BIRDS AND THE ANT × ACACIA INTERACTION IN CENTRAL AMERICA, WITH NOTES ON BIRDS AND OTHER MYRMECOPHYTES

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This paper discusses the trophic and nesting relationships between birds, and swollen-thorn acacias and their ant occupants. It is part of a study of the ecological position of myrmecophytes (plants that have a mutualistic interaction with the ants that live in them) in lowland Central American plant communities (Janzen 1966, 1967a, 1967b) and refers primarily to the ant-occupied acacias of the New World, which are found only in the lowlands of Central America and northern Colombia. The very meager information available on other myrmecophytes and their interactions with birds is included in context. There are fewer than 10 references to birds and myrmecophytes in over 400 references on myrmecophytes cited by Wheeler (1922), and subsequent summaries of insect-bird nesting interactions (Meyers 1929, 1935; Moreau 1936, 1942) contain no information on bird relations with myrmecophytes.

The mutualistic interaction between ants and acacias has been experimentally analyzed and described in detail (Janzen 1966, 1967a, 1967b) and a brief summary follows.

A colony of obligate acacia-ants (*Pseudomyrmex ferruginea*, *P. nigrocincta*, *P. belti*, *P. venefica*, etc.) lives in the swollen, stipular thorns of one to several individual shrubs or trees, referred to as swollen-thorn acacias (*Acacia cornigera*, *A. collinsii*, *A. hindsii*, *A. sphaerocephala*, *A. cookii*, etc.), in the lowland moderately dry tropics of Central America. These acacias differ from other acacias in having (1) large partially hollow thorns in which the ants live (figs. 2, 4), (2) modified leaflet tips called Beltian bodies which constitute the primary protein and oil source of the ant colony, (3) greatly enlarged foliar nectaries which are the sugar source of the ant colony, (4) year-round leaf production on most individuals, providing a relatively constant food source for the ant, and (5) absence of chemical and structural traits that protect other acacias from most herbivores in the environment. The swollen-thorn acacias differ ecologically from other acacias in that they cannot survive to reproductive maturity without the patrolling activities of a large colony of obligate acacia-ants which remove herbivores (primarily insects) and intrusive vegetation by biting and stinging. The ants are virtually never found as a viable colony living elsewhere than in the swollen-thorn acacia. They replace the chemical and physical ability of the plant to deal with its consumers and competitors. This interaction occurs in virtually all lowland Central American semi-deciduous and deciduous secondary vegetation with a dry season of six months or less and no annual burning or plowing.

BIRD PREDATION ON ACACIA-ANTS

An occupied swollen-thorn acacia, with one-fourth to three-fourths of the thorns filled with ant larvae, is an obvious and potentially important food source for insectivorous birds. There may be as many as 0.8 g of live larvae (up to 0.6 g dry weight) in one thorn and 40 g of live larvae in a tree 2 m tall. This highly localized food is present all year, but its potential importance is greatly increased during the dry season when most diurnal insects are in a secluded and inactive stage (Janzen and Schoener 1967). However, predation on these larvae is only rarely encountered in active colonies. This is complicated by the fact that, in nearly three years of field work on this interaction, a bird has not yet been observed actually opening a thorn, and A. Skutch, probably the most experienced Central American bird biologist, informs me that he has never observed it. However, the circumstantial evidence points to birds as the predators because insects are not strong enough, bill marks are seen on some thorns, and mammals leave tooth marks when opening thorns.

The bird either splits the thorn from one tip to the base (fig. 1), breaks the thorn (fig. 2) or punches a hole through the dorsal or ventral thorn wall near the base (fig. 3). Since thorns are dead tissue there is no reaction by the plant to this damage. Forcing the beak into the entrance hole apparently splits the thorn and spreading the bill probably opens it further. This "gaping" ability is pronounced

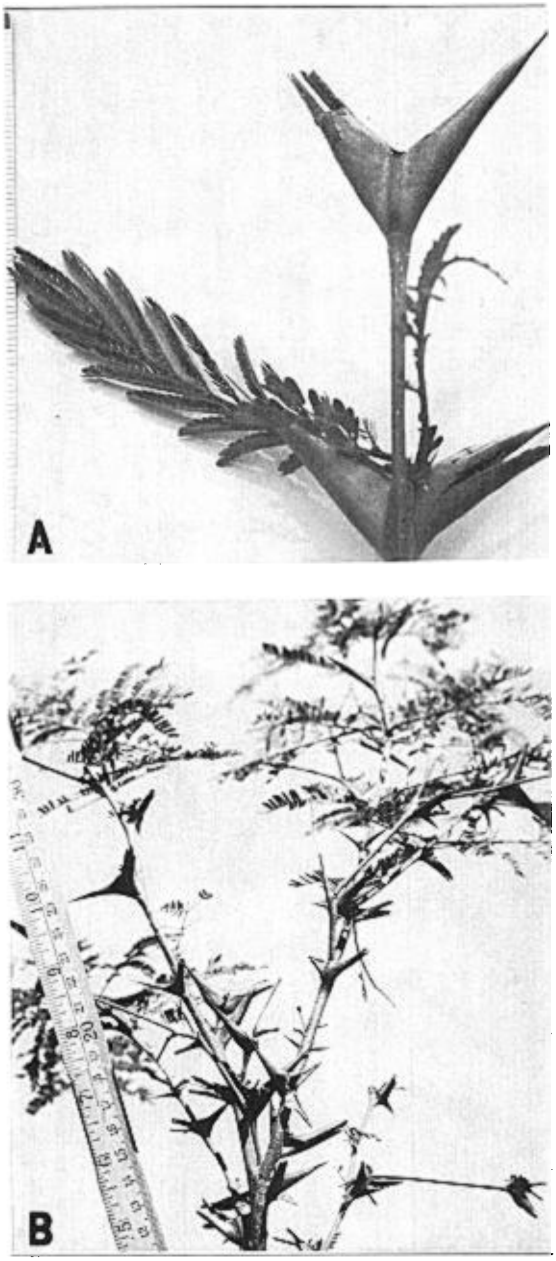

FIGURE 1. Acacia thorns split from one tip to the base. A. Split type A thorns of *Acacia hindsii* that were occupied by *Pseudomyrmex venefica* (9 June 1967, 15.9 mi. E Concordia, Sinaloa, México). B. *Acacia hindsii* branch presumably thoroughly worked over by a bird (tree occupied by *Pseudomyrmex ferruginea*, 2 August 1967, 22.2 mi. SW San Pedro Sula, Cortés Prov., Honduras). Splitting thorns in this manner is the commonest type of predation encountered.

in Icteridae (Beecher 1950), which are abundant in acacia habitats. The split side of the thorn is almost invariably that with the ants' entrance hole, leaving the ants no exit. Bill marks indicate that a thorn is broken by holding it at right angles to the bill, biting hard, and twisting. This is difficult to duplicate even with heavy forceps. The break may be on any part of the thorn and often the workers could escape through the entrance hole in the other side of the thorn. Only rarely are both sides of the thorn broken (fig. 2E). Thorn opening could be initiated after a bird sees an ant disappear into the entrance hole. Larvae and workers of *Pseudomyrmex ferruginea* have been taken from oriole gizzards (*Icterus* spp.) in the state of Veracruz, México, and the birds were probably foraging by one of the three methods described here. Orioles observed creating a strong disturbance reaction by pecking at the seed pods were found to have 500–800 worker ants in the gizzard (Janzen 1967b).

All thorn opening recorded has occurred during weather when ant activity on the surface of the acacia is at it lowest, i.e., during the occasional cool spells in December and January and during the peak of the dry season in late March and early April. At these times worker ants may be virtually absent outside the thorns of auxiliary-shoots and at very low densities on queen-shoots. The density of other insects in the habitat is lowest during the cool periods, dry periods, or both (Janzen and Schoener 1968), so the causal basis for the correlation between predation and the dry and cool season may be two-fold.

