

On the Mass Aggregations of *Polistes versicolor* (Olivier) (Hymenoptera: Vespidae) along the Northern Cordillera of Venezuela, South America

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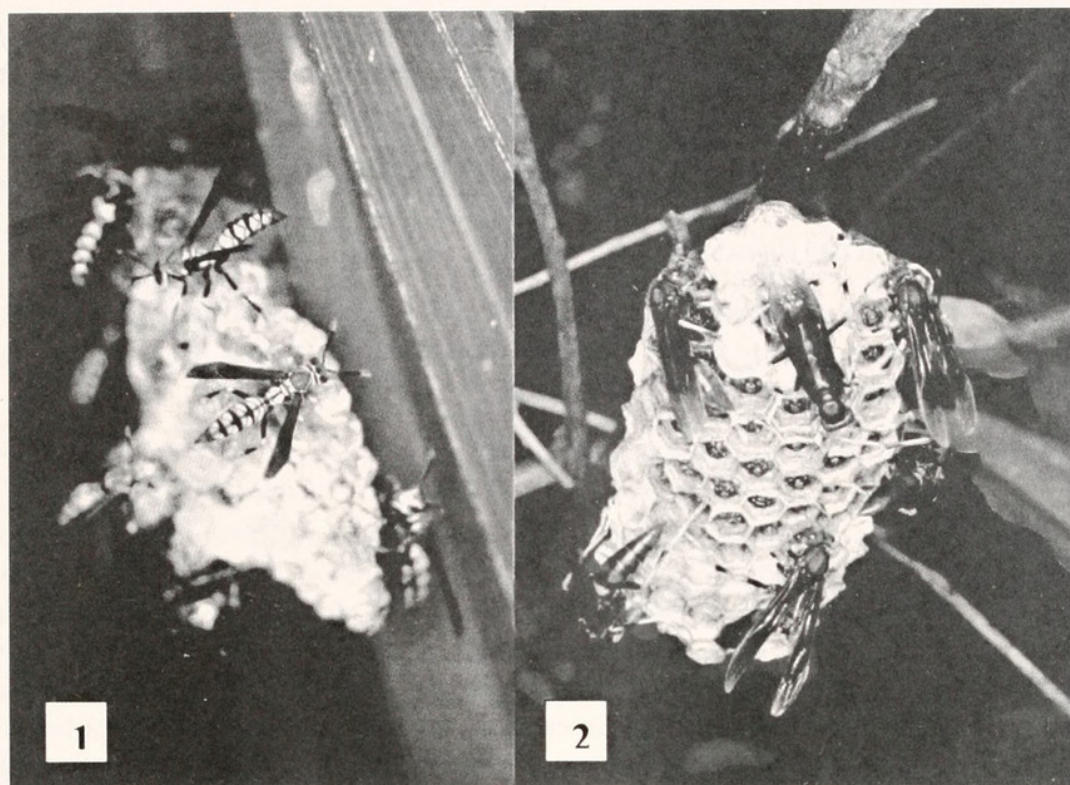
Abstract.—Aggregations of diapausing *Polistes versicolor* were observed and sampled at three sites in the Venezuelan Northern Cordillera (ca 2,400 m) during the dry season (November to April). During the wet season (May–October), *Polistes versicolor* occupies lowland areas where food supply appears to be abundant year round. Here it coexists with *P. canadensis* which does not move to the mountains during the dry season so there seems to be no basis for a seasonal diapause in *P. versicolor*. The phenomenon is compared with a conspecific population in Brazil that also has been reported to aggregate. Energy savings, escape from predators, and the presence of a pronounced dry season at lower elevations are some of the possible reasons for this behavior.

Resumen.—Agregaciones de *Polistes versicolor* en diapausa fueron observadas y colectadas durante la época seca (Noviembre a Abril), en tres lugares diferentes de la Cordillera de la Costa Venezolana (ca 2.400 m). Durante la época húmeda (Mayo–Octubre), *P. versicolor* ocupa áreas en Venezuela donde el suministro de alimentos es abundante todo el año. Aquí coexiste con *P. canadensis*, la cual no se mueve hasta las montañas durante la época seca, de manera que no pareciera existir una base para que tenga una diapausa estacional. El fenómeno es comparado con una población coespecífica estudiada en Brasil, la cual ha sido reportada en agregaciones. Ahorro energético, escape de depredadores o que la presencia de la época seca demanda la aparición de una diapausa, se mencionan como algunas de las razones para exhibir este comportamiento.

