

## Seasonality and Colony Composition in a Montane Tropical Eusocial Wasp<sup>1, 2</sup>

*Key words:* cloud forest; colony development; enforced sterility; foundress associations; *Mischocyttarus mastigophorus*; phenology; rainfall; Vespidae.

POPULATION-LEVEL ANALYSES OF COLONY DEVELOPMENT have enhanced our understanding of the origins and maintenance of eusocial behavior in insects (Jeanne & Davidson 1984, Tschinkel 1991, Wcislo & Danforth 1997). Variation in seasonal climatic regimes affects insect colony development, both at large spatial scales (e.g., between temperate and tropical regions) and at more local scales (e.g., among sites at similar latitudes that have different rainfall patterns; Strassmann & Hughes 1986, Richards & Packer 1996, Field *et al.* 1998). Climatic factors impose a number of constraints on colony productivity. For example, seasonal changes in the availability of nectar resources for adult nutrition, and of insect prey for larval nutrition, can restrict opportunities for nest founding and offspring growth. Climatic constraints may result in the evolution of species-level and population-level differences in social behavior.

Colony phenology data are especially important from tropical eusocial insects, for two reasons. First, the effects of seasonality on colony development likely differ between tropical and better-studied temperate habitats. Second, the early evolutionary stages of insect eusociality may have occurred in tropical habitats. Patterns of species distribution, species richness, and phylogeny suggest that independent-founding eusocial paper wasps evolved in the tropics (Vespidae: Polistinae; Vecht 1965, Reeve 1991, Wenzel & Carpenter 1994). Therefore, tropical independent-founding wasps are key subjects for understanding the evolutionary origins and maintenance of eusocial behavior in Vespidae. The few long-term studies of colony development in independent-founding paper wasps have demonstrated considerable variation among species and populations, but the degree of population-level synchrony in wasp colony development appears to be determined largely by seasonal climatic factors (Suzuki 1986, O'Donnell 1996). Synchrony of colony foundation and reproduction can have important implications for the maintenance of eusociality. For example, the schedules of producing reproductive females (gynes) and males, and the longevity of males, determine the temporal distribution of mating and nesting opportunities for emerging adult females (Alexander 1974, Yanega 1988, Hunt 1994). In this study, we quantified seasonal patterns of colony development and social composition in a population of the montane tropical paper wasp *Mischocyttarus mastigophorus* Richards (Hymenoptera: Vespidae) and related these patterns to seasonal climate variation. The *M. mastigophorus* subject population occurs at higher elevations than previously studied tropical paper wasps and is therefore exposed to a different seasonal climatic regime. We also surveyed the abundance of adult males during different seasons to assess whether or not male absence could enforce female sterility and thereby favor female worker behavior in this population.

*Mischocyttarus* is one of the largest genera of eusocial Vespidae, with *ca* 200 described species (Richards 1978, Gadagkar 1991). Species of *Mischocyttarus* occur from temperate areas in the northwestern United States and southwestern Canada to northern Chile and Argentina (Gadagkar 1991). The few *Mischocyttarus* species that have been studied for extended periods (*i.e.*, over several seasons or years) exhibit diverse seasonal patterns of colony development (Jeanne 1972; Litte 1977, 1979; Stiller 1989). Such behavioral diversity, coupled with the wide latitudinal and elevational range occupied by *Mischocyttarus* wasps, permits comparative analyses of climatic effects on colony structure.

We collected data in the vicinity of Monteverde, Costa Rica (10°18'N, 84°48'W). The Monteverde area includes a well studied tropical cloud forest (Hartshorn 1983, Nadkarni & Wheelright 2000). *Mischocyttarus mastigophorus* nests are restricted to elevations above *ca* 1450 m in the tropical lower montane wet forest life zone (Holdridge 1967, O'Donnell & Joyce 1999, O'Donnell 2000). The elevational range of *M. mastigophorus* is characterized by extensive cloud cover and precipitation, including rain and wind-driven mist for much of the year (Clark *et al.* 2000); however, average monthly rainfall

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changes seasonally. Daily rainfall data were collected in Monteverde at 1500 m elevation from 1971 to 1998 (J. Campbell & A. Pounds, pers. comm.), and temperature data were collected from July 1981 to December 1998 at 1350 m elevation (R. Laval, pers. comm.). We used these weather data to assess relationships between seasonal climatic variation and *M. mastigophorus* colony phenology.

