

Behavior of the primitively social wasp *Montezumia cortesioides* Willink (Vespidae Eumeninae) and the origins of vespid sociality

MARY JANE WEST-EBERHARD

Smithsonian Tropical Research Institute, c/o Escuela de Biología, Universidad de Costa Rica, Costa Rica (E-mail: mjwe@sent.com)

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Montezumia cortesioides is of special interest for studies of insect social evolution because it belongs to the primarily solitary-nesting subfamily (Eumeninae) of wasps that is most closely related to the subfamilies (Stenogastrinae, Polistinae, Vespinae) that contain eusocial species. It is one of a few eumenines that are primitively social, with more than one reproductive female on the same nest without a division of labor between sterile workers and egg-laying queens. Most of the 17 known progressively provisioning eumenines nest as solitary females, but there is an association between progressive provisioning and nest sharing: all of the three nest-sharing eumenines whose behavior has been observed progressively provision their larvae. Of those species, the behavior of *M. cortesioides* most closely resembles that of the eusocial (worker-containing) wasps, in nest-sharing, reuse of brood cells, progressive provisioning, and strong aggressive competition among resident females for empty cells. Observations suggest that groups are formed when offspring females remain on the maternal nest. A male repeatedly visited a nest and paired with a newly emerged female. Prey theft from the open cells of nestmates (intranidal prey theft) was associated with episodes of self-grooming and brief repetitive superficial inspections of prey-containing cells.

KEY WORDS: group life, mutualism, mating behavior, intranidal prey theft, monandry, social evolution, progressive provisioning, displacement activity.

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INTRODUCTION

Primitively social behavior, defined as nest sharing without a reproductive division of labor between queens (egg-layers) and workers (non-egg-laying helpers), has been observed previously in only two species of eumenine wasps, *Zethus miniatus* (*Z. lobulatus* in DUCKE 1914) (DUCKE 1914, DRUMMOND 1986, WEST-EBERHARD 1987a) and *Xenorhynchium nitidulum* (Fabricius) (WEST-EBERHARD 1987b). Nest sharing has been observed or deduced to be likely in three additional species: in the Philippine wasp *Odynerus xanthozonatus* [= *Epsilon dyscherum* (de Saussure)] (two females observed on one nest) and the British Guianan wasp *Montezumia dimidiata* (de Saussure) [*Montezumia infundibuliformis* (Fabricius) of WILLIAMS 1928] (two females observed on a nest of five cells). In both of these species, associated females passed the night ensconced facing outward in partially provisioned larva-containing cells (WILLIAMS 1928: 81-82). A collected nest of *Abispa australiana* contained two females and two larvae of similar ages suggesting that they were being provisioned simultaneously (MATTHEWS & MATTHEWS 2004). In addition, several females of *Zethus laevinodus* shared an entrance to a complex of cells in tunnels in wood, but each may have tended her own cluster of cells within (BOHART & STANGE 1965); similarly, two or three females of a *Zethus* species (near *Z. westwoodi*) shared the entrance to tunnels leading to ramifying galleries in the fruiting body of a basidiomycete fungus (FLÓREZ 1996). In tunnel nesting wasps it is difficult to discern whether females share the same cell cluster ("nest") or maintain strict spatial separation on separate cell clusters connected only by a common entrance.

I report here observations of primitively social behavior in the neotropical eumenine, *Montezumia cortesioides* Willink. Although brief and incomplete, I record the observations in some detail because such examples are rare in the literature, and they revealed several critical aspects of natural history relevant to understanding the evolutionary transition between solitary and group life, as well as the origin of a reproductive division of labor in wasps.

Montezumia Saussure is a neotropical genus of eumenine wasps whose 48 species (WILLINK 1982) range from Argentina to the southwestern United States (Arizona). Most of the known species (38 of 52 species and subspecies; WILLINK 1982) are South American. Despite their wide distribution and the relatively large size of the wasps, the behavior of *Montezumia* species has not previously been studied and the nests have been described for only eight definitively identified species (*ferruginea*, *dimidiata*, *cortesioides*, *vechti*, *pelagica*, *brethesi*, *platinia*, and *petiolata*) (reviewed in WILLINK 1982). This is unfortunate, for the genus is of special interest for illuminating the origins of group life and eusociality (social behavior characterized by a reproductive division of labor between egg-laying queens and sterile workers). *Montezumia* belongs to a vespidae subfamily (Eumeninae) of primarily solitary wasps which are closely related to the eusocial vespidae of the subfamilies Epiponinae and Polistinae; and the species discussed here, *M. cortesioides*, exhibits several behaviors similar to those of primitively eusocial wasps.