Some *Polistes* wasps from temperate regions form autumnal aggregations prior to a hibernation period (Hermann and Gerling 1974, Krispyn 1975, Rau 1930, 1931, Takamizawa 1981, West-Eberhard 1969). In contrast to the annual hibernation cycle of temperate *Polistes*, swarming followed by continued nest construction is generally associated with tropical members of the genus (Rau 1929, 1930, 1931, 1941). Despite the general nesting patterns for tropical species, mass aggregations of *Polistes* wasps have also been seen and reported from Brazil (Gobbi 1977, Gobbi and Zucchi 1985, González et al. 2002, Hughes 2002, Ihering 1904), Costa Rica

(Hunt et al. 1999, J. Pickering, pers. comm.), Cuba (J. Genaro, pers. comm.), Mexico (J. Strassmann, pers. comm., J. Hunt, pers. comm.), and Venezuela (Bequaert 1948, Manzanilla et al. 2000, Menke 1988, Steyermark 1945).

Polistes versicolor and *P. canadensis* (Figs 1–2) are two of the most common paper wasps below 1,000 m throughout the Neotropics from Costa Rica to Argentina (Carpenter 1996a, Ihering 1904, Mac Callan 1954, Richards 1978). In Venezuela, one of the areas where both species are sympatric is the slopes and lowlands along the Northern Cordillera or Coastal Mountainous System which lies between about 10 °



Figs 1–2. 1. *Polistes versicolor*; 2. *Polistes canadensis*. Both from Maracay, Aragua, Venezuela (450 m).

and 11 ° N, and 62 to 68 ° W, interrupted at the east by the Unare Depression. Its maximum heights are Naiguata peak (2,765 m) in the central area and Turimiquire peak (2,595 m) to the east.

During the dry season, from November to April, large aggregations of *P. versicolor* are regularly found along the highlands of some areas of the Northern Cordillera (P. Berry, F. Bisbal, J.B. Rodríguez, M.T. Badaraco, pers. comm.; L.J. Joly, J.L. García, F. Bisbal in Manzanilla et al. 2000) where it does not occur during the wet season. However, despite the common occurrence of this phenomenon, and the easy access to some sites it has been poorly documented. As a contribution to the overall knowledge of *Polistes* biology we review published material on tropical *Polistes* aggregations and report information from field collected mass-aggregated specimens of *P. versicolor* from Venezuela.