Generally one out of 100–500 occupied swollen-thorn acacias at a given site (0.5–10 ha) shows predation by birds of the type illustrated in figures 1 and 2. Thorn opening occurs throughout the range of all swollen-thorn acacias but varies in frequency from site to site. An average of about one per cent of obligate acacia-ant colonies appear to be subject to thorn opening by birds during their lifetime. Damage to a single tree is probably done by a single bird. When a colony in a single acacia has been thoroughly raided by a bird, up to 200 out of 250 thorns may have been split or broken and the colony is nearly always killed, owing to both the predation and colony disorganization. In those *Pseudomyrmex* species that have only one queen (*P. ferruginea*, *P. belti*, *P. nigrocincta*, *P. spinicola*, etc.), this colony mortality indicates that the queen-thorn was opened. However, since she is often in the largest and strongest thorn on the tree, generally a type B thorn after the tree is two years old (fig. 4A), the bird may miss her (at least in *P. ferruginea* and *P. belti*, on which most of the observations have been

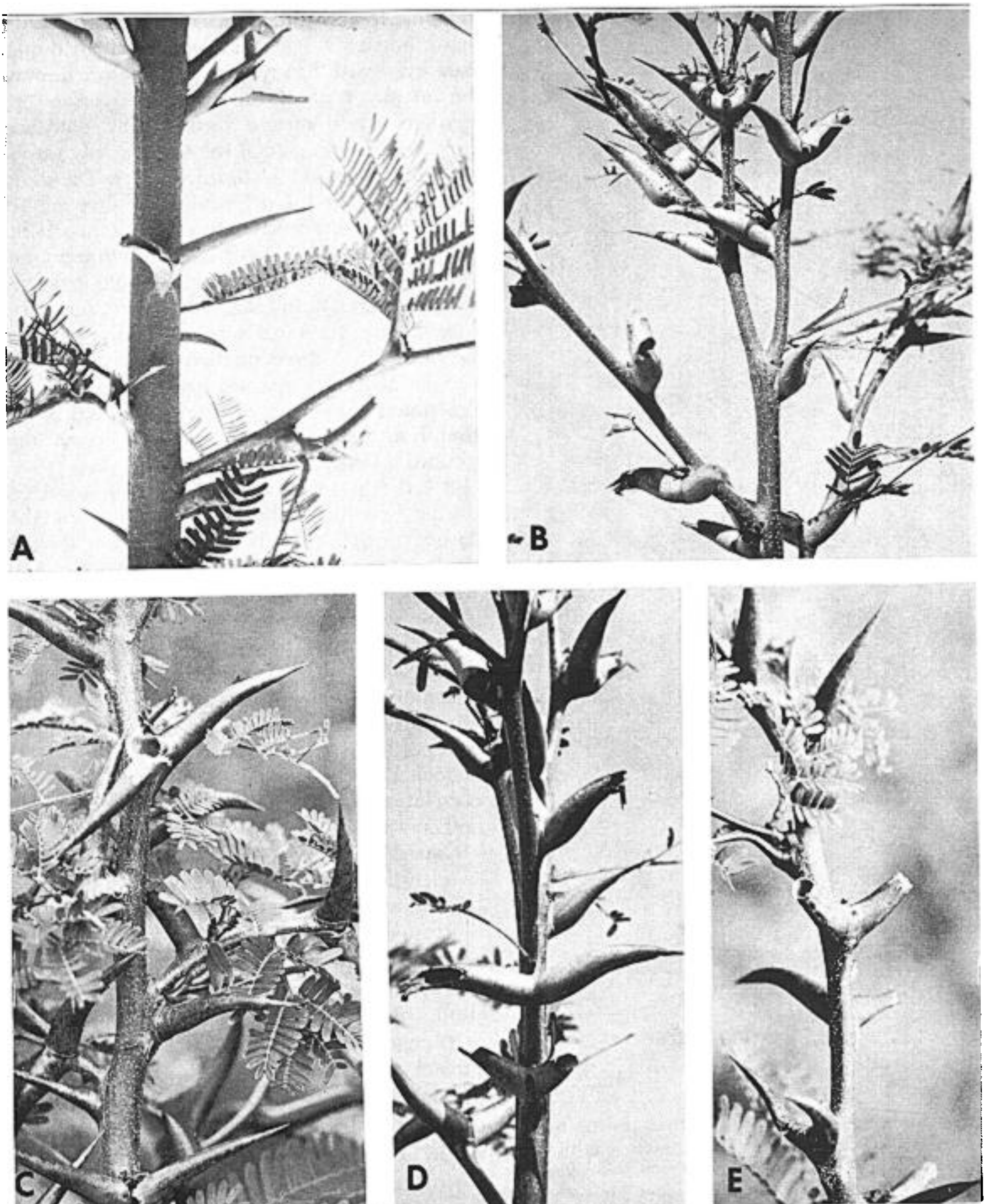

FIGURE 2. Broken acacia thorns. A. Type A thorns of *Acacia cornigera* that were occupied by *Pseudomyrmex ferruginea* (2 August 1967, 14.2 mi. S San Pedro Sula, Cortés Prov., Honduras). This tree shows splitting and breaking (upper right). B. Type A thorns of *Acacia collinsii* that were occupied by *Pseudomyrmex belti* (28 July 1967, 8 mi. E San Benito, Depto. de Managua, Nicaragua). The tips of all the thorns in the photograph have been broken off, presumably by a bird. C. Type A thorns of *Acacia collinsii* that were occupied by *Pseudomyrmex nigrocincta* and broken at the thorn base (28 July 1967, 10.9 mi. NE Sebaco, Matagalpa, Nicaragua). D. Type A thorns of *Acacia collinsii* that were occupied by *Pseudomyrmex belti* (28 July 1967, 8 mi. E San Benito, Depto. de Managua, Nicaragua). E. Type A thorns of *Acacia collinsii* that were occupied by *Pseudomyrmex belti* (28 July 1967, 10.9 mi. NE Sebaco, Matagalpa, Nicaragua). Breaking of both ends of the thorn is relatively uncommon.

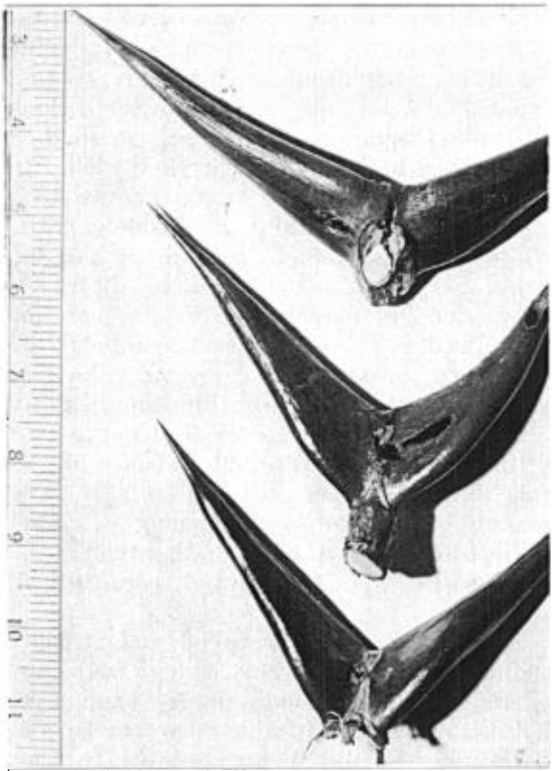

FIGURE 3. Thorns of *Acacia hindsii* with a hole punched in their bases by a bird (woodpecker?) preying on *Pseudomyrmex venefica* (5 June 1967, 23.5 mi. SW El Palmito, Sinaloa, México). Uppermost thorn was split with a knife along midline. Hole in right tip of middle thorn is ant entrance hole.

made). Type B thorns have never been found split by birds, although in some cases there are puncture holes at the base of the thin-walled type B thorns of *A. hindsii.* In this case, the colony is greatly decimated but not killed. In species with multiple queens (*P. satanica*, *P. venefica*, etc.) scattered among the larger thorns, the bird will eat many, but probably not all.

More commonly, only those thorns on 2–30 per cent of the lateral branches of an acacia are split or broken. These are exclusively type A thorns with thin straight-grained walls (fig. 4B) and virtually never contain the colony queen though they are often full of brood. In most cases the queen is not in danger at all, as an ant colony commonly occupies 2–10 acacias. Since the sites of such larval predation are negatively correlated with the density of patrolling worker ants, the queen-shoot with its high density of ants and more severe disturbance reaction is the least likely part of the colony to be raided by a bird. There is ample evidence that worker ants will attack a predating bird, but the bird probably eats

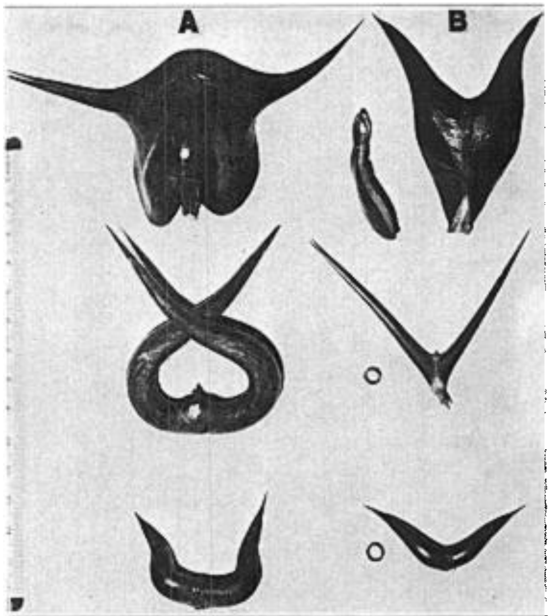

FIGURE 4. Comparison of type A and B thorns from three acacias. Row A. Top: type B thorn of *Acacia hindsii* from Retalhuleu, Retalhuleu, Guatemala. This thorn type is on rare occasions opened by a bird that punctures the thorn close to its base, but the thorn walls are at best 1–2 mm apart and thus the ants can probably partly escape. Middle: type B thorn of *Acacia cornigera* from Temascal, Oaxaca, México. This thorn type has never been found opened by birds. It has thick walls (up to 3 mm) and a twisted grain making it very difficult to break. It is usually wrapped around the stem bearing it. Bottom: type B thorn of *Acacia collinsii* from an area south of Comitán, Chiapas, México. This thorn type has never been found opened by birds (many of them are more recurved). While its thorn walls are thinner than those of *Acacia cornigera*, they are also harder and very tightly appressed to the branch bearing them; they often occur in very tight clusters. Row B. Thorns from the same plants as in Row A. Top: type A thorn with an adjacent cross section from a similar thorn. The thin walls of these thorns are apparently easily split or punctured by birds, and may be up to 4–5 mm apart. Middle: type A thorn with an adjacent cross section from a similar thorn. These thorns are commonly split, but rarely punctured. Bottom: type A thorn with adjacent cross section from a similar thorn. These thorns are most commonly broken in the middle or across one side of the thorn.

them unless they become so numerous that it cannot catch them all, and then it may be driven from the tree. Evidence of this is occasionally found when just one centrally located thorn on a heavily occupied tree has been opened.