EVANS (1973) collected a nest of *M. cortesia* Saussure (now called *cortesioides* Willink) on 14 January 1972 at the locality of the present study (EVANS 1973¹) (Fig.

¹ The article by EVANS (1973) contains several important typographical errors and omissions (H.E. EVANS personal communication): on p. 286, line 9, the center heading should read *Montezumia cortesia* Saussure (now *cortesioides* Willink) rather than *Montezumia dimidiata* Saussure, and footnote 3 does not apply to that species. Footnote 3 applies instead to the heading *Montezumia*

1). The nest was 17 cm long at the upper margin and was composed of 17 cells and contained three females and a male. The subcylindrical cells were 9 by 20 mm in inside dimensions, and were "barely evident from the exterior", for "the outside of the nest was well plastered with soil" (EVANS 1973: 286). Like all of the nests of the present study, this nest was located on a dry area of a vertical surface, in this case a rock. Seven of the eight *Montezumia* species whose nests have been described build nests of several mud cells attached to a surface above the ground, as in *M. cortesioides*. One species (*M. petiolata*) builds a nest in the soil.

EVANS (1973) found that two egg-containing cells lacked prey, while one with a small larva contained several tiny microlepidopterous caterpillars, suggesting progressive provisioning — gradual feeding of the growing larva. This is a pattern that contrasts with mass provisioning, or placement of prey sufficient to rear a larva in an egg-containing cell, which is then sealed. It was not known how many of the three females were active in building and provisioning the nest, but EVANS suggested that the species might be reproducing communally (EVANS 1973).

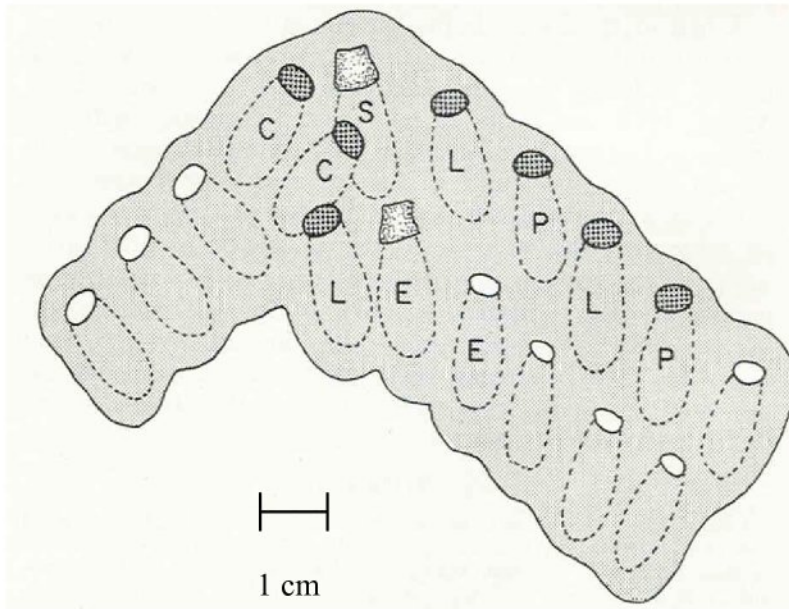


Fig. 1. — Nest of *M. cortesioides* with seven cells closed (heavily shaded) and the remaining 10 open. Contents of open cells (with number of each in parentheses): no shading or letter = empty (8); E = egg (2); S = small larva (1). In sealed cells (shaded tops): L = large larva (3); C = cocoon (2); P = parasite pupa (2). After EVANS (1973).

dimidiata Saussure (p. 287, line 14). In addition, the figure legends were omitted. Figure 1 from EVANS (1973) and its footnote are therefore included here (Fig. 1). Figures 2, 3, and 4 of EVANS (1973) show, respectively, a nest of *M. dimidiata* from Restrepo, Colombia; the egg of *M. cortesioides*; and an adult *M. cortesioides* on the nest. The *Montezumia dimidiata* listed as a nest-sharing species in table 1 of WEST-EBERHARD (1978) and in the review by COWAN (1991) is in fact the *M. cortesioides* of the present study.