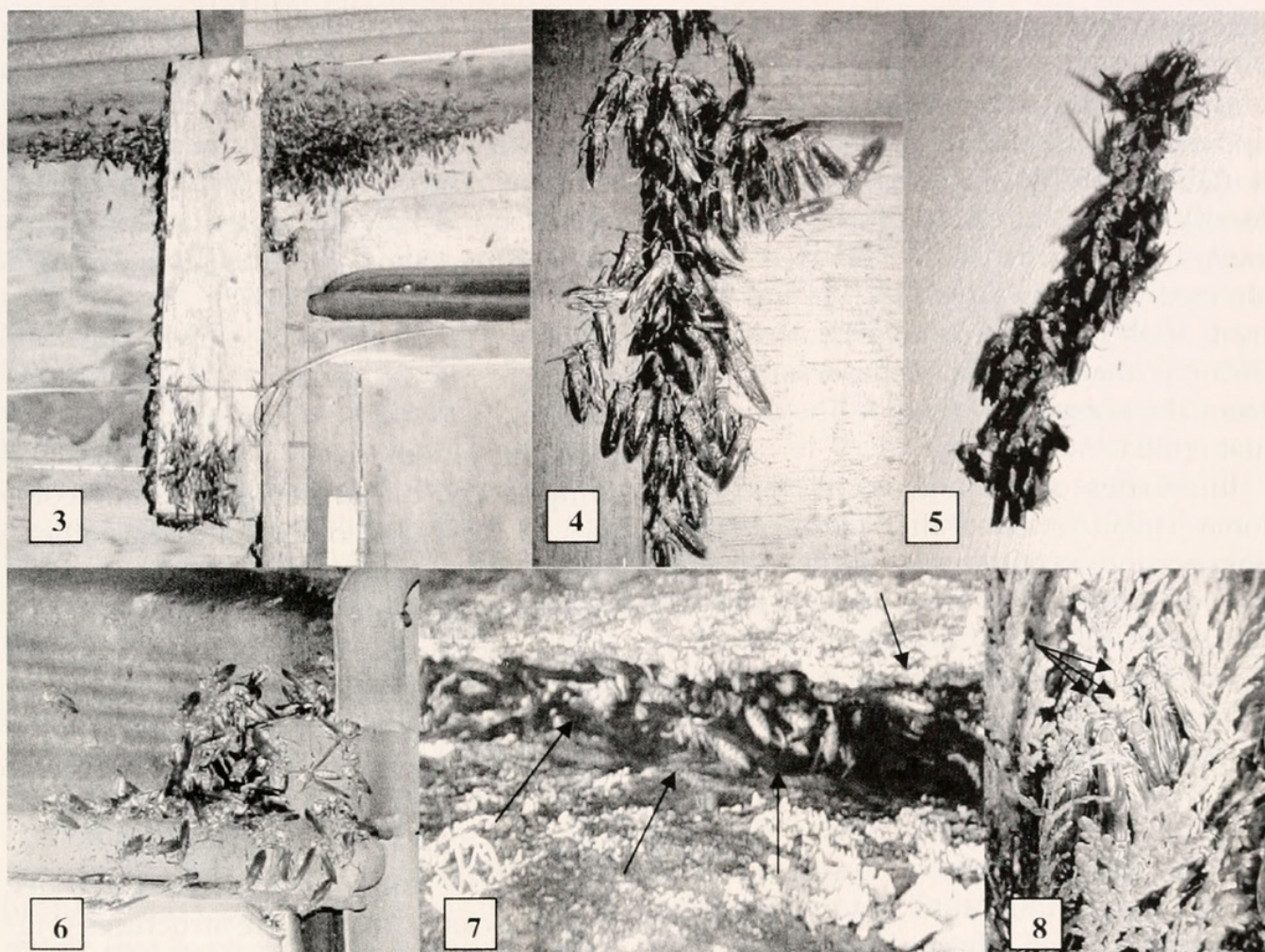
MATERIALS AND METHODS

Study sites.—Sites 1 and 2 were located at opposite ends of Colonia Tovar town (Northern Cordillera; 50 km west of Ca-

racas; Approximate Annual Mean: Temp. 15.8 ° C; 85 % RH) (Site 1: West of Colonia Tovar; Sector La Lagunita, Via Colonia Tovar—La Victoria, Aragua, Aprox. 2,400 m; Site 2: East of Colonia Tovar; Sector Geremba, Topo Botiquín, Miranda, 2 km from the Road Colonia Tovar—El Jarillo, 2,345 m). The life zone of sites 1 and 2 is that of a cloud forest characterized by a wet evergreen forest, with many hours of mist, mostly from mid afternoon to mid morning, with a temperate climate (Fernández-Badillo 1997, 2000).

Site 3 is located at Topo Galindo, Miranda, 2,550 m (Approximate Annual Mean: Temp. 10 ° C; 86 % RH). This site can be characterized as a subpáramo zone with shrubby vegetation, with almost constant mist (Fernandez-Badillo 2000, Ortiz and Fernández-Badillo 2004).

Collection of specimens.—Wasps were collected on January 1st, 2004 from man-made structures, but they were also observed on vegetation at sites 1 and 2 (Figs 3–7), while at site 3 they were collected on February 4th, 2004 from natural crevices. A total of 128 wasps were collected from



Figs 3–8. Mass aggregation of *Polistes versicolor*, 3. inside a shack; 4. behind door; 5. cement wall crevice; 6. corner of rolling door; 7. rock crevice; 8. inside branches of *Cupressus lusitanica*. All photographs were taken with flash, since the wasps were in dark places. Arrows in figures 7 and 8 signal the wasps. Photographs 3–5, 8 from Sector Geremba, Topo Botiquín, Miranda, Venezuela; 6 from Sector La Lagunita, Vía Colonia Tovar-La Victoria, Aragua, Venezuela; 7 from Topo Galindo, Miranda.

the three sites (38 from Site 1; 41 from Site 2; 49 from site 3). Ten wasps from each site were dissected to determine sex and condition of the reproductive system, and also if food was present in the midgut. Extent of wing tip wear of every wasp was also recorded.