There has probably been selection not only for generally strong thorn walls to reduce larval predation by birds, but also for the production of a few large and very thick-walled thorns for protection of the queen as

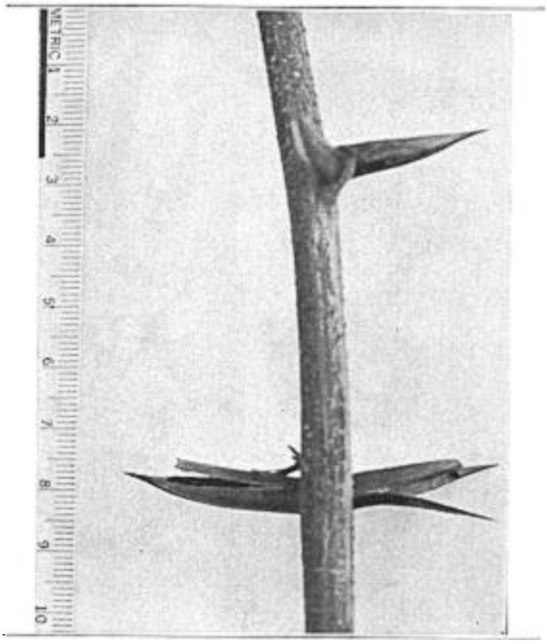

FIGURE 5. Thorns, apparently split by a bird, of a hybrid (F_1) of *Acacia hindsii* with an unidentified species of acacia not associated with ants (6 August 1967, 17.1 mi. NW Santa Ana, Santa Ana, El Salvador). Only founding queens of obligate acacia-ants (*Pseudomyrmex* spp.) were in these thorns. Both sides of these hard, brittle, and easily split thorns are often opened by birds.

well. On two occasions queen-shoots of *A. cornigera* were found with virtually every type A thorn split, but with the two large type B thorns undamaged. On both occasions the *P. ferruginea* queen was in one of these latter thorns. I have nine records of an entire colony (*A. cornigera* and *A. collinsii*; *P. ferruginea*) being removed by a bird when queen-shoots lacked type B thorns. As a consequence, the tree will be without its protective ant colony when the rainy season begins and the tree starts to grow. The detrimental effect of this on the acacia is well documented (Janzen 1967b). It may be significant that *A. hindsii*, which has type B thorns with exceptionally weak walls, is occupied over the majority of its range by multiple-queen species of obligate acacia-ants (and the loss of some queens is less critical).

Puncturing the thorn base (fig. 3) is much less obvious and more rarely encountered than thorn splitting. Puncturing usually occurs on a series of 8–10 consecutive thorns along the main central axis, indicating that a stronger support is needed by this bird than by the ones that split or break thorns. This implies that a perching bird splits thorns, while a climbing bird such as a woodpecker (*Centurus* spp.?) punctures them. A single or double small hole is made and the entire thorn content removed, suggesting a bird with a long versatile tongue that could be extended at right angles to the bill tip when in the hole. In some cases the bill is inserted parallel to a thorn axis at the ventral point of contact of the thorn with the branch; here the entire bill could be pushed up through the thorn. At times, the bill may be pushed through the lateral wall in a direction nearly parallel to the thorn axis, but in these cases the hole is so small that gaping is probably not involved. Since these birds forage in the central part of the tree, they have a better chance of getting the queen than do thorn splitters. The majority of cases of hole punching are found in the thin-walled *A. hindsii* rather than in the thick-walled type B thorns (*A. cornigera*, *A. collinsii*).

Selection for thicker walled and stronger thorns is also evidenced by the high frequency of thorn splitting found on F_1 (and F_2?) hybrids of *A. hindsii* with other acacias (*A. cochliancantha* and *A. macracantha*) not associated with ants. The hybrids have brittle and easily split thorn walls (fig. 5), and very often both sides of the thorn are split. This is complicated by the fact that these hybrids are very poorly patrolled, if at all, by worker ants, and therefore the higher frequency of thorn splitting may be due simply to the lack of colony defense. However, young and unoccupied swollen-thorn acacias, even though their thorns have the same content as the hybrid's thorns (founding queens and young colonies), virtually never have split or punched thorns. Holes have never been found punched in the bases of hybrid acacia thorns, but these have very tough bases. Founding queens often cannot remove the tough parenchyma in the bases of hybrid acacia thorns and thus there is no empty cavity for a bird to break into by punching a hole.

Specialized deterrent traits of thorns vary among species of swollen-thorn acacia. All species show some thickening and toughening of the walls of type B thorns. *A. cornigera* in the lowlands of eastern México has highly recurved type B thorns that are extremely difficult to split with a knife or by hand, but they are only slightly recurved in the rest of Central America (south to Guanacaste, Costa Rica). *A. collinsii* (Colombia to México) and an undescribed swollen-thorn acacia in southwestern Costa Rica have a heavy internal ridge or bump at the site where, in other species, the bird punches a hole. *A hindsii* has no apparent modification except that the thorn is very flat (fig. 4). The walls are 1–2 mm apart in many places, and it is probably difficult for the bird to probe all the crevices if it does enter.

In heavily shaded sites, young swollen-thorn acacias have very thin thorn walls. These plants do not reach reproductive maturity, but founding queens do establish young colonies in the thorns. An unknown bird(s) breaks the thorns at the midline (as in the mature tree in fig. 2C). Even when a thorn is opened the queen ant stays in one end of the thorn with her head blocking the entrance hole and can be easily caught. This has been especially evident with *A. melanoceras* in 40–80-year-old second growth in Panamá and with *A. hindsii* in 2–5-year-old second growth in Guatemala, and occurs at all times of the year.

Thorns opened by birds are not reused by the ants; but until they rot off the tree, they do form a refuge for spiders that prey on ants.

At the end of the dry season, new soft and green unoccupied thorns are occasionally found crushed by birds (evidenced by bill marks and direct observation of a small passerine on one occasion). This very likely has nothing to do with predation on ants since only the newest green thorns are damaged and the thorns are thoroughly crushed from one end to the other. These thorns are filled with a sweet parenchyma not unlike fresh celery stalks in water content, and probably are used by birds as water sources and perhaps for sugar.

The thorns of unoccupied adult swollen-thorn acacias are often occupied by other genera of ants (*Crematogaster, Azteca, Pseudomyrmex, Paracryptocerus, Camponotus,* etc.) more normally found living in dead twigs. These thorns are usually partly rotted and have weak and fragile walls. Thoughout the year but more frequently in the dry season these acacias are found with many hundreds of their thorns freshly split or punctured at the base. While most obligate acacia-ant workers remain in the opened thorn, workers of other genera of ants burst out, running in all directions. This appears to be a mechanism to avoid predation and is common to many twig-inhabiting species of ants. There is no evidence that these other ants would attack a bird.

Ants living in most other myrmecophytes are subject to an unknown amount of predation by birds. The hollow stems and trunks of *Cecropia* spp. (Moraceae), occupied by ants of the genus *Azteca* (Dolichoderinae) in Central America (Wheeler 1942; Eidmann 1944), are often ripped open, apparently by woodpeckers. A Lineated Woodpecker (*Dryocopus lineatus*), collected while eating ant larvae from near the top of a *Cecropia* 14 m tall (Puerto Viejo, Heredia Prov., Costa Rica; 26 June 1965, L. L. Wolf), had broken through the stem wall and sorted the larvae and pupae (in cocoons) from the workers, as shown by the absence of worker ants among the approximately 2 cc of *Azteca alfari* brood in the gizzard. Although adult ants of this species have a very strong alarm odor and despite the ants strong alarm reaction (at least 3 per cm^2 of bark surface) the woodpecker had opened six different internodes. Skutch (1945) reports that this woodpecker opens *Cecropia* internodes to eat *Azteca* brood, and also that it eats the worker ants from the surface of the tree. He also notes that this woodpecker, like flickers (*Colaptes* spp.), feeds its young by regurgitation and this may be associated with the small particle size of its food.

