5. GUILDS

- One reason ecologists study population interactions is to understand how ecological communities are organized. In other words, what are the interspecific interactions (e.g., competition, mutualism) in a community that help explain the coexistence of different species? **Research Connection 1** highlighted a study of two coexisting populations that were competing for the same resource. **Research Connections 2** highlighted a study of two coexisting populations that had a mutualistic relationship. Some ecologists have found that one way some communities are organized is by interspecific competition among a group of more than two populations in a community that form a **guild**.

- A guild is a group of populations that compete for the same class of resources in a similar way. One famous example of a guild is the "oak foliage-gleaning guild" which includes five different bird populations (Root 1967): warbling vireo (*Vireo gilvus*), Hutton's vireo (*Vireo huttoni*), orange-crowned warbler (*Vireo celata*), plain titmouse (*Parus inornatus*), and blue-gray gnatcatcher (*Polioptila caerulea*). To be considered a member of this guild, a large portion of each bird species' diet must consist of insects (i.e., the same class of resources) gleaned from oak leaves (i.e., exploited in a similar way). Note that despite the similarities among guild members, there still must be sufficient difference in resource use such that there is no **competitive exclusion** (see **Research Connection 1**).

- Populations within a guild may be from closely related taxonomic groups, such as the five bird species in the above example. Alternatively, populations within a guild may be from diverse taxonomic groups, such as the granivorous guild discussed in **Research Connection 1**. This guild consisted of three species of kangaroo rats and five species of smaller granivores from different taxonomic groups: banner-tailed kangaroo rats (*Dipodomys spectabilis*), Merriam's kangaroo rats (*D. merriami*), Ord's kangaroo rats (*D. ordi*), desert pocket mouse (*Chaetodipus penicillatus*), silky pocket mouse (*Perognathus flavus*), cactus mouse (*Peromyscus eremicus*), deer mouse (*Peromyscus maniculatus*), and western harvest mouse (*Reithrodontomys megalotis*).

- Membership in a guild is based on competition for the same resource, but a guild also includes other interactions. Guild members may be a group of predators (e.g., birds) competing for the same prey (e.g., arthropods). Alternatively, a guild may include a group of mutualists. For example, the guild may be a group of bee species (i.e., pollinators) competing for access to the same flower species or it may be a group of flower species competing for the same bee species. **Research Connection 4** presents the well-known example of mutualism between ants and acacia trees; the guild comprises different ant species competing for nesting sites in the trees.

© 2003 University of Calgary Kananaskis Field Stations
Alberta Innovation & Science ISRIP Science Awareness &Promotion Program

RESEARCH CONNECTION 4

Interspecific competition within a guild of African Acacia-ants.

Source: Stanton, M.L., T.M. Palmer, and T.P. Young. 2002. Competition-colonization trade-offs in a guild of African acacia-ants. *Ecological Monographs* **72**: 347-363.

Background:

- In the Laikipia District of central Kenya is an extensive bushland savannah, which is a grassland with shrubs and trees. The tree canopy is dominated by a single species of swollen-thorn acacia tree, *Acacia drepanolobium* (Figure 4.1). The savannah is frequently burned by fire and trampled by elephants and is host to numerous herbivores and browsers.

Figure 4.1 *Acacia drepanolobium*, a species of swollen-thorn acacia found in the bushland savannah of central Kenya *(Photo by Todd Palmer)*.

- This savannah is home to a guild of four ant species, *Tetraponera penzigi, Crematogaster nigriceps, C. mimosae*, and *C. sjostedti* (Figure 4.2). Each species forms a mutualistic relationship with the *Acacia* trees. The ants help defend the trees against small- to medium-sized herbivores; in return the trees provide the ants with nest sites and nectar which the ants eat.

