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Dry Season Migration by Costa Rican Lowland Paper Wasps to High Elevation Cold Dormancy Sites[1]

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We report observations here of aggregating behavior by social wasps in the genera *Polistes* and *Mischocyttarus* during the nonnesting phase of their colony cycle in Guanacaste Province, Costa Rica, a tropical locale with a pronounced dry season. The aggregating wasps are from many different nests, and they aggregate in a cold, high elevation habitat during the dry season, a time when they are nearly absent from the low elevation habitat where they build nests and reproduce during the rainy season. The aggregating behavior, which occurs after the wasps have seasonally migrated to the upper elevation aggregation site from the lowlands, strongly resembles that of temperate zone *Polistes* during winter, but it differs by the incorporation of the seasonal migration.

Polistes is the sister taxon to all other polistine wasps (Hymenoptera: Vespidae, Polistinae; Carpenter 1991), and life cycles of extratropical species are well-known (reviewed in Evans & West Eberhard 1970, Reeve 1991, Yamane 1996). Males and reproductive females are produced primarily late in the nesting season (*e.g.,* West Eberhard 1969). Mating occurs before winter dormancy (but *cf.* Hermann & Gerling 1974) and has been reported at dormancy sites (*e.g.,* Kasuya 1981) and on nests (Kundu 1967), as well as at sites away from either (reviewed in Wenzel 1987), but observations of matings are rare. Mated females aggregate in sheltered hibernacula where they overwinter (*e.g.,* Rau 1930). Males typically die at the end of the nesting season (but *cf.* Brimley 1908; Hermann & Gerling 1974).

Tropical *Polistes* species have colony cycles that vary from strongly seasonal (in areas with a pronounced dry season) to apparently continuously brooded (in areas with little rainfall seasonality; West Eberhard 1969). Matings can occur at newly founded nests (West Eberhard 1969) or at leks away from nests (Polak 1992). How *Polistes* in seasonal sites pass the dry (unfavorable) season has been little studied; *P. major* near Cañas, Guanacaste Province, Costa Rica, have been seen to aggregate during the dry season in a crevice *ca* 5 cm from their empty natal nest under the roof of a small building (JHH, pers. obs.).

Polistes instabilis de Saussure is distributed from Mexico to Costa Rica (Richards 1978) and is one of the most common *Polistes* species in the dry forest region of northwestern Costa Rica. New colonies may be initiated by lone, inseminated females or by foundress associations of several inseminated females (Rau 1940). Large, successful colonies have at-nest populations of <100 individuals. In the highly seasonal dry forests of northwestern Costa Rica (*e.g.,* Sector Santa Rosa, Área de Conservación Guanacaste), a few colonies with brood can be found at any time of year in areas of human habitation (JHH, pers. obs.), but virtually all colonies in wild forest are strongly seasonal (DHJ, pers. obs. spanning 35 years) in concert with the wet/dry climate pattern that is described in Janzen (1993). Most *P. instabilis* nests are initiated at the start of the rainy season (mid-May), and those that are not lost to predators or parasites generally terminate late in the rainy season (typically October/November). The last month of the rainy season (December) and the onset of the dry season are marked by the disappearance of these wasps from the lowlands, synchronous with their appearance in very large numbers in the evergreen wet forest (middle elev. to cloud forest) at 1000–1400 m elevation on the very steep isolated cones of Volcan

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FIGURE 1. A portion of a dry-season aggregation of inseminated females (gynes) of the independent-founding paper wasp, *Polistes instabilis,* at Estación Cacao, Área de Conservación Guanacaste, Guanacaste Province, Costa Rica. The wasps are clustered near the uppermost part of the west wall at the southwest corner of a small wooden building.