The woodpecker holes in the damaged trunk are filled by callus tissue ("wound tumor," Skutch 1945) after several months. Neither mature colonies nor founding queens use opened internodes. Some species of *Azteca* fill the hole with carton of vegetable origin. At some sites, 1–2-m *Cecropia* are commonly encountered (Osa Peninsula, Puntarenas Prov., Costa Rica; Yucatán Peninsula, México; lowland southwestern Guatemala) with nearly every internodal chamber opened and the entire colony missing. The internodes of young *Cecropia* sometimes are opened and the founding queens are eaten, greatly lengthening the time required for a colony to develop on the tree. Destruction of the stem wall leads to reduction in height increment and the holes admit rainwater, which is associated with fungal attack of the stem. Skutch (1945) reports that *Cecropia* often break off at the point where the woodpecker has done an exceptional amount of damage, though my field notes indicate that this actually happens to somewhat less than 0.1 per cent of the population at any one site. Similarly, Escherich (1911) reports that birds split the internodal domatia of *Humboldtia laurifolia* (Leguminosae) in India to eat the ants living within and regards this as evidence that the ants are detrimental to the plant.

Surprisingly, there are no records of bird predation on the ants living in thin-walled saccate domatia of the common myrmecophytes in the understory of primary wet lowland forest of Central and South America (Melasto-

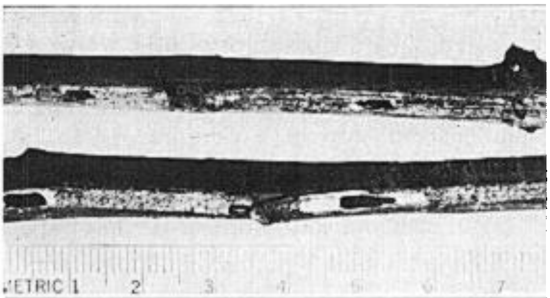

FIGURE 6. Sections of a branch that contained an ant nest and was apparently raided by an Olivaceous Piculet (*Picumnus olivaceus*) in a brushy pasture near Palmar Sur, Puntarenas Prov., Costa Rica (22 August 1965).

mataceae, especially *Tococa* and *Clidemia*), although the occupant ants are small and not generally aggressive to humans. However, Kerr (1912), in describing the interaction of *Dischidia rafflesiana* (an epiphytic vine in the Asclepiadaceae, dry forests of southeast Asia) with its occupant ant (*Iridomyrmex* in the Dolichoderinae), interprets holes in the pitcher-like foliar domatia as evidence of bird predation.

The type of predation described above is not peculiar to myrmecophytes. Predation on twig-inhabiting ant colonies by woodpeckers in lowland Central America ranges from sporadic to common. Splitting of twigs has not been recorded, but rather a series of holes are punched through the wall of the twig at 3–5-cm intervals (fig. 6). The spacing and size of the holes vary between twigs, and several species of woodpecker may be involved. The bird appears to start at the terminal end and move toward the base, thus trapping the remaining part of the ant colony against the end without an entrance. Brood and worker ants of obligate twig-nesting species of one *Pseudomyrmex* and three *Camponotus* colonies were found in the gizzards of four *Centurus hoffmannii* in lowland Guanacaste, Costa Rica, during the rainy season (July 1965). The tiny woodpecker known as the Olivaceous Piculet (*Picumnus olivaceus*) has been recorded "pecking at slender twigs" (Upper Térraba River Valley, Costa Rica; Skutch 1960), and a female shot near Palmar Sur, Puntarenas Prov., Costa Rica (L. L. Wolf, 20 August 1965) had the remains of workers and larvae from a small yellow *Pseudomyrmex* ant colony in its gizzard; this ant was often collected from twigs the size of those in figure 6. Otvos (1967) reports *Pseudomyrmex*, *Camponotus*, and *Crematogaster* ants (all twig-inhabiting species) in three of these little

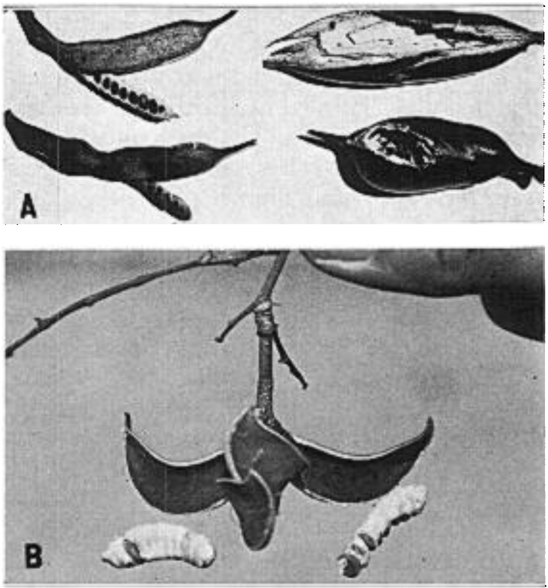

FIGURE 7. Acacia pods and seed clusters that are eaten by birds dispersing the seeds. A. On the right, two dark red indehiscent pods of *Acacia cornigera* that have been opened by birds (31 March 1967, Cañas, Guanacaste Prov., Costa Rica). All seeds have been removed from the upper pod. On the left are two brown pods of *Acacia hindsii* (9 June 1967, Acaponeta, Nayarit, México). The valves dehisce on one side only, and the seeds imbedded in a bright yellow pulp (aril?) project downward. If not picked off by a bird, the cluster of seeds eventually falls from the gradually separating valves. B. Two bright yellow seed clusters of *Acacia collinsii* hanging below the fully opened valves of two pods (8 February 1966, Playa Coco, Guanacaste Prov., Costa Rica). The seed clusters are suspended on 2–5 thin strands 1–2 cm long and the bird can pick them off without even stopping in the tree (orioles, *Icterus* sp., have been observed to do this).

woodpeckers from the same locality. Slud (1964) reports that this bird pecks "the twiglets sharply" and prefers "viny twiggy tangles." In twig-inhabiting ant species, as with the obligate acacia-ants, the colony is subdivided into a number of units. The loss of one unit from one twig is therefore usually not fatal since the queen is usually in the cavity with the strongest and thickest walls. In those species where there are many queens, the woodpecker will get some but not all. When one of these twigs is split, the reaction is immediate flight by nearly all adults.

DISPERSAL OF SEEDS

Bird dispersal of the seeds of the polyphyletic Central American swollen-thorn acacias is of unusual interest because the other 700-plus species in the genus have seeds dispersed by gravity, rodents, water, and large browsing mammals. *A. arabica* of South Africa (Bews

1917) and *A. caven* of Argentina (Havrylenko, in litt.) may, however, also be bird dispersed.

All the swollen-thorn acacias have a sweet pulp (aril?) around the seeds. The red, maroon, or yellow indehiscent pods of *A. sphaerocephala* and *A. cornigera* are split (fig. 7A) by woodpeckers, orioles (*Icterus* spp.), saltators (*Saltator* spp.), and Great Kiskadees (*Pitangus sulphuratus*), or eaten entirely by Brown Jays, *Psilorhinus morio* (Janzen 1967b). The legume valves of *A. collinsii* and *A. hindsii* open and the row of seeds, enclosed in lemon-yellow pulp, protrudes or swings below on very thin and fragile fibers (fig. 7B) which the bird flies to and picks up, sometimes without landing. Other swollen-thorn acacia pods split on one or two sides and the white or yellow pulp containing the seeds is picked out. The sweet and sticky pulp around the seeds is very difficult to remove, but saltators remove most seeds before swallowing the fruit (*A. cornigera* in Veracruz and Oaxaca, México; Janzen 1967b). The seeds are 3–7 mm long, 2–5 mm wide, and 1–3 mm thick. By Temperate Zone standards, these seeds are rather large to be bird dispersed; however, they are not extraordinary for tropical seeds dispersed following ingestion by birds. For example, the seeds of *Calathea* (Marantaceae), *Heliconia* (Musaceae), *Protium* (Burseraceae), *Byrsonima crassifolia* (Malpighiaceae) are ingested by birds and are as large as, or larger than swollen-thorn acacia seeds. The seeds of *A. cornigera*, *A. sphaerocephala*, *A. hindsii*, and *A. collinsii* have all been germinated after being taken from the feces of birds. Seeds of swollen-thorn acacias will not germinate until the seed coat is damaged, and the grinding in the bird gizzard may therefore be of significance. However, seeds taken from the gizzards and intestines of *Psilorhinus morio* required further seed coat damage (filing) to germinate.

Irrespective of whether this dependence on birds is a convergence or a product of introgression of the same genome (reticulate evolution is most likely; Janzen 1966), there appears to be a selective pressure acting on all the swollen-thorn acacias that favors bird-dispersal of seeds. First, swollen-thorn acacias occurred, prior to human interference, in widely scattered segments of young, natural, and wetter second growth along rivers, landslides, and similar places, rather than in essentially continuous, drier, and widespread areas as do most other members of the genus (and as do the swollen-thorn acacias at present: in pastures, roadsides, and other human disturbance sites). In these habitats birds are the only biotic dispersal agents that regularly travel long distances (0.1–15 km) across habitats inimical to development of swollen-thorn acacia seedlings. The birds that distribute these seeds are found primarily in second growth. Also, birds can move in and out of the acacia more easily than can mammals without being attacked. Those species of swollen-thorn acacia (*A. collinsii*, *A. cornigera*, *A. hindsii*, *A. sphaerocephala*) whose seeds are most quickly removed by birds are those with the broadest distributions, while those that are less rapidly removed (*A. cookii*, *A. chiapensis*, *A. melanoceras*, and two undescribed species) have been very slow to move into human disturbance sites and have very spotty distributions (there are other reasons for this as well). The former three species also have the largest geographic distribution and *A. collinsii* occurs naturally on Old Providence Island, 120 miles off the coast of Nicaragua.