Voucher specimens have been deposited at the Entomological Collection of the Museum of Natural History of the University of Georgia, Georgia, USA, as well as the Museum of Instituto de Zoología Agrícola of the Universidad Central de Venezuela, Maracay, Venezuela.

RESULTS

Aggregations of *P. versicolor* wasps were observed at three sites located in the

northern Cordillera of Venezuela at two neighbor states (Aragua and Miranda). They were located inside man-made structures (holes and crevices in walls—Figs 3–6), and also in natural crevices and inside the branches and leaves of some plants (Figs 7–8). Most wasps were clustered but at sites 1 and 2 some were observed flying on the vegetation, especially on flowers, and also around the aggregation groups. Some wasps in the aggregations were also clearly engaged in trophallaxis. No movements out of the hibernating groups were noticed in Site 3, probably due to rain and the low temperature during the day of collection.

All wasps collected at the three sites were females, and sub-samples showed

that most had undeveloped ovaries [Stage A (Gobbi 1977)]. A few of the collected wasps had large ovaries but no eggs (with apparent egg reabsorption signals) [Stage K (Gobbi 1977)]. No solid remains were found inside the guts of the dissected wasps. A minority of the collected wasps showed wing tip wear (15, 18, and 16 % from sites 1 to 3 respectively), a clear indication that at least some wasps were from the season previous to the one that just ended.

Interviews of some peasants from Colonia Tovar revealed that massive wasp aggregations occur annually from November to April, and treating the wasps with pesticides has been a common practice. According to all interviewed persons, the numbers of these aggregations have decreased over the years.

DISCUSSION

Mass aggregations of adult *Polistes* wasps were thought to occur mostly in temperate zones where the phenomenon is clearly related to hibernation (Hermann and Gerling 1974, Kryspin and Hermann 1977, Matsuura 1980, Takamizawa 1981). However, some *Polistes* species from different species groups [1, 2, 3 & 5 (Richards, 1973)] but of the same subgenus (Richards 1978, Carpenter 1996b) are known to gather in mass aggregations in tropical regions (*P. versicolor* (Gobbi 1977, Manzanilla et al. 2000); *P. instabilis* in Costa Rica, *P. cf. canadensis* in Mexico, *P. cubensis* in Cuba—J. Pickering, J. Strassmann, J. Genaro, respectively, pers. comm., Hunt et al. 1999) where there would seem to be no apparent seasonal demand for diapause.

Polistes versicolor has been reported in such abundance in some areas than it has become a major threat to some vertebrates (Grant and Grant 1997, Heraty and Abedrabbo 1992).

In Venezuela, this wasp species is commonly found north of the Orinoco River, mainly in the lowlands along the Andes

and the Northern Cordillera (Bequaert 1948, McCallan 1954). Manzanilla et al. (2000) also observed high densities of these wasps in the easternmost section of the Turimiquire massif, in Northern Venezuela, and they attributed the phenomenon to seasonal migration, associated with the dry season.

The areas of occurrence of *P. versicolor* are agricultural lands that appear to provide these and other wasps, with enough food supply the whole year. While the sympatric *P. canadensis* initiate new colonies and enlarge older ones throughout the year, *P. versicolor* wasps stop making nests and start moving in large groups to higher elevations of the Northern Cordillera by November. Flying in such large masses is not uncommon and seems to be a regular behavior of this species (Heraty and Abedrabbo 1992). Once the high altitudes (> 2,000 m) are reached, these wasps hide along crevices in rock walls, under rocks or man-made structures (Figures 3–7) where they spend the colder months until April when they return to warmer lands. While in these aggregations, they also hide or remain still on tree-trunks, branches, inside bushes, and other small plants (Fig 8) (Manzanilla et al. 2000, Steyermark 1945). It looks like the first known report of these mass aggregations in Venezuela was the one made by the famous botanist Julian Steyermark who observed "... billions of semi-dormant hibernating wasps covering the trees on the summit of Cerro Peonía or Pajaritos", a mountain located at the Turimiquire, in Anzoátegui State (Menke 1988, Steyermark 1945). Manzanilla et al. (2000) reported high densities from Cerro La Laguna also, which is located in the same mountainous region of Steyermark's observations. A similar situation was reported by Gobbi (1977) in Sao Paulo, Brazil, where *P. versicolor* have been found to hibernate in masses during the dry season, in geographic and weather conditions

similar to those we described for Venezuela.

