Stone Dropping by *Conomyrma bicolor* (Hymenoptera: Formicidae): A New Technique of Interference Competition

Michael H.J. Möglich* and Gary D. Alpert

Museum of Comparative Zoology Laboratories, Harvard University, Cambridge, Massachusetts 02138, USA

Summary. 1. The dolichoderine ant *Conomyrma bicolor* interferes with the activity of other desert ants when their nest entrances are in close proximity. *C. bicolor* workers surround these nests, pick up small stones and other objects with their mandibles, and drop them down the nest entrances.

2. Interactions of *C. bicolor* with three species of *Myrmecocystus* (*M. mexicanus, M. mimicus,* and *M. depilis*) were investigated. 'Stone dropping' and associated behaviors prevent the *Myrmecocystus* colonies from foraging. Periodic checks throughout the summer revealed a consistently adverse effect on these *Myrmecocystus* species.

3. Considerable overlap in food resources, activity times, as well as space among *C. bicolor* and the *Myrmecocystus* species suggest that 'stone dropping' is a technique of interference competition.

4. We were not able to completely analyze the mechanism which keeps the victimized colonies from foraging. However, we report circumstantial evidence supporting the hypothesis that the stones function as a mechanical signal.

Introduction

Competitive interactions play an important role in the structure of ant communities. Two categories have been recognized: exploitation and interference. In the first case the access to the limiting resource is free for both competitors but the outcome of competition is determined by their relative abilities to use the resource efficiently (Miller, 1969). The other possibility is to interfere with a competitor in order to prevent his access to the resource in question. For example, the myrmicine ants *Solenopsis fugax* and *Monomo-*

rium pharaonis use similar techniques in dominating food resources (Hölldobler, 1973). After discovering a food source they discharge a secretion from the poison gland which repels other ant species from approaching the food.

In studying the dolichoderine *Conomyrma bicolor* we discovered a completely different type of interference behavior which is employed not at the food source itself but at the nest entrance of competitors. Workers of *C. bicolor* surround the nest of *Myrmecocystus* during their foraging period and drop small stones or other objects down the entrances. This unique interference behavior among ants prevents the affected colonies from foraging.

We investigated the behavioral ecology of this interference behavior, with emphasis on the experimental analysis of the behavioral mechanisms employed by *C. bicolor* to successfully interfere and thus compete with three species of *Myrmecocystus* (*M. mexicanus, M. mimicus,* and *M. depilis*).

Materials and Methods

Study Area

Fieldwork was conducted in an area two miles northeast of Portal, Arizona, in Cochise County. Two study sites 100 m apart were located on an aluvial fan (elevation 1410 m) formed by drainage from the eastern foothills of the Chiricahua Mountains. Each site consisted of 1 ha of open rangeland with a surface mixture of sand and soil to a depth of 0.5 m underlaid by caliche.

Dominant vegetation in the area are tarbush (*Flourensia cernua*), saltbush (*Atriplex canescens*), and Mormon tea (*Ephedra trifurca*). Most of the ground between these shrubs is clear of vegetation and this is where nests of *Conomyrma bicolor* and four species of *Myrmecocystus* were found. Other ant genera common in the study area are *Novomessor, Pogonomyrmex, Pheidole, Formica,* and *Forelius*.

In southeastern Arizona there are two rainfall periods, one during the winter months and another during the summer. Mean annual precipitation for the area is 276 mm, with about 80% occurring during July and August.

* Present address: Am Löwentor 15, D-6100 Darmstadt, Federal Republic of Germany

General Biology

Conomyrma bicolor prefers to nest in very arid areas from west Texas to southern California (Creighton, 1950). There has been no report yet on the ecology or ethology of this rather common species even though it has been recorded as a house pest in southern California (Mallis, 1941).

The ants most commonly affected by the interference competition of *C. bicolor* in southeastern Arizona are species of honey ants in the genus *Myrmecocystus*. This genus is notable for its 'replete' caste of workers that store liquid food in greatly distended gasters. Four sympatric species of *Myrmecocystus* (*M. mexicanus, M. mimicus, M. navajo,* and *M. depilis*) inhabit our desert study area (Snelling, 1976).