Orosi and Volcan Cacao (Sector Cacao, Área de Conservación Guanacaste), 2–15 km east of the dry forest lowlands (DHJ & W. Hallwachs, pers. obs.). We interpret this seasonal movement as the wasps putting themselves into "cold storage," where they pass the time of year when Lepidoptera larvae, their normal food for rearing brood (*e.g.,* Rabb 1960), are virtually nonexistent in the lowlands (Janzen 1993). During the first rains in the lowlands they abruptly disappear from their upper elevation aggregations, and newly founded nests appear in the newly leafing dry forests of the lowlands. Disappearance of the aggregations is not due to predation or starvation; rather, the wasps simply fly away from the aggregations (DHJ & W. Hallwachs, pers. obs.). Hundreds of *P. instabilis* aggregations have been seen in the understory of old growth forest on the slopes of Volcan Cacao at 1000–1400 m during the dry seasons of 1986–1997; the wasps aggregate in hollow trees, old buildings, and vegetation masses. Nonnesting aggregations of this (or any other) social wasp have not been observed in the dry forest lowlands below Volcan Cacao at any time of the year (DHJ & W. Hallwachs, pers. obs.). Observation of large numbers of *P. instabilis* on mountains in Veracruz, Mexico, at a time when no active nests were present in adjacent lowlands (R. L. Jeanne, pers. comm.), suggests that elevational migration may occur at sites throughout the species' range.

We investigated several of the dry season aggregations of *P. instabilis* on 31 January–1 February 1993 and 29–31 January 1995, in and near several wooden buildings at Estación Cacao, at 1000 m elevation on the western slope of Volcan Cacao, Área de Conservación Guanacaste, Guanacaste Province, Costa Rica. The aggregations (Fig. 1) occurred primarily in the upper corners of room interiors, especially on southwestern but also southeastern exposures. Five aggregations inside buildings in 1993 ranged from 17 to >400 wasps; seven similar aggregations in 1995 ranged from *ca* 40–300 wasps. Aggregations of 500–2000 individuals (one aggregation was estimated at 7 liters; DHJ, pers. obs.) have been found at this time of year in old unused buildings and in hollow trees in the nearby forest (DHJ & W. Hallwachs, pers. obs.). Most of the wasps in aggregations are females, but at least one 1995 aggregation included a few males; some males have been seen in aggregations in other years. We dissected 30 females in 1993 and 34 in 1995; all were inseminated, and none had enlarged ova in the ovaries. While some had slight wing wear, most had none. Wasps flying solitarily in the old growth forest understory and forest edges 100 m or more from the buildings were collected for one hour periods on two sunny, warm afternoons

in 1995. Of 20 *P. instabilis* thus collected, 7 were female and 13 male. These free-flying wasps are individuals roused from aggregations by disturbance or, more commonly, by heating of hollow trees through direct insolation; many return to hollow trees in the afternoon. Aggregations on leafy vegetation of no more than ten wasps each—all of which were males in the few such aggregations that we inspected—seemed to be the primary source of males we captured in flight. However, when the weather is cloudy and cold for several consecutive days, these small aggregations disappear from the foliage (DHJ, pers. obs.), and the wasps in them presumably join larger aggregations in more sheltered sites.

In 1993, females from three aggregations of >30 wasps each were color-marked on the thorax with a spot of enamel paint. Triads of wasps, 2 from one aggregation and 1 from another, were established in petri dishes; each of six possible combinations of wasps from the three aggregations was replicated five times. Ten control dishes of 3 wasps from the same aggregation were also established. The wasps exhibited substantial activity in the dishes, and over the course of 4–5 hr we observed neither associative nor aggressive behaviors among any of these wasps. We marked 200 wasps from the largest aggregation with one of two colors. Wasps of one color ($N = 100$) were released within the building at the site of the original aggregation; wasps of the other color were released outside, 100 m from the building. One day later, 17 of the wasps released at the original site were in a smaller aggregation at the same site; none of the 100 wasps released 100 m away had returned. In 1995, an aggregation of *ca* 40 wasps was roused by an attempted capture; no wasps were found at this same site on later days. The very large size of some of the aggregations precludes the possibility that wasps therein are progeny of a single nest. Our observations further show that there is no tendency for wasps to be attracted to other wasps of a particular aggregation nor to a particular aggregation site.