Progressive provisioning, either complete (continued until the larva ceases to feed) or truncated (ending with rapid provisioning of larva that is still feeding) has been documented in 17 eumenines (Table 1). In eumenines fully progressive provisioning occurs only in tropical species, despite many studies of species in the temperate zone, and in species that build cells of mud or leaves, never in the many twig-nesting or burrowing species that have been studied (KROMBEIN (1978)). The three eumenines definitively known to be primitively eusocial are progressive provisioners (Table 1), as are two (*O. xanthozonatis* and *M. dimidiata*) of the three species (above) thought to possibly share nests (WILLIAMS 1928). This association suggests that something about progressive provisioning predisposes populations to the evolution of group life.

Some degree of progressive provisioning may occur in *Odynerus oahuensis* (WILLIAMS 1927: 454); *Ancistrocerus taihorinshoensis* (= *Parancistrocerus taihorinshoensis*; GIORDANI SOIKA 1994) and *Subancistrocerus sichelii* (IWATA 1976: 270); *Euodynerus auranus* (Cameron) (EVANS 1977); and *Abispa meadowaldoensis* (MATTHEWS & MATTHEWS 2004). In these species females have been observed provisioning an open cell containing a young larva and numerous prey, so these may be instances of either full progressive provisioning or of "delayed provisioning" (delayed mass

Table 1.
Progressively provisioning eumenine wasps.

Species	References	Obsolete or incorrect species names used in some references
<i>Synagris cornuta</i>	ROUBAUD 1910 LONGAIR 2004	
<i>Antepipona tropicalis</i>	ROUBAUD 1916	<i>Odynerus tropicalis</i>
<i>Zethus miniatus</i>	DUCKE 1914 DRUMMOND 1986 WEST-EBERHARD 1987a	<i>Zethus lobulatus</i>
<i>Calligaster cyanoptera</i>	WILLIAMS 1919	<i>Zethus cyanoptera</i>
<i>Epsilon dyscherum</i>	WILLIAMS 1928	<i>Odynerus xanthozonatus</i>
<i>Montezumia dimidiata</i>	WILLIAMS 1928	<i>M. infundibuliformis</i>
<i>Montezumia cortisioides</i>	EVANS 1973 Present Study	<i>M. cortesia</i> <i>M. dimidiata</i>
<i>Paraleptomenes miniatus</i>	JAYAKAR & SPURWAY 1966 KROMBEIN 1978	<i>Paraleptomenes mephitis</i>
<i>Orancistrocerus drewseni</i>	IWATA 1976	
<i>Pararhynchium ornatum</i>	IWATA 1976	
<i>Xenorhynchium nitidulum</i>	WEST-EBERHARD 1987b	
<i>Abispa splendida</i>	MATTHEWS & MATTHEWS 2004	
<i>Synagris spiniventris</i> *	ROUBAUD 1916	<i>Synagris calida</i>
<i>Synagris calida</i> *	ROUBAUD 1916	<i>Synagris sicheliana</i>
<i>Delta emarginatum</i> *	ROUBAUD 1916	<i>Eumenes maxillosus</i>
<i>Eumenes pomiformis</i> *	DELEURANCE 1946	
<i>Discoelius japonicus</i> *	ITINO 1992	

Asterisk (*) indicates facultative (condition-dependent) progressive provisioning.

provisioning), in which the egg is laid before provisioning is complete and the cell is still open and the egg hatched before the cell is closed, as in *Odynerus xanthozonatus* (= *Epsilon dyscherum*) (WILLIAMS 1928).

The present study confirms EVANS' conclusion that *M. cortesioides* females, like eusocial (worker-containing) wasp species, are progressive provisioners. It also confirms his suspicion that they form communal groups, with several females rearing brood on the same nest, each one attending primarily her own offspring. The nest-sharing females of *M. cortesioides*, like those of *Z. miniatus*, exhibit several behaviors of kinds that could have contributed to the origin of workers (eusociality) in the ancestors of eusocial wasps.

METHODS

Six nests of *M. cortesioides* were observed for a total of 15 hr, or 72.5 wasp hours (wasp hours = number of hours a nest was observed multiplied by the number of adult wasps resident on the nest). Because there were never more than six individuals present on a nest at one time, the activities of all could be recorded simultaneously. Dates and durations of observation periods, numbers of females present, and nest contents are given in Table 2. All nests were located at Anchicayá, Departamento del Valle, Colombia, South America (4° N latitude) at the site of a hydroelectric dam 40 km east of Cali on the old road to Buenaventura. This is an area of tropical rain forest with very high annual rainfall and little seasonal change in the abundance of nesting wasps (see WEST-EBERHARD 1969). Wasps were marked for individual identification without removal from nests, using quick-drying colored paints. Voucher specimens were deposited in the Museum of Natural History, London, and the Insituto Miguel Lillo, Tucuman, Argentina. O.W. Richards identified the species as *M. cortesia* (now *cortesioides* WILLINK 1982). WILLINK (1982) confirmed that both the wasps that EVANS studied and those of the present study are of this species.