Fieldwork

Fieldwork was carried out in July and August 1976 and 1978 and from June to September 1977. *Myrmecocystus* nests located on both study sites were flagged, numbered, and mapped. A survey of the study area was continuously made to determine the extent to which different ant species were victimized by *C. bicolor* interference behavior.

Evaluation of behavioral scenes was augmented by the use of a 16-mm Beaulieu movie camera and a single-frame analyzer. Additional methodological details will be given with the description of the individual experiments.

Results

Description of the Interference Behavior

We observed at both study sites that *Conomyrma bicolor* dropped stones down the nest entrances of *Myrmecocystus mimicus, M. depilis, M. navajo, M. mexicanus, Novomessor cockerelli,* and *Pogonomyrmex desertorum.* The 'stone dropping' seemed to be the same with all species. We concentrated in our study on the nocturnal honey ant, *M. mexicanus,* because of its relative abundance in the area and the frequency of interactions with *C. bicolor. Conomyrma insana* (species complex) also occurred in the same area but was never seen to interfere with other ant species.

M. mexicanus colonies have a single nest entrance surrounded by a crater of small pebbles. Before the start of their normal foraging period, a few *M. mexicanus* workers come up to the top of the entrance and assume a guarding position. *C. bicolor* workers in the area encounter these guards and quickly surround the nest entrance. Soon thereafter the first *C. bicolor* workers can be observed picking up small particles in their mandibles, carrying them over the crater rim, and dropping them down the inside slope of the entrance. The initiation of interference behavior is correlated with the occurrence of *M. mexicanus* workers in the crater (Fig. 1).

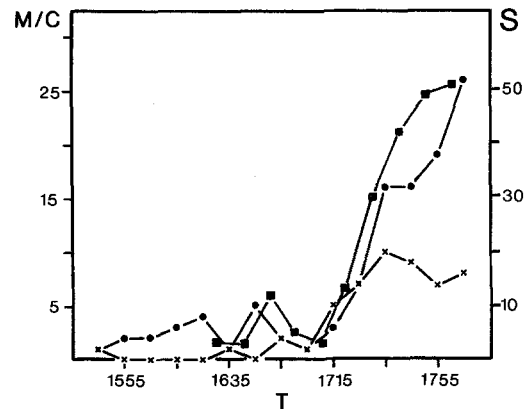Since the majority of objects released are small

Fig. 1. Initiation of interference behavior by *C. bicolor*. x, number of *M. mexicanus* (*M*) workers in the nest entrance; ●, number of *C. bicolor* (*C*) workers present in a circle of r=10 cm around the nest entrance; ■, number of stones (*S*) dropped per 5 min; *T*, time of day

stones, the term 'stone dropping' will be used throughout this study to indicate the behavior of carrying an object to the nest entrance of a different species and releasing it there. Interference behavior refers to both stone dropping and other behavioral interactions by the *C. bicolor* as they surround a given nest entrance. Figure 2 depicts a typical interference scene including stone dropping by *C. bicolor* against *M. mexicanus.*

The stones are picked up in the immediate vicinity of the crater, on the average only 7 cm from the nest opening (range: 1–23 cm, $n=19$). An individual *C. bicolor* worker typically dropped 1–2 stones per minute (mean interval 45 s, range: 8–15 s, $n=19$). The initiation of a typical stone-dropping episode is shown in Fig. 1. We observed frequencies of 200 stones or more during 5-min intervals. The distribution of stone-dropping frequencies at one nest of *M. mexicanus* at different hours of day and night is demonstrated in Fig. 3. Stone dropping occurred throughout the night. The range of frequencies when the behavior is in full progress is 9–81 per 5 min, with a mean of 42 ± 22 ($n=24$).