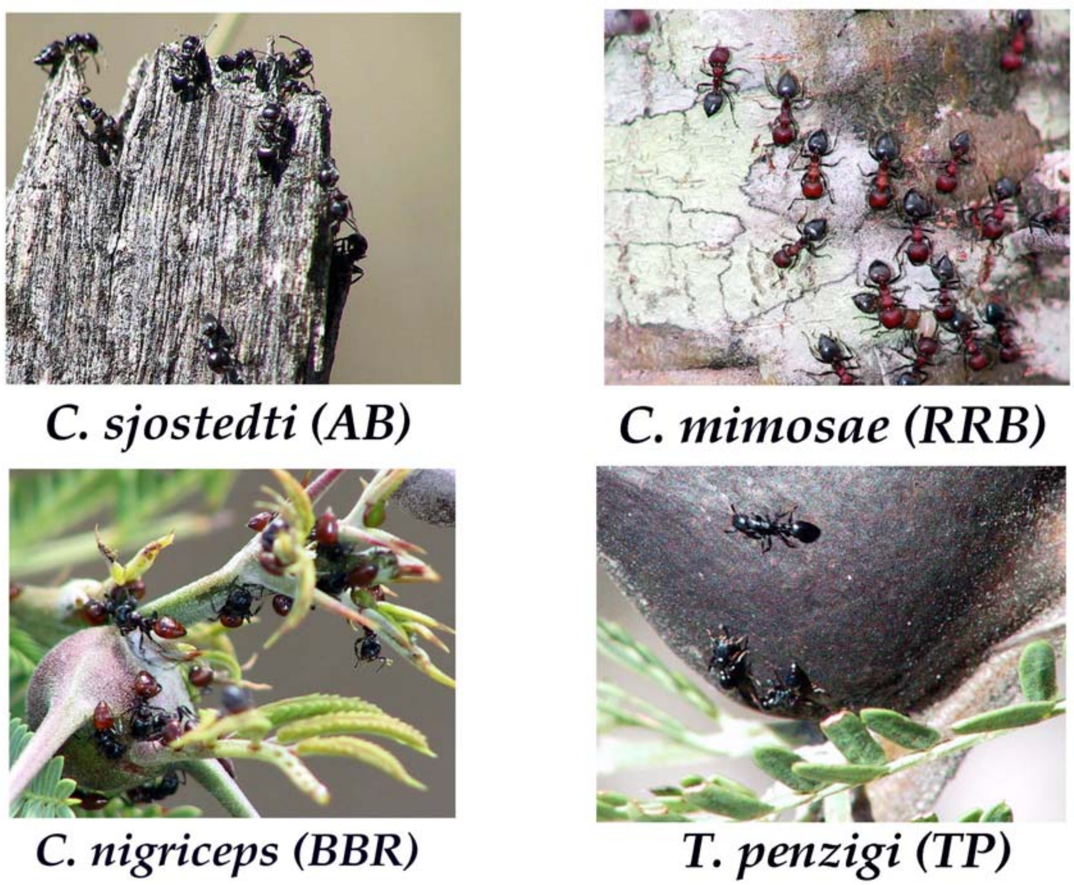

Figure 4.2 The guild of four ant species found in the savannah of central Kenya. Each species forms a mutualistic relationship with *Acacia* trees *(Photos by Todd Palmer)*.

- The ants nest inside swollen cavities that are found at the base of some of the *Acacia* trees' thorns (Figure 4.3). Ants gain access to and nest in these inflated thorns by chewing a hole through the cavity wall. *Acacia* trees also provide ants with nectar, which is produced in 1-3 extrafloral nectaries at the base of their leaves (Figure 4.4). Extrafloral nectaries are specialized plant cells that secrete nectar (most plants have nectaries only at the base of the inside of their flowers).

© 2003 University of Calgary Kananaskis Field Stations

Figure 4.3 A view looking up from the base of an *Acacia drepanolobium* tree. Note the swollen cavities at the base of some of the tree's thorns. These swollen cavities are inhabited by ants *(Photo by Todd Palmer)*.