Table 2.

Characteristics of nests and groups of *Montezumia cortesioides* on dates observed, and duration of observations.

Nest	Date	Hours/nest	Wasp hours	Cells				
				females	males	total	open	closed
N1	1 July 1972	1.0	1	1	—	2	1	1
N2	1 July 1972	2.5	5	2	—	3	2	1
N3	1 July 1972	1.0	1	1	—	2	1	1
N4	19 Oct 1972	—	—	1	—	3	6	9
N5	25 May 1974	0.5	0.5	1	—	4	1	3
	8 June 1974	0.5	0.5	1	—	4	1	3
	18 June 1974	0.5	0.5	1	—	4	2	2
N6	25 May 1974	3.0	24	7	1	17	7	10
	9 June 1974	5.0	35	6	1	17	3	14
	18 June 1974	1.0	5	5	—	19	5	14

RESULTS

Nests and nest building

All of the six nests of Table 2 were built on rocks. A seventh nest was located on a vertical, dry board of a building. In small, evidently younger nests the shapes of the elongate cells were easily distinguished. A recently constructed cell of N2 measured 3 cm wide by 1.3 cm long; another, on N6, measured 2.5 × 1.25 cm, with an opening of 0.8 cm in diameter. The largest nest I found is not included in Table 2 because its location high up on a building made it difficult to observe or collect. It contained 14 open cells and many sealed ones, uncountable due to the much-modified surface of the nest.

Most open brood-containing cells on N6, and those of the nest observed by EVANS (1973), had the entrance produced as a lip 1-6 mm high, termed a "turret" by EVANS (1973) (Fig. 1). Female F6 constructed a turret on a newly vacated cell within 2.5 hr of occupying it, soon after the cell was cleaned. Turrets were never found on closed cells. The mud of the turret may be used to seal the cell, as in *Abispa epihippium* (MATHEWS & MATTHEWS 2004; after MCKEOWN 1932), for mud was commonly moved from one place to another on the nest. On June 9, female F5 of N6 made many brief trips from the nest and returned with water, which she regurgitated onto dry mud of the nest. She then removed moistened mud small bits at a time, creating a small pit in the nest surface. She applied the mud in thin plaques nearby. When the nest was observed nine days later (18 June) there was a new cell located where she had been applying the mud. Females also removed mud from inside vacated brood cells prior to re-using them.

Water-collection trips, recognizable by regurgitation of liquid upon the female's return, were very brief. One water-collecting female made seven trips from the nest in 30 min, an average of one trip every 4.3 min. A timed trip took 1 min. Sometimes females moved bits of dry material from one place to another on the nest surface before collecting water, then returned to the loosely attached bit of dry mud, mix it with regurgitated water, and apply it elsewhere. One female collected water from water-laden leaves 2-3 m from her nest.

Nest growth is evidently slow. Even though seven females were active on N6, and on 9 June there was an excess of females (six present) relative to the number of available empty cells (three), only two cells were added during the 3 weeks spanned by this study (Table 2). During the same period no new cells were added to N5, composed of four cells and attended by one female. If nest growth is usually this slow, the large size attained by one nest (above) suggests that nests can be maintained for long periods of time.

Slow nest enlargement is due at least in part to extensive reuse of vacated cells. Females built new cells only when no empty cells were available: when female F5 initiated preparations for a new cell on N6 on June 9 there was a shortage of empty cells, only three on a nest with seven active females. One of the other cell-less females was relatively inactive and evidently young (newly marked). The other two females without cells, F2 and F6, were more than 2 weeks old, having been marked while attending brood cells on May 26. They aggressively competed for a vacant cell (see *Interactions among females*, below). The 3-weeks without cell additions on N5 was a period when there was never more than one female present, and there was always an empty cell available.