Our observations revealed that although sometimes 10–30 workers surround the entrance of a *M. mexicanus* nest, less than 5 are sufficient for a constant stone-dropping rate which produces an impact on the colony to be described later in this paper.

How do workers of *M. mexicanus* react to the approaching *C. bicolor* worker and to the stone-dropping behavior? Only in extremely few cases were we able to observe physical contact between the two ant species. Sometimes a fast retreat of *M. mexicanus* workers could be observed when a *C. bicolor* approached or dropped a stone. We could not detect
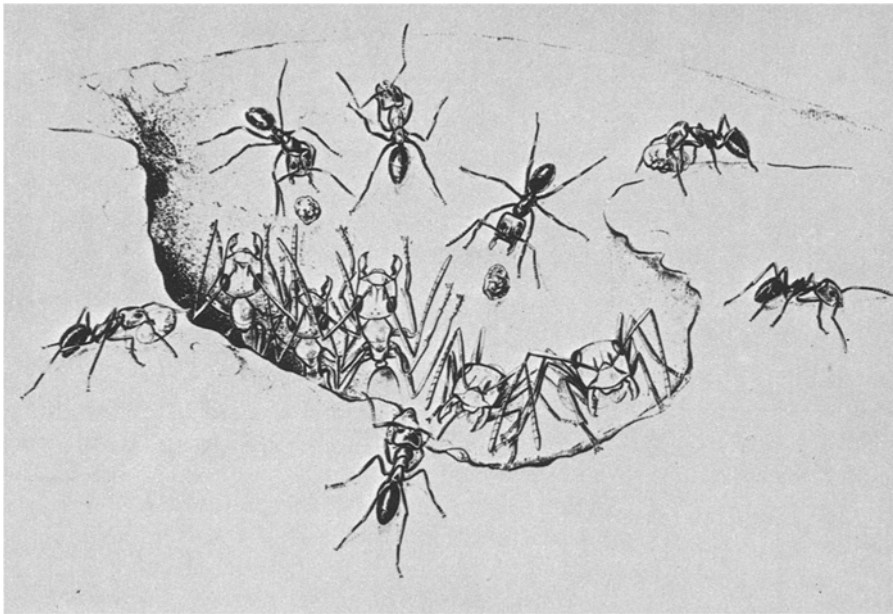
Fig. 2. Typical stone-dropping episode seen at the lower portion of a *M. mexicanus* nest entrance crater. For further explanation see text. (Drawing by Turid Hölldobler)
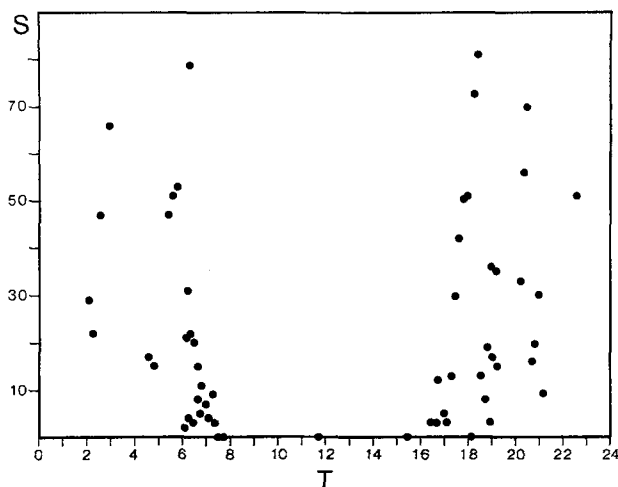

Fig. 3. Frequencies of stone dropping at different times of the day recorded at *M. mexicanus* colony 505 throughout the summer. *S*, number of stones dropped per 5 min; *T*, time of day

a significant behavioral difference toward ants carrying stones in comparison to those without stones. *M. mexicanus* guards frequently opened their mandibles and turned their bodies in the direction of the intruder. Sometimes a guard lunged forward very quickly. Although a dropped stone may hit a guard directly, many observations as well as slow-motion cinematography failed to reveal a direct mechanical effect in most of the cases.

