

Observations on Two Neotropical Swarm-Founding Wasps, *Agelaia yepocapa* and *A. panamaensis* (Hymenoptera: Vespidae)

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ABSTRACT In northwestern Costa Rica, *Agelaia yepocapa* (Richards) nests in cavities within living hollow trees in lower montane mesic forests; *A. panamaensis* (Cameron) nests in very large cavities in premontane gallery forests. Nests of both species have vertical combs with horizontal cells that face outward from the nest center; the nests have no enclosing envelope. In January 1996, an *A. yepocapa* colony was in full brood production, while an *A. panamaensis* colony was in the last stage of colony decline, and a nearby *A. panamaensis* colony had terminated only weeks before. The appearance of a small aggregation of *A. panamaensis* in a montane cloud forest site, too small to support a colony as large as those that had recently reached the end of a colony cycle in a nearby premontane gallery forest, suggests that the colony cycle of *A. panamaensis* in northwestern Costa Rica has a seasonal pattern that includes elevational migration and possible non-nesting quiescence at cool high elevations. Morphometric contrasts of queen and worker *A. yepocapa* confirm caste dimorphism that has been reported for other *Agelaia* species. The multivariate analysis presented here reveals caste differences that can only have occurred as a result of a dichotomy in developmental pathways during larval growth. Individuals of both species performed the behavior of gaster flagging during colony defense. The role of gaster flagging in these wasps is unknown. Near-nest aggressiveness of cavity-nesting wasps is higher than that of wasps that nest in exposed locations, perhaps as a correlate of the scarcity of suitable cavities for nesting. The sting of *A. panamaensis* is particularly painful. The *A. panamaensis* colony that was in decline was host to diverse inquilines and a parasitoid. The *A. yepocapa* nest collection included two parasitoid species.

KEY WORDS *Agelaia yepocapa*, *Agelaia panamaensis*, caste, colony, inquilines, morphometrics

EPILONINI, THE ECOLOGICALLY dominant social wasps of the Neotropics (Jeanne 1991), are the most diverse of four independent lineages of swarm-founding Polistinae (Carpenter 1991). More than 200 species in 20 genera are distributed from subtropical Texas, U.S.A., in the north to subtropical Argentina in the south (Richards 1978, Raw 1985, Carpenter et al. 1996, Carpenter et al. 2000). Few taxa likely surpass their ecological significance as insectivores in the habitats in which they are found. Yet despite their abundance, diversity, distribution, and ecological significance, the vast majority of genera and species are known only taxonomically, with the basic natural history of some genera poorly known (e.g., *Clypearia*, *Chartergellus*) or virtually unknown (e.g., *Marimbonda*). Only *Polybia*, the most species-rich epiponine genus, can be said to be relatively well known (Jeanne 1991), with even that knowledge restricted to a few of the genus' 50+ species. Research on *Metapolybia* and *Parachartergus*

has illuminated focal aspects of epiponine biology such as queen determination (West-Eberhard 1978) and patterns of intra-colony relatedness (Strassmann et al. 1991), although basic natural history of even these genera remains only partially known.

Agelaia, formerly *Stelopolybia* (Carpenter and Day 1988), is the third-largest epiponine genus with 29 species (J. M. Carpenter, personal communication). *Agelaia* exhibits the greatest intra-generic diversity of nest architecture among Epiponini (Jeanne 1975; Wenzel 1991, 1998), and the range of body sizes across species is among the largest in Epiponini. All known *Agelaia* species have caste dimorphism, with queens larger than workers (Jeanne and Fagen 1974, Noll et al. 1997). *Agelaia* is one of only two epiponine genera in which foragers are known to regularly include carrion among provisions for larvae (O'Donnell 1995), although recruitment of foragers to food is apparently lacking (Jeanne et al. 1995a). Many species achieve large colony sizes, with *Agelaia vicina* (Saussure) reaching the largest colony size of any nonadventive wasp, having populations estimated at up to 1 million adults (Zucchi et al. 1995). *Agelaia* foragers are often locally more abundant than those of other Epiponini or second in abundance to those of *Polybia*, which often come from smaller, more numerous colonies.

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Agelaea yepocapa (Richards) is patterned in black and yellow and has one of the smaller body sizes in the genus; it ranges from Guatemala to Ecuador (Richards 1978). The all-black *Agelaea panamaensis* (Cameron) is one of the larger *Agelaea* species; it ranges from Mexico to Peru (Richards 1978). Both species occur in premontane and lower montane wet forest and rain forest habitats in mid-elevation slopes of mountains in Costa Rica. Here we report findings on nest site, nest architecture, colony composition, colony cycle/phenology, behavior, and nest associates of both species. A morphometric contrast of queen and worker castes in *A. yepocapa* is given, as are observations that suggest a seasonal colony cycle in *A. panamaensis*.