Nest foundation and group formation

Females attended one brood cell at a time, and each brood cell housed only one egg, larva or pupa. The smallest nests observed, N1 and N3, were composed of only two cells each, and each was attended by a single female. On N1 there was one sealed cell containing a large pupa, already pigmented and therefore nearly mature; and one large larva provisioned with two large prey. Similarly, N3 contained one sealed cell with an advanced (fully featured) but still white pupa; and one large larva provisioned with three prey. The nests were probably initiated by a single female, who had constructed two cells in succession, the first soon to produce an offspring and second about to be sealed.

N2 contained three cells (one closed, two with small larvae and small prey) and was attended by two females (Table 2). One of these was older (with darker abdominal apodemes) than the other, suggesting that this was a mother-daughter pair. N5 contained four cells, three of them sealed and one with an egg attended by a single female, suggesting that this female had constructed four cells before any of her offspring had emerged. Nest 4 consisted of nine cells, six closed and three open, each open cell attended by one of six resident females. If this nest was founded by a single female as suggested for nests N2 and N5, and a single female can begin her fourth offspring prior to the emergence of the first (as was evidently the case for N5), then the age composition of the wasps of N4 suggests that it was producing at least its third generation of offspring. All of these observations are consistent with the conclusion that nests were founded by a single female, and that groups were formed when female offspring remained on the maternal nest.

Provisioning: hunting, and intranidal prey theft

As reported by previous authors (reviewed in EVANS 1973 and WILLINK 1982), females of *M. cortesioides*, like those of other *Montezumia* species, provision their larvae with caterpillars of Lepidoptera, which are placed whole in the brood cells. The size and number of the prey varied with the size of the larva being provisioned. Combining the data of EVANS (1973) with those of the present study ($n = 11$ brood cells), egg-containing cells ($n = 5$) contained no prey. In cells containing small larvae with prey ($n = 3$) the prey were small compared to those in cells with large larvae ($n = 2$), and the prey were small in number (2, 2, and 1 caterpillars, compared to 2 and 3 caterpillars, respectively). On one occasion a large larva was provided with three large caterpillars in a single morning (N6; 26 May), and another received a succession of five prey, three large prey brought from outside the nest, and two by intranidal theft from another cell (N6; female F3, 9 June). Two timed successful hunting trips took 30 and 50 min, respectively. If this small sample is representative, the increased size and number of prey provided to relatively large larvae would imply that a provisioning female can judge the size or stage of her larva, and that she is able to adjust the size and quantity of prey hunted accordingly.

Prey theft from the cells of other females on the same nest, or *intranidal prey theft*, was observed three times on N6 during 5 hr of observation (7-12 a.m.) on June 9. This was usually preceded by cell inspection — antennation or head-first entry into the cell of another female. The first observed episode of theft occurred after a provisioning female (F9) returned without prey following a long absence from the nest (she was last recorded present 48 min before). Upon return to the

nest she first inspected her own cell, then went directly to the cell of absent female F3, removed a caterpillar, flew with it briefly off the nest, then returned and placed the caterpillar in her own cell. She then immediately left the nest, leaving one other caterpillar in the raided cell and refrained from stealing in subsequent visits to the raided cell that same day following repeated trips to and from the nest. Once, after returning loadless, F9 inspected her own cell, groomed, and then started to place her head into the cell of F3, but stopped when another female neared the nest. F9 then groomed and inspected her own cell deeply, then repeatedly groomed and slowly approached the cell of F3 without entering. Finally, after 5 min of this behavior she antennated the entrance to the cell of F3, groomed again, and left the nest. These observations indicated one instance of arrested entry into a previously raided cell upon the approach of another female, and several instances of inspections of a prey-containing cell without robbing, by an actively provisioning robber female, who thus, even after several returns without prey, did not immediately steal available prey from cells unguarded by their owners.

Later the same day, female F3 stole two prey in quick succession from the cell of female F9. Prior to stealing, F3 had been notably successful in hunting, having brought three prey to the nest with no returns without prey. After returning with the third prey, which was unusually large, she immediately stole the two caterpillars from the unguarded cell of F9. A N6 female (F6) provisioning more slowly on May 26 failed to steal prey, even after long trips away from the nest followed by returns without prey and repeated inspections of unguarded prey-containing cells. Then, after she returned to the nest with a prey, she stopped making trips to and from the nest and inspecting the cells of others, and remained ensconced in her own cell. These observations indicate that prey theft occurred when two females were provisioning large larvae simultaneously, and that it sometimes, but not necessarily, occurs following hunting failure. Perhaps, as in another eumenine with intranidal prey theft, *Zethus miniatus* (MURILO 1986, WEST-EBERHARD unpublished), prey theft is associated with provisioning of an advanced larva just prior to cell closure.