Acute Effects of Interference Behavior

Twenty-four percent of all *Myrmecocystus* nests in our study sites were observed to be affected by *C.*

bicolor stone-dropping behavior. This percentage was approximately the same for *M. mexicanus* and *M. depilis*. *C. bicolor* nest entrances were very common and were predominately located in the open areas between desert shrubs in loose, sandy soil. But we also found areas outside our study where the number of *C. bicolar* nests per area was considerably lower and, accordingly, the *Myrmecocystus* nests were less frequented by *C. bicolor*. The impact of this relatively common interference behavior on the activity of *Myrmecocystus* species will now be described.

The most dramatic effect of interference behavior by *C. bicolor* is the almost complete cessation of foraging by *M. mexicanus* colonies. During the nightly foraging period of an unaffected *M. mexicanus* colony, many single workers can be seen in the area around the nest entrance. In comparison, at a colony which is victimized by *C. bicolor*, none or only a few *M. mexicanus* workers can be detected outside the nest. To quantify this observation we counted returning foragers per 10 min during several nights in July (Fig. 4). The mean number of foragers returning to their nest per 10 min was only 13 for victimized colonies. Control nests in the same area which did not have *C. bicolor* present were checked on the same nights at the same time. Although there was considerable variation in foraging activity of unvictimized colonies, these nests had a mean of 109 foragers returning per 10 min. The difference between both nests was highly significant ($P < 0.0001$; *t*-test). Foragers of victimized colonies experienced difficulty in penetrating the circle of *C. bicolor* workers around their nest entrance and were frequently repulsed.
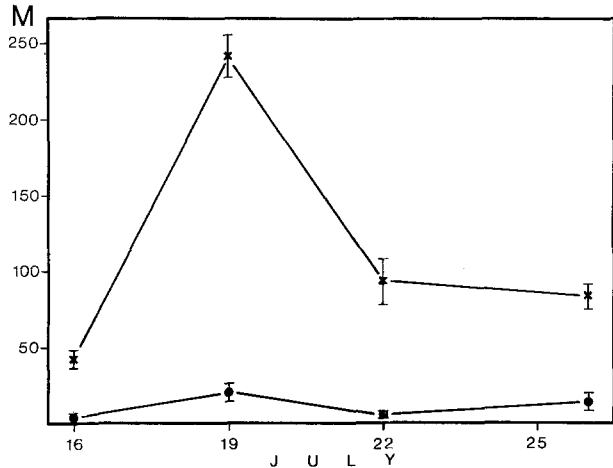
Fig. 4. Effect of interference behavior on the foraging activity of *M. mexicanus* colonies during different nights in July 1977. x, unaffected colonies; ●, affected colonies; *M*, number of *M. mexicanus* workers returning per 10 min; *bars* indicate the standard error of the mean

Fig. 5. Seasonal activity of stone-dropping behavior during the months of June, July, and August 1977 at two different colonies of *M. mexicanus* (x, —), and one colony each of *M. mimicus* (●) and *M. depilis* (+). 0, days on which no interference behavior was observed; days without symbols had not been checked

This interference behavior and corresponding significant decrease in number of foragers occurred during the entire active period for *M. mexicanus*. Once a colony of *M. mexicanus* was affected by stone-dropping behavior in the early part of their foraging period, the interference continued throughout the night until sunrise when *M. mexicanus* workers retreated into the nest. *C. bicolor* appeared to be diurnal as well as nocturnal, only ceasing activity during the hotter hours of midday. Thus it interfered with nocturnal (*M. mexicanus*, 1625–0630 hours) and diurnal (*M. depilis* and *M. mimicus*, 0600–1000 hours and 1600–1835 hours) species during their foraging periods.

The decrease in number of foragers was not as marked for *M. depilis* and *M. mimicus* because workers foraged when highly excited in spite of the presence of *C. bicolor* and also during the hotter hours of the day when *C. bicolor* was relatively inactive. Interference behavior on the part of *C. bicolor* did not appear to adversely affect the foraging activities of *Pogonomyrmex desertorum*. In fact, *C. bicolor* could approach *P. desertorum* workers very closely without eliciting an aggressive response.