Materials and Methods

Study and Collection Sites. Behavior observations and colony collections were made 3–11 January 1996 in the neighboring communities of Monteverde (elevation $\approx 1,450$ m) and San Luis (elevation $\approx 1,100$ m), $10^{\circ} 18' N$ and $84^{\circ} 9' W$, Puntarenas Province, Costa Rica. Residents directed us to two colonies of *Agelaea yepocapa*, both active, and three colonies of *A. panamaensis*: one active, one recently exterminated, and a recently abandoned nest. The abandoned nest is known to have been constructed by *A. panamaensis*, due to its size, site, architecture, and based on first-hand knowledge of a local resident who had encountered the colony when it had been active and who identified it by its unique common name. Using standard aerial nets and plastic bags, collections were made, during daytime, of nest comb, brood, and adults from one active nest of each species. Nest comb and asphyxiated occupants of the two collected colonies were examined carefully within hours of each collection, and vouchers were preserved of the adult wasps, parasitoids, and commensals. Vouchers of the wasps have been placed in the Museum of Natural History of the University of Missouri-St. Louis, the Museo Nacional de Costa Rica, and the Universidad de Costa Rica. Vouchers of the associated species are in collections of the specialists who determined them.

Morphometrics. Queens and workers of *A. yepocapa* are unambiguously separable by size (queens are larger) and color pattern. Pinned specimens of 50 queens and 50 workers were prepared for morphometric analysis by removing the legs and left wings; the left forewing of each wasp was attached to a glass slide by clear tape and numbered to correspond to the wasp from which it came. For each specimen, 13 dimensions, defined by Jeanne et al. (1995b) (Fig. 1), were measured to the nearest 0.01 mm using a dissecting microscope equipped with video camera and computer programmed with DIAS, Digital Image Analysis System (C-Squared Corporation, Tamarac, FL). Data were analyzed using SAS (SAS Institute 1990). Importance of the 13 dimensions for distinguishing between queens and workers was assessed by means of individual *t*-tests as well as by stepwise discriminant analysis with a significance level of 0.10 for entry and removal of variables. The Mahalanobis distance (D^2 ;

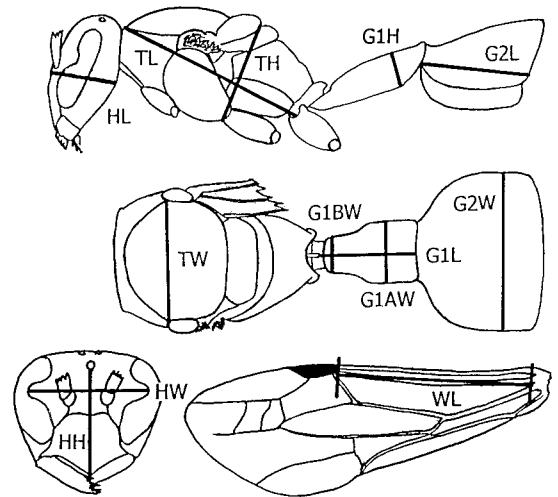


Fig. 1. Line drawing of an *Agelaea yepocapa* queen to illustrate the 13 dimensions measured for morphometric analysis. HH = head height, HW = head width, HL = head length, TH = mesosoma height, TW = mesosoma width, TL = mesosoma length, WL = wing length, G1H = height of first gastral segment, G1BW = basal width of first gastral segment, G1AW = apical width of first gastral segment, G1L = first gastral segment length, G2W = second gastral segment width, G2L = second gastral segment length.

Rao 1973) was also calculated as a measure of the difference between queens and workers.

Parasites, Parasitoids, and Inquilines. Fluid-preserved specimens of Acari were cleared in a lactophenol solution and mounted in Hoyer's medium on glass slides for microscopic examination (Krantz 1978). Fluid-preserved specimens of Diptera and parasitoid Hymenoptera were submitted to specialists for taxonomic determination.

Results

Nest Sites. Both colonies of *A. yepocapa* observed in January 1996 were in living in hollow trees in open pastures in Monteverde. The trees were 0.5–0.75 m diameter at breast height (dbh), and access to the interior was via branch scars with $\approx 25\text{-cm}^2$ openings. One nest entrance was ≈ 1.5 m above the ground; the other ≈ 4 m.

Two of three colonies of *A. panamaensis* were in similar sites in gallery forests in San Luis. One was inside the hollow of a large tree (>1 m diameter) that had fallen from the eroded bank of a rushing stream; the other was under a horizontal buttress of a very large tree (>2 m diameter) that had fallen near a small creek. Access to the first nest was via an opening of several hundred square centimeters at the base of the upturned tree and ≈ 2 m above the stream bed; the second nest was mostly concealed from view by the overhanging, curved buttress but was fully exposed from beneath and ≈ 1 m above the ground. The first nest was damaged by the collecting process but in every regard appeared to be similar to the second,

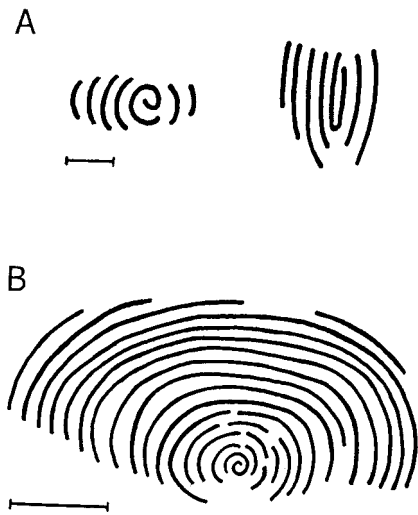


Fig. 2. Schematics redrawn from field sketches to show the arrangement of combs in (A) the collected nest of *A. yepocapa* and (B) the abandoned nest of *A. panamaensis*. For *A. yepocapa*, the scale bar equals ≈ 10 cm, and comb arrangement is shown in both horizontal cross section (left) and vertical cross section (right). For *A. panamaensis*, the scale bar equals ≈ 25 cm, and comb arrangement is shown in horizontal cross section. In both, nest cells faced outward from the nest center. Inter-comb distances were more uniform than in these schematics. The outward-facing, more exposed side of the *A. panamaensis* nest faces the bottom of this figure.

which had been abandoned by its colony only 2–3 wk before. The third *A. panamaensis* colony differed from the first two. It was located at ground level in a living hollow tree in the Monteverde Cloud Forest Preserve at $\approx 1,550$ m elevation. Access was via an opening of ≈ 25 cm², and the tree hollow appeared to be no larger than a few liters in total volume. The wasps had moved into the site only 2–3 d before and had been chemically exterminated only hours before our arrival. No nest comb was seen, although view of the tree interior was limited.

Nest Architecture. The collected *A. yepocapa* nest is presumed to be typical for the species. Combs were vertical, with cells extending horizontally from one side. The central comb was attached to a stalactite-like piece of wood that hung vertically within the tree hollow. The attachment was by means of several discrete horizontal petioles, and the comb spiraled from its innermost edge around the piece of wood to which it was attached. Cells faced outward from the nest center. Other combs were concentric about the first (Fig. 2A), with cells facing outward. Each comb was attached to the next by several independent horizontal petioles. The dimensions of the combs seemed constrained by dimensions of the tree hollow; it appeared that without constraint the marginal combs would have continued around the central comb. The nest had no surrounding envelope.

The *Agelata panamaensis* nest beneath the buttress consisted of vertical sheets of comb arranged concen-

trically about a central comb (Fig. 2B). Cells were horizontal and faced out from the center. Combs were ≈ 1.7 cm apart and attached to one another by multiple horizontal petioles. Combs were also attached to the overhanging buttress by multiple vertical and subvertical petioles at the comb margins. The space between the combs and tree was constant and approximately equal to the distance between adjacent combs in a design strongly reminiscent of “bee space” in a Langstroth *Apis* hive. The combs were fully exposed, with no enclosing envelope. The nest’s overall dimensions were ≈ 1 m long, ≈ 0.6 m wide, and ≈ 0.5 m high. The largest comb, # 10 from the center, was estimated to have 4,000 cm² surface area and 20,000 cells.

Colony Composition. The collected *A. yepocapa* colony was estimated to contain 4,000 wasps. The uncollected *A. yepocapa* colony, judging by volume of forager traffic, was 25–50% larger than the collected colony. About 3,000 wasps were collected from the first colony, all of which were female, including 250 queens by direct count. Queens are larger and darker in coloration than workers and are easily discriminated. Forty queens were dissected; all had developed ova; spermathecae were not checked for insemination. Twenty workers were dissected; all had filamentous ovaries. The colony was in full brood production, with all stages from eggs to pupae present and few, if any, empty nest cells. The central nest comb and combs at the nest margin contained only eggs; larvae and pupae were present in an age-graded series in the intermediate combs, with pupae adjacent to the egg-containing central cells and ever-younger brood toward the egg-containing cells at the nest margins.

The number of wasps in the collected *A. panamaensis* colony was estimated at 5,000. Of the estimated 3,000 of these that were collected, approximately two-thirds were worker females and one-third males. No queens were present among the collected wasps. The nest comb contained no eggs or larvae. A few hundred pupal cocoons were present, with most pupae pigmented and near emergence. Sex of the pupae was not determined. The dead wasps in the small cloud-forest colony of *A. panamaensis* were drenched with insecticide, and none were collected. The number of dead wasps appeared to be in the hundreds.

Caste Dimorphism. Means and standard deviations for each of the 13 morphological measurements of 50 queens and 50 workers of *A. yepocapa* are given in Table 1, along with *t* statistics and associated probabilities for between-caste comparisons. Queens are significantly larger than workers in 12 of the 13 variables, with only head width having statistical nonsignificance. Stepwise discriminant analysis applied to the full data set selected five variables as contributing significantly to queen-worker discrimination (Table 2): apical width of the first gastral tergite (GIAW), mesosoma length (TL), head width (HW), mesosoma width (TW), and length of the second gastral tergite (G2L). Relationships between apical width of the first gastral tergite and mesosoma length are illustrated in Fig. 3A and between head width and mesosoma length in Fig. 3B. There is no overlap in size between castes

Table 1. Means (mm) and standard deviations of 50 queens and 50 workers of *Agelaia yepocapa* for each of 13 morphological measurements named in the text, ratios of means between castes (Q:W), and calculated *t* statistics and associated probabilities for between-caste differences

Variable	Queen		Worker		Q:W ratio	<i>t</i>	Pr > <i>t</i>
	Mean	SD	Mean	SD			
HW	2.136	0.044	2.117	0.058	1.009	1.82	0.072
HH	1.949	0.078	1.911	0.061	1.020	2.73	0.008
HL	1.278	0.101	1.154	0.059	1.107	7.47	0.001
TL	4.003	0.110	3.447	0.123	1.161	23.89	0.001
TH	2.274	0.073	2.058	0.072	1.105	14.94	0.001
G1H	0.837	0.050	0.641	0.050	1.306	19.39	0.001
G2L	2.248	0.133	1.815	0.133	1.239	16.32	0.001
TW	2.029	0.060	1.785	0.061	1.137	20.07	0.001
G1L	1.580	0.155	1.345	0.151	1.175	7.68	0.001
G1BW	0.525	0.029	0.414	0.029	1.268	18.88	0.001
G1AW	1.138	0.052	0.898	0.037	1.267	29.67	0.001
G2W	2.581	0.080	2.206	0.088	1.170	22.24	0.001
WL	5.921	0.156	5.160	0.211	1.147	20.45	0.001

in either mesosoma length or apical width of the first gastral tergite, but head widths span the same range of sizes for both castes.

In accord with similar multivariate analyses of other social wasp taxa (Jeanne et al. 1995b, Hunt et al. 1996), and to examine differences in shape rather than absolute size, mesosoma length (TL) was used to calculate relative dimensions. That is, each of the 12 other variables for a wasp was divided by that wasp's mesosoma length to yield 12 new, relative variables. Stepwise discriminant analysis of these 12 relative variables selected five variables as contributing significantly to queen-worker discrimination (Table 3): relative head width (rHW), relative apical width of the first gastral tergite (rG1AW), relative length of the second gastral tergite (rG2L), relative head height (rHH), and relative mesosoma width (rTW).

Based on the 13 original dimensions, the Mahalanobis distance between queens and workers was $D^2 = 54.17$. The 12 size-adjusted variables gave $D^2 = 45.25$ ($F = 83.68$; $df = 12, 87$).

Behavior and Stings. Both of the study species have been seen at meat and honey baits during other investigations in the region (O'Donnell 1995). During the present investigations we also observed large numbers of *A. panamaensis* foragers at sugar feeders used to attract hummingbirds. The wasps, large and menacing in appearance, are capable of driving humming-

Table 2. Significant morphometric discriminators between queens and workers of *A. yepocapa* as revealed by stepwise discriminant analysis of original data in millimeters^a

Step	Variable entered	Partial R^2	<i>F</i>	Prob > <i>F</i>
1	G1AW	0.8789	711.55	0.0001
2	TL	0.2608	34.22	0.0001
3	TW	0.0863	9.07	0.0033
4	HW	0.0733	7.51	0.0073
5	TW	0.0347	3.38	0.0690

^a A significance level of 0.10 was used as the criterion for entering and removing variables in the stepwise selection method.

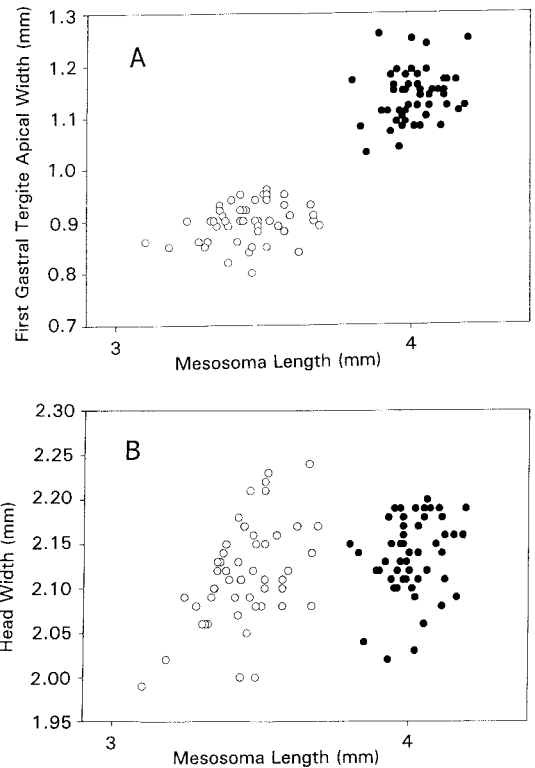


Fig. 3. (A) Relationship between apical width of the first gastral tergite (G1AW) and mesosoma length (TL) in queens (filled circles) and workers (open circles) of *Agelaia yepocapa*. (B) Relationship between head width (HW) and mesosoma length (TL) in queens (filled circles) and workers (open circles) of *Agelaia yepocapa*.

birds from the feeders and are considered a nuisance by hummingbird aficionados.

Wasps of each collected colony exhibited concerted, sustained defensive behaviors during the collection process. During defense, several individuals of each species were observed to display a behavior in which a wasp would use its mandibles to grasp some part of an attacker (e.g., a glove) or the tree near the nest entrance and hold on firmly for several minutes. The wasp's coxae would be appressed to the substrate

Table 3. Significant morphometric discriminators between queens and workers of *A. yepocapa* as revealed by stepwise discriminant analysis of relative data for which each of 12 measurements for each wasp has been divided by that wasp's mesosoma length (TL)^a

Step	Variable entered	Partial R^2	<i>F</i>	Prob > <i>F</i>
1	rHW	0.8378	506.01	0.0001
2	rG1AW	0.3665	56.12	0.0001
3	rG2L	0.0751	7.80	0.0063
4	rHH	0.0486	4.85	0.0301
5	rTW	0.0479	4.73	0.0321

^a A significance level of 0.10 was used as the criterion for entering and removing variables in the stepwise selection method.



Fig. 4. Workers of *A. yepocapa* at the entrance to the nest of the uncollected colony in Monteverde. The nest was being aggressively disturbed by the photographer; in response, the wasp in the left center is holding its gaster aloft in a posture called gaster flagging. The gaster is elevated at a 90° angle from the long axis of the body, but the wings are in repose as are those of all other wasps in the photo, which are not gaster flagging. This wasp is not grasping the substrate with its mandibles nor pressing its coxae to the substrate, as was done by some of the gaster-flagging wasps of the collected *A. yepocapa* colony. Scale bar = ≈5 mm.

with the legs splayed out to the sides; the wings were in repose as if at normal rest, but the gaster was held fully erect between the folded wings at an elevation of 90° to the longitudinal body axis. At least some wasps that adopted this posture were seen to expose their sting. The behavior has been termed "gaster flagging" (Obin and Vander Meer 1985) and described for epiponine wasps more fully elsewhere (O'Donnell et al. 1997). Attempts to arouse the second *A. yepocapa* colony and induce the behavior met with only meager success (Fig. 4), apparently because there was no forced entry to the nest chamber and, accordingly, a lower level of alarm by the wasps.

Wasps of both species, striking protective screens over the collectors' faces, expelled venom that was highly irritating to the eyes. A pronounced odor of venom and/or pheromone was apparent during collection of the *A. panamaensis* colony. The aroma was musty, somewhat like the smell of wet meconium in nests. Inhalation of the chemical(s) caused a very runny nose and upper throat irritation in the collectors, but these symptoms had abated by 0.5 h after the collection. Similar respiratory symptoms occurred in researchers collecting a colony of *Agelaiia vicina* (F. B. Noll, personal communication). Several *A. panamaensis* were able to grasp a collector's gloves with their tarsi and forcefully sting just above the gloves through the protective nylon bee suit being worn. Of five stings thus received, two caused pain far exceeding any experienced (by J.H.H.) in dozens of stings from tens of species of social wasps. Localized swelling lasted two days versus a typical response of 0.5 h for taxa such as

Polistes, *Vespula*, *Dolichovespula*, and diverse Epiponini. Two-millimeter-diameter lesions at the envenomation sites persisted for 1 mo afterward. Red spots at the lesion sites were visible 3 mo after the event. D. P. Janos (personal communication) experienced similar long-lasting lesions following *A. panamaensis* stings.

Parasites, Parasitoids, and Commensals

Acari. A series of 28 gamasid mites were collected from the nest of *A. panamaensis*. The mites were found within and around the cells of the nest, none being directly associated with the wasps. Twenty-seven of the mites were nymphs; only one (a female containing an egg) was an adult. The opithosoma of the female was 0.4 mm in length and 0.25 mm in width. Lateroventral stigmatal openings were present at the level of coxae III–IV. Observations of the chaetotaxy indicate that these animals are trigynaspids, but further classification was extremely doubtful.

Diptera. The *A. panamaensis* colony collection included stages II, III, and IV larvae and a pupa of *Clogmia albipunctata* (Williston) (Psychodidae, Psychodinae). Eight larvae of *Copestylum* sp. (Syrphidae) were found amid the wasp comb, and three *Copestylum* sp. puparia were firmly affixed within wasp nest cells. The puparium of a cycloraphous fly was found with the *A. yepocapa* nest collection.

Hymenoptera. The *A. yepocapa* colony collection included two species of parasitoid Hymenoptera: one female *Xanthogonales robertibuyssoni* Schulz, 1907 (Trigonidae) and one male *Nomadina* sp. (Trigonidae). The *A. panamaensis* colony collection included five specimens of *Nomadina smithii* Westwood 1868 plus a xanthic specimen probably of the same species.

Discussion

All *Agelaiia* for which nest sites are known, except *A. areata* and *A. flavipennis*, build nests without an envelope in sheltered or enclosed sites (Jeanne 1975; Wenzel 1991, 1998). In this regard, the nest sites of *A. yepocapa* and *A. panamaensis* are typical of the majority of species in the genus. Nest locations reported here are apparently typical for each species. *Agelaiia yepocapa* nests have previously been reported in living trees (Richards 1978, O'Donnell and Jeanne 1990, O'Donnell and Joyce 1999), as we report here, but the wasps have also been seen to nest in bird boxes and in a standing dead tree snag (S.O'D., unpublished data). "A nest [of *A. panamaensis*] was seen by Dr. W. D. Hamilton in Panama in a hollow log on the ground" (Richards 1978). D. P. Janos (personal communication) encountered a nest of *A. panamaensis* in January 1997, at 1,710 m in Parque Nacional Braulio Carillo on the eastern (north facing) slope of the Cordillera Central of Costa Rica. The habitat at this location is lower montane rain forest that receives an estimated 5 m of rain annually. The wasps were in a large, tent-like shelter the shape of a half-cylinder ≈3.5 m in diameter and 6 m in length. The wasps entered the

closed shelter through an opening of ca. 3 cm at the apex of one end; nest comb had been attached to the steel frame that supported the vinyl covering. The dimensions of the shelter are larger than but roughly analogous to the two sites in which we found large nests in San Luis, which reinforces our impression that nest sites of adequate dimension for a reproductive colony may be a limiting resource for this (and other) cavity-nesting *Agelaia* species.

O'Donnell and Jeanne (1990) reported that *A. yepocapa* reoccupied a nest that had been raided by army ants, and they speculated that nest site tenacity and aggressive nest defense may be more characteristic of cavity nesting wasps than of aerial nesting wasps. An example of this phenomenon may also occur in cavity-nesting *Polistes*: *P. carolina* (L.) is unique among the seven *Polistes* in Missouri because it nests in cavities such as hollow trees and wall voids, and it is the most aggressive of the seven species in defense of its nest (J.H.H., unpublished data). Similarly, *P. canadensis* (L.) often nests in cavities in the dry forests of Guanacaste Province, Costa Rica, where it is a notably aggressive *Polistes* species (J.H.H. and S.O'D., unpublished data). It is interesting to speculate that the extreme aggressiveness we report here for *A. panamaensis*, in defense of a nest that contained no brood other than a few pupae, is a correlate of extreme scarcity of suitably spacious sites such as the vinyl shelter in Braulio Carillo observed by D. P. Janos and the tree sites we observed in San Luis. At its peak, the collected *A. panamaensis* colony could have had a population of 15–20 thousand adults, each as large as a midsize *Polistes*. The nest of the abandoned colony was up to twice as large as that of the collected colony; that colony therefore could have had a population of 30,000 or more adults with 100,000 or more immatures. The size and aggressiveness of these wasps and the severity of their stings would place such colonies among the most formidable of social wasps.

Great nest architectural diversity occurs in *Agelaia* (Wenzel 1991, p. 507) and includes one or several interconnected spherical combs expanding spirally from a central point or axis in nests of *A. areata* (Say) (Jeanne 1973) and *A. flavipennis* (Ducke) (Wenzel 1991), stacked horizontal combs with downward-facing cells in *A. vicina* (Zucchi et al. 1995), and vertical combs with cells on both faces in *A. lobipleura* (Richards) (Richards 1978). Most species have vertical combs with cells on one side only (Jeanne 1975; Wenzel 1991, 1998). In this regard, the nest architectures of *A. yepocapa* and *A. panamaensis*, which have not been previously described, are typical of the majority of species in the genus. Illustrations of a nest of *A. p. pallipes* (Olivier) in Noll et al. (1997, their Fig. 2 B–D) resemble the nests of *A. panamaensis* that we saw in terms of comb orientation and multiple petiolar attachment to the substrate.

Gaster flagging occurs in *A. yepocapa* and *A. panamaensis* in response to assault on a nest by a predator (e.g., the investigators), but the communicative mode and function of gaster flagging are not yet demonstrated. Gaster flagging in epiponine wasps might

serve as a visual assembly signal from a wasp to its nestmates or as a visual warning signal to potential predators (O'Donnell et al. 1997). Dissemination of an alarm or assembly pheromone seems more likely, especially in those cases in which the sting is extruded in concert with gaster flagging, because venom is known to excite alarm in epiponines (Jeanne 1981). Support for this supposition can be drawn from the demonstration of venom dispersal via gaster flagging in the imported fire ant *Solenopsis invicta* Buren (Obin and Vander Meer 1985). However, gaster flagging occurs in ants such as *Cataglyphis bicolor* F. (see figure 10–3 in Hölldobler and Wilson 1990) and *Camponotus chilensis* (Spinola) (J.H.H., unpublished data) that forage solitarily and in which alarm or warning signaling would seem uncalled for. The role and significance of gaster flagging in epiponine wasps remains to be elucidated.

Monteverde has rainy and nonrainy seasons, but tradewind-induced clouds maintain mesic conditions throughout the year at Monteverde's upper elevations, and so the colony cycle of *A. yepocapa* at Monteverde could be aseasonal or asynchronous among colonies. The collected *A. yepocapa* colony was in full brood production, and the volume of forager traffic at the second colony suggested a similar condition. The absence of males coupled with full brood production suggests that reproductive swarming was not imminent, but swarming could have occurred a month or more later following emergence of the substantial brood being reared at the time of collection. The attack of army ants on a colony of *A. yepocapa* in Monteverde in late July (O'Donnell and Jeanne 1990) is evidence that brood was also being reared at that time of the year.

That queens of *A. yepocapa* were significantly larger than workers is in accord with expectation based on previous analyses of other *Agelaia* species (Jeanne and Fagen 1974, Richards 1978, Noll et al. 1997). The stepwise discriminant of raw morphometric data incorporated between-caste size difference. Therefore, to contrast castes independently of size, relative (size-adjusted) values were calculated by dividing each of the other 12 variables by mesosoma length (TL). Whether based on original measurements or on size-adjusted dimensions, the resulting linear discriminant function correctly classified all wasps in the sample according to caste. We interpret these results as demonstration that queen and worker *A. yepocapa* differ significantly in morphometrics even when between-caste difference in size is controlled for. The Mahalanobis distance and corresponding *F* test based on the 12 size-adjusted variables also support this conclusion. The plotted measurements of Fig. 3 illustrate this interpretation by showing that head width does not scale allometrically to body size; instead the overall smaller workers have relatively larger heads. The clear implication is that castes in *A. yepocapa* differentiate discretely during larval development; that is, caste in *A. yepocapa* is preimaginally determined by a developmental switch that directs a female larva onto either

the queen or worker pathway (Wheeler 1986, O'Donnell 1998).

For the honey bee, *Apis mellifera* L., Evans and Wheeler (1999) have shown that the well-known larval dichotomy in caste developmental pathways (Winston 1987) incorporates caste-specific expression of several genes. These differences in gene expression must necessarily follow from the differences in larval nourishment that have long been known to accompany honey bee caste differentiation (Winston 1987). The discrete differences in queen and worker castes that we report here for *A. yepocapa* probably reflect a difference in gene expression during larval growth analogous (if not homologous) to that now known in honey bees. Such a difference in gene expression may be modulated by larval nourishment. We did not find nest cells larger (for queens) than others (for workers and males), nor have nest cell size differences been reported in any epiponine wasp. Zucchi et al. (1995) reported that queens of *A. vicina* are produced from cells that have higher pupal cocoons than do workers. We observed a small number of pupal cocoons in the collected *A. yepocapa* colony that stood above the large number of surrounding cocoons, but these cells contained larvae rather than pupae, so we could not determine whether they contained developing queens.

The high number and diversity of inquiline species associated with the *A. panamaensis* colony probably reflect colony decline, with lowered vigilance against intruders and resistance to parasites. The psychodid *Clogmia albipunctata* is found in tropical and warm temperate regions throughout the world and is especially common in tree holes containing water (F. Vaillant, personal communication). Presence of these flies with the wasp nest collection may thus be coincidental, reflecting the preference of both species for tree cavities. Coincidence due to similar habitat choice is a less apparent explanation for presence of the syrphid immatures, because puparia were attached within wasp nest cells. However, colony decline may have enabled the flies to enter the nest for pupation following larval growth elsewhere in the tree hollow.

This is the first host record for the genus *Xanthogonalos* (Hymenoptera: Trigonaliidae) (D. Carmean, personal communication). A specimen of *X. robertibuyssoni* has previously been taken (by malaise trap?) in the same region of Costa Rica: Prov. Guanacaste, SW Volcan Cacao, Est. Mengo, 1,100 m, August 1988, leg. I. Gauld. The *Nomadina* species taken with *A. yepocapa* is most likely *N. smithii* Westwood 1868, but it is not as dark as reference specimens (D. Carmean, personal communication).

Our observations suggest that *A. panamaensis* colonies in San Luis may have annual cycles, terminating in December/January, which is at the onset of the dry season in the region surrounding the gallery forests in which the colonies were sited (Janzen 1993). The small colony in the cloud forest above Monteverde was near a well-used trail, and its detection a few days before our study probably coincided closely with the arrival of the wasps at the site. The number of wasps

was many fewer than would have been in a mature colony in San Luis, and the tree hollow that they occupied was much too small to have contained a nest such as those in San Luis. The presence of 5,000 wasps, but apparently no queens, in the declining colony in San Luis suggests that one or more reproductive swarms had departed that colony rather than the entire colony departing synchronously. The abandoned nest was reported to us to have been occupied 2–3 wk before our study. The termination of colonies in San Luis at the end of the rainy season and the synchronous appearance of a small swarm in the cool mesic cloud forest suggests the possibility of a colony cycle that includes an annual elevational migration and quiescent colonies during the season unfavorable for brood rearing at lower elevations. Seasonal migrations by swarm-founding wasps are known with certainty only in the epiponine *Protopolybia acutiscutis* (Cameron) in Panama (Naumann 1970), but observations suggest seasonal migration in the epiponine *Apoica pallens* (F.) in Venezuela (Hunt et al. 1995) and in the swarm-founding ropalidiine *Ropalidia montana* Carl in India (Jeanne and Hunt 1992). The independent-founding polistines *Polistes instabilis* Saussure, *Polistes pacificus* F., and *Mischocyttarus angulatus* Richards migrate elevationally in concordance with wet/dry seasonality in the lowlands west and northwest of Monteverde (Hunt et al. 1999); they nest in lowlands but pass the dry season in quiescence at cool moist high elevations. Colony cycles of swarm-founding wasps, including possible seasonal migrations and non-nesting swarms or nonreproducing nests, merit thorough investigation.

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