Defense of nest and of individual brood cells

The nest of *M. cortesioides* collected by EVANS (1973) (Fig. 1) produced two ichneumonid parasitoids, which emerged in the laboratory 3 weeks after the nest was captured. In an attempt to provoke defensive behavior I placed a ponerine ant on N6 when five female wasps were present. It walked around the nest and briefly entered the unguarded cell of F7. Although female F6 was facing directly toward the invading ant, she did not visibly respond to it. Female F1, which was on the surface of the nest gathering mud, appeared to arrest her activity slightly, but did not drop her mouthful of mud to attack and did not back into her unguarded cell, nor did any of the ensconced wasps move out of their cells to approach the intruder.

This passivity toward an intruding ant contrasted with reactions by females attending brood cells in the presence of nestmates on the surface of the nest, toward which they often darted aggressively. Females commonly inspected the entrances to cells of other females, using their antennae and extruding their mouthparts to seemingly "lick" the surface of the nest near the entrances of neighboring cells, as well as their own. They often inspected both empty and partially provisioned cells deeply, inserting the head far into the cell. Prey-containing cells of other females were sometimes inspected without stealing prior to trips from the nest, as already

described. It was also common for females to groom themselves after such inspections (see *Miscellaneous notes*, below).

Some behaviors, such as arrested movement, indicated caution on the part of females when approached by others, and ensconcement in the brood cell upon the approach of another female indicated protective behavior toward their cells when other females were nearby.

Cell reuse and competition for empty cells

As already noted, a cell vacated by an emerging female on N6 was occupied by an older female within 15 min of her emergence, and there was no instance of an empty cell on a nest along with females not attending cells. Prior to the emergence of the female on N6, three females without cells on that nest spent much time walking briskly around the nest and inspecting the nest surface, acting "nervous" or "uneasy" in that they turned away from, rather than approaching others. They sometimes darted mildly at one another without fighting. The advent of an empty cell created by the emergence of an offspring female led to marked aggression between two of these females (F2 and F6) after female F6 began to enter and remove debris from the empty cell. Aggressive behaviors included pushing against each other near the cell entrance, biting, climbing on top of the opponent, and mutual stinging movements. During an especially violent fight the two females fell grappling from the nest. Female F6 soon returned and continued cleaning the cell, then occupied it facing outward. F2 returned briefly and once antennated F6, but did not bite at the ensconced female. When the nest was observed 10 days later (June 18) F2 was not present.

Several observations indicated costs and possible advantages of cell reuse. Female F6, who won the contest for an empty cell, had to fight and clean the cell, but avoided the delays and possible dangers of foraging for mud and water away from the nest. The construction of a new cell by F5 was still in the very early stages of moving and smoothing mud at the site of the new cell, with the construction of the cell proper not yet begun, at the end of 3 hr of work involving many brief trips from the nest (7 trips in 30 min) to bring water. A cost of cell construction by use of mud from outside the nest is suggested by the extensive reuse of mud by moving it around on the nest. Females that worked inside cells prior to oviposition also applied mud from inside the vacated cell to other parts of the nest, and on one occasion the unusually dark color of a small amount of material taken from inside a recently vacated cell and applied to the nest surface suggested that the meconium might have been used along with mud. This idea was supported when another female antennated the newly applied material, whereas she ignored other regions of newly applied mud.

It is worth noting, however, that females without cells did not attempt to usurp the brood-containing cells of other females even though they were unattended for extended periods while provisioning females were away from the nest.

Male behavior and mating

A male, easily recognized by the tightly curved tips of his antennae, alighted briefly 3 times (with little movement while present) on nest N6 on the morning of

26 May. The females on the nest did not react to his presence, nor did the male show any special behavior toward them.

When N6 was observed on 9 June a male appeared on the nest at about the time females were beginning to be active (8:14 hr), and was paint-marked for individual identification. He went toward a cell-inspecting female, which acted alert (hesitated briefly while facing him) but showed no other special reaction. Female F3, which was inspecting the surface of the nest and inside cells, avoided the male. When he bit at her she left the nest.