Frequently a guarding *M. mexicanus* worker would fall down the entrance, carrying with it several large stones from the crater. Because these larger stones were not immediately carried out when *C. bicolor* was present, we wanted to determine whether nest-cleaning activity was also prevented. This was assessed by painting two sets of 120 stones with fluorescent dye and dropping one set down a nest victimized by *C. bicolor* and the other set down a control
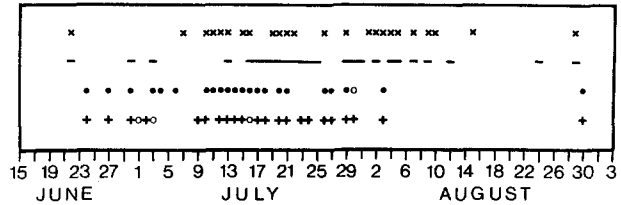
nest. An ultraviolet light was used to detect stones carried to the surface. Within 11 h, 107 stones were found scattered up to 3 m from the control nest. The victimized nest had only 9 stones removed up to a distance of 1.5 m after 24 h. However, in contrast to *M. mexicanus*, very pronounced cleaning behavior was observed when *C. bicolor* dropped stones down the entrance to *M. mimicus* or *M. depilis* colonies.

Chronic Effects of Interference Behavior

The seasonal pattern of interference by *C. bicolor* with individual colonies of the three species of *Myrmecocystus* reveals an even more dramatic effect. Each symbol in Fig. 5 represents a positive recording of stone-dropping behavior at a particular day during the normal foraging hours of the species in question. Observing four individual *Myrmecocystus* colonies over a 2-month period we recorded *C. bicolor* dropping stones on 96% (*M. depilis*), 88% (*M. mimicus*), and 100% (*M. mexicanus*) of the days checked. It was impossible to check every colony on a daily basis to achieve a continuous record, but frequent checks during periods in July closely approach constant observation. During this time it seems very likely that the interference behavior occurred regularly during every foraging period. This must greatly diminish a colony's food intake, considering that the interference behavior stops the foraging activity of the victimized colony almost completely.

M. mexicanus colonies 447 and 505 had been under constant stone-dropping interference for several weeks. Thus they were almost entirely deprived from any food intake. During this time, a day with special weather conditions provided us with a natural field experiment by altering temporarily the activity periods of both *C. bicolor* and *M. mexicanus*. The sky was fully overcast and we recorded low temperatures and light rains during the morning hours till early afternoon. During the rain *C. bicolor* ceased its activity completely, whereas the two *M. mexicanus*
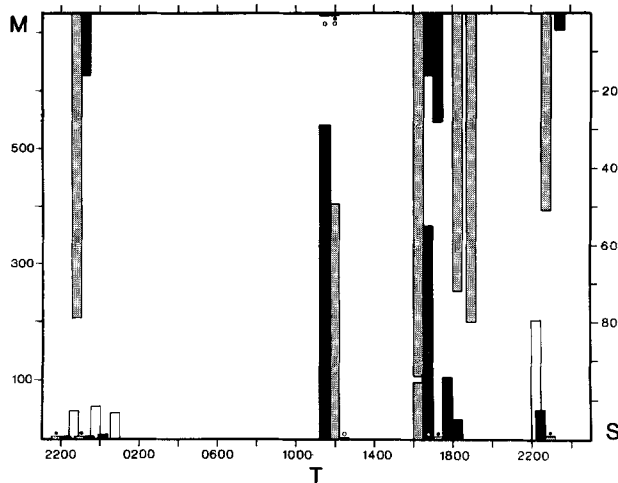
Fig. 6. Foraging and stone-dropping behavior during a 24-h period with unusual weather conditions (July 23, 1977) at 3 different colonies of *M. mexicanus. Stippled bars*, colony 505; *black bars*, colony 447; *open bars*, control colony 507; *Standing bars*, number of *M. mexicanus* workers leaving the nest per 5 min (scale on the left side, *M*); *hanging bars*, number of stones dropped by *C. bicolor* per 5 min (scale on the right side, *S*). (Counts of 0 are indicated by *very small bars* carrying the number *0. Small stippled bars* carry in addition a small black dot, •.) *T*, time of day. For further explanation see text