- Previous studies showed that this guild of ant species compete intensely for possession of *Acacia* host trees by **displacing one another from inhabited trees**. *C. sjostedti* colonies can competitively displace *C. mimosae* colonies, *C. sjostedti* and *C. mimosae* can displace *C. nigriceps*, and all three *Crematogaster* species can displace *T. penzigi*. *T. penzigi* rarely displaces the other species. Therefore, the competitive hierarchy of these ant species in terms of their ability to displace other species from **inhabited trees** is:

***C. sjostedti* > *C. mimosae* > *C. nigriceps* > *T. penzigi*.**

© 2003 University of Calgary Kananaskis Field Stations
Alberta Innovation & Science ISRIP Science Awareness &Promotion Program

Figure 4.4 Ants feeding from the extrafloral nectaries at the base of some *Acacia* tree leaves. These nectaries are specialized plant cells that secrete nectar, which ants eat *(Photo taken by Todd Palmer; photo appears on front cover of Ecology **84** (11) Permission granted © Ecological Society of America)*

Description of Research:

- In the Laikipia District of central Kenya, *T. penzigi*, *C. nigriceps*, *C. mimosae*, and *C. sjostedti* are intolerant of one another and compete intensely for possession of *Acacia* trees. As shown by previous studies, there is a competitive displacement of ant species from **inhabited** trees such that there is a competitive hierarchy: *C. sjostedti* > *C. mimosae* > *C. nigriceps* > *T. penzigi*. If the only way that these ant species could expand their colonies was by competitive displacement from inhabited trees, then it is predicted that **competitive exclusion** may result, with *C. sjostedti* becoming the dominant ant species in this region.

- However, these ant species are able to coexist at a very fine spatial scale, such that all four species are likely to be found within any given 0.1 - 0.2 hectare area. Therefore, Stanton and her fellow researchers investigated whether the coexistence of these four ant species could be explained by

© 2003 University of Calgary Kananaskis Field Stations
Alberta Innovation & Science ISRIP Science Awareness &Promotion Program

differences among species in their ability to colonize **uninhabited** *Acacia* trees.

- This study examined the colonization of three categories of **uninhabited** trees.

  1) **Empty, moderately-damaged mature trees**: These become available when mature, drought-stressed trees are abandoned by resident ants or when moderate-intensity fires kill resident ants. The damage to trees by drought or moderate-intensity fires is relatively minor such that undamaged parts of the tree can be re-colonized.
  2) **New shoots from large, severely-damaged trees**: These become available when previously healthy, large trees are severely damaged by fire or elephants, and resident ants are killed. Vigorous new shoots quickly grow from surviving stem tissues and produce swollen thorns and leaves with nectaries, becoming attractive targets for colonization.
  3) **Small saplings and their new shoots:** Small saplings become available when seedlings grow into saplings. New shoots grow from the base of these small saplings when they are eaten by herbivores. The saplings and new shoots occur at high densities but produce fewer swollen thorns and leaves than large trees. Therefore, they are less desirable colonization sites.

- This study examined differences among ant species in their ability to colonize **uninhabited** trees in one of two ways:

  1) **worker ants from a mature colony** spreading from adjacent trees to expand the size of the colony, or
  2) an egg-laying "**foundress queen**" ant dispersing independently to initiate a new ant colony.

<u>Methods:</u>

- The colonization of uninhabited *Acacia* trees was monitored to determine which species occupied each tree and if colonization was by **mature colonies** that spread from nearby trees or by **foundress queen** dispersal.

- Colonization was monitored in three categories of unoccupied *Acacia* trees:
  1) empty, moderately-damaged mature trees,
  2) new shoots from large, severely-damaged trees,
  3) small saplings and their new shoots.

- Stanton and her fellow researchers used two types of experimental manipulation to create these three categories of unoccupied *Acacia* trees. Then they monitored colonization by colony expansion and foundress

© 2003 University of Calgary Kananaskis Field Stations

queens. They documented patterns of colonization on naturally occurring small saplings within permanent plots.

- They also examined the competitive outcome between foundress queens attempting to occupy the same nesting sites by locating thorns containing the queens of two species.

Results:

- The results in Figures 4.5 – 4.8 are a comparison of expected and observed frequencies. The expected frequency is based on the frequency of each ant species or queen in the study site. For example, if an ant species occupied 50% of trees in the study area, then it would be expected to colonize about 50% of the uninhabited trees in that area. If it colonizes more empty trees than expected (observed frequency > expected frequency), then it is a better colonizer compared to species colonizing fewer empty trees than expected.

1) Colonization by **Expansion of Mature Colonies**

- **Empty, moderately-damaged mature trees** were occupied more often than expected by the expansion of mature colonies of all *Crematogaster* species, especially *C. nigriceps* (*Cnig*), and to a lesser extent *C. mimosae* (*Cmim*) (Figure 4.5A). *C. sjostedti* (*Csjo*) occupied empty, moderately-damaged trees only slightly more often than expected. *T. penzigi* (*Tpen*) was the least likely species to occupy these empty mature trees by colony expansion.

- The **new shoots from large, severely-damaged trees** were occupied more often than expected by the expansion of mature colonies of *C. nigriceps* (Figure 4.5B). *T. penzigi* did not occupy these new shoots by colony expansion.

© 2003 University of Calgary Kananaskis Field Stations

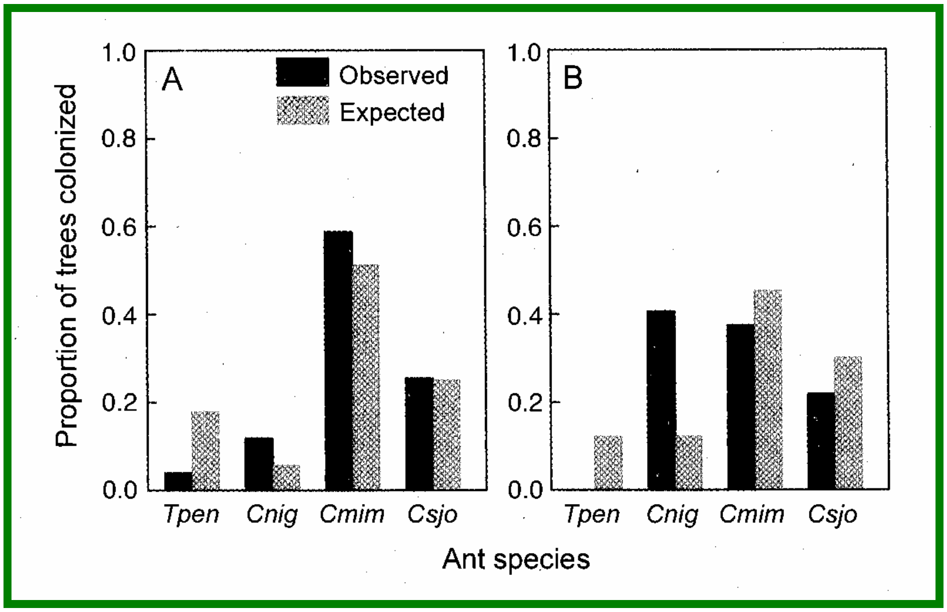

Figure 4.5 The proportion of A) empty, moderately-damaged mature trees, and B) new shoots from large, severely-damaged trees colonized by each of the four ant species by expansion of nearby mature ant colonies *(Adapted with permission from: Figure 1, Pg. 354. Stanton et al. (2002). © Ecological Society of America)*

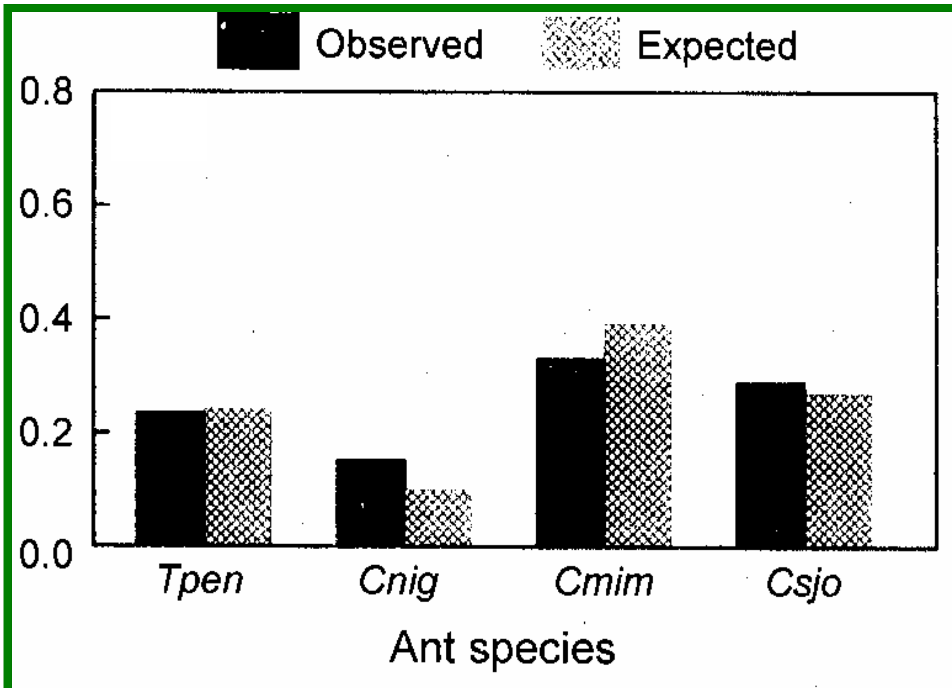

Figure 4.6 The proportion of small saplings and their new shoots occupied by workers from nearby mature ant colonies. *(Adapted with permission from: Figure 2A, Pg. 355. Stanton et al. (2002). © Ecological Society of America)*

- **Small saplings and their new shoots** were occupied by mature colonies of all species spreading from adjacent trees; there were no significant differences between the expected and observed frequencies (Figure 4.6).

2) Colonization by **Foundress Queens**

- On **empty, moderately-damaged mature trees**, and **new shoots from large, severely-damaged trees**, foundress queens of *T. penzigi*, and to a lesser extent *C. nigriceps*, were far more common than would be expected from their local frequencies (Figure 4.7A and B). In contrast, foundress queens of *C. mimosae* were rarely found, and *C. sjostedti* queens were virtually absent.

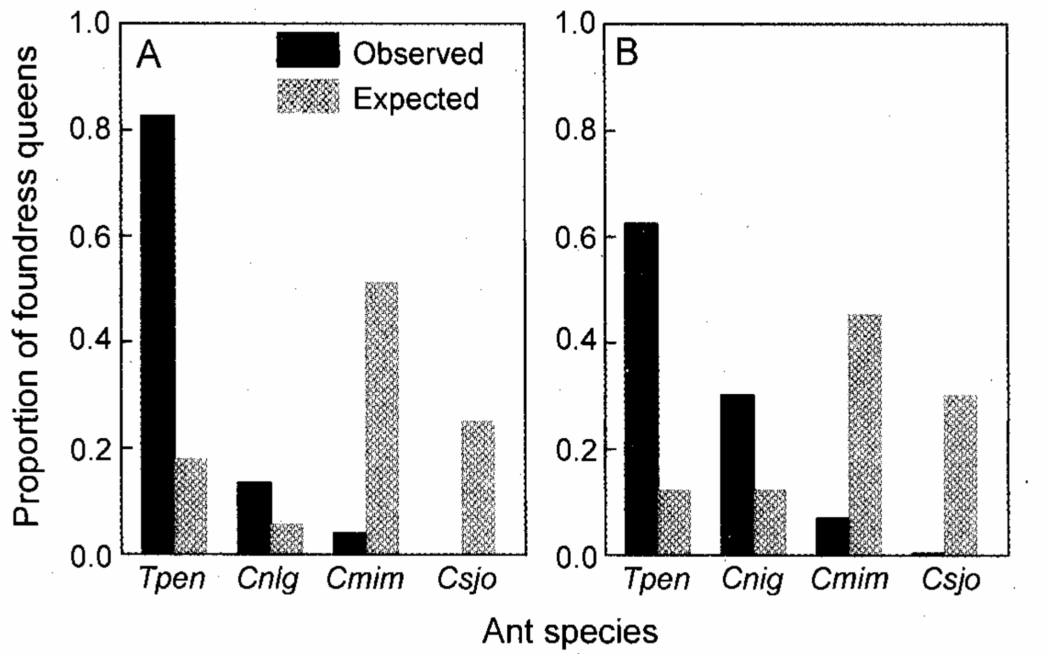

Figure 4.7 The proportion of queens of each ant species found on A) empty, moderately-damaged mature trees, and B) new shoots from large, severely-damaged trees. *(Adapted with permission from: Figure 3, Pg. 356. Stanton et al. (2002). © Ecological Society of America)*

- On **small saplings and their new shoots**, queens of *C. mimosae* were more frequent than expected from their local frequencies, whereas *C. sjostedti* queens were extremely rare (Figure 4.8).

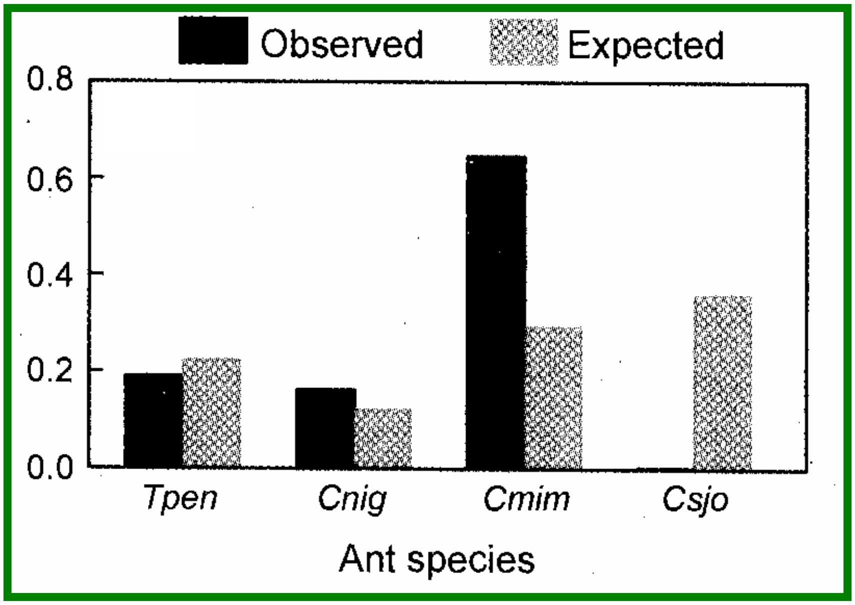

Figure 4.8 The proportion of queens of each ant species found on small saplings. *(Adapted with permission from: Figure 4A, Pg. 357. Stanton et al. (2002). © Ecological Society of America)*

3) Mortality of Queens in **Interspecific Queen-to-Queen Combat**

- To examine the competitive outcome between queens attempting to occupy nesting sites, swollen thorn cavities were surveyed for thorns containing the queens of two species. In thorns with two queens, *T. penzigi* queens had the highest survival rate, *C. nigriceps* had the second highest survival rate, and *C. mimosae* had the lowest survival rate (Figure 4.9, solid bars). No *C. sjostedti* queens were found in thorns occupied by two queens. Therefore, the competitive hierarchy of these ant species in terms of the ability of foundress queens to displace other species from **uninhabited trees** is:

***T. penzigi* > *C. nigriceps* > *C. mimosae* > *C. sjostedti*.**

- For comparison, Figure 4.9 also includes the results of a previous study that examined the competitive outcome of mature colonies displacing one another from **inhabited trees** (see bottom of page 24 for competitive hierarchy of inhabited trees). Notice that the ranking of ant species by the combative ability of their foundress queens is the reverse of the ranking seen among mature colonies that displaced one another from inhabited trees.

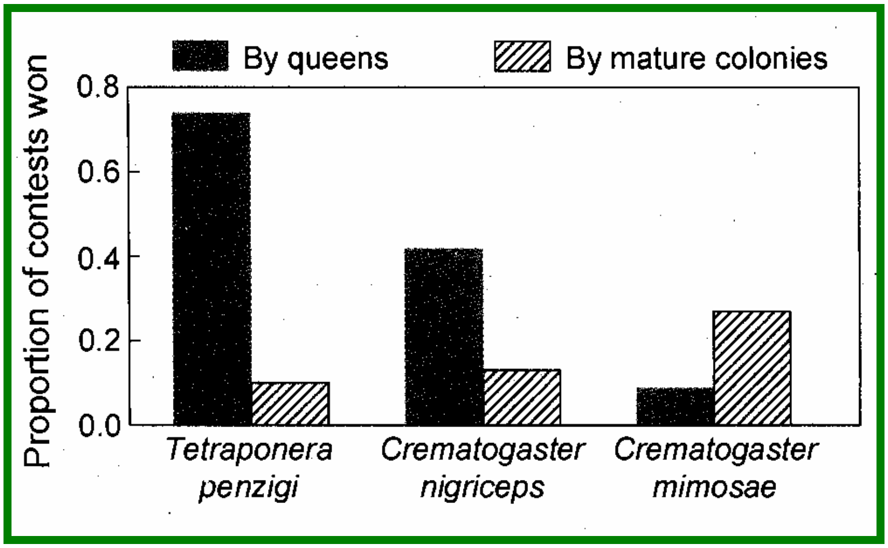

Figure 4.9 Survival of ant foundress queens after interspecific combat over nest sites. *(Adapted with permission from: Figure 6, Pg. 358. Stanton et al. (2002). © Ecological Society of America)*

Conclusions:

- Coexistence among members of this *Acacia*-ant guild appears possible because there are competition-colonization trade-offs between two stages of colony development: competitive colony expansion onto nearby **inhabited** or **uninhabited** trees, and **competition among foundress queens** for nest-initiation sites.

- Some species expand their colonies primarily by competitively displacing resident species from inhabited trees, other species expand their colonies primarily by workers spreading to adjacent uninhabited trees, and still other species form new colonies primarily by having competitively superior foundress queens that win battles over nest sites in empty trees.

- *C. sjostedti* is competitively superior at displacing colonies from inhabited trees; however it is a relatively poor colonizer when it comes to occupying empty, moderately-damaged mature trees, or new shoots from large, severely-damaged trees. Also, foundress queens of *C. sjostedti* rarely start independent colonies. Therefore, *C. sjostedti* expands its colonies primarily by driving off resident ants from nearby inhabited trees.

- *C. mimosae*, the second best competitor at displacing colonies from inhabited trees, is also relatively successful in colonizing empty, moderately-damaged mature trees. *C. mimosae* foundress queens are rarely found starting independent colonies on new shoots from large, severely-damaged trees; however they were found more frequently than expected on small saplings and their new shoots, the least desirable sites. Therefore, *C. mimosae* expands its colonies primarily by displacing resident colonies from inhabited trees or colonizing empty, moderately-damaged mature trees and its foundress queens initiate new colonies on small saplings and their new shoots.

- *C. nigriceps* is competitively inferior at displacing colonies from inhabited trees; however it is better than other species at colonizing empty, moderately-damaged mature trees and its foundress queens outcompete all species except *T. penzigi* when competing for nest sites in mature trees. Therefore, *C. nigriceps* colonizes primarily empty, moderately-damaged mature trees by colony expansion onto nearby trees, and by its competitively superior foundress queens initiating new colonies.

- *T. penzigi* colonies rarely displace resident ant colonies from inhabited trees and they rarely occupy empty, moderately-damaged mature trees by colony expansion; however its foundress queens are superior competitors in direct encounters for occupied nest sites. Therefore, *T. penzigi* forms new colonies primarily when its foundress queens colonize uninhabited trees.

© 2003 University of Calgary Kananaskis Field Stations