Later that morning (8:55 hr) a female began to chew out of her sealed cell. She seemed simply to bite at the dry mud with her mandibles without moistening it, in contrast to some other mud-nesting species, where there is conspicuous moistening of the mud (e.g., EBERHARD 1972; additional references in COWAN 1991). Female nestmates paid no attention to the emerging female, but the marked male stood vigil with his head directly over the cell of the emerging female, where he remained until she emerged 25 min later. Before emerging the female antennated the male and came partially out of the cell, but withdrew when the male moved. She later came part way out, and then withdrew again and continued to bite at the remaining mud seal of the cell. For a time she pushed outward repeatedly, without getting her thorax past the mouth of the cell.

As soon as the female emerged from the cell the male mounted her with his body above and parallel to hers, and his antennae held straight upward and backward so that they resembled horns, with his mandibles positioned between the female's head and thorax. When a female returned to the nest the pair flew off in tandem. The male returned alone 22 min later and rested for 4 min on the nest, repeatedly extruding and retracting his genitalia. I noted that he had white powdery material on his face, possibly pollen from some plant. He returned briefly twice more during the remaining 2 hr of observation.

About 2 hr after the mating pair had left the nest, an unmarked female flew to the nest with a slow, circuitous approach. This was probably the newly emerged female, since all other females associated with the nest had been marked. This female departed when I approached. The observations had to be ended without waiting to see if an unmarked wasp would return.

Miscellaneous notes

On 9 June I captured female F3 of N6, leaving her large larva an orphan provisioned with a total of at least five prey, one of them unusually large. At that time there were two females without cells present on the nest. I especially hoped to test the responses of female F2, which had just lost a fight over an empty cell, to the presence of an unguarded cell containing a nearly mature well-provisioned orphaned larva, but unfortunately F2 left the nest following her defeat and was not seen again. Nine days later (18 June) the orphaned cell had been sealed. It contained a living larva without prey. If this was the larva of captured female F3, given its age, more than 24 days old, and its large supply of prey when orphaned, it was unusually small, even smaller than another larva which had been preserved prior to cell closure along with three prey. Alternatively, the orphaned larva may have been replaced by the offspring of another female.

Females without brood cells on N6 did not pass the night on the nest, but returned in the morning well after sunrise and at about the same time that

ensconced females first became active on the nest outside their cells. On 9 June observations started at 7:00 hr and the first arrival by a marked resident was at 7:55 hr; the first trip out from the nest by females ensconced there overnight with brood was at 8:29 hr.

Self-grooming (rubbing the front legs on other parts of the body) was common. Social grooming (mouthing and antennating the bodies of others) was not observed. Self-grooming, along with brief repeated cell inspections — entering a cell without provisioning, stealing or ensconcing — was a conspicuous activity of a thief female. One recorded sequence included more inspections the thief's own cell (12) than of the one robbed (six).

DISCUSSION

Several behaviors associated with group life in *M. cortesioides* resemble those of eusocial wasps and contrast with those usual in solitary eumenines. Such behaviors invite consideration as factors that could have contributed to the evolution of group life and colony organization as seen in the wasps.

Genetic relatedness among nestmates

Although it is possible for a division of labor to evolve in an association of non-relatives, as in obligate symbioses between different species, all of the primitively social and eusocial groups in wasps that have been genetically analysed to date, are evidently composed of relatives (individuals genetically more closely related to each other than they are to the population at large) (WEST-EBERHARD 1978, QUELLER et al. 1988, QUELLER & STRASSMANN 1998) and are therefore subject to kin selection (HAMILTON 1964). So factors increasing kinship within groups are of special interest, alongside other factors that may contribute to the evolution of group formation itself. In *M. cortesioides*, two factors suggested by the observations of this study would increase genetic relatedness among nestmates in *M. cortesioides* if regularly occurring in the species: nest foundation by a single female with offspring that remain at the maternal nest; and single-mating (monandry) of females. Most solitary bees and wasps are monandrous (THORNHILL & ALCOCK 1983), including most eumenine wasps, especially those which, like *M. cortesioides*, mate upon female emergence (review in BUDRIENÉ 2004; see also COWAN 1991).

Progressive provisioning

Progressive feeding and contact with the growing young are not prerequisites of eusocial behavior, for some eusocial bees are mass provisioners (LIN & MICHENER 1972). But they do characterize the biology of all eusocial wasps. FIELD & BRACE (1994) showed that in some sphecoid wasps (*Ammophila* species) progressive provisioning effectively protects the vulnerable egg, by delaying the beginning of provisioning until the less vulnerable larval stage; and it protects the mother from investment in parasitized offspring because provisioning females detect and abandon parasitized larvae. Thus, progressive provisioning can enable a female to monitor the

condition of young and to terminate maternal investment in the event of parasitic attack or illness (ITINO 1986, FIELD & BRACE 2004).