Fig. 7. Distance relationship between 3 colonies of *Myrmecocystus* (*hexagon*, *M. mexicanus*; *square*, *M. mimicus*; *large circle*, *M. depilis*) and a surrounding polydomous *C. bicolor* colony (*small circles* each depicting one nest entrance). All 3 colonies of *Myrmecocystus* were stone dropped against

colonies switched to diurnal activity. Since *C. bicolor* was not active they did not interfere with *M. mexicanus* and thus allowed them to forage in high numbers. The quantitative record of this natural experiment is given in Fig. 6.

During the previous night, when both *M. mexicanus* colonies were still victimized by *C. bicolor*, less than 10 workers returned to the nest per 10 min. During the rain on the next day there was no stone dropping at the two nests, and accordingly we recorded up to 530 foragers per 5 min. We were never able to observe such high frequencies under normal circumstances.

A second step of this natural experiment was caused by the fact that the light rain stopped sometime between 1400 and 1600 hours, allowing *C. bicolor* to resume activities again. Between 1600 and 1800 hours they dropped stones with high frequency (90+ per 10 min), sharply decreasing the number of returning foragers of *M. mexicanus*. Thus although there were higher numbers of *M. mexicanus* workers out foraging compared to regular periods, *C. bicolor* still managed to push these colonies back and prevent them from further foraging. This natural experiment demonstrates two aspects of this technique of interference behavior: (1) Constant suppression of foraging of victimized *M. mexicanus* colonies is strong enough to cause the ants to switch to diurnal activity, provided the weather conditions allow it. Nonvictimized
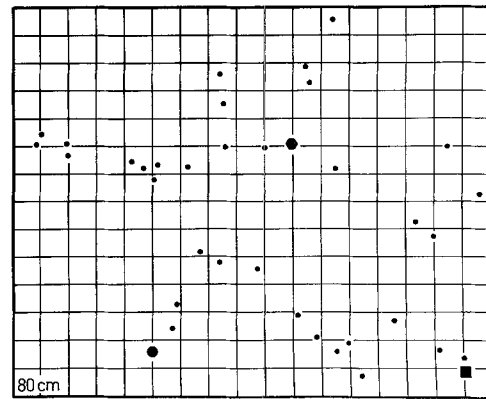
colonies did not forage at all during daytime. (2) Even colonies which were able to start heavy foraging could be quickly pushed back by *C. bicolor* workers resuming interference behavior.

Niche Overlap: Space and Food

The total area of a *C. bicolor* colony could not be determined precisely because of a lack of aggression between ants of different entrances. Based on observations of frequent worker movement and brood transport between adjacent entrances, each colony seemed to have numerous nest entrances (20 to 50+).

The density of nest entrances of *C. bicolor* around victimized *Myrmecocystus* colonies was determined by mapping an area around a colony of *M. mexicanus* (447) which had been regularly stone dropped against during the summer of 1977 (see Fig. 7). The average distance between *C. bicolor* entrances was 65 cm. In the same vicinity were colonies of the diurnal *M. mimicus* (447a) and *M. depilis* (447b). Thus at night *C. bicolor* dropped stones into the nest entrance of *M. mexicanus*, and during the day it switched to the two colonies of the other species.

