



Elevational Patterns of Diversity and Abundance of Eusocial Paper Wasps (Vespidae) in Costa Rica

Anjali Kumar^{1,4}, John T. Longino², Robert K. Colwell³, and Sean O'Donnell¹

¹Animal Behavior Group, Department of Psychology, Box 351525, University of Washington, Seattle, Washington 98195, U.S.A.

²The Evergreen State College, Olympia, Washington 98505, U.S.A.

³Department of Ecology and Evolutionary Biology, University of Connecticut, U-43 Storrs, Connecticut, 06269, U.S.A.

ABSTRACT

We used a standard sampling protocol to measure elevational patterns of species richness and abundance of eusocial paper wasps (Hymenoptera: Vespidae) in Costa Rica. The sample transect of six sites spanned approximately 2000 m in elevation from lowland to montane forest. Species accumulation curves and species richness estimates both document a low elevation peak in paper wasp species richness at 50 and 300 m asl, with a decline in species richness at higher elevations. Comparison of species composition among elevations revealed strong species turnover from a rich lowland fauna to a depauperate, but distinct, montane fauna. We also observed a general trend toward a greater abundance of paper wasps at higher elevations, a pattern not usually observed in eusocial insects. Army ant species that prey on paper wasps declined in abundance with elevation across the sample transect, a pattern that has been observed at other sites. We discuss the possibility that elevational changes in predation pressure affect variation in paper wasp abundance and species richness. Eusocial paper wasp species employ one of two modes of colony founding, independent and swarm founding. We found that the total abundance of individual swarm-founding wasps was higher at all elevations than the abundance of independent-founding wasps, supporting previous suggestions that Neotropical swarm founders are more successful ecologically.

Key words: army ant; colony founding; elevation gradient; Hymenoptera; Neotropical; species richness; swarm founding.

A CENTRAL AIM IN ECOLOGY is to explain the heterogeneous distribution of species richness among different taxa and at different geographical scales. Previous work focused heavily on latitudinal gradients of species richness, but elevational patterns of diversity are receiving increased attention (Rahbek 2005). In part, this interest is motivated by evidence for directional changes in the abiotic conditions of montane habitats (Pounds *et al.* 1999, Lomolino 2001, Parmesan & Yohe 2003, McCain 2004, Colwell *et al.* 2008). However, biotic factors such as interspecific interactions can also influence patterns of species richness.

Measures of turnover in species composition among elevational zones can indicate how community structure changes with biotic and abiotic environmental pressures (Shmida & Wilson 1985, Condit *et al.* 2002). Faunal turnover along elevational gradients should be relatively rapid in the tropics (Janzen 1967, Ghalambor *et al.* 2006). Tropical organisms are expected to have narrow elevational ranges because they are exposed to, and potentially adapted to, relatively constant local environmental conditions (Janzen 1967, Olson 1994). Insects have numerous advantages for testing patterns and causes of elevational variation in community structure. Insect communities can be thoroughly sampled within a relatively short period of time (Erwin 1982, Gullan & Cranston 2000). Their small body size (high surface area/volume ratio) makes them sensitive to temperature and humidity variation (Deutsch *et al.* 2008), and their potential for rapid adaptation to environmental change may contribute to their high species richness (Janzen *et al.* 1976, Gullan & Cranston 2000, Rahbek 2005).

Using a standard sampling protocol, we quantified changes in species richness and species composition for eusocial paper wasps (Hymenoptera: Vespidae: Polistinae) along a 1950-m elevational gradient (the Barva Transect) in Costa Rica. Eusocial insects, particularly species of Hymenoptera (eusocial ants, bees, and wasps), are excellent subjects for the analysis of geographic patterns of species richness (Kaspari *et al.* 2000, Longino *et al.* 2002). Eusocial insects are ecologically dominant in many terrestrial habitats (Erwin 1982, Wilson 1990). Although vespidae community ecology is poorly studied (Jeanne 1991), paper wasps are likely to influence many other species in terrestrial tropical ecosystems. Paper wasps are predators on insects and other arthropods (Wenzel 1998, Richter 2000). As prey items, paper wasps represent an important food resource for predators such as army ants and some insectivorous birds (Windsor 1976; Chadab 1979a, b; Strassmann 1981; Rettenmeyer *et al.* 1983; Kumano & Kasuya 2006).

Social wasps are easily sampled because foragers depart from and return to a central place (the nest), and because workers are active in all seasons in most tropical ecosystems (O'Donnell 2000). Paper wasp colonies have low mobility because their nests are sessile and many species are philopatric when choosing nest sites (Wenzel 1991, 1998). This reduced mobility may cause paper wasps to adapt to local climatic regimes (Wenzel 1991, Hozumi *et al.* 2005). Since climate changes quickly with elevation, even at tropical latitudes (Pounds *et al.* 1999, Clark *et al.* 2000, Colwell *et al.* 2008), wasp species may be restricted to narrow elevational ranges. There is evidence that the montane paper wasp species assemblage at Monteverde, Costa Rica is distinct from adjacent lower elevation communities (O'Donnell 2000, O'Donnell & Joyce 2001). However, the elevational distributions of tropical paper wasp species, and

Received 14 January 2008; revision accepted 17 September 2008.

⁴ Corresponding author; e-mail: anjali2@u.washington.edu

patterns of turnover in species composition among elevations, are largely unknown.

Ants, particularly army ants (Ecitoninae), are major predators on Neotropical paper wasps. Ants have affected the evolution of paper wasp behavior, including colony founding, nest architecture, and nest-site selection (Jeanne 1970, 1975; Chadab 1979a, b; O'Donnell & Jeanne 1990; Bouwma *et al.* 2007). Predation pressure on wasp brood by ants decreases strongly with increasing latitude (Jeanne 1979) and probably decreases with increasing elevation as well. Army ant foraging activity declines with elevation in Costa Rica (O'Donnell & Kumar 2006). Paper wasp colonies are favored prey of some of the most common army ant species, and many paper wasps show specific defensive responses to army ants, suggesting that army ants are particularly important natural enemies of social Vespidae (Chadab 1979a, b; Rettenmeyer *et al.* 1983; Gotwald 1995). In this study we sampled the abundance of aboveground army ants that could potentially prey on paper wasp colonies along the sample transect. We asked whether army ant abundance corresponds to elevational patterns of paper wasp community structure.