From wasps collected at three different sites of the Northern Cordillera of Venezuela we found that they were only females, with large amounts of fat body, and subsamples showed that most had undeveloped ovaries, as expected for hibernating wasps (Hunt et al. 1999, Spradbery 1973). The relatively low incidence of wing wear among the aggregating wasps indicates that most are young. These characteristics were also found in hibernating aggregates of *P. versicolor* wasps found in Ribeirao Preto, Brazil (Gobbi 1977), but also noted in *P. instabilis* aggregations from Costa Rica (Hunt et al. 1999).

Once aggregations are in place, some individuals make short flights, probably to gather some "maintenance" food during periods of warmer temperatures, usually around mid-day. This behavior was also observed by Manzanilla et al. (2000). Gobbi (1977) and Gobbi and Zucchi (1985) also found that even while hibernating, some individuals of *P. versicolor* had solid food remains in their midgut. Additionally, these authors reported trophallaxis to be common among the individuals composing the aggregates. In our sample of wasps from each site no solid remains were found inside the midgut. Manzanilla et al. (2000) mentions also that residents of the Turimiquire area confirmed the occurrence of the aggregating phenomenon for "at least ten consecutive years". Based on Steyermark's (1945) remarks, the presence of aggregating wasps in this region is even older. According to residents of Colonia Tovar, the first wasps appear in these mountains around November, or about the end of the wet season. The numbers increase as the dry season starts. They fly in large groups and invade natural and artificial crevices, and any place where they can "hide". A common comment among the people in the area was that they have known the wasps "forever", and that the wasps were more numerous many years

ago, but since these insects "are annoying for agricultural and other activities", residents have normally sprayed them with pesticides. Daniel H. Janzen has noticed that the cloud level has moved to higher elevations in Costa Rica due to global warming (J.H. Hunt pers. comm.), this could be also another possible explanation why these wasps are less abundant than before in the surrounding areas of Colonia Tovar. Even though the wasps are not aggressive in these aggregations, they can sting if bothered. The wasps seem to "disappear" from the area after April.

The northernmost range of *P. versicolor* is Costa Rica and Panama where the species seems to swarm throughout the year but does not mass-aggregate (J. Pickering, pers. comm.). In Trinidad, where the mountains are lower than 1,000 m, neither these wasps, nor others in the genus appear to mass-aggregate at any season (C.K. Starr, pers. comm.)

In the tropics, *Polistes* species are basically lowland creatures; besides, *P. versicolor* occupies agricultural areas in Venezuela and in Brazil where food supply should be expected to be abundant year around, which would seem to make a need for a seasonal diapause unnecessary. However, the phenomenon is clear, common and happens every year, in both Brazil and Venezuela. *Polistes canadensis* and *P. versicolor* have broadly overlapping ranges in northern Venezuela, but while *P. canadensis* nests year-round, *P. versicolor* disappears during the dry season. Three of the many plausible reasons for *P. versicolor*'s aggregating behavior could be either that they go to a colder place for energetic savings, and metabolic costs would be minimal, and/or to escape from predators, who might find inactive wasps exceptionally vulnerable in the lowlands, or, as suggested by Hunt et al. (1999), the presence of a severe dry season is indeed a clear seasonal demand for diapause. Furthermore, even though *P. canadensis* remain active through the dry season in the

lowlands, in Costa Rica it has been observed that they sharply diminish productivity that increases only with the onset of the rainy season (J. Hunt, pers. comm.). Something similar could actually be happening in the Venezuelan lowlands during the dry season. Further and more detailed studies of this phenomenon will be needed to provide more insights into this particular behavior.

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