Second, birds begin dispersal of seeds as soon as the fruits are ripe. This is important to a plant that loses 60–100 per cent of a particular seed crop to damage by the larvae of pea weevils (Bruchidae; Janzen 1967b, 1969). Since the first infestation generally destroys 40–80 per cent of the seeds, and within two months after seed maturation all seeds remaining on the tree have usually been killed, rapid seed removal by birds is probably critical to survival of the acacia species (Janzen 1967b). The beetle larvae in infested seeds do not survive the trip through the bird; these seeds are broken up and the bird undoubtedly obtains some nourishment from them. Although other acacias also sustain high percentage of seed loss by bruchids, they are not dependent on long distance dispersal (several miles or more) to new localized disturbance sites at each generation, and therefore probably require fewer viable seeds per plant to maintain a given population density.

The intermediate stages in the evolution of bird-dispersed acacia seeds may be functional. When the rainy season begins and soaks the legume liner of some non-myrmecophytic acacias, the fermenting material attracts insects (Nitidulidae, Anobiidae, Tenebrionidae, fly larvae, etc.). If the birds go to these pods for insect food then there may be occasional seed ingestion. Birds that serve as dispersal agents at present are both insectivorous and frugivorous. The higher the sugar content the more likely the bird will eat the pulp and ingest some seeds, and the quicker the fruits will be eaten, raising the probability that the seeds will be removed before the bruchid beetle larvae can damage them.

Three other groups of lowland Central American myrmecophytes have bird-dispersed seeds. Brown Jays (*Psilorhinus morio*), woodpeckers (*Centurus* sp.), and many unidentified passerine birds have been observed frequently eating the pendant elongate fruits of *Cecropia peltata*, *C. sandersoniana* and *C. obtusifolia* (Moraceae). The 2-mm-diameter flat yellow seeds are often seen in bird droppings on foliage. Skutch (1945) lists oropendolas, toucans, barbets, cotingas, and finches as feeding on *Cecropia* fruits and adds that "in the Térraba Valley of Costa Rica, these catkins are probably the most important food of frugivorous birds during the early months of the year, when fruits of other sorts are scarce." While other fruits are in fact very abundant during the dry season ("early months of the year") (Janzen 1967c), *Cecropia* is nevertheless an important food source at that time. Of probably greater importance, it is also one of the few trees that bears fruit during a major part of the rainy season when fruits on trees are very scarce. Wheeler and Darlington (1930) list six species of birds that feed on *Cecropia* fruit in Colombia (*Forpus spengeli* = *Forpus xanthopterygius*, Blue-winged Parrolet; *Brotogeris jugularis*, Orange-chinned Parakeet; *Momotus momota*, Blue-crowned Motmot; *Pteroglossus torquatus*, Collared Araçari; *Centurus rubricapillus*, Red-crowned Woodpecker; *Thraupis episcopus*, Blue-gray Tanager). *Azteca* ants do not patrol the fruits of *Cecropia* with any regularity and a bird sitting in the canopy causes virtually no general disturbance. Bats are the only other likely candidates for seed dispersal of *Cecropia*, and Wheeler and Bequaert (1929) report this for *Cecropia* in the Amazon basin. Skutch (1945) reports howler monkeys (*Alouatta alouatta*) feeding on *Cecropia* fruits in Panama but gives no details as to whether the plants were occupied by *Azteca*. The small pale fruits of the myrmecophytic tree *Cordia alliodora* (Boraginaceae) are eaten by small passerine birds, but the occupant *Azteca* do not appear to bother them. The blue fruits of myrmecophytic *Tococa*, *Conostegia* and *Clidemia* (Melastomataceae) are eaten by small passerine birds in the heavily shaded understory of primary and old secondary forests in the wet lowlands of Central America.

The preponderance of bird dispersal of seed of Central American myrmecophytes is undoubtedly primarily associated with the selective factors that have led to the very high proportion of bird-dispersed fruits among all plants in the second growth tropical wet habitats that swollen-thorn acacias inhabit. *Triplaris americana* (Polygonaceae) is the only wind-dispersed Central American myrmecophyte.

BIRDS NESTING IN SWOLLEN-THORN ACACIAS

Throughout the range of swollen-thorn acacias, active bird nests are commonly encountered on the thorn-covered branches during the last month of the dry season and the first three months of the rainy season (fig. 8). In areas where swollen-thorn acacias occur at low density (e.g., one or less per mile of roadside), over 50 per cent of the acacias over 3 m tall have at least one nest or nest remnant in them. Wheeler (1942) reports unidentified bird nests in swollen-thorn acacias in Nicaragua, Guatemala, and Panamá. Skwarra (1934a, b) saw orioles (*Icterus* sp.) and Kiskadees (*Pitangus sulphuratus*) nesting in swollen-thorn acacias in Veracruz, México, and used this point to support her erroneous conclusion that the ants were unable to protect the tree against herbivores (Janzen 1967b). Skutch (1945) says that "birds of numerous kinds place their nests in the bullhorn (swollen-thorn) acacias, evidently taking advantage of the protection afforded by the fiercely stinging ants that dwell in the thorns." Sutton (1948) and Sutton and Pettingill (1942) reported *P. sulphuratus* and *Nannorchilus leucogaster* (= *Uropsila leucogastra*, White-bellied Wren) nesting in swollen-thorn acacias in northeastern México.

Casual observation gives the impression that birds select these trees or bushes as nest sites over other plants, as has been postulated for birds nesting near ant and wasp nests in both the Old and New World (Meyers 1929, 1935; Moreau 1936, 1942). This impression is complicated by the fact that swollen-thorn acacia canopies are relatively open and the nests therefore very easy to see. The exposed position would seem to make the acacia a very poor site for nesting in terms of escaping from inclement weather, predators, and parasites.

To examine the density of nests in acacias, two road censuses were conducted in southern and western México.

Census 1. Between San Blas, Nayarit, and México Highway 15, there is an old asphalt road 22.6 miles long (Nayarit Highway 46) rising from sea level mangrove swamps to 300 m elevation (rolling hills). It is bordered on both sides by fields and second growth vegetation 1–70 years old and 1–50 m tall

TABLE 1. Results of census of bird nests along 22.6 miles of road between San Blas and México Highway 15, Nayarit, México (10 June 1967).

	No. of nests	% of total	Height above ground (m)		
			$\bar{x}$	S.D.	Range
Nests in *Acacia hindsii*					
Pendant	114	45.0	6.04	3.10	2–18
Sessile	45	17.7	5.42	4.39	2–13
Nests in other plants					
Pendant	54	21.3	18.19	8.84	2–40
Sessile	40	15.8	16.55	10.81	2–40

(very tall trees are probably riparian remnants of primary forest). Beginning at the inland edge of the mangrove swamp, *A. hindsii* is a very abundant roadside plant. It is occupied by *Pseudomyrmex venefica* (black with red markings on the petiole) and an undescribed species of obligate acacia-ant (brown). Both of these ant species have multiple queens and therefore the colony often occupies a large clump of acacias (5–500 trunks; 4–300 m^2). These clumps are scattered with a density of at least one (and often more) visible per 0.1 mile on each side of the road. On 10 June 1967 (still dry season) one census of the nests along this road (table 1) was made at 20–25 mph with two observers, one at each car window.

All bird nests seen in all kinds of vegetation were recorded, along with their height, type, and species of substrate plant. It is impossible to know which nests were occupied or active, but it has been my experience that nearly all old bird nests in swollen-thorn acacias have disintegrated (partly by weather and partly by ant cleaning activity) by the end of the previous rainy season, and thus the nests were probably all from 1967. Pendant nests (fig. 8A) were definitely in the process of being constructed by Yellow-winged Caciques (*Cassiculus melanicterus*) and an unidentified species of oriole (*Icterus* sp.). Sessile nests (fig. 8B, C, D; fig. 9) were all covered to various degrees with nest material, were approximately spherical, and ranged from 15 to 30 cm in diameter; they probably belonged to several species of bird (*Thryothorus* spp.?). There was no obvious segregation of nest sizes or types (pendant or sessile) between swollen-thorn acacias and other plants. The only road margins along which nests were conspicuously absent, but with ant-occupied acacias densely present, were those bordered on both sides by plowed fields 5–20 ha in extent. A mean of about one nest per five clumps of *A. hindsii* was recorded, but very often there were two to five nests in a clump (pendant and/or sessile).

Table 1 shows a clear difference between the number of pendant nests in *A. hindsii* and in other plants. This is even more meaningful considering that there are easily 1000 branch ends in the vegetation examined for every *A. hindsii* branch end. I conclude that the birds that build pendant nests are seeking out *A. hindsii* as a nest site.

The similarity of number of sessile nests in the two groups of plants must be considered in the light of the fact that, in the area censused, not over 0.1 per cent of the roadside canopy volume is *A. hindsii*. Thus less than 0.1 per cent of the vegetation contained over 50 per cent of the sessile nests observed. This indicates a preference for *A. hindsii* by the birds that build sessile nests in exposed sites in roadside plants.