We censused or collected *M. mastigophorus* colonies during seven survey periods from 1994 to 2000 as follows: dry season (January 1996), onset of wet season (May 1994, May 2000), mid wet season (July 1997, July 1999), and later wet season (August 1997, October–November 1995). Each survey period provided a cross-sectional sample of colony developmental stages in the population during a single season. To locate colonies, we searched the eaves of buildings in the elevational range of *M. mastigophorus* (ca 1450–1700 m at Monteverde; O'Donnell & Joyce 1999). We collected additional data opportunistically from colonies at other locations, typically under leaves at forest edges and on rootlets in road-cut banks. For each colony, we recorded adult composition and developmental stage, noting the date on which the colony was collected or surveyed, and the location of the nest site. To determine developmental stage, we examined whether nests contained pupal caps that were opened. Colonies having nests that did not show evidence of cells with opened pupal caps were assumed not to have produced adults, and these were categorized as preemergence colonies. Colonies with nests containing cells with opened pupal caps were assumed to have produced adult offspring and were categorized as postemergence colonies. We noted whether adult males were present on or near nests; male *M. mastigophorus* are readily distinguished by their elongate antennae and silvery pubescence on the face (O'Donnell 1999).

We located a total of 108 colonies. A subset of the colonies ( $N = 47$ ) were examined *in situ* in the field at night, and the adult wasps of each sex were counted. When possible, we also counted the number of adults present on colonies that were surveyed in daylight hours. The numbers of adults on colonies surveyed in daylight hours may have been underestimated because individuals were away foraging or on mating trips. This bias could be especially important for preemergence colonies in which only one female was present at the time of the survey, as it could have reduced estimates of the rate of cooperative colony foundation (pleometrosis). We indicate when the data included colonies surveyed during daylight hours. Some of the subject colonies ( $N = 45$ ) were collected and the adults counted. The collections were performed at night to ensure that all adults would be present. Colonies were collected by placing a plastic bag or plastic jar containing an ether-soaked cotton ball over the nest. Any escaping adults were noted. For colonies collected during October–November 1995 (late wet season), adult females were killed by freezing until immobile and immediately dissected. Relative ovary development was examined with a binocular microscope at 20 to 40 $\times$  magnification.

Mean temperature varied little among months. In contrast, average monthly rainfall was highly seasonal, and variation in *M. mastigophorus* colony development was associated with seasonal rainfall variation (Fig. 1). Postemergence colonies were found in all population samples, but the relative frequency of preemergence colonies differed among months (Fisher's exact test:  $P = 0.00002$ ). Preemergence colonies comprised the smallest proportion of nests at the onset of the wet season (May). Relatively more preemergence colonies were located during later wet season surveys; across years, newly founded colonies increased in relative frequency through the wet season and into the onset of the dry season (from 13% in May to 80% in January; Fig. 1). Proportions of preemergence colonies from different years' samples did not differ in May (Fisher's exact test  $P = 0.103$ ), July (Fisher's exact test:  $P = 1.00$ ), or during late wet season (August 1997 and October–November 1995; Fisher's exact test:  $P = 1.00$ ).

Foundress numbers ranged from one to seven for preemergence colonies that were surveyed or collected at night ( $\bar{x} = 2.7$ ;  $N = 22$  colonies). Most newly founded colonies included more than one female: 77 percent of night-surveyed foundress associations included multiple females (51% of  $N = 43$  foundress associations included multiple females if day-observed colonies are included in the sample). For night-surveyed colonies, single-foundress nests occurred only in an early wet season sample (July 1997). Males were present in two preemergence colonies, one in January 1996 and one in May 2000. Multiple females with well developed ovaries were present in two of the ten foundress associations that were collected and dissected in the late wet season (October–November 1995).

Postemergence colonies ranged in size from 2 to 128 adults ( $\bar{x} = 23.9$ ;  $N = 30$  night-collected colonies). Adult female numbers in postemergence colonies ranged from 2 to 86 ( $\bar{x} = 14.9$ ). Numbers of adult females in postemergence colonies did not differ significantly among seasons (Kruskal-Wallis test:  $\chi^2 = 3.55$ ,  $df = 2$ ,  $P > 0.10$ ). Adult males were present in 68 percent of postemergence colonies

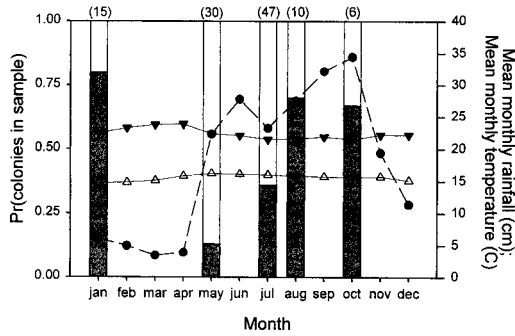


FIGURE 1. Relative abundance of preemergence (shaded portion of bars) and postemergence (open portion of bars) *Mischocyttarus mastigophorus* colonies sampled in different months at Monteverde, Costa Rica. Number of colonies sampled is in parentheses above bars. Also plotted are monthly means of rainfall (dashed line, filled circles), maximum temperature (filled triangles), and minimum temperature (open triangles).

( $N = 54$ ; ten colonies were built too high above the ground for the sexes of wasps to be determined). Males were observed flying and perching in the vicinity of nests, or on nests, during all surveys. When males were present on postemergence nests, they comprised 11.1 to 67.5 percent of the adults, but females outnumbered males in most colonies (Fig. 2). Colonies with larger numbers of females were more likely to include males (Wilcoxon two-sample test:  $Z = -2.33$ ,  $P < 0.05$ ), and the number of males in colonies increased with the number of females in colonies (Fig. 2;  $R^2 = 0.58$ ,  $N = 32$ ,  $P < 0.001$ ).

Active *M. mastigophorus* colonies were present at Monteverde during all population surveys, but the distribution of colony developmental stages varied among seasons. Our data suggest that monthly variation in the amount of rainfall influenced the probability of new colony foundation. Apparently, fewer new colonies were initiated during (or survived) the latter part of the dry season. Our across-year data suggest that new colonies can be initiated over a period spanning at least nine months, and new colonies may be initiated throughout the year. Several subtropical and tropical *Mischocyttarus* species have been

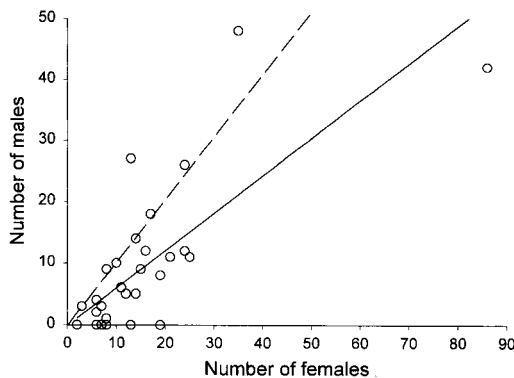


FIGURE 2. Relationship between numbers of adult males and adult females on postemergence nests of *Mischocyttarus mastigophorus* collected at Monteverde, Costa Rica. The dashed line represents a slope of unity; the solid line indicates the best-fit simple linear regression line for these variables.

found to exhibit relatively asynchronous colony foundation, with colonies of all stages present for much or all of the year (Jeanne 1972; Litte 1977, 1981). In marked contrast, temperate populations exhibit highly synchronized colony foundation over a span of several days to three weeks (Litte 1979, Stiller 1989). Similar latitudinal effects on nest founding synchrony have been observed in temperate and tropical *Polistes* species (West Eberhard 1969). Low monthly variation in temperature and day length at tropical sites, including Monteverde, contrast with seasonal climatic variation in the temperate zone. Seasonal variation in mean monthly rainfall, however, was greater at Monteverde than at many lowland wet or moist forest sites, and total annual rainfall was lower (Coen 1983, Clark *et al.* 2000). Previous studies of *Mischocyttarus* colony phenology were conducted at temperate latitudes, or at lower elevations in relatively aseasonal tropical areas (<400 m). The Monteverde population of *M. mastigophorus* was intermediate between temperate and lowland tropical *Mischocyttarus* populations with respect to synchrony of colony foundation (Jeanne 1972; Litte 1977, 1979, 1981; Stiller 1989). These patterns suggest that elevational and latitudinal climatic effects can combine to determine seasonal constraints on insect colony growth and development.

Cooperative colony foundation by several females (pleometrosis) was common in *M. mastigophorus*. Some of the *M. mastigophorus* foundress associations and postemergence colonies that we collected in the late wet season had multiple females with developed ovaries. We did not determine if multiple active eggs layers were present in foundress associations. Behavioral observations on postemergence colonies suggest that a single functioning queen dominates *M. mastigophorus* societies (O'Donnell 1998). Other females with developed ovaries may succeed the queen or replace it if it is lost (Jeanne 1972, Litte 1979). Snelling (1953) reported the occurrence of polygyny in postemergence *M. flavitarsis* colonies in California, but did not present quantitative data or describe how polygyny was determined.

Cooperative nest foundation has occurred at varying rates in all temperate and tropical *Mischocyttarus* populations studied to date (Snelling 1953, Itô 1984), except in an *M. flavitarsis* population in eastern Colorado (Stiller 1989). Rates of cooperative founding vary among species and populations in other genera of paper wasps as well. In *Polistes* wasps, the proportion of cooperatively founded colonies increases from temperate to tropical latitudes (Reeve 1991). A similar general pattern appears in the genus *Mischocyttarus*, although fewer species have been studied (Litte 1979, Stiller 1989, Clouse 1994). We observed single-female preemergence *M. mastigophorus* colonies only in the early wet season sample (excluding day-observed colonies), at the start of a period when new colonies are founded at high rates. Some of these lone females may have been joined later by cofoundresses, since additional foundresses can join paper wasp colonies up to several weeks after nest initiation (West Eberhard 1969, Jeanne 1972). Litte (1977) found that *M. mexicanus* colonies were cooperatively founded more often in the fall (November–January) than during winter/spring (January–May); the seasons differed in day length and mean temperature, but not in rainfall, since all of Litte's (1977) data were collected during the Florida dry season.

Increased probability of male presence with larger numbers of females, and therefore presumably with greater colony age, indicated that *M. mastigophorus* colonies may produce female offspring before males (protogyny). Males were occasionally observed on preemergence nests, but males were not present on the smallest postemergence nests. Mating has not been observed on *M. mastigophorus* nests, and a possible off-nest mating aggregation was observed in 1997 (O'Donnell 1998, 1999). In other tropical independent-founding wasps, males are typically produced after adult females emerge on their nests (West Eberhard 1969, Jeanne 1972, Litte 1981). Colony-level protogyny is expected to occur in independent-founding wasps because early investment in males (instead of female workers) can reduce colony productivity. Males consume food resources but typically do not perform tasks for the colony (*cf.* O'Donnell 1995). The costs of males may be especially high for *M. mastigophorus*, in which males are dominant over females, reside on natal nests for long periods, and consume much of the food collected by foragers (O'Donnell 1999); however, even if colony-level protogyny occurred, it did not result in a period of male absence in the *M. mastigophorus* population.

Because of their haplodiploid sex determination, hymenopteran females that emerge when males are absent from the population cannot produce female worker offspring of their own. The enforced sterility hypothesis asserts that such unmated females will be likely to help their mothers rather than attempt to initiate new colonies (Alexander 1974, Suzuki 1986, Yanega 1988, Hunt 1994). We predict that the conditions for enforced sterility are less likely to occur in tropical Hymenoptera populations. That is,

colony-level protogyny alone would seem inadequate to enforce female sterility when nest initiation and adult male production are asynchronous in the population.

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