

## 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

<sup>1</sup> Received 7 August 2000; revision accepted 15 December 2000.

<sup>2</sup> We dedicate this paper to the memory of John Campbell, whose diligence in collecting Monteverde weather data provided a valuable information base for analyzing tropical climatology.