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Azteca ants in *Cecropia* trees: taxonomy, colony structure, and behaviour

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Introduction.

The most conspicuous ant-plant association in the wet neotropics is that of *Azteca* ants and *Cecropia* trees. In most low-elevation, wet regions of the neotropics, *Cecropia* is an ubiquitous and important invader of man-made clearings (Uhl *et al.* 1981; Brokaw 1987). The open, candelabra-shaped crowns of *Cecropia* often appear as the sole emergents over dense vine tangles in abandoned fields. The hollow internodes of these trees are almost always occupied by biting ants in the genus *Azteca*, each tree typically containing a single colony (Bequaert 1922; Wheeler 1942; Benson 1985).

In spite of being a common and species-rich ant-plant symbiosis, the *Azteca-Cecropia* association is only now receiving more than cursory investigation, with major research efforts underway in Costa Rica, Peru, and Brazil. Which *Azteca* species are obligate to *Cecropia* has been obscured by taxonomic uncertainty, past misidentifications, and inadequate collections (e.g. Wheeler 1942). It is important to provide a firm descriptive background to establish:

1. the data necessary for reconstruction of the evolutionary history of the relationship;
2. a basis for ecological studies of *Cecropia* and *Azteca*.

With the work of Harada (1982), Benson (1985), Harada and Benson (1988), Davidson and Fisher Chapter 20, this volume), and myself, involving surveys of *Cecropia*-inhabiting ant communities, a clearer picture is emerging.

Here I present a general description of *Azteca* and *Cecropia*, a discussion of the taxonomy of *Cecropia* ants (Table 19. 1), and a more detailed account of *Azteca* species in Costa Rica, contrasting their colony structure and behaviour (Table 19. 2), and their habitat and host use (Table 19. 3).

***Cecropia* (Cecropiaceae) and *Azteca* (Dolichoderinae)**

Cecropia is a strictly neotropical genus (introduced elsewhere, see Ake Assi 1980; Putz and Holbrook 1988) related to the Urticaceae and Moraceae

Table 19.1. *Cecropia*-inhabiting *Azteca* and their status as obligate *Cecropia* inhabitants.

	Type locality	Status
<i>constructor</i> Emery (1896)	Costa Rica	1
var. <i>guianae</i> Wheeler (1942)	Guyana	2
<i>muelleri</i> Emery (1893)	Brazil	1
var. <i>brunni</i> Forel (1909)	Brazil	3
var. <i>janeirensis</i> Forel (1912)	Brazil	3
var. <i>nigella</i> Emery (1893)	Brazil	3
var. <i>nigridens</i> Forel (1908)	Brazil	3
var. <i>pallida</i> Stitz (1937)	Mexico	3
var. <i>wacketi</i> Emery in Forel (1908)	Brazil	3
subsp. <i>terminalis</i> Mann (1916)	Brazil	3
<i>xanthochroa</i> (Roger (1863))	Mexico	1
subsp. <i>costaricensis</i> Wheeler (1942)	Costa Rica	2
subsp. <i>isthmica</i> Wheeler (1942)	Panama	2
subsp. <i>australis</i> Wheeler (1942)	Bolivia	2
subsp. <i>salti</i> Wheeler (1942)	Colombia	2
<i>coeruleipennis</i> Emery (1893)	Costa Rica	1
<i>alfari</i> Emery (1893)	Costa Rica	1
<i>ovaticeps</i> Forel (1904)	Brazil	1

1: Known obligate *Cecropia* inhabitant. 2: Taxonomic status (i.e. valid name or junior synonym) unknown, usually known only from type specimens, but types collected from *Cecropia*. 3: Taxonomic status unknown; no biological data with type description.

Table 19.2. Nest structure and behaviour of obligate *Cecropia* ants in Costa Rica.

<i>Azteca</i> species	Nest organization	Aggression	Herbivory
<i>A. constructor</i>	Centralized in main stem	high	low
<i>A. xanthochroa</i>	Centralized in main stem	high	low
<i>A. coeruleipennis</i>	Polydomous in branch tips	?	?
<i>A. alfari</i>	Polydomous in branch tips	low	high
<i>A. ovaticeps</i>	Polydomous in branch tips	low	high

Table 19.3. Habitats and host species used by *Cecropia*-inhabiting *Azteca* in Costa Rica. + = present and common, r = present but rare, ? = present in habitat but not recorded from host, 0 = not present at locality.

Locality*	<i>Azteca</i> species†				
	<i>con</i>	<i>xan</i>	<i>coe</i>	<i>alf</i>	<i>ova</i>
La Selva					
second growth, saplings, and small trees	+	+	0	+	+
primary forest, mature <i>C. obtusifolia</i>	+	+	0	?	?
primary forest, mature <i>C. insignis</i>	?	?	0	?	+
Peñas Blancas					
sapling and mature <i>C. insignis</i>	+	+	0	0	r
Monteverde					
sapling <i>C. polyphlebia</i> ‡	r	r	0	0	0
sapling and mature <i>C. obtusifolia</i>	+	+	r	r	0
Guacimal					
sapling and mature <i>C. peltata</i>	+	r	+	+	0

* Prov. Heredia, La Selva Biological Station, 50 m elevation; Prov. Alajuela, Río Peñas Blancas, 800 m; Prov. Puntarenas, Monteverde, 1300–1500 m; Prov. Puntarenas, Guacimal, 12 km SSW Monteverde, 500 m.

† *con* = *A. constructor*, *xan* = *A. xanthochroa*, *coe* = *A. coeruleipennis*, *alf* = *A. alfari*, *ova* = *A. ovaticeps*.

‡ *Cecropia polyphlebia* Donn. Sm. is a non-myrmecophytic cloud forest species, the mature trees of which never contain *Azteca* colonies, but whose saplings exhibit myrmecophytic traits and sometimes attract colonizing queens.

(Berg 1978a). It exhibits a very regular modular structure. The basic unit of stem elongation is the internode, a cylinder bearing a single, long-petioled, palmately lobed leaf. Initially, the internode centre is filled with a soft pith. The pith is surrounded by a thin layer of extremely hard sclerenchyma, which is continuous across the two ends of the internode, and thus forms durable septa between the internodes (Bailey 1922a). The cambium, and hence all wood growth, is external to this capsule of horny tissue.