A. hindsii differs from other plants in several respects of probable importance to nesting birds. The large stiff thorns on stiff branches that retain many of their leaves through the dry season offer many points of attachment for nest material in contrast to the relatively smooth branch surfaces of other plants. This interpretation is supported by the very heavy use of unoccupied swollen-thorn acacias as standards by vines (the ants in occupied trees kill the vines), in contrast to other plants from which the tendrils slip repeatedly (Janzen 1967b).

Secondly, the extreme thorn development on *A. hindsii* could well serve as a deterrent to large arboreal mammals. That this is, however, probably not very important to the bird is shown by the absence of nests in other moderately spiny trees (e.g., *A. farnesiana*, *A. cochliancantha*, *A. macracantha*, and various other Mimosoidea), except those of cactus wrens (*Campylorhynchus* spp.) in cactus.

Thirdly, and probably most important, the large ant colony is likely a deterrent to any climbing vertebrate or flying vertebrate that sits in the tree before entering the bird nest. The low positions of both sessile and pendant nests (table 1) indicate that the ants can substitute for height as a predator deterrent. The acacias chosen by birds are in the 2–20-year age class and have well-developed lateral branches at least 1.5 m above the ground. The nests may be in the top center or edge, or lower down in the canopy. The bird does not seem to discriminate between occupied and unoccupied acacias; by the end of the dry season up to 20 per cent may be unoccupied through natural colony mortality and colony consolidation into certain plants.

TABLE 2. Results of census of bird nests along 141.2 miles of road between Arriaga and Tapachula, Chiapas, México (21 June 1967).

	No. of nests	% of total	Height above ground (m)		
			$\bar{x}$	S.D.	Range
Nests in *Acacia hindsii* or *Acacia cornigera*					
Pendant	65	12.1	3.06	1.01	1–8
Sessile	332	62.2	3.09	1.29	2–8
Nests in other plants					
Pendant	119	22.3	16.35	7.01	5–40
Sessile	17	3.1	13.65	7.22	4–25

There is no evidence that birds choose *A. hindsii* because of the proximity of food; I have no records of thorn opening by birds in the San Blas area. They may, however, be eating adult ants from the acacia surface.

Census 2. Between Arriaga and Tapachula, Chiapas, México, there is an asphalt road 141.2 miles long across coastal plain of not over 150 m elevation. It is bordered on both sides by fields, brushy pastures, and regenerating second growth 1–15 years old and 1–12 m tall, with occasional large trees that may be remnants of primary forest. Most of the swollen-thorn acacias (*A. hindsii* and *A. cornigera*) in this vegetation are in ravines, roadside wasteland, swamps, and fields abandoned over 2–3 years previously. In contrast to the San Blas area described above, the acacias are occupied by single-queen species of obligate acacia-ants (*P. ferruginea* and an undescribed species) and the result is that most acacias occur as separate plants rather than as clumps. This had no obvious influence on bird nesting patterns. The density of swollen-thorn acacias within 100 m on each side of the road was almost never less than one per 0.1 mile and often as high as 100–200 per 0.1 mile.

On 21 June 1967 (rainy season about one month old) this route was driven at an average speed of 45 mph. At this speed, all individual acacias could not be examined closely, but two observers examined carefully a total of 1561 distinctly separate swollen-thorn acacias in the 2–8-m size class (table 2). Trees below 2 m almost always lack nests and are much more abundant and difficult to observe than the taller trees. The mean number of nests per acacia examined was 0.25; the number of nests per acacia with nests ranged from one to eleven, with a mean of about two. Between the acacias the vegetation was examined intently for nests. All nests seen in other species of trees were single nests with no other nests within 20–50 m. The acacias constituted less than 0.1 per cent of the vegetation volume in the 2–12-m size class. A major part of the plants in this size class are common woody shrubs and small trees of second growth, and many have individuals with a general life form and foliage density similar to that of the acacias, e.g., *Muntingia calabura, Guazuma ulmifolia, Trema micrantha*, juvenile *Enterolobium cyclocarpum, Luehea* sp., *Byrsonima crassifolia*, and *Cordia allidora* (a myrmecophyte which virtually never has bird nests in it).

There were more pendant nests in all other plants than in the swollen-thorn acacias. In terms of total volume of vegetation, however, there was still a very strong indication of preference for swollen-thorn acacias. Orioles (*Icterus* spp.) were the only birds seen to leave the pendant nests. The three reasons for nesting in acacias given for the San Blas sample apply here as well. However, the presence of 119 pendant nests in other plants indicates that the birds are very capable of building there, so it is doubtful that structural suitability can be cited as the sole reason for nesting in the acacia. Similar nests in acacias and other vegetation were often within sight of each other, and it is not clear why all members of these species of birds do not nest in the acacias. It may be that there is genetic continuity with those portions of the species living in areas where swollen-thorn acacias are absent or rare, or there may be disadvantages in nesting in swollen-thorn acacias (e.g., these nests, being low, are more susceptible to fire than those high in other trees, although swollen-thorn acacias generally have a "fire-break" around them cut by the ants; Janzen 1967a).

A comparison of the heights of the two groups of pendant nests (table 2) strongly indicates that the ants are effective in deterring climbing animals. The bottoms of some pendant nests in acacias were not over one meter off the ground. It should be noted however that the acacias do not extend over 8 m tall and most are in the 3–6-m size class, and therefore it is impossible to have as high a mean height for nests in acacias as for nests in other plants. The differences in nest heights may be due to differential preferences of two or more species of birds, but, whatever the reasons, it is clear that some birds that build pendant nests seek out swollen-thorn acacias for nest sites and are willing to build nests much lower on these acacias than those built on other plants.

In terms of the nests visible from a moving car, there is a clear preference for swollen-thorn acacias by birds building sessile nests

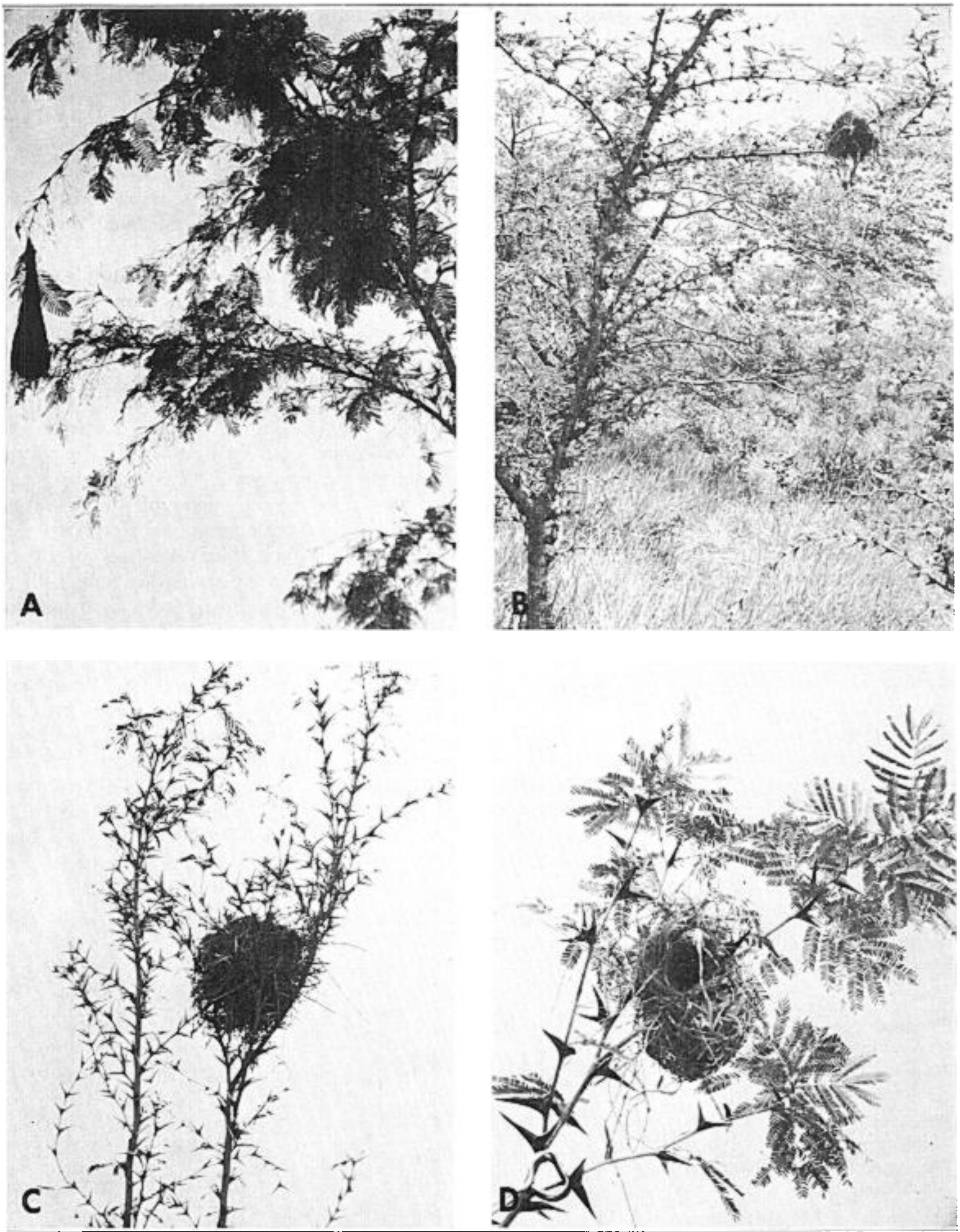

FIGURE 8. Placement of nests on acacia branches. A. An active pendant icterid nest in *Acacia hindsii* occupied by *Pseudomyrmex ferruginea* (19 June 1967, 17.9 mi. N Puerto Escondido, Oaxaca, México). Note that attachment is nearly terminal so that the nest obstructs ant traffic flow to a minor degree. Further, the branch supporting the nest is a flowering branch and such branches are generally poorly patrolled. B. An active sessile nest of a wren-like bird in *Acacia hindsii* occupied by *Pseudomyrmex belti* (7 August 1967, 9.3 mi. NE Jutiapa, Jutiapa, Guatemala). Note that nest is on a lateral branch and very exposed. C. Inactive sessile nest in *Acacia globulifera* (2 August 1967, 19.9 mi. SW San Pedro Sula, Cortés, Honduras). Plant virtually leafless owing to insect damage since acacia is unoccupied. D. Active sessile nest of a wren-like bird in a branch of *Acacia collinsii* occupied by *Pseudomyrmex ferruginea* (26 June 1967, 12 mi. NE Palmar Sur, Puntarenas Prov., Costa Rica). Note that nest obstructs ant traffic to only five thorns.

(presumably *Campylorhynchus* wrens although at least two sessile nests belonged to birds that looked like Barred Antshrikes, *Thamnophilus doliatus*). There were as many as eight sessile nests in one acacia; the mean was about two per tree. In my limited experience, wren nests not in acacias are usually well hidden in very dense tangles of vegetation. This means, of course, that many would be missed in a census such as the one conducted. On the other hand it also indicates that there is something sufficiently different about acacias as nest sites to bring the birds out to the most exposed site possible (see canopies in figs. 8B, C, D, and fig. 9). In contrast to pendant nests, sessile nests are built at all heights in the tree. That the mean height of non-acacia sessile nests is lower than that of non-acacia pendant nests is probably in part due to the difficulty of seeing a sessile nest in the dense foliage of a tall tree. However, nearly all tall trees were isolated and thus provided good visual access.

General observations. Since obligate acacia-ants are very aggressive toward foreign objects on the acacia (Janzen 1967b), it should be asked how the bird can build a nest and rear young. The age and size of the tree and ant colony, the species of ant, acacia, and bird, the time of year, and the type of nest are all variables in the answer to this question.

That a bird can rear nestlings to maturity in a nest in a heavily occupied swollen-thorn acacia is shown in table 3. When found, these nests had either eggs or very recently hatched young in them, and they were observed sporadically at least until the young birds were old enough to flutter from branch to branch when removed from the nest. It appears significant that once a nest was located with eggs or young in it, these were never removed by a predator (or other agent) during the period of observation, despite the fact that the contents were examined as often as twice a day. The above statement covers a total of 29 nest records for at least eight species of birds, and 10 of these nests were observed until young fledged (included in table 3). This is in contrast to other bird nests that I have examined in the same habitats in Central America, where, almost without exception, on a second visit to a nest that had had eggs or young, they were gone. This indicates that predation rates on the young of birds nesting in swollen-thorn acacias may differ from the rates on the young birds nesting in other species of plants, at least in the zone 1–3 m off the ground. A more rigorous study could easily be made since the nests are so easily located.

The acacias chosen for nesting throughout lowland Central America are 2–20 m tall, usually three or more years old, and lightly to moderately occupied by the ant colony (a heavily occupied colony may have 5000 worker ants per m^3 of canopy volume). Only twice in four years have I found a sessile nest in a 1-m

TABLE 3. Successful nests of birds in swollen-thorn acacias in Central America. Only those that fledged young while under observation are recorded.

Bird Species	*Acacia*	Ht. of nest (m)	Date of fledging	Nest type	Vegetation type	Site
Pitangus sulphuratus	*cornigera*	2.5	10 August 1962	sessile, covered	brushy pasture	Veracruz, México
Pitangus sulphuratus	*cornigera*	2.0	2 July 1964	sessile, covered	brushy pasture	Veracruz, México
Thamnophilus doliatus	*collinsii*	2.0	12 July 1967	sessile, covered	20 year 2nd growth	Palmar Sur, Costa Rica
Thamnophilus doliatus	*cornigera*	1.5	1 July 1962	sessile, covered	brushy pasture	Veracruz, México
Scardafella inca	*cornigera*	1.5	20 July 1962	open flat	brushy pasture	Veracruz, México
Amblycercus holosericeus	*cornigera*	3.0	1 July 1962	pendant	brushy pasture	Veracruz, México
Icterus sp.	*cornigera*	2.0	6 June 1964	pendant	10 year 2nd growth	Veracruz, México
Icterus sp.	*cornigera*	3.0	28 June 1962	pendant	brushy pasture	Veracruz, México
Campylorhynchus rufinucha	*collinsii*	1.5	16 June 1965	sessile, covered	brushy pasture	Cañas, Costa Rica
Campylorhynchus rufinucha	*cornigera*	2.5	17 June 1965	sessile, covered	brushy pasture	Cañas, Costa Rica

tall acacia, and on both occasions all the vegetation within at least 500 m was of the same height. Birds nest to the tops of the tallest acacias in a given area, but are not concentrated in them. I have never seen a nest in an acacia occupied by a very strong colony (e.g., 20,000 workers in a 3-m single-trunk acacia). Very strong colonies produce strong alarm reactions with light shaking of a major branch at all times of the year and at all usual temperatures. Worker ant densities may increase to 2 per cm^2 within one minute of disturbance in such cases. The density is so high even on an undisturbed tree that ants new to a point (e.g., a nest attachment site) on the tree may appear at that point at least once a minute on a warm day. Therefore, there is very little habituation to disturbances by the group of ants that patrol a given branch or branch cluster, and this is probably discouraging to a bird seeking a nest site. On several occasions in Guanacaste, Costa Rica, very new partly constructed bird nests have been found abandoned and swarming with excited worker ants on heavily occupied trees.

Further, there is little herbivorous insect damage to heavily occupied trees and the tree tends to grow straight upward with few lateral branches that would make good nest attachment sites. There appears to be no distinction made by the birds as a group between moderately-occupied, lightly-occupied and unoccupied acacias, although different bird species might be expected to show such distinctions. As the acacia gets older, the density of patrolling ants decreases on branches over two years old and these are usually the support branches for bird nests. Bird nests have never been observed entangling the central terminal shoot while it is growing; this site has the highest density of patrolling of any point on the acacia. Bird nests are usually out of the path of the major part of ant traffic. Pendant nests attached to the end of a branch do not obstruct ant passage at all, and sessile nests are usually placed distally along lateral branches. Those few thorns on the branch beyond the nest are often without ant brood to start with during the dry season, and if brood is present it is often neglected by the worker ants (apparently associated with the obstruction on the branch).

Swollen-thorn acacias vary considerably in life-form, both intra- and interspecifically, and this appears to influence their use by birds, but at least a few nests have been observed in the canopies of all 12 species of Central American swollen-thorn acacias. *A. collinsii* north of Honduras has very few lateral branches, and where it and the much bushier *A. hindsii* grow side by side, birds building sessile nests seem to prefer the latter. A swollen-thorn acacia from southwest Costa Rica has widely spaced strongly attenuated branches, and sessile nests built in these trees are so poorly secured that they can often be shaken from the tree. In central Nicaragua, trees of *A. collinsii* have extremely compact canopies when occupied by *P. ferruginea*, which cause multiple branching by killing shoot tips. Bird nests have not been seen in such trees.

Obligate acacia-ants vary considerably in aggressiveness and patrolling thoroughness. Acacias occupied by species with smaller and less aggressive workers (e.g., *P. nigrocincta*) appear to contain more nests than those occupied by other species in a mixed species stand. Birds have been observed building and using nests in acacias occupied by each of the 13 species of obligate acacia-ants. A highly subjective estimate is that nesting density is lowest in acacias occupied by *P. ferruginea* in that portion of its range from Nicaragua south to western Panamá, and by *P. satanica* in the northern part of the Canal Zone. However, in the case of *P. satanica*, there are no other species of obligate acacia-ants in the area for comparison. Non-aggressive ants that often nest in the thorns of unoccupied swollen-thorn acacias (*P. nigropilosa*, *Crematogaster* spp., *Camponotus planatus*, *Paracryptocerus minutus*, *P. gracilis*, etc.) appear to have no influence on the presence or absence of birds.

Detailed studies of the behavior of *P. ferruginea*, and preliminary studies of other obligate acacia-ants, indicate that all species can become habituated to certain patterns of plant disturbance. Most of the worker ants on a particular branch patrol that branch for major parts of the day and for many days consecutively. If the branch is shaken lightly, it usually creates a general disturbance among them. If the disturbances are similar qualitatively and quantitatively, the workers begin to ignore them within 5–10 trials. Thus if a bird builds a nest in a regular manner, it is not surprising that it does not create a continuous strong alarm reaction. As the nest material builds up, there are always some worker ants that continue to bite, sting, and pull at it. After a day or two, they generally cease and treat the nest as part of the branch, (perhaps because it acquires a colony odor). The ants have large eyes, and sudden motions near them can cause a disturbance reaction, usually directed at the moving object. Within

FIGURE 9. Two sessile bird nests near a vespid wasp nest in *Acacia hindsii* occupied by *Pseudomyrmex belti.* The nest on the right had eggs of a wren-like bird in it (7 August 1967, 9.3 mi. NE Jutiapa, Jutiapa, Guatemala).

a short time, however, the birds are inside their nest and movements can only be felt by the workers. In short, the reaction to the bird nest is not unlike that to dead vegetation under the tree; the ants walk over it, bite, pull, or sting it now and then until it rots or is dragged away, and it probably becomes contaminated with "trail substance" or whatever the "colony odor" is composed of.

For unexplained reasons the ants have not been observed to enter the nest entrance hole. An occasional worker ant must attack a bird or its nestlings, but the single sting should do no more than raise a welt on a nestling or an adult, and the ant would either be picked off or eaten.

The importance of the habituation of the workers to the bird's movements is illustrated by the fact that when a branch end is pulled down slightly to look in a nest, there is generally strong disturbance reaction by the workers on that branch, but the bird landing on the branch does not cause such a disturbance. Moreau (1936) has also pointed this out for wasp nests near bird nests in Africa. Presumably the same would apply to a climbing mammal. Both arboreal snakes and lizards placed quietly in an acacia are strongly bitten and stung by a large ant colony and quickly leave.

While the selection of the acacia as a nest site is consistent in some bird species over much of lowland Central America, there are many areas where these birds occur and the swollen-thorn acacias are absent. Nests of *Pitangus sulphuratus*, orioles, and the Yellow-winged Cacique (*Cassiculus melanicterus*) are found in acacias and in other species of plants at the same site. In starting the nest, some tolerance or avoidance of the ants must be necessary. This is further indicated by the fact that the nests in acacias are often adjacent to hanging wasp nests (fig. 9; Vespidae such as *Polybia*, *Brachygastra*, *Synoeca*, *Epipona*, *Protopolybia pumila*, *Parachartergus*, and *Stelopolybia*) and near *Trigona* bees nests in other plants (caciques; M. Naumann, pers. comm.). In the Guanacaste area where many of the observations reported in this paper were made, Slud (1964) reported that the nest of *Campylorhynchus rufinucha capistratus* is "often placed near the tip of a leafy branch or, in the drier portions of the range, beside a wasp nest in a defoliated, ant-infested bull's-horn acacia." Although it probably creates a similar mild disturbance each time it arrives, the bird enters the nest upon arrival and is thus out of sight of the wasps; probably few successful attacks by the wasps result (cf. Moreau 1936).

Patrolling by the ant colony is reduced during the last month of the dry season, when most nests are built in the acacias. Not only is colony size reduced (leaving some trees with very few worker ants on them) but the remaining ants have a tendency to stay in the thorns, except to patrol the parts of the tree that still have leaves. While swollen-thorn acacias do not drop all their leaves, in many areas (especially rivers and swamps) they are among the more sparsely-leaved species and thus the nest is quite exposed to the sun. On the other hand, in completely deciduous forest, the swollen-thorn acacias are among the few plants to retain some leaves (e.g., *A. hindsii* to the south and east of Mazatlán, Sinaloa, México) and thus the nest is comparatively shaded. That nesting occurs during the driest part of the year may appear anomalous, but it should be pointed out that this synchronizes the time of fledging with the large burst of insect activity shortly after the rains begin.

Nesting in other myrmecophytes. I have no records of bird nests in the other common myrmecophytic trees of Central America (*Cecropia* spp., *Triplaris americana*, *Cordia alliodora*), but Skutch (1945) reports that the Social Flycatcher (*Myiozetes similis*) "not infrequently" builds nests in *Cecropia* branch crotches (Río Térraba Valley, Costa Rica).

These trees are not thorny and have relatively open canopies and smooth branches. The *Pseudomyrmex* species in *T. americana* are not nearly as aggressive as those in swollen-thorn acacias. The *Azteca* ant species in both *Cecropia* and *Cordia alliodora* tend to swarm heavily for hours over an intruding object. Bird nests artificially placed on *Cecropia* branches are covered, inside and out, with ants within 10–20 min. Finally, *Azteca* ants are essentially ignored by arboreal snakes placed on the plant (*Azteca* has no sting, but may place anal and mandibular gland fluids in a shallow wound cut with its mandibles). The swollen-thorn acacias of Africa (independently evolved system) are occupied by *Crematogaster* spp., and Sjostedt (1908) reports the Rufous Sparrow (*Passer iagoensis*) nesting apparently unmolested in *Acacia seyal*.

While the several species of trees occupied by the arboreal ant *Oecophylla longinoda* in Africa are not regarded as myrmecophytes, Maclaren (1950) has demonstrated an association of birds with these trees. Their attraction to nesting birds appears to be based on the same protective function as that ascribed to the obligate acacia-ants above.

OTHER USES OF MYRMECOPHYTES BY BIRDS

Shrikes (*Lanius ludovicianus*) do not occur south of the Isthmus of Tehuantepec in México (Blake 1953) but an unidentified bird with similar behavior apparently does. On three occasions in central Nicaragua (8 mi. E. San Benito, Depto. de Managua, 28 June 1967) large melolonthine scarab beetles were found impaled 3 m off the ground on thorns of *A. collinsii* (fig. 10). In July 1963 two large acridid grasshoppers were found impaled in the same manner in the top of a 5-m tall *A. collinsii* near Santa Ana, San José Prov., Costa Rica. Sjostedt (1908) encountered many insects impaled on the thorns of *A. seyal* by "shrikes" in the area of Mt. Kilimanjaro, East Africa. This species of swollen-thorn acacia is occupied by moderately aggressive ants of the genus *Crematogaster*. Sjostedt feels that lack of occupation by ants of the acacias involved was responsible for their use by birds, but if the bird works rapidly, or is not sensitive to the chemical defense of this ant (or the sting of *Pseudomyrmex*), it should have little difficulty using the tree in this manner.

In addition to crushing green thorns for fluid in the dry season, birds may gain some food from those myrmecophytes that bear food bodies normally harvested by the ants

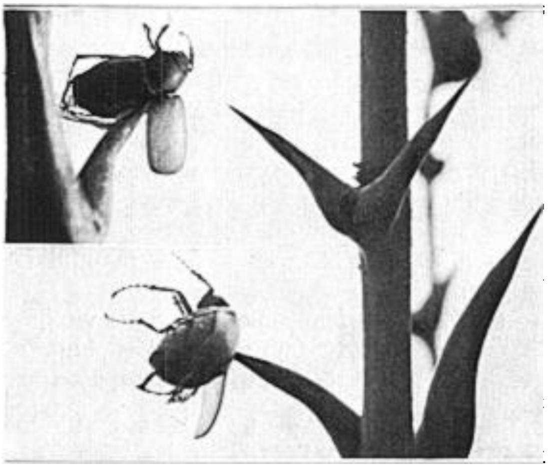

FIGURE 10. A melolonthine scarab (*Phyllophaga* sp.) presumably impaled by an undetermined bird on a thorn of *Acacia collinsii* occupied by *Pseudomyrmex belti* (28 July 1967, 8 mi. E San Benito, Depto. de Managua, Nicaragua). Inset: dorsal view of same insect.

(*Cecropia* and *Acacia* in Central America). Skutch (1945) and others have observed small passerine birds eating the small (1–1.5 mm long) white food bodies (Mullerian bodies) at the trichilia (pad at petiole base) of *Cecropia* in Costa Rica. These are normally harvested very rapidly by the ants but in cold or rainy weather, or on unoccupied trees, there may be a delay in harvest and the food body density may build up.

CONCLUSION

There is no evidence of a specific mutualism developing between birds and the interaction between ants and plants in Central America. The dispersal of seeds is of obvious benefit to the plant (and indirectly to ant species) since this is a plant of secondary vegetation and must therefore be repeatedly dispersed to newly disturbed sites. However, no evidence has been gathered to show evolution of a specific adaptation to swollen-thorn acacias or *Cecropia* as fruit sources.

There is no indication that nesting by birds in the acacia is in any manner beneficial to the ants, although it probably is of value to the bird, clearly a mildly persecuted myrmecophile. Adaptations of the bird to the acacia and its ants are not clear but probably involve discrimination between the acacia and other plants, tolerance of an occasional sting, and persistence in the face of being occasionally driven out of a heavily occupied tree.

Predation on the ants is clearly detrimental to the ant × acacia system, and it may be that this has been a selective force in the evolution of strong thorns. The adaptation on the part of the bird appears primarily associated with opening thorns (splitting, breaking, puncturing), persistence in the face of the inevitable attack of the worker ants, and knowing that food is in the thorns. All three of these processes, especially the last two, probably involve learning as well as a genetic background.

In all three circumstances cited above there is an opportunity for coevolution, but the predation and nesting aspects are unlikely to lead to mutualism.

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