There are two major grades of social structure based on modes of colony founding in eusocial paper wasps: swarm founding and independent founding. Independent-founding species initiate colonies with a lone inseminated queen (Gadagkar 1991, Reeve 1991). In contrast, swarm-founding species initiate colonies with a large number of workers accompanied by a smaller number of queens (Jeanne 1991). In a review of individual and colony-density data in the Neotropics, Jeanne (1991) posited that swarm-founding paper wasps are ecologically more successful than independent-founding species. Under the assumption that worker density of a species reflects its relative contribution to local biomass, the relative abundances of different species at a locality can be used to estimate species differences in the ability to capture available energy, which is an indicator of ecological success (Jeanne 1991). However, no previous study of paper wasp density and diversity employed a repeatable, systematic sampling protocol. In this study, we used data collected by the Arthropods of La Selva project (Project ALAS, <http://purl.oclc.org/alas>) to test the assertion that swarm founders are ecologically more successful than independent-founding species, and to examine whether this pattern holds across elevations.

By analyzing the density and species richness of paper wasps and their army ant predators at different elevations along an elevational transect, we answered the following questions: (1) How do paper wasp species richness and abundance change with elevation? Are species richness and abundance related? (2) What are the patterns of elevational turnover of paper wasp species (beta-diversity) among elevations? (3) How does social structure (independent- vs. swarm-founding paper wasps) affect the above patterns? (4) Do aboveground army ants vary in abundance over the elevational gradient, such that they could affect observed patterns of paper wasp community structure?

METHODS

STUDY AREA.—The ALAS project was a large-scale inventory of Neotropical invertebrate species richness for which insects and other

arthropods were sampled at a range of elevations using standardized protocols along a transect on the slopes of Barva Volcano (the Barva Transect), located on the Caribbean slope of Costa Rica. The transect extended from La Selva Biological Station, at 50 m asl elevation (10°26' N, 83°59' W) to a site near the peak of Barva Volcano, at 2200 m asl (10°11' N, 84°07' W), over a linear distance of 35 km. The forested land along the transect has protected status, forming the northwestern edge of Braulio Carrillo National Park. Project ALAS carried out a program of quantitative sampling at six different elevations along the transect, with one field site sampled each year from 2001 to 2005, except for the La Selva site that was sampled at the same time as the 300 m asl site in 2004 (see the Project ALAS website, <http://purl.oclc.org/alas> for details). Sampling was carried out each year from February to April (during the dry season). Sampling consisted of three 2-wk expeditions separated by 2-wk intervals (during which malaise traps continued to operate; see below). Permanent members of the ALAS staff were present during all expeditions and at least one parataxonomist was based in the ALAS lab in La Selva for the entire sampling period.

SAMPLING METHODS.—Paper wasp samples were collected at six elevations: 50 m asl (2004), 300 m asl (2004), 500 m asl (2003), 1100 m asl (2001), 1500 m asl (2005), and 2000 m asl (2002). Sites were randomized with respect to sampling year to avoid confounding effects of elevation and time. The sampling protocol was similar for all years for two sampling methods, malaise and flight-intercept traps, except for the 50 m asl site (2004), where half as many malaise traps were run, but for the same length of time. Additional sampling was conducted at La Selva (50 m) in 1993 and 1994, but the methodology was not standardized to the subsequent years. Paper wasp species that were collected during 1993 and 1994 are noted in Table 1, but they were not included in the quantitative analyses.

MALAISE TRAPS.—Twenty malaise traps were established during the first two days of each year's sampling period. The trapping sites were in small clearings or treefall gaps. Ten of the traps were also used as flight-intercept traps (described below). Samples were harvested from the malaise traps at 2-wk intervals, five intervals for each trap (10 wk total, five collections for each trap) for a total of 100 collections per elevation (20 traps × 5 samples). For La Selva (year 2004), 10 malaise traps were established and samples were harvested from the malaise traps at 2-wk intervals, five intervals for each trap (10 wk total, five samples for each trap) for a total of 50 samples (10 traps × 5 samples). For the statistical analyses of wasp abundance, all data for each trap were combined, and each trap was treated as a single independent sampling unit, for a total of 20 data points at each elevation. All insects in the traps were collected into 95 percent ethanol and transported to the ALAS laboratory at La Selva Biological Station, where the ethanol was changed once and the insects were placed in a freezer.

FLIGHT-INTERCEPT TRAPS.—Flight-intercept samples were taken by placing 10 plastic trays with soapy water beneath the center pane of each of 10 malaise traps. During each 2-wk expedition specimens were collected from the trays and accumulated into 95 percent

TABLE 1. Species and sampling elevations where each species was found. Species are ordered by the elevation of their lowest observed occurrence. Bold entries are independent-founding paper wasp species. Entries marked with X are species that were found only at 50 m elevation in 1993 and 1994, but were not included in the analyses due to the use of different sampling methods in those years. The values in the table cells are the proportion of traps in which each species was found, by elevation.

Species	50 m	300 m	500 m	1100 m	1500 m	2000 m
<i>Polybia bribri</i>	0.2	0.6	0.45	0.85	0.15	0.75
<i>Polybia raii raii</i> (Bequart 1933)	X	0.05		0.3		0.1
<i>Agelaia areata</i> (Say 1837)	0.2		0.3	0.3		
<i>Polybia diquetana buyssoni</i> (Buysson 1905)	X	0.05	0.1	0.2		
<i>Leipomeles dorsata</i> (Fabricius)	0.1	0.4	0.15			
<i>Polybia nidulatrix</i> (Bequart 1933)	0.1	0.3	0.55			
<i>Polybia scrobalis surinama</i> (Richards 1970)	X	0.05	0.05			
<i>Polybia selvana</i> (Carpenter 2002)	0.1	0.2	0.2			
<i>Parachartergus apicalis</i> (Fabricius 1804)	X		0.05			
<i>Polybia occidentalis bohemani</i> (Olivier 1791)	X		0.05			
<i>Protopolybia exigua exigua</i> (Saussure 1906)	0.1		0.05			
<i>Mischocyttarus melanarius</i> (Cameron 1906)	X	0.1				
<i>Agelaia cajennensis</i> (Fabricius 1798)	X					
<i>Agelaia centralis</i> (Cameron 1907)	0.2					
<i>Agelaia melanopyga</i> (Cooper 2000)	X					
<i>Epipona niger</i> (Brethes 1926)	X					
<i>Mischocyttarus tolensis</i> (Richards 1941)	X					
<i>Synoeca chalybea</i> (Saussure 1852)	X					
<i>Polistes aterrimus</i> (Saussure 1853)		0.05		0.05	0.05	
<i>Mischocyttarus nigroclavatus</i> (Zikan 1949)		0.05	0.05	0.6		
<i>Polybia flavitincta</i> (Fox 1898)		0.05	0.1	0.55		
<i>Angiopolybia zischkai</i> (Richards 1978)		0.1		0.25		
<i>Polybia occidentalis nigratella</i> (Olivier 1791)		0.2				
<i>Protopolybia exigua binominata</i> (Saussure 1906)		0.3				
<i>Polybia aequatorialis tristis</i> (Zavattari 1906)			0.4	0.2	0.6	1
<i>Epipona guerini</i> (Saussure 1854)			0.15		0.05	0.35
<i>Agelaia angulicollis</i> (Spinosa 1851)			0.15	0.05	0.15	
<i>Agelaia panamaensis</i> (Cameron 1906)			0.1	0.95	0.95	
<i>Polybia barbouri</i> (Bequart 1943)			0.1	0.35		
<i>Protopolybia wheeleri</i> (Bequart 1944)			0.1	0.05		
<i>Apoica thoracica</i> (Buysson 1906)			0.1			
<i>Mischo. carbonarius tibialis</i> (Saussure 1854)			0.1			
<i>Polybia flavifrons hecuba</i> (Smith 1857)			0.15			
<i>Polybia bistriata</i> (Fabricius 1804)			0.1			
<i>Polybia emaciata</i> (Lucas 1879)			0.1			
<i>Polybia simillima</i> (Smith 1862)			0.1			
<i>Protopolybia picteti fulvotincta</i> (Saussure 1854)			0.15			
<i>Synoeca septentrionalis</i> (Richards 1978)			0.05			
<i>Agelaia xanthopus melanotica</i> (Saussure 1854)				0.15	1	0.7
<i>Apoica pallens</i> (Fabricius 1804)				0.1	0.05	
<i>Agelaia yepocapa</i> (Richards 1878)				1	0.45	
<i>Mischocyttarus</i> nr. <i>costaricensis</i> (Richards 1945)					0.25	
Total species observed per elevation	7 (18)	14	26	16	10	5

ethanol. One sample comprised two weeks of accumulated specimens from one trap, for a total of 30 samples for each site (10 traps \times 3 samples). For the statistical analyses of wasp abundance,

all data for each trap were combined, and each trap was treated as a single independent sampling unit, for a total of 10 data points. Paper wasp samples were transported to the ALAS laboratory at La

Selva Biological Station where the ethanol was changed once and the samples were placed in a freezer.

ARMY ANT ABUNDANCE.—We estimated abundance of aboveground army ants across the ALAS elevational gradient from leaf litter arthropod samples, following the 'miniWinkler' extraction method (Fisher 1999). Straight-line transects, 250 m in length, were marked with flags at 5-m intervals, yielding 50 individual sampling points per transect. The compass orientation of transects was varied within elevations. After a period of at least 24 h with no rain, a sample was taken at each flagged spot on the transect. A 1-m² area was delimited, and the litter and dead wood inside was minced with a machete. Litter was sifted until all the litter in the plot was sifted or 2 L of siftate was obtained, whichever came first. When there was more than enough litter to produce 2 L of siftate, the different kinds of litter in the plot (*e.g.*, leaves on soil vs. litter from a rotten log) were subsampled so that all were represented. The siftate was returned to the base camp and hung in Winkler bags for 3 d. Arthropods were collected directly into Whirlpac bags containing 95 percent ethanol. The number of plot samples varied among elevations, from 150 (at the 300 and 1100 m asl sites) to 541 (at the 50 m asl site). Leaf litter sampling was carried out in the same weeks as the paper wasp sampling for all sites except the 50 m asl site. We report the proportion of litter samples that contained army ant species that are known to raid aboveground paper wasp nests as an indicator of army ant density at each elevation.

SPECIES IDENTIFICATION.—Army ants were identified to species by JTL. All paper wasp species from malaise and flight-intercept traps were sent in 95 percent ethanol to the University of Washington for identification and quantitative analysis by AK. To identify paper wasps we examined each specimen at 10× or greater magnification under a dissecting microscope with a fiber optic illuminator. We consulted published keys (Richards 1978, Carpenter 2004), and identifications were confirmed by J. Carpenter (J. Carpenter, pers. comm.). We counted the number of individuals (abundance) of each species in each sample.

DATA ANALYSIS OF SPECIES RICHNESS PATTERNS.—Species accumulation curves were calculated for each elevation. We calculated Mao-Tau sample-based rarefaction curves (Colwell *et al.* 2004) using EstimateS software (Colwell 2005, version 7.5). Because paper wasp density was uneven among elevations, we followed the recommendations of Gotelli and Colwell (2001) for species accumulation curve analysis. We generated the x-axes (number of individuals) for the species accumulation curve plots by multiplying sample number by the average number of individuals per sample. This approach allows sites with greatly varying density of individuals to be compared, by plotting multiple curves on a common x-axis. In the species accumulation curve analyses, 2-wk malaise samples and 2-wk flight-intercept samples were treated as independent sample units (this approach does not require statistically independent samples [Colwell *et al.* 2004]), for a total of 130 samples per site (100 malaise + 30 flight intercept).

We also computed estimates of asymptotic local species richness for each elevation using the Abundance-based coverage estimator (ACE) (Chao & Lee 1992) in EstimateS (Colwell 2005, version 7.5). ACE estimates total species richness at a location, including an estimate of species that were present but not collected, based on the observed number of species and the rate of occurrence of rare species in the sample.

BETA DIVERSITY PATTERNS.—We analyzed the degree of species sharing among wasp assemblages among elevations (an inverse measure of turnover, or beta diversity). We used the abundance-based estimate of the Chao–Jaccard similarity measure (Chao *et al.* 2005), computed using EstimateS (Colwell 2005, version 7.5). This statistic is based on the probability that a wasp randomly drawn from each of two samples will belong to a species that is shared between the communities, adjusted for undetected, shared species (Chao *et al.* 2005).

MODE OF COLONY FOUNDING AND ABUNDANCE DIFFERENCES.—We used general linear models (GLM) implemented in SAS software (version 9) to analyze the relationship of elevation with paper wasp abundance and mode of colony founding. For this analysis we analyzed the per-trap total individual abundances of paper wasps at each elevation, testing for effects of mode (independent or swarm founding) and elevation. Only the traps for which there was a combination of malaise and flight-intercept sampling were used ($N = 10$) in order to standardize sampling effort across elevations.

RESULTS

SPECIES COMPOSITION.—In all, 42 species of eusocial Vespidae from 11 genera were captured among the six elevations during standardized sampling (Table 1). This total represents 40.3 percent of the 104 species known from Costa Rica (J. Carpenter, pers. comm.). Six species were independent founding while 36 species were swarm-founding wasps (Table 1). An additional 11 species of paper wasps were collected at La Selva (50 m asl) in 1993 and 1994.

ELEVATIONAL PATTERNS OF ESTIMATED SPECIES RICHNESS.—MaoTau species accumulation curves revealed a low elevation species richness peak spanning the 50–500 m asl elevations. At the three lowest elevations, species richness was increasing rapidly with respect to sampling effort (as measured by the number of individuals collected) at the end of the study, suggesting that not all paper wasp species at these elevations were collected during our sampling (Fig. 1A). Species richness per sampling effort declined with elevation above 500 m asl, with the lowest species richness per effort at 2000 m asl (Fig. 1A). The MaoTau species accumulation curves for the three highest elevations (1100–2000 m asl) showed asymptotic trends, suggesting that nearly all paper wasp species at these elevations were captured during sampling (Fig. 1A). The ACE extrapolated species richness estimates mirror the patterns of the MaoTau species accumulation curves (Fig 1B).

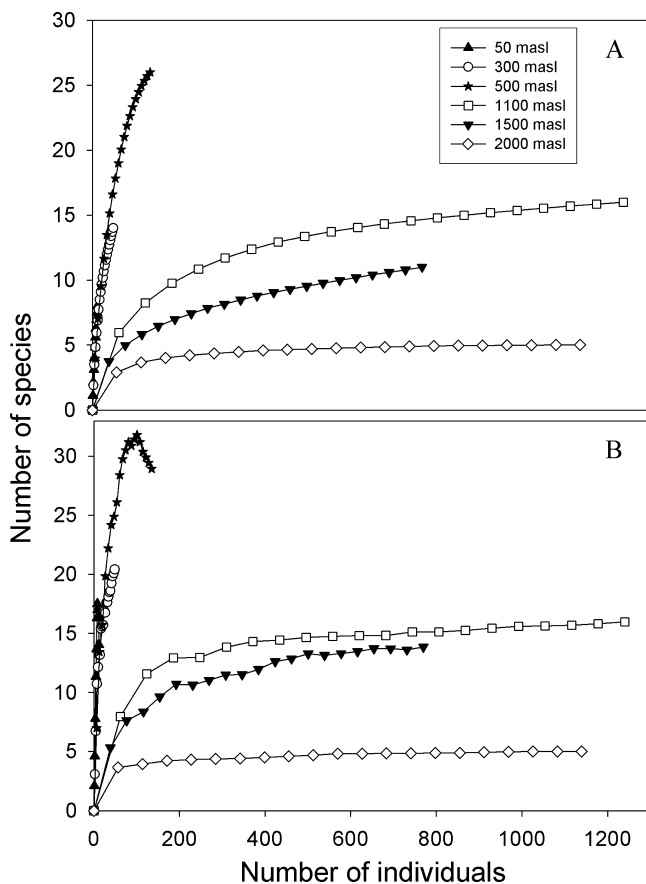


FIGURE 1. (A) MaoTau species accumulation curves showing expected species richness versus sampling effort (number of individuals encountered). Malaise and flight intercept trap captures were included in the analysis. A separate curve is plotted for each sampling elevation. (B) Abundance-based coverage estimator (ACE) estimates of asymptotic species richness, plotted against sampling effort (number of individuals encountered). A separate curve is plotted for each sampling elevation.

SPECIES SHARING AMONG ELEVATIONS.—Paper wasp communities showed elevational turnover in species composition. Only one species was found at every elevation (*Polybia bribri*); an additional species (*P. rauti*) spanned the entire elevational range of our sampling, but was not detected at all sites. In general, sites that were farther apart elevationally (and in map distance) were less similar in species composition. The level of compositional similarity was highest between the 1100 and 1500 m asl sites (0.90; Table 2) and the 1500 and 2000 m asl sites (0.71; Table 2). Similarity was lowest between 50 and 1500 m asl (0.004; Table 2) and between the 300 and 1500 m asl (0.006; Table 2). Considered together with the species accumulation curve analyses, these patterns suggest a strong turnover from a rich lowland fauna to a depauperate, but distinct, montane fauna.

INDIVIDUAL ABUNDANCE, ELEVATION AND MODE OF COLONY FOUNDATION.—A total of 85.7 percent of species and 98.3 percent

TABLE 2. Estimates of similarity in species composition and number of shared species of paper wasps among all possible elevation pairs using the Chao-Jaccard abundance-based similarity estimator.

(m asl)	50	300	500	1100	1500
300	0.551	—			
500	0.591	0.558	—		
1100	0.122	0.161	0.219	—	
1500	0.004	0.006	0.196	0.896	—
2000	0.066	0.056	0.249	0.123	0.710

of individuals were swarm founders (Fig. 2). There were highly significant main effects of both elevation and mode of colony founding on the per-trap total individual abundances of wasps at each elevation (Elevation: $F_{1,116} = 34.6$, $P < 0.0001$; Mode of colony founding: $F_{1,116} = 67.5$, $P < 0.0001$; Fig. 2). Paper wasps were more abundant overall at higher elevations and swarm-founding wasps were more abundant than independent-founding wasps at all elevations. There was a dramatic increase in individual paper wasp abundance from 500 to 1100 m asl and above, particularly for swarm founders (Fig. 2). Increased paper wasp abundance at higher elevations was due mainly to the presence of one or two common swarm-founding species at each site (Table 1). At 1100 m asl, the most common species was *Agelaia yepocapa* (72.8% of all wasp individuals collected). At 1500 m asl, the two most common species were *A. xanthopus* (66.3%) and *A. panamaensis* (21.3%), whereas at 2000 m asl the most common species was *Polybia aequatorialis tristis* (76.6%).

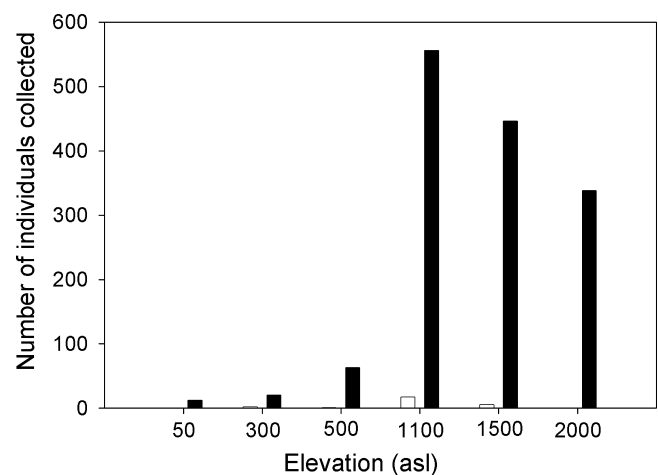


FIGURE 2. Total number of wasps collected at each elevation, all species and traps combined. Vertical bars indicate swarm (black) and independent (white) founders. Only traps that were a combination of malaise and flight - intercept ($N = 10$) were used for the analysis, to make all six elevations directly comparable.

ELEVATION AND ARMY ANT ABUNDANCE.—Leaf litter sampling for army ants was done at all six elevations, and army ants were collected at all elevations except the 1500 m asl site. However, large-bodied army ant species that raid by climbing into vegetation, and therefore potentially prey upon paper wasp colonies, were restricted to two of the lowland sites: three wasp-preying army ant colonies were encountered at the 50 m asl site (0.275 colonies/50-plot transect) and one was encountered at the 500 m asl site (0.20 colonies/50-plot transect).

DISCUSSION

ELEVATIONAL PATTERNS OF PAPER WASP DENSITY AND SPECIES RICHNESS.—Elevation had strong effects on paper wasp community composition. Other eusocial insect taxa show elevational species richness gradients (Wolda 1987, McCoy 1990, Sanders 2002, Hodkinson 2005), and both mid-elevation and low elevation peaks in species richness have been observed in insects (Lawton *et al.* 1987, Wolda 1987, McCoy 1990, Rahbek 2005), including both patterns for different insect taxa on the Barva Transect (Brehm *et al.* 2007, Colwell *et al.* 2008). For paper wasps, our analysis of species accumulation curves strongly supported a low elevation (50–500 m asl) peak in species richness. Our data further suggest that there is a distinct, species poor community at higher elevations (> 500 m asl). Species turnover at 500–1100 m asl was relatively rapid, with relatively little turnover > 1100 m asl. Elevation also showed a strong relationship with the abundance of paper wasp individuals, which was significantly greater at higher elevations.

ABIOTIC FACTORS.—The interaction between high elevation weather and paper wasp physiology may in part account for the higher numbers of paper wasps caught at high elevations. For flying terrestrial ectotherms, flight often requires that body temperature be higher than ambient temperature (Chai & Srygley 1990). Many high elevation paper wasps have dark colored bodies that may aid in physiological adaptation to cool temperatures and limited insolation (O'Donnell 2000; A. Kumar, pers. obs.). However, it is possible that at higher elevations, paper wasps were caught early in the morning when their body temperatures were not at the optimum for locomotion (Heinrich 1974) and their ability to avoid or escape from the traps was reduced. This is a potential source of bias in the sampling protocol that may have affected our estimates of individual paper wasp abundance. However, the fact that we recorded much higher species richness based on substantially fewer individuals at lower elevations than at higher elevations suggests that our estimates of the magnitude of elevational gradients of paper wasp species richness are conservative.

Year-to-year variation in wasp population densities might affect both individual wasp density and species richness estimates. Samples taken in 1993 and 1994 and in 2004 at the 50 m asl site were consistent, both samples indicating high paper wasp species richness and low abundance, although the data were not collected in identical ways. Furthermore, because we randomized our elevational sampling order among years, year-to-year variation would serve as a source of random variation for this study, rather than

a source of bias. It is also possible that seasonality affects species richness and abundance of wasps. Because the sampling was carried out in the same months each year, however, the season of sampling was consistent among years. Seasonality, particularly in precipitation, can affect paper wasp colony life history (O'Donnell & Joyce 2001). However, between 1000 and 1600 m asl in Monteverde, Costa Rica, there is little evidence that seasonality restricts either nest initiation or colony development by swarm-founding species (O'Donnell 2000). It is likely that since seasonality is less pronounced in the wet tropics than the dry tropics or temperate zones, paper wasp reproduction is relatively aseasonal, and many species would be active throughout the entire year (O'Donnell 2000).

BIOTIC FACTORS.—The increase in abundance of preferred paper wasp prey items at higher elevations may contribute to the higher abundances of paper wasps at 1100 m asl and above. Paper wasps primarily collect herbivorous insects, especially caterpillars, to feed their larvae (Rabb 1960). Along the ALAS transect, species richness of Lepidoptera (geometrid moths) showed a hump-shaped pattern with a maximum between 500 and 2100 m asl, and the abundance of lepidopteran individuals also showed an increase from 1070 to 2730 m asl, similar to the elevational pattern of density we have documented in paper wasps (Brehm *et al.* 2007).

We suggest that elevational gradients in predation pressure may also, in part, explain both low abundance and high species richness at lower elevations. In our samples, and at other sites, army ant predators of paper wasps decreased in abundance with elevation (Kaspari & O'Donnell 2003, O'Donnell & Kumar 2006). High rates of predation by army ants could be one factor promoting low paper wasp density and high species richness at lower elevations. Many elements of paper wasp behavior suggest adaptations to reduce predation by ants in general, and by army ants in particular, including nest-site selection, nest architecture, and nest defense (Jeanne 1970, 1975; Carroll & Janzen 1973; Chadab 1979a, b; O'Donnell & Jeanne 1990; Bouwma *et al.* 2007). Vespid wasps are favored prey of several species of Neotropical army ants (Carroll & Janzen 1973, Chadab 1979b, Jeanne 1979, Rettenmeyer *et al.* 1983, O'Donnell & Jeanne 1990). Army ant presence and absence may thus explain some of the variation in abundance that we documented, and could also be linked to species richness. Regular army ant predation may regulate eusocial vespid populations, both by reducing colony densities and by keeping colony size low, especially at lower elevations (Forsyth 1978).

SWARM- AND INDEPENDENT-FOUNDER DENSITY DIFFERENCES.—In the Neotropics, 315 species of independent-founding Polistinae (58%) and 232 swarm founders (42%) are currently known (West-Eberhard *et al.* 2006; J. Carpenter, pers. comm.). We observed a much higher abundance of swarm-founding wasps. This pattern held at both lower elevations, where species richness of swarm founders was high, and at higher elevations, where one or two species of swarm founders dominated. To the extent that numerical abundance of workers correspond to biomass and energy capture differences, the high swarm-founder abundance suggests that swarm founding is an ecologically more successful behavioral

strategy. The evolution of swarm founding brought with it two advantages that could promote ecological success (Jeanne 1991). First, queen mortality is reduced: swarm-founding workers are responsible for scouting nest sites, and the queens are protected within the founding group. Second, the evolution of the swarm also allowed for larger colony sizes. Because swarm founders typically have multiple queens, the rate of egg laying and colony growth is rapid in comparison with independent-founding species. Larger swarm-founder colony sizes and complex nests may also provide defense against larval predators, including ants, in tropical forests (Wenzel 1991, Smith *et al.* 2001).

CONCLUSIONS.—We show that Neotropical paper wasp communities are structured with respect to elevation. Both abiotic and biotic factors may contribute to elevational changes in paper wasp density and species richness. Paper wasps exhibit moderate species richness (104 species known in Costa Rica: J. Carpenter, pers. comm.), and they are taxonomically well characterized. Paper wasps are also conspicuous and relatively easily sampled, making them a tractable indicator taxon for analyzing climate-related changes in community structure along elevational gradients.

The pattern of increased paper wasp abundance at higher elevation may be due, in part, to changes in the regime of predators that attack paper wasp colonies. Our findings indicate that army ants deserve particular consideration as predators that may contribute to reduced paper wasp density at lower elevations. Reduced paper wasp abundance at lower elevations may be causally linked to higher species richness in the lowlands because high predation pressure is thought to promote prey species richness by preventing competitive exclusion by dominant prey taxa (Paine 1966, Shurin & Allen 2001). We therefore suggest that army ant predation is one factor that may shape geographic and elevational patterns of Neotropical paper wasp abundance and species richness.

A striking pattern in the ALAS data was the high abundance of swarm founding relative to independent-founding paper wasps. Swarm founders were captured at higher rates at all elevations. In Costa Rica, total species richness of independent and swarm founders is similar, and our species accumulation curves suggested that richness of the independent-founding fauna was comparable to, if not greater than, that of the swarm-founding fauna. However, swarm founders were 88 times more abundant than independent founders overall. Similar swarm-founder and independent-founder density discrepancies were noted by Heithaus (1989) for workers visiting flowers, and by Erwin (cited in Jeanne 1991) for canopy fogging samples. These data suggest that Neotropical predators (and prey) interacting with paper wasps are much more likely to face swarm founders. The ALAS data set represents the first critical test of Jeanne's (1991) assertion that swarm founders are more ecologically successful than independent founders. The fact that many independent founders apparently mimic swarm founder models lends credence to the notion of swarm-founder ecological dominance (O'Donnell & Joyce 1999). Reasons for swarm-founder success are not known, but the efficient division of labor and effective communication of swarm founders may bolster their colony productivity (Smith *et al.* 2001).

ACKNOWLEDGMENTS

We thank the personnel of Project ALAS, especially the parataxonomists who sorted the Vespidae for our samples. Special thanks to J. Carpenter for his expert help with paper wasp species identification. Institutional support from the Organization for Tropical Studies, the Instituto Nacional de Biodiversidad (Costa Rica), The Evergreen State College, and the University of Connecticut has been crucial to the success of ALAS. Project ALAS was supported by National Science Foundation grants: BSR-9025024, DEB-9401069, DEB-9706976, DEB-0072702, and National Geographic Society grants: 7331-02 and 7751-04. SO'D was supported by National Science Foundation grant IBN-0347315, and AK and SO'D were supported by the University of Washington Royalty Research Fund. RKC was supported by National Science Foundation grant DEB-0072702. JTL was supported by National Science Foundation grant DEB-0640015. The research presented was additionally supported by the National Science Foundation while SO'D. was working at the foundation. Any opinions, findings, and the conclusions or recommendations are those of the authors, and do not necessarily reflect the views of the National Science Foundation. Thanks to anonymous reviewers for helpful comments that improved the paper.

LITERATURE CITED

- BOUWMA, A. M., K. J. HOWARD, AND R. L. JEANNE. 2007. Rates of predation by scouting-and-recruiting ants on the brood of a swarm-founding wasp in Costa Rica. *Biotropica* 39: 719–724.
- BREHM, G., R. K. COLWELL, AND J. KLUGE. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecol. Biogeogr.* 16: 205–219.
- CARPENTER, J. M. 2004. Synonymy of the genus *Marimbonda* Richards, 1978, with *Leipomeles* Möbius, 1856 (Hymenoptera: Vespidae: Polistinae), and a new key to the genera of paper wasps of the New World. *Am. Mus. Novitates* 3465: 1–16.
- CARROLL, C. R., AND D. H. JANZEN. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4: 231–257.
- CHADAB, R. 1979a. Early warning cues for social wasps attacked by army ants. *Psyche* 86: 115–124.
- CHADAB, R. 1979b. Army ant predation on social wasps. PhD Dissertation. University of Connecticut-Storrs, Connecticut.
- CHAI, P., AND R. B. SRYGLEY. 1990. Predation and the flight, morphology, and temperature of Neotropical rain-forest butterflies. *Am. Nat.* 135: 748–765.
- CHAO, A., AND S.-M. LEE. 1992. Estimating the number of classes via sample coverage. *J. Am. Stat. Assoc.* 87: 210–217.
- CHAO, A., R. L. CHAZDON, R. K. COLWELL, AND J. SHEN. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8: 148–159.
- CLARK, K. L., R. O. LAWTON, AND P. R. BUTLER. 2000. The physical environment. *In* N. M. Nadkarni, and N. T. Wheelwright (Eds.). *Monteverde: Ecology and conservation of a tropical cloud forest*, pp. 15–38. Oxford University Press, Oxford, UK.
- COLWELL, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- COLWELL, R. K., C. X. MAO, AND J. CHANG. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85: 2717–2727.

- COLWELL, R. K., G. BREHM, C. CARDELÚS, A. C. GILMAN, AND J. T. LONGINO. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322: 258–261.
- CONDIT, R., N. PITMAN, E. G. LEIGH, JR., J. CHAVES, J. TERBORGH, R. B. FOSTER, P. NÚÑEZ, S. AGUILAR, R. VALENCIA, G. VILLA, H. C. MULLER-LANDAU, E. LOSOS, AND S. P. HUBBELL. 2002. Beta-diversity in tropical forest trees. *Science* 295: 666–669.
- DEUTSCH, C. A., J. J. TEWKSBURY, R. B. HUEY, K. S. SHELDON, C. K. GHALAMBOR, D. C. HAAK, AND P. R. MARTIN. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. USA* 105: 6668.
- ERWIN, T. L. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. *Coleopterists Bull.* 36: 74–75.
- FISHER, B. L. 1999. Improving inventory efficiency: A case study of leaf litter ant diversity in Madagascar. *Ecol. Appl.* 9: 714–731.
- FORSYTH, A. 1978. Studies on the behavioral ecology of polygynous social wasps. PhD Dissertation. Harvard University, Cambridge, Massachusetts.
- GADAGKAR, R. 1991. *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*. In K. G. Ross, and R. W. Matthews (Eds.). *The social biology of wasps*, pp. 149–160. Cornell University Press, Ithaca, New York.
- GHALAMBOR, C. K., R. B. HUEY, P. R. MARTIN, J. J. TEWKSBURY, AND G. WANG. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Compar. Biol.* 46: 5–17.
- GOTELLI, N. J., AND R. K. COLWELL. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4: 379–391.
- GOTWALD, W. H. 1995. *The biology of social predation*. Cornell University Press, Ithaca, New York.
- GULLAN, P. J., AND P. S. CRANSTON. 2000. *The insects: An outline of entomology*. Blackwell Science, Oxford, UK.
- HEINRICH, B. 1974. Thermoregulation in endothermic insects. *Science* 185: 747–756.
- HEITHAUS, E. R. 1979. Community structure of Neotropical flower visiting bees and wasps: Diversity and phenology. *Ecology* 60: 190–202.
- HODKINSON, I. D. 2005. Terrestrial insects along elevational gradients: Species and community responses to altitude. *Biol. Rev.* 80: 489–513.
- HOZUMI, S., S. YAMANE, S. MIYANO, S. MATEUS, AND R. ZUCCHI. 2005. Diel changes of temperature in the nests of two *Polybia* species, *P. paulista* and *P. occidentalis* (Hymenoptera, Vespidae) in the subtropical climate. *J. Ethol.* 23: 153–159.
- JANZEN, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101: 233–249.
- JANZEN, D. H., M. ATAROFF, M. FARIÑAS, S. REYES, N. RINCON, A. SOLER, P. SORIANO, AND M. VERA. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8: 193–203.
- JEANNE, R. L. 1970. Chemical defense of brood by a social wasp. *Science* 168: 1465–1466.
- JEANNE, R. L. 1975. The adaptiveness of social wasp nest architecture. *Q. Rev. Biol.* 50: 267–287.
- JEANNE, R. L. 1979. A latitudinal gradient in rates of ant predation. *Ecology* 60: 1211–1224.
- JEANNE, R. L. 1991. The swarm founding Polistinae. In K. G. Ross, and R. W. Matthews (Eds.). *The social biology of wasps*, pp. 191–231. Cornell University Press, Ithaca, New York.
- KASPARI, M., AND S. O'DONNELL. 2003. High rates of army ant raids in the Neotropics and implications for ant colony and community structure. *Evol. Ecol. Res.* 5: 933–939.
- KASPARI, M., S. O'DONNELL, AND L. ALONSO. 2000. Three energy variables predict ant abundance at a geographic scale. *Proc. R. Soc. Lond. B* 267: 485–490.
- KUMANO, N., AND E. KASUYA. 2006. An alternative strategy for maintenance of eusociality after nest destruction: New nest construction in a primitively eusocial wasp. *Insect Soc.* 53: 149–155.
- LAWTON, J. H., M. MACGARVIN, AND P. A. HEADS. 1987. Effects of altitude on the abundance and species richness of insect herbivores on bracken. *J. Anim. Ecol.* 56: 147–160.
- LONGINO, J., R. K. COLWELL, AND J. A. CODDINGTON. 2002. The ant fauna of a tropical rainforest: Estimating species richness three different ways. *Ecology* 83: 689–702.
- LOMOLINO, M. V. 2001. Elevation gradients of species-density: Historical and prospective views. *Global Ecol. Biogeogr.* 10: 3–13.
- MCCAIN, C. M. 2004. The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *J. Biogeogr.* 31: 19–31.
- MCCOY, E. D. 1990. The distribution of insects along elevational gradients. *Oikos* 58: 313–322.
- O'DONNELL, S. 2000. Eusocial wasps (Vespidae: Polistinae). In N. M. Nadkarni, and N. T. Wheelwright (Eds.). *Monteverde: Ecology and conservation of a tropical cloud forest*, pp. 129–131. Oxford University Press, Oxford, UK.
- O'DONNELL, S., AND R. L. JEANNE. 1990. Notes on an army ant (*Eciton burckelii*) raid on a social wasp colony (*Agelaia yepocapa*) in Costa Rica. *J. Trop. Ecol.* 6: 507–509.
- O'DONNELL, S., AND F. J. JOYCE. 1999. Dual mimicry in the dimorphic eusocial wasp *Mischocyttarus mastigophorus* Richards (Hymenoptera: Vespidae). *Biol. J. Linn. Soc.* 66: 501–514.
- O'DONNELL, S., AND F. J. JOYCE. 2001. Seasonality and colony composition in a montane tropical eusocial wasp. *Biotropica* 33: 727–732.
- O'DONNELL, S., AND A. KUMAR. 2006. Microclimatic factors associated with elevational changes in army ant density in tropical montane forest. *Ecol. Entomol.* 31: 491–498.
- OLSON, D. M. 1994. The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *J. Trop. Ecol.* 10: 129–150.
- PAINE, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65–75.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- POUNDS, J. A., M. P. L. FOGDEN, AND J. H. CAMPBELL. 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611–615.
- RABB, R. L. 1960. Biological studies of *Polistes*. North Carolina (Hymenoptera: Vespidae). *Ann. Entomol. Soc. Am.* 53: 111–121.
- RAHBEK, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* 8: 224–239.
- REEVE, H. K. 1991. *Polistes*. In K. G. Ross, and R. W. Matthews (Eds.). *The social biology of wasps*, pp. 99–148. Cornell University Press, Ithaca, New York.
- RETTENMEYER, C. W., R. CHADAB-CREPET, M. G. NAUMANN, AND L. MORALES. 1983. Comparative foraging by Neotropical army ants. In P. Jaisson (Ed.). *Social insects in the tropics*, Vol. 2, pp. 59–73. Proceedings of the 1st International Symposium of I.U.S.S.I. and Sociedad Mexico Entomologia, Coyoyoc, Morelos, Mexico, Nov. 1980 Université Paris-Nord, Paris, France.
- RICHARDS, O. W. 1978. *The social wasps of the Americas excluding the Vespinae*. British Museum of Natural History, London, UK.
- RICHTER, M. R. 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu. Rev. Entomol.* 45: 121–150.
- SANDERS, N. J. 2002. Elevational gradients in ant species richness: Area, geometry, and Rapoport's rule. *Ecography* 25: 25–32.
- SHMIDA, A., AND M. V. WILSON. 1985. Biological determinants of species diversity. *J. Biogeogr.* 12: 1–20.
- SHURIN, J. B., AND E. G. ALLEN. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. *Am. Nat.* 6: 624–637.
- SMITH, A. R., S. O'DONNELL, AND R. L. JEANNE. 2001. Correlated evolution of colony defense and social structure: A comparative analysis in eusocial wasps (Hymenoptera: Vespidae). *Evol. Ecol. Res.* 3: 331–344.
- STRASSMANN, J. E., 1981. Parasitoids, predators, and group size in the paper wasp, *Polistes exclamans*. *Ecology* 62: 1225–1233.

- WENZEL, J. W. 1991. Evolution of nest architecture in social vespids. *In* K. G. Ross, and R. W. Matthews (Eds.). *The social biology of wasps*, pp. 480–519. Cornell University Press, Ithaca, New York.
- WENZEL, J. W. 1998. A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *Am. Mus. Novitates* 3324: 1–40.
- WEST-EBERHARD, M. J., J. M. CARPENTER, AND P. E. HANSON. 2006. Familia Vespidae. *In* P. E. Hanson, and I. D. Gauld (Eds.). *Hymenoptera de la región Neotropical*, pp. 617–644. *Memoirs of the American Entomological Institute*.
- WILSON, E. O. 1990. *Success and dominance in ecosystems: The case of the social insects*. Ecology Institute, Oldendorf/Luhe, Germany.
- WINDSOR, D. M. 1976. Birds and predators on the brood of *Polybia* wasps (Hymenoptera: Vespidae: Polistinae) in a Costa Rica deciduous forest. *Biotropica* 8: 111–116.
- WOLDA, H. 1987. Altitude, habitat and tropical insect diversity. *Biol. J. Linn. Soc.* 30: 313–323.