The cyclic change in behavior of progressively provisioning females may have facilitated the origin of a division of labor: females alternate between cell building or (as in *M. cortesioides*) aggressive cell acquisition by females with a mature egg, and brood care by females that have recently produced an egg. This alternation between queen-like and worker-like phases during the reproductive cycle has been hypothesized to set the stage for a separation of worker and queen reproductive tasks (WEST-EBERHARD 1987a, 1996, 2003).

Reuse of brood cells and competition to obtain them. As in all eusocial wasps, eggs are laid in cells vacated by emerged adult offspring, after being cleaned by removal of the meconium and other debris left in the cell. Ability to reuse vacated cells can shorten the period between opportunities to oviposit for aggressive females able to defend empty cells. But in nests attended by more than one female access to vacated cells may require them to engage in costly fights: falling and stinging fights of the type observed in this species are sometimes injurious or fatal to wasps (WEST-EBERHARD 1969). The opportunity to obtain cells without building them is a reason for females not to disperse from the natal nest, and therefore a potential cause of the origin and maintenance of groups.

An important difference between *M. cortesioides* and the eusocial wasps is the strict attendance of the eumenine to one offspring at a time, despite the presence of empty cells in which to oviposit. In the *M. cortesioides* nest observed by EVANS (1973) females already tending a cell did not oviposit in empty cells even though many (8) were available, but persisted instead in the solitary-wasp pattern of rearing one offspring at a time. In primitively eusocial wasps such as *Polistes*, by contrast, an empty cell stimulates oviposition (DELEURANCE 1950). In wasps, where there is positive feedback between oviposition activity and (increased) ovarian development, as well as between failure to oviposit and ovarian regression (reviewed in WEST-EBERHARD 1996), simultaneous reuse of brood cells where many are available on a large nest could lead automatically to a self-accelerating process of differentiation between reproductive and non-reproductive females beginning with small initial variation in egg-production rates of females. Given that feedback mechanism, competition over empty cells of the kind observed in *M. cortesioides* as well as in *Zethus miniatus* and the eusocial wasps, is a key element in the evolution of a division of labor, where the winners in social competition for cells become queens, and the losers become workers.

Stealing/sharing of prey. Intranidal prey theft involves tension between social cohesion and parasitic competition among nestmates. It occurs in some other primitively social (nest-sharing, workerless) wasps, including *Trigonopsis cameroni* (EBERHARD 1972), *Zethus miniatus* (WEST-EBERHARD 1987a) and *Auplopus irenangelus* (WCISLO et al. 1988). Since these are the only communal progressive-provisioning wasps in which marked females have been observed, intranidal prey theft may prove common or universal in communal wasps, especially in view of the fact that internidal prey theft sometimes occurs between neighboring nests of solitary wasps, as does theft from prey-laden females outside of nests (FIELD 1989). The distinction between intranidal prey theft and theft between nests is important (FIELD 1992 lumps them as "theft from nests"), however; because intranidal theft may grade (or evolve) into food sharing, whereas that possibility is less likely for prey theft between nests or species.

As emphasized by FIELD (1992), intraspecific parasitism, including intranidal prey theft, is a conditional alternative tactic of provisioning females, which

can switch between hunting and stealing of prey. Females of *Trigonopsis cameroni* (see EBERHARD 1972) and *Zethus miniatus*, like those of the present study, sometimes show what appears to be “restraint” in theft; observed robber females sometimes inspect prey-containing cells without stealing, then continue to bring prey from outside the nest; and *Zethus miniatus* females steal primarily during the final rapid phase of provisioning a large larva (DRUMMOND 1986). If costs and benefits are adjusted to benefit, or not unduly harm, the other females in the group, then intranidal prey theft could be regarded as mutualistic (individually beneficial, with net benefit to all) and not parasitic or dissolutive in its effect on groups under natural selection, and could actually promote rather than undermine the maintenance of group life. As pointed out by FIELD (1992), “if subordinate females tend to be provisioners while dominants tend to parasitize their prey or cells, the system starts to resemble a caste system”.

In conclusion, the social biology of *M. cortesioides*, in which there is nest-sharing by adult females, reuse of brood cells, strong aggressive competition for empty cells, and evidence for genetic relatedness of nestmates, suggests that this species, of the three primitively social eumenines thus far observed, is the one whose behavior most closely resembles that of caste-containing (eusocial) vespids.

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