In most of the more than 100 *Cecropia* species, there is a suite of characters which relate to ant association. First, the internode pith splits and retracts during internode development, leaving a hollow internode with a thin layer of spongy pith on the walls. The hollow internodes form the domatia which ants inhabit. Secondly, each internode has a preformed thin

spot, the prostoma, which lacks latex ducts (Bailey 1922*a*). The prostoma is often a well-defined oval depression in the wall, and is typically excavated and used as an entrance hole both by founding ant queens and workers of established colonies. Thirdly, the base of each petiole bears a trichilium, a pad of densely packed trichomes, from which sprout 1–2 mm long, glycogen-containing beads called Müllerian bodies (Rickson 1971). In Costa Rica, only the terminal two or three trichilia on leafy branches of mature trees produce Müllerian bodies; production ceases abruptly on more proximal leaves. Most ant inhabitants of *Cecropia* harvest Müllerian bodies as their primary food source.

Cecropia saplings, prior to the establishment of a single colony large enough to occupy all internodes, form stacks of potentially semi-autonomous nest sites for ants. Saplings frequently contain numerous incipient colonies in separate internodes (Longino 1989*a*; Davidson *et al.* 1990). The uppermost internodes typically contain live queens of the local species of *Azteca* that are obligate inhabitants of *Cecropia*. Internodes below those housing live queens routinely contain dead *Azteca* queens, evidence of colony failures. These failures occur inside sealed internodes, and so are not due to interactions with other colonies. Queens are sometimes killed by hymenopteran parasitoids (*Conoaxima*: Eurytomidae, Wheeler 1942), which may be locally abundant (see Chapter 20). At some point during sapling growth colonies begin to survive, producing workers that reopen the prostoma and begin gathering Müllerian bodies from trichilia. How reduction in the number of colonies occurs, such that one *Azteca* colony comes to dominate the sapling, is poorly understood as yet, but is currently under investigation (D. Perlman, personal communication).

In the sapling stage, incipient and mature colonies of a variety of arboreal ants may be found inhabiting lower internodes. The species list is large and includes the genera *Gnamptogenys*, *Heteroponera*, *Pachycondyla*, *Pseudomyrmex*, *Crematogaster*, *Solenopsis*, *Pheidole*, *Wasmannia*, *Zacryptocerus*, *Procryptocerus*, *Camponotus*, and *Myrmelachista*. These include species that are known to be nest-site generalists and some that may be specialized inhabitants of sapling *Cecropia*. However, only two non-*Azteca*, a *Pachycondyla* and a *Camponotus* from Peru, are known to have persistent, dominant colonies in mature *Cecropia* (see Chapter 20).

Azteca is a diverse genus, with over 150 nominal taxa, which exhibits a variety of nesting habits (Emery 1893, 1912; Forel 1929). Many *Azteca* use carton, a cardboard-like construction material fabricated by the ants (Wheeler 1910*a*; Longino 1986). Some species build large carton nests which hang exposed from branches. Others build carton nests within dead branches or hollow trunks. Still others inhabit live stems, and exhibit varying degrees of host specificity. Among this group at least six species are obligate inhabitants of *Cecropia*. Harada and Benson (1988) also review the *Cecropia* ants, and discrepancies between their work and this need to be resolved.

Taxonomy of *Cecropia*-inhabiting *Azteca*

Worker size polymorphism and gradual changes accompanying colony ontogeny greatly compromise the utility of workers in species identification. In contrast, queens are monomorphic and exhibit greater structural diversity than workers, and so are often essential for the identification of a species. Several characters are of critical importance in the species-level taxonomy of *Azteca*. First, the abundance of erect setae on the scapes and tibiae varies between species, and this character is expressed similarly in workers and queens. Secondly, the shape and size of the queen head varies greatly, ranging from extremely elongate (twice as long as wide) to broadly heart-shaped and wider than long. Thirdly, colour, although rarely used by ant taxonomists, is stable for some *Azteca* species and may be a very useful field character.

The common *Cecropia*-inhabiting *Azteca* species can be unequivocally divided into two groups: those with and those without abundant setae on scapes and tibiae. The former group is the more diverse, containing *A. constructor*, the *A. muelleri* and *A. xanthochroa* species complexes, and *A. coeruleipennis*. The group with bare tibiae contains only two species, *A. alfari* and *A. ovaticeps* (Longino 1989b).

A few other *Azteca* have been reported as *Cecropia* ants, but so infrequently that they are either obligate to *Cecropia* and very rare, or they have a variety of nest sites and only occasionally occur in *Cecropia*. Colonies of the *A. schimperi* species complex have been found nesting on *Cecropia* trees (Benson 1985). Unlike the foregoing species, workers totally lack erect setae on the thorax, and they build external carton nests. Their status as obligate *Cecropia* ants is uncertain. *Azteca minor* Forel was collected once from a *Cecropia* in Brazil. I have seen what may be conspecific material from myrmecophytic melastomes from Amazonia and thus doubt that it is an obligate *Cecropia* ant. These species will not be discussed further here.

Azteca constructor occurs in northern South America and Central America. The queen is solid black, with the head about as long as it is wide (Fig. 19. 1(a)). The erect setae on the thoracic dorsum are long and extremely dense, a condition unique to this species. The workers are chocolate brown, and are often difficult to distinguish from workers of *A. xanthochroa*.

Azteca muelleri, the species originally observed by Müller (1876; 1880–1881), occurs in southern Brazil, but its morphological variability and range are unknown. Queens from the type locality (Santa Catarina state) have a head shape very similar to *A. constructor*, but the thoracic setae do not form as dense a brush, and the colour is a mottled orange-brown. There are seven infraspecific taxa, whose status and affinities are completely unknown (Table 19. 1).

The taxonomy of *A. xanthochroa* and its four infraspecific nominal taxa is in a state of flux. All of them live in *Cecropia* and have queens with body colour solid orange, or the ground colour orange with some darkening in the

centre of the head and on the extremities. Distributional disjunctions and geographical variation confuse the species-level taxonomy. Queens from Mexico, the type locality of *A. xanthochroa* s.s., have heads that are somewhat elongate, with sides slightly convex, and the petiolar apex bears 0–4 weak setae. Moving south, the head generally becomes larger, more elongate, and with very straight sides, until an extreme is reached in Costa Rica, the type locality of the subspecies *costaricensis* (Fig. 19.1(b)). A disjunction occurs across northern South America, *A. xanthochroa*-like forms occurring again in the highlands of Peru and Bolivia, and extending

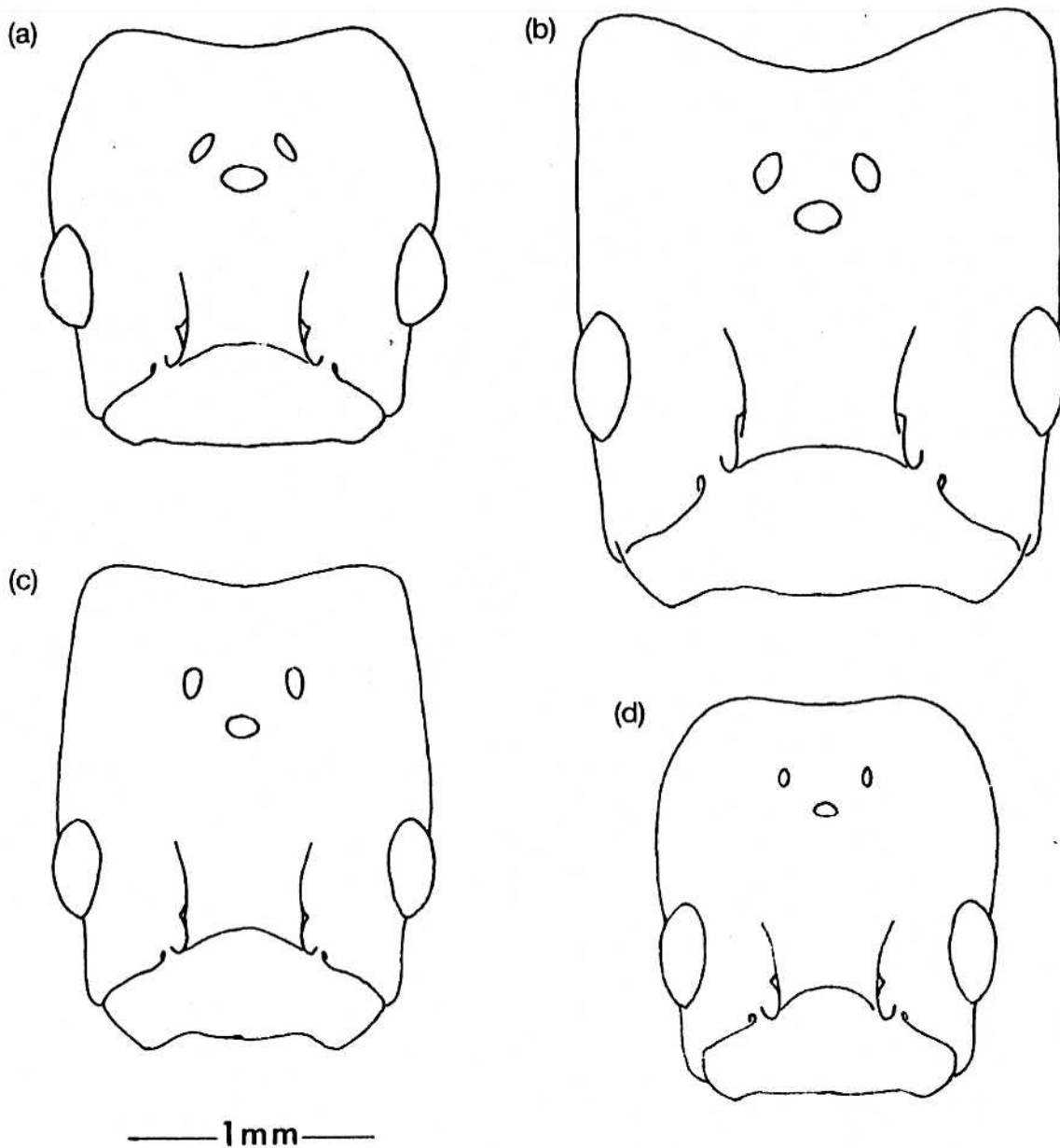


Fig. 19.1. Heads of queens of the major groups of obligate *Cecropia*-inhabiting *Azteca*. (a) *Azteca constructor*. (b) *Azteca xanthochroa*. (c) *Azteca coeruleipennis*. (d) *Azteca alfari*. All were drawn from Costa Rican specimens in the author's collection.

along the eastern slopes of the Andes and across the Amazon basin. Queens from the Andean highlands, the type locality of the subspecies *australis*, are nearly identical to queens from Mexico, but decrease substantially in size in the Amazonian lowlands (*A. xanthochroa* of Harada 1982). Thus, when queens from Costa Rica and the Amazon basin are placed side by side, they are strikingly different, yet they can be connected by a continuous series of intermediates.

In contrast to *A. xanthochroa* s.s., several geographically isolated forms in northern South America have a conspicuous tuft of erect setae on the petiolar apex. These include the subspecies *isthmica* in Panama and northern Colombia, the subspecies *salti* from the Sierra Nevada de Santa Marta, Colombia, and an undescribed species from the coastal mountains of Venezuela. Subspecies *isthmica* is the smallest form in the *A. xanthochroa* species complex, with the head about as long as it is wide, and presents a strong contrast to the largest members of the complex which are found in neighbouring Costa Rica.

The *A. muelleri* and *A. xanthochroa* complexes are poorly known and probably are not distinct groups on either phenetic or phylogenetic grounds. At one site in the Venezuelan Andes I observed two new species of *Cecropia*-inhabiting *Azteca*: one was intermediate between *A. muelleri* and *A. xanthochroa*, the other was intermediate between *A. muelleri* and *A. constructor*. Harada (1982) reported subspecies *isthmica* from the Manaus area, but her description and measurements suggest a distinct species. Two sympatric *A. xanthochroa*-like species have been found in eastern Bolivia (P. S. Ward, personal communication), one of which is certainly new. These new species suggest that there is an unexplored diversity of related species throughout the South American tropics.

Azteca coeruleipennis, presumably of Mesoamerican origin, has a range from southern Mexico to the Pacific coast dry forest of Costa Rica. The setae are fine and difficult to see, which has resulted in frequent misidentification of this species as *A. alfari*. The workers are always concolorous yellow-orange, and the queen is a lustrous solid black. The name refers to the smokey blue reflections on the wings of alate queens. The queen head is somewhat rectangular and longer than it is wide (Fig. 19.1 (c)).

Workers and queens of the *A. alfari* species group can be distinguished from all other obligate *Cecropia* ants by the absence of erect setae on the scapes and tibiae. The queens are small relative to queens in the other species groups. The head is slightly longer than it is wide and the posterior border is evenly rounded to flat, never strongly cordate, or angulate (Fig. 19. (d)). Two species are recognized in this group, *A. alfari* and *A. ovaticeps* (Longino 1989b), which differ in the degree of pilosity. The two species are broadly sympatric, both geographically and at the micro-habitat scale. This species group has the widest range of any obligate *Cecropia* inhabitant, occurring from southern Mexico to Argentina, and on several Caribbean islands.

Nest structure and behaviour of Costa Rican species of *Azteca*

Azteca constructor

A mature colony of *A. constructor* inhabiting a *C. obtusifolia* Bertol. tree near Monteverde was dissected (Fig. 19. 2). The colony centre was a spindle-shaped carton nest. To accommodate the nest, extensive excavation had occurred in the wood external to the hard, internodal capsules, the remains of which were incorporated into the carton. A major exit hole, 110 × 3 mm, was adjacent to the carton nest, and exit holes were common above and below the nest. The single carton nest contained the lone colony queen, all brood, all cached Müllerian bodies, abundant males, and abundant alate queens. No carton, brood, or sexuals were found elsewhere in the tree. The central nest communicated internally with every branch tip, the septa having been largely removed throughout, and passages maintained at branch junctions. All branch tips contained many exit holes, abundant workers, and Coccoidea. Eight branches from other *C. obtusifolia* trees containing *A. constructor* colonies in the area were all occupied throughout the 1–2 m of branch. All contained workers and Coccoidea only, with no carton, brood, or sexuals.

When the trunks of the trees occupied by *A. constructor* were tapped or shaken, workers poured from the central fissure and blackened the trunk near the internal carton nest. Workers also issued forth in numbers from all the branch tips. Workers responded similarly when branches were prodded with a pole. Even without disturbance, workers were often seen patrolling leaf surfaces (in part to tend Pseudococcidae, which were found tucked in the sinuses where the primary leaf veins radiate from the petiole). Leaves from the dissected tree and the eight branch samples were nearly devoid of other insects, and had almost no trace of herbivore damage.

Anastasio Alfaro claimed that *A. constructor* was the most aggressive of the Costa Rican *Cecropia* ants (in Emery 1896); I have also found this to be true. The behaviour and nest structure of *A. constructor* are similar to *A. muelleri* inhabiting *C. adenopus* in southern Brazil. Both Müller (1876; 1880–1881) and Eidmann (1945) observed that mature colonies of *A. muelleri* construct large, spindle-shaped carton nests in the boles of *Cecropia* trees, causing a swelling in the trunk which is visible from outside. Both Müller and Eidmann described *A. muelleri* as an extremely aggressive ant.

Azteca xanthochroa

A mature colony of *A. xanthochroa* inhabiting *C. obtusifolia* near Monteverde was dissected (Fig. 19. 3). The colony centre was a cylindrical carton nest filling two internodes in the centre of the trunk. To accommodate the nest a small amount of wood had been excavated exterior to one of the hard

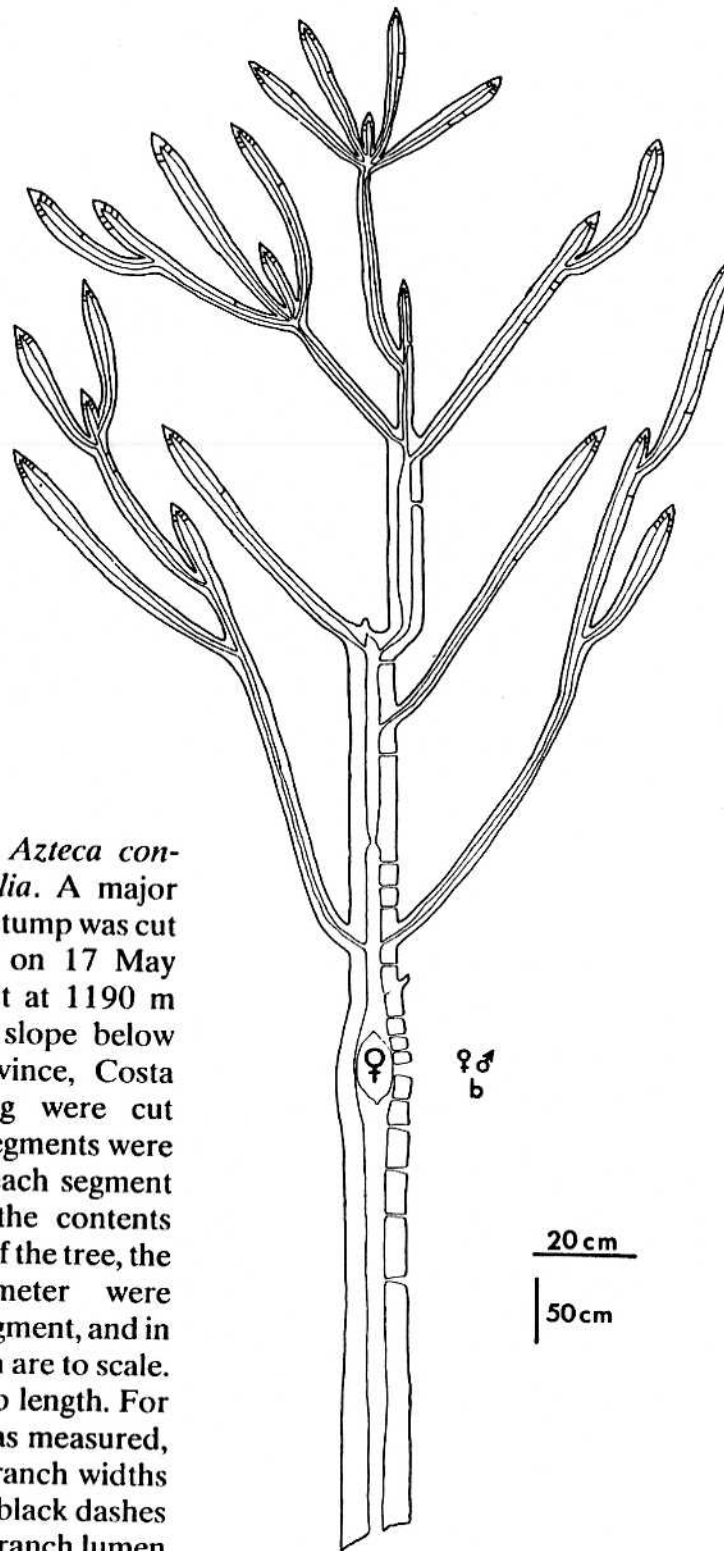


Fig. 19.2. Nest structure of *Azteca constructor* in *Cecropia obtusifolia*. A major stem from a coppice on an old stump was cut and dissected in its entirety, on 17 May 1989, in second growth forest at 1190 m elevation, on a steep Pacific slope below Monteverde, Puntarenas Province, Costa Rica. Segments 50 cm long were cut sequentially with a bow-saw. Segments were examined for exit holes, and each segment was split longitudinally and the contents examined. For the central axis of the tree, the internal and external diameter were measured at the base of each segment, and in the figure both width and length are to scale. Width is exaggerated relative to length. For lateral branches, length only was measured, thus widths are not to scale. Branch widths were mostly 5 cm or less. Small black dashes at branch tips, connecting the branch lumen to the exterior, and gaps in the right side of the central axis, are exit holes. The bold-face female symbol is where the physogastric colony queen was found. Smaller male and female symbols are where adult sexuals (males and alate queens) were found. 'b' is where brood was found.

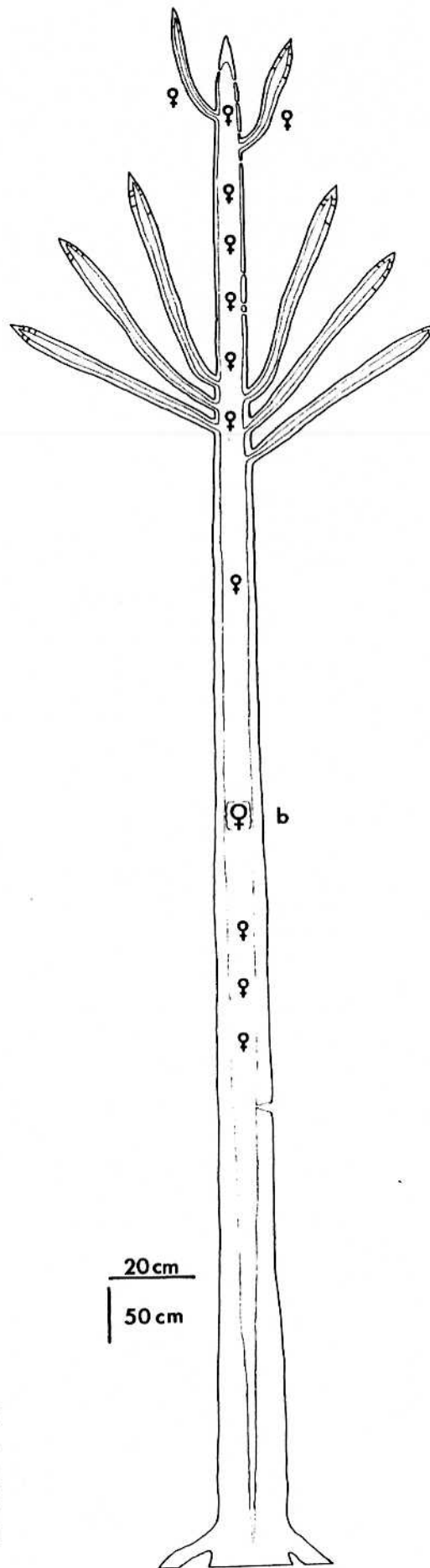


Fig. 19.3. Nest structure of *Azteca xanthochroa* in *Cecropia obtusifolia*. A free-standing stem was cut and dissected in its entirety, on 25 May 1989, within 20 m of the stem shown in Fig. 19.2. Methods and symbols are as in Fig. 19.2.

internodal capsules, but there was no external sign of the nest location. There were no exit holes near the carton nest. The only exit hole below the carton nest was a 4 cm long longitudinal fissure 4 m above the ground and 2 m below the carton nest. The next exit hole was over 4 m above the carton nest, near the branch tips. The single carton nest contained the lone colony queen, all brood, all cached Müllerian bodies, and abundant alate queens. Alate queens were also found scattered throughout the main trunk of the tree. The internodal septa were largely removed and the nest communicated internally with all branch tips, and all branch tips contained exit holes, workers, and Coccoidea, but no carton or brood.

Fifteen 1–2 m long branches were sampled from other *C. obtusifolia* trees containing *A. xanthochroa* colonies near Monteverde, and an additional three branches from La Selva Biologica Station, Heredia Province, Costa Rica. All were continuously occupied throughout, none contained brood, two contained very small amounts of carton, 13 contained sexuals (males, alate queens, or both), and all contained Coccoidea.

The colonies observed maintained a longitudinal fissure near the base of the tree, and major workers emerged from this fissure when the tree was tapped or shaken. Although they had large heads and strong mandibles, they had difficulty obtaining a grip on a flat surface such as a collector's hand. In contrast, smaller workers were fierce biters. When branches were prodded with a pole, workers issued from the branch tips vigorously and in large numbers. Workers patrolled leaves of undisturbed trees, the leaves were largely free of other insects, and there was minimal herbivore damage.

Alfaro (in Emery 1896) made similar observations of Costa Rican *A. xanthochroa* colonies. He observed that the nest entrance was a longitudinal fissure, and that workers emerged with their gasters elevated but did not bite the hand of the collector. The *A. xanthochroa*-like species in the eastern Amazon has a nest structure similar to that described here (D. W. Davidson, personal communication), and I have observed a similar nest structure in a related species from Venezuela.

Azteca coeruleipennis

A mature colony of *A. coeruleipennis* inhabiting a *C. peltata* L. tree near Monteverde was dissected (Fig. 19. 4). This tree was growing in a seasonally dry habitat, and, perhaps reflecting slow growth rates, the internodes were very compressed vertically and had small diameters relative to wood thickness. The colony was polydomous, with colony fragments occupying 23 separate branch tips and four separate cavities in the central axis. Brood and sexuals were evenly spread throughout the colony space. The colony queen was in a very protected region, surrounded by four large knots of dense wood, at a site where four branches had radiated from the central axis. Although adjacent portions of the queen's nest cavity contained abundant workers and small brood, the internode in which the queen was found and

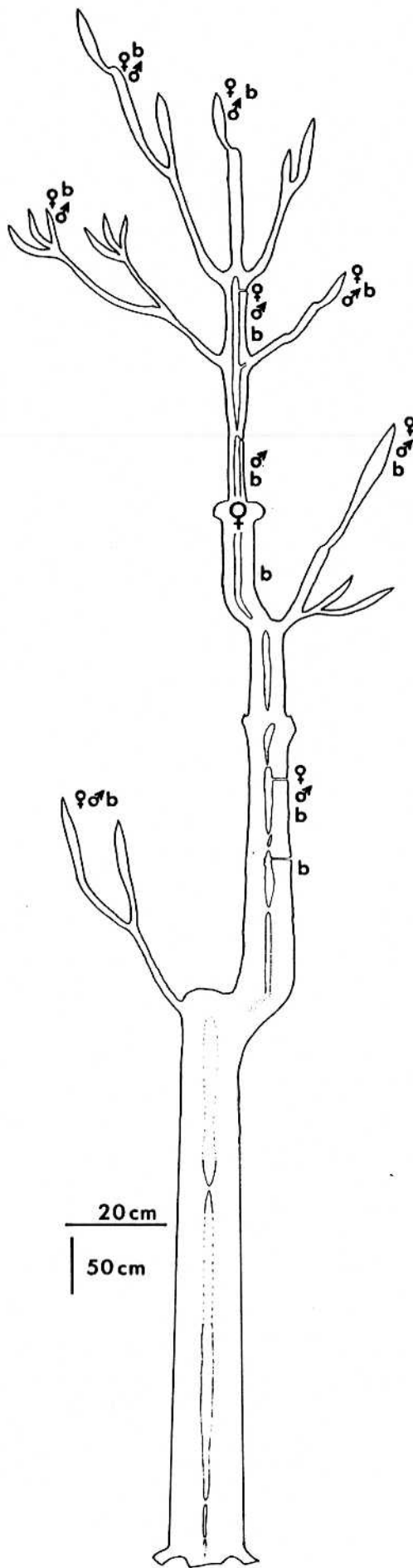


Fig. 19.4. Nest structure of *Azteca coeruleipennis* in *Cecropia peltata*. A free-standing stem was cut and dissected on 28 May 1989, in scrubby vegetation on a steep river bank, at 840 m elevation along the Rio Guacimal, on the Pacific slope below Monteverde. Methods and symbols are as in Fig. 19.2, except that lateral branches were not all cut and split, and so lumens are not drawn in the figure. All branches were inhabited and contained workers, brood, and sexuals. Not all of the 23 branch tips are shown in the figure because many broke in the felling and their positions were uncertain.

the adjacent four to five internodes were devoid of brood. In contrast to *A. xanthochroa domatia*, there was no trace of carton anywhere in the tree. In general, the septa were perforated with small holes, little larger than the workers themselves, and the lumens of lateral branches did not communicate with the central axis.

Eight branch tips were sampled for detailed dissection. Every branch contained workers, brood, adult males, alate queens, and Coccoidea. There were two species of Coccoidea, one of which was common in shoot apices, the other occurred more basally, 20–30 internodes down.

Azteca coeruleipennis was chary with its exit holes. Each of the four occupied nest spaces in the central axis had a single 2–3 mm diameter, round exit hole near the top of the cavity. Branch tips had very few exit holes, and these were often located 10–20 internodes below the active branch tip. This contrasts sharply with *A. constructor* and *A. xanthochroa*, which typically maintain 4–7 exit holes in the top ten internodes.

Workers responded to trunk tapping or shaking by descending to the trunk base, but their response was not as vigorous as *A. constructor* or *A. xanthochroa* colonies. The exit holes were small and inconspicuous; small yellow workers seemed to suddenly appear from nowhere, swarming over the crown and trunk. The leaves were free of other insects and herbivore damage was low. However, I have no data on patrolling, nor on between-tree or seasonal patterns of herbivory.

Azteca alfari group

A mature colony of *A. alfari* inhabiting *Cecropia insignis* Liebm. at La Selva Biological Station was dissected (Fig. 19.5). The nest was polydomous, occupying only the terminal 1–3 m of most branch tips. The single colony queen was in a small carton nest in the lowermost occupied internode of the central axis of the tree. The carton nest was small, occupying only a portion of the internode, and it contained only a few workers and a small mass of eggs and first-instar larvae. Small carton nests, brood, males, and alate queens were spread diffusely throughout the entire colony space. Coccoidea were present in every occupied branch tip. The colony occupied 22 separate branch tips, none of which communicated internally. Internodal septa had 1–3 perforations which were little larger than the workers, in contrast to the extensive septum removal displayed by *A. constructor* and *A. xanthochroa*. Branch and trunk interiors basal to the inhabited regions generally exhibited evidence of former occupation (perforate septa, pith removed from internode walls), but there were scattered blocks of internodes that had clearly never been entered. Small colonies of two other ant species, a *Camponotus* and a *Pachycondyla*, were found basally in branch space formerly occupied by *Azteca*.

Sixteen branches were sampled from other *Cecropia* trees inhabited by *Azteca alfari* group colonies at La Selva (two *C. insignis* with *A. ovaticeps*,

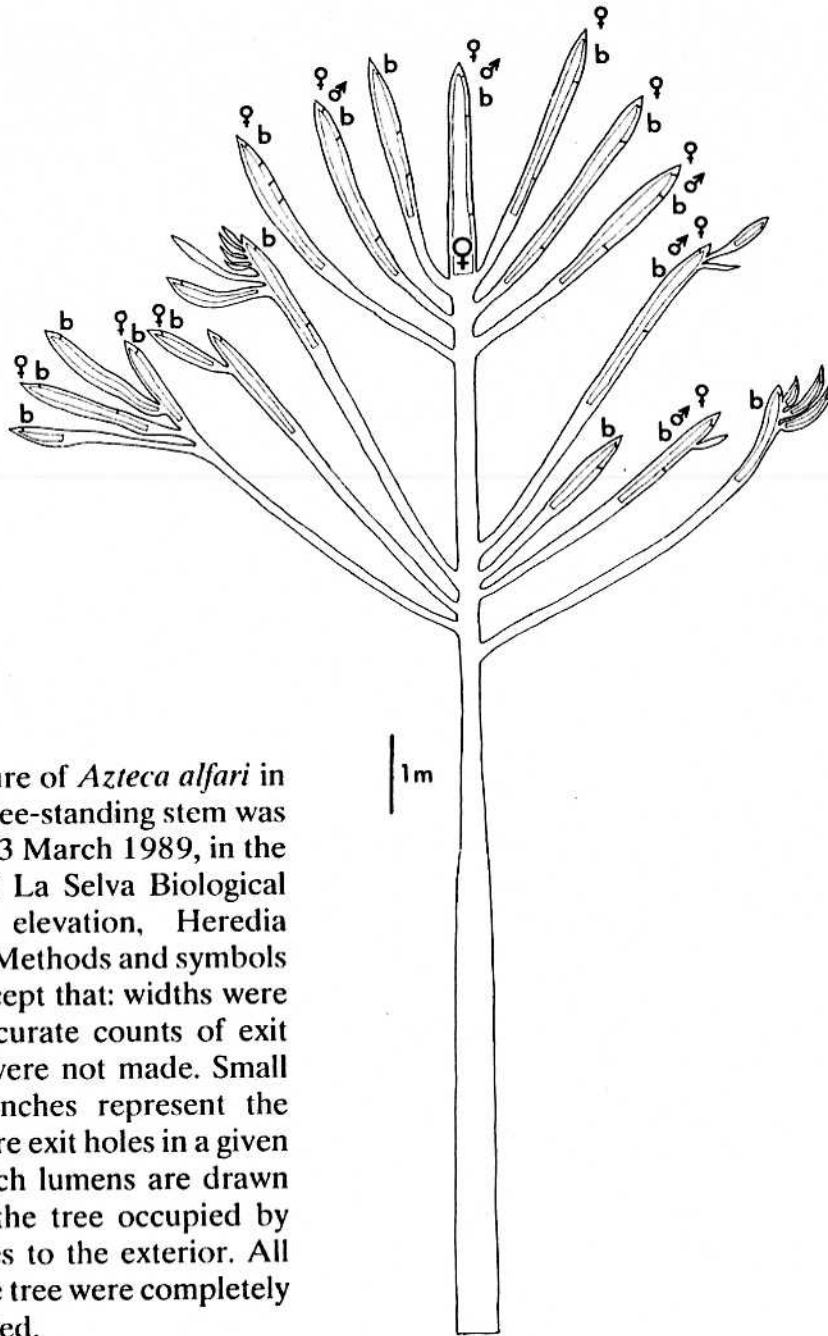


Fig. 19.5. Nest structure of *Azteca alfari* in *Cecropia insignis*. A free-standing stem was cut and dissected on 13 March 1989, in the laboratory clearing of La Selva Biological Station, at 50 m elevation, Heredia Province, Costa Rica. Methods and symbols are as in Fig. 19.2, except that: widths were not measured and accurate counts of exit holes at branch tips were not made. Small black dashes on branches represent the presence of one or more exit holes in a given 50 cm segment. Branch lumens are drawn only for portions of the tree occupied by *Azteca*, with exit holes to the exterior. All other internodes of the tree were completely sealed.

ten *C. obtusifolia* with *A. ovaticeps*, and four *C. obtusifolia* with *A. alfari*). Carton, brood, and Coccoidea were present in all of them; 13 contained sexuals. Most of the branches were long enough to observe a basal, unoccupied region and an apical, occupied region. One branch from a *C. obtusifolia* inhabited by *A. alfari* at Monteverde followed the same pattern, with an unoccupied base and workers, carton, brood, Coccoidea, and alate queens found in the inhabited apex.

When mature, branching *Cecropia* trees inhabited by *A. alfari* or *A. ovaticeps* were tapped or shaken, usually nothing happened. When branches

were prodded with a pole, workers either did not emerge at all, or did so only in small numbers. If a few workers did emerge they were aggressive and bit, and when branches were cut large numbers of workers emerged and presented just as much of an irritation as *A. constructor* or *A. xanthochroa* workers.

I never observed workers of *A. alfari* group species patrolling leaf surfaces. Leaves from the La Selva branch samples supported a complex arthropod community, including nymphs and adults of Miridae and Tingidae (Hemiptera), lepidopteran larvae, spiders, and other species of foraging ants in the genera *Camponotus*, *Solenopsis*, and *Procryptocerus*. Six of the 16 sampled branches were heavily infested with a myrmecophilous caterpillar (*Theope* aff. *decorata* G. & S., Riodinidae, P. J. DeVries, personal communication) which was always tended by an abundant Diplorhoptum *Solenopsis* species. Leaves from the 14 *C. obtusifolia* branch samples were heavily damaged, speckled throughout with small holes and necrotic spots, and some showed the characteristic feeding damage of *Theope* larvae near the petiolar insertion. The two *C. insignis* branches were less damaged.

The non-aggressive nature of Costa Rican *A. alfari* and *A. ovaticeps* should not be assumed in other parts of their ranges. P. S. Ward (personal communication) observed aggressive responses of *A. alfari* in southern Mexico, and D. W. Davidson (personal communication) observed *A. ovaticeps* near Manaus 'swarming over its host *Cecropia latiloba* Miq.'.

Inside *Cecropia domatia* inhabited by *Azteca xanthochroa* and *A. constructor*, there are regular mounds of brown, sticky, bran-like material. Müller (1880–1881) called these mounds 'knollen'. They have a uniform texture and are composed partly, if not entirely, from pith scraped from the internode walls. They are crawling with small fly larvae and nematodes, but there are no insect parts. Common inquilines are flies, especially a milichiid and a psychodid running freely and rapidly inside of the branches. Other inquilines (beetles, silverfish, cockroaches, Hymenoptera) seem to be extremely rare.

Phylogenetic considerations

Benson (1985) suggested that obligate *Cecropia* use arose many times in the genus *Azteca*, and the evidence presented here supports this conclusion. Structural and behavioural data strongly support an independent origin of *Cecropia* use in the *A. alfari* group, while the number of origins represented by the remaining *Cecropia* ants is unclear.

In many parts of the wet, lowland neotropics the canopy contains *Azteca* species that share the following characters:

1. external, pendent carton nests, in which all brood and sexuals are concentrated;

2. satellite carton shelters which house scale insects, Coccoidea;
3. queens with short, broad heads;
4. workers and queens with densely hairy tibiae and scapes; and
5. fierce defence of the main carton nest.

Azteca constructor and the *A. muelleri* complex share all these characters, except that they have moved into *Cecropia* trees and shelter their Coccoidea in branch tips. The construction of a bulging carton nest in the bole, with its requisite wood excavation and consequent deformation of the tree, and the maintenance of many large exit holes near the carton nest are probably retained characters which are not particularly adaptive to nesting in *Cecropia* trees.

In contrast to the builders of exposed carton nests, there is a large and little known set of *Azteca* species that nest in live stems of a variety of plants. Some nest in recognized ant plants such as *Cordia* (Boraginaceae), *Triplaris* (Polygonaceae), and *Tachigali* (Caesalpinaceae), while others occupy a wide variety of canopy and understorey vegetation. These *Azteca* are often found in plants that do not have preformed domatia, and it is unknown whether the ants excavate the stems themselves or opportunistically follow other stem-boring insects. These species typically have small queens with narrow, elongate heads. They are polydomous with the colony spreading out in shoot tips, progressively moving into new growth and abandoning older stems. Part of the reason that they are so poorly known is that they are often cryptic, tending Coccoidea inside the live stems and not actively patrolling the plant surface. Workers and queens of these species often have greatly reduced pilosity, with no or few erect setae on scapes and tibiae. Some of these species have strong associations with particular myrmecophytes, for example several species are obligate to *Cordia alliodora* Cham. (Wheeler 1942; J. T. Longino, personal observation). The *A. alfari* group clearly belongs with these stem-nesting *Azteca*, on both behavioural and morphological grounds.

The affinities of *A. xanthochroa* and *A. coeruleipennis*, and whether they share close ancestry, are unknown. Based on queen head shape, male genital characters, and the centralized carton nest, species in the *A. xanthochroa* complex may be related to the *A. muelleri* complex and to *A. constructor*. There are no obvious species groups of *Azteca* with which *A. coeruleipennis* can be allied. Thus, for the non-*alfari* group of *Azteca* it is unknown whether the *Cecropia* specialists are one lineage within which the habit arose once, or multiple lineages with independent colonization of *Cecropia*.

Which ant behavioural traits are adaptations specific to association with *Cecropia*? The trait which all obligate *Cecropia* ants must share is host-specific searching by founding queens, and in a species such as *A. constructor* this might be the only specialized trait. The lack of exit holes in the vicinity of the colony queen, a character shared by *A. xanthochroa* and *A. coerulei-*

pennis, could be a specialized adaptation which takes advantage of *Cecropia* architecture to protect the queen from predators or parasites. The total lack of carton, and the location of the queen in a highly protected part of the tree, may also be specialized traits that have evolved in *A. coeruleipennis*. Thus, these two species may be the most specialized occupants of *Cecropia*, representing plant-ants which have undergone extensive modification in response to the *Cecropia*-nesting habit.

More detailed knowledge of how, and how many times, obligate use of *Cecropia* has arisen will require phylogenetic analysis, and the mapping of behaviour onto structure-based cladograms (see Chapter 22). Museum collections of full caste series, species-level taxonomy, and field observations of behaviour and nest structure for a range of *Azteca* species are essential.

Ecological consequences of *Azteca* behaviour

It has been observed that species of *Azteca* and species of *Cecropia* sort by habitat (Harada 1982; Benson 1985; Davidson *et al.* 1990; Longino 1989*a, b*), with the *A. alfari* group occupying open, disturbed habitats, and *A. constructor* and *A. xanthochroa* being more common in closed forest. A summary of these habitat relationships for Costa Rica is presented in Table 19. 3. Davidson *et al.* 1990 and Davidson and Fisher (Chapter 20, this volume) have proposed a mixture of ultimate and proximate causes for the observed habitat partitioning. The ultimate causes pertain to resource availability and herbivore defence. The suggested proximate causes are active habitat selection by flying queens and/or habitat-specific outcomes of competition between newly emergent workers and founding queens in saplings.

With such strong behavioural differences between *Azteca* species inhabiting *Cecropia*, the species of ant occupant probably influences tree growth and survivorship, providing an additional explanation for habitat partitioning. If *A. alfari* fails to protect its host tree, trees occupied by *A. alfari* may selectively die during succession. At La Selva Biological Station, Costa Rica, I have observed that:

1. at the founding stage, saplings of *C. obtusifolia* contain queens of a full range of species: *A. constructor*, *A. xanthochroa*, *A. alfari*, and *A. ovaticeps*;
2. small trees with one dominant colony contain a similar range of species; and
3. large *C. obtusifolia* trees in the forest canopy contain only *A. constructor* or *A. xanthochroa*.

If active habitat selection by queens or habitat-specific outcomes of competition are occurring, the effects are not strong. These observations suggest that either trees containing *A. alfari* are dying early or that there is a succession of

Azteca species in a tree after a dominant colony has emerged. There is no evidence for the latter.

The length of time a colony takes to reproduce could also enhance habitat partitioning. Sexualls of *A. alfari* and *A. ovaticeps* occur in branches of small trees, but sexualls of *A. xanthochroa* occur only in branches of large trees (J. T. Longino, personal observation). If *A. alfari* group species reproduce early, in small trees, and *A. xanthochroa* and *A. constructor* delay reproduction until their colonies and trees are larger, then *A. alfari* group species would be dominant in pastures and along river edges, where trees would be either cut or washed out before *A. xanthochroa* or *A. constructor* could reproduce.

A pattern of within-habitat partitioning, which none of the above hypotheses explains, occurs on Costa Rica's Atlantic slope. At La Selva Biological Station, a lowland site, canopy *C. obtusifolia* are dominated by *A. constructor* and *A. xanthochroa*, while canopy *C. insignis* are dominated by *A. ovaticeps*, an *A. alfari* group species (D. and D. Clark, personal communication). At higher elevations, where *C. insignis* occurs alone, *A. xanthochroa* and *A. constructor* dominate and *A. ovaticeps* is extremely rare or absent. The mechanism resulting in host partitioning of forest *Cecropia* is unknown. A related question is how *A. ovaticeps*, whose behaviour appears to be identical to *A. alfari*, can be both a common, early-reproducing 'parasite' of second-growth *C. obtusifolia* and the primary occupant of mature *C. insignis*, a long-lived canopy species.

The study of the community ecology of the *Azteca*-*Cecropia* association is in its infancy. The following questions should be addressed by further observation and experiment:

1. Do founding queens exhibit habitat-specific host choice?
2. Are there deterministic competitive relationships between *Azteca* species, and are they affected by host tree species or habitat?
3. For each *Cecropia* species, how is host-tree demography (and ultimately fitness) affected by species of ant occupant and habitat?

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Part 5

Pollination, ant exclusion, and dispersal