In 1995, we found an aggregation of 18 *Polistes pacificus* F. clustered under a leaf of a coffee tree in a clearing near the buildings of Estación Cacao. Eleven of the wasps were female; 7 were male. Seven of the females were inseminated, and in 4 we could not tell. A second aggregation of 5 inseminated female *P. pacificus* was found in interstices of a damaged and abandoned nest of *Polybia diguetana* du Buysson at the same site. No *P. pacificus* were seen flying on sunny days.

In 1995, we also examined an aggregation of *Mischocyttarus a. angulatus* Richards taken from beneath a leaf at the margin of a woodland trail near Estación Cacao. All of the 40 wasps were female. We dissected 10; all were inseminated. As with *P. instabilis,* small aggregations of apparently all males of *M. angulatus* could be found on leafy vegetation. Sixty-four of 66 *M. angulatus* collected individually while flying on two sunny afternoons were males.

None of these three species nest in the evergreen old growth forest where these aggregations occur; *Polybia diguetana* is the only social wasp that is present in this forest (DHJ & W. Hallwachs, pers. obs. spanning 11 years). However, all three of the aggregating species nest abundantly in the seasonal lowlands at 0–300 m elevation, 2–15 km west of where we studied these aggregations. Thus, the off-nest aggregations of *P. pacificus* and *M. angulatus* that we report here also reflect altitudinal migration, as do the more apparent *P. instabilis* aggregations. Although on sunny days both males and females may be seen on the wing, we did not see them at water or food sources, nor have migrant wasps been observed feeding or drinking at other times (DHJ, pers. obs.). In contrast, Strassmann (1979) reports that gynes of *Polistes annularis* in Texas, U.S.A., that emerge from their hibernacula on warm midwinter days may feed on honey stored in their natal nests. A consequence of the elevational migration that we describe here is that the wasps are quiescent in cool, mesic conditions in which metabolic costs would be minimal. The aggregating wasps are behaving in a manner directly analogous to coccinelid beetles (*Hippodamia convergens*) in the high Sierras of California (Hagen 1962), noctuid moths [*Euxoa* (*Chorizagrotis*) *auxiliaris*] in the Rocky Mountains (Pruess 1967), and bogong moths (*Agrotis infusa*) in the Great Dividing Range of Australia (Common 1954)—all of which pass an unfavorable season by migrating into aggregations at cool, high elevations.

Occurrence of both males and females on mountains that are the most prominent topographic feature in the region is suggestive of "hilltopping," an apparent mating strategy found in several insect orders in which which females of hilltopping species seem scarce or widely scattered (Thornhill & Alcock 1983). Hilltopping has been ascribed to *Polistes canadensis navajoe* in Arizona, U.S.A. (Alcock 1978) and to *P. canadensis* and *P. carnifex* in Guanacaste Province, Costa Rica (Polak 1993). Hilltopping may be a component of an elevational migration that occurs in the three species of social parasitic *Polistes* in Italy (Cervo & Dani 1996). Although we cannot rule out hilltopping as a component of the aggregation

behavior described here, we have not observed male territorial behavior or any mating behaviors among the migrant wasps at Estación Cacao. Instead, the dry-season aggregations of paper wasps at Estación Cacao resemble the winter aggregations of *Polistes* in temperate zones in that all females are inseminated. Matings in the temperate wasps may occur with males that defend territories near aggregation sites as females assemble (*e.g.,* Post & Jeanne 1983), but we have not observed territorial behavior in the wasps reported here.

The elevational migration and aggregating behavior that we describe also have similarities to the swarming of *Polistes* sexuals at prominent anthropogenic features such as towers described by Reed and Landolt (1991)—notably that "most females were inside enclosed areas near the tops of the towers and most males were in dispersed swarms around the outside of such areas." The presence of males at Volcan Cacao of all three observed species suggests that observations of overwintering males in extratropical species by Brimley (1908) and Hermann and Gerling (1974) are not anomalies but rather document uncommon extratropical occurrences of a phenomenon more common in tropical taxa.

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