To determine whether stone-dropping behavior was correlated with the proximity of foreign nests, measurements were taken of the distance from 96 nest entraces (representing four species of *Myrmecocystus*) to the closest entrance of a *C. bicolor* colony. If stone-dropping behavior could be observed in at least one of three checks, the colony was considered to be victimized (Fig. 8). The results indicate clearly that stone-dropping behavior occurs if the
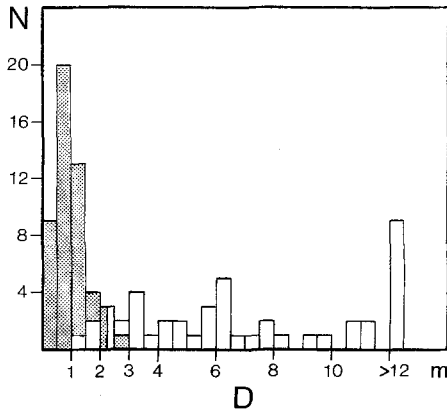
Fig. 8. Occurrence of stone-dropping behavior at colonies of *M. mexicanus* in comparison to the distance to the closest *C. bicolor* nest entrance. *Stippled bars,* at least one recording of stone dropping out of 3 checks at different days during regular interference hours; *open bars,* no interference behavior observed; *N,* number of *Myrmecocystus* nests; *D,* distance in meters

Fig. 9. 'Plugging experiment' at a nest of *M. mexicanus,* which was victimized by *C. bicolor* prior to the experiment. The nest entrance had been sealed with a tight cotton plug early in the morning. ↓, time at which plug had been removed; *S,* number of stones dropped per 5 min; *T,* time of day

closest nest entrance of *C. bicolor* is less than 1.5 m away from the *Myrmecocystus* colony in question. If the distance between nests exceeded 3 m, no stone dropping was observed. Observations of *C. bicolor* foraging showed that workers forage over distances greater than 3 m, thus they are able to encounter nests in those areas where no stone dropping occurs. The absence of interference behavior in such colonies demonstrates that a spatial component of the competitive relationship exists.

Besides this overlap in foraging time and nest space, accounts in the literature and our own observations indicate that there is also an overlap in utilization of food sources. *C. bicolor* (*C. pyramicus,* for taxonomic details see Creighton, 1950) is predacious but will feed on honeydew when available. For *Myrmecocystus,* Snelling (1976) lists insect fragments and a large number of nectar sources as food. We found *C. bicolor* in June tending aphids for their honeydew on yucca and observed both competitors foraging on the same termites and other arthropods.

However, these are only preliminary observations and a separate detailed study would be necessary to provide evidence that food is the limiting resource.

Stimuli Releasing Interference Behavior

We have so far established two requirements for the occurrence of stone dropping: inter-nest proximity and activity of the affected species (Fig. 1). The latter suggests that the nests themselves are not effective in releasing stone-dropping behavior. It seems more likely that the first ants coming up the crater serve as a releaser for the behavior.
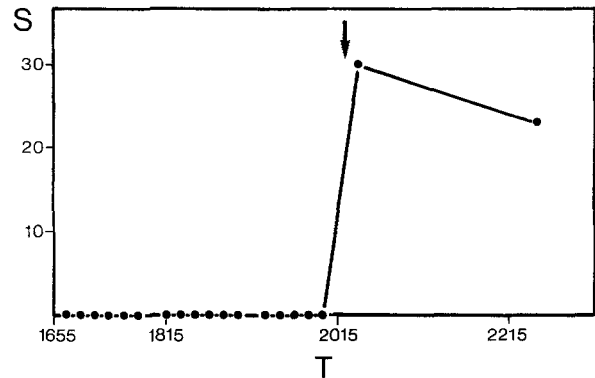
To test this hypothesis we conducted the following experiment. *M. mexicanus* workers were prevented from coming up nest entrances by plugging the entrances tightly with cotton during noontime, and this was performed on a colony normally subject to strong interference. No stone dropping occurred following plugging (Fig. 9) although a few *C. bicolor* workers approached the nest entrance of *M. mexicanus* from time to time. In controls we plugged only half of the nest entrance. In four cases we observed normal stone-dropping behavior, indicating that the cotton itself did not prevent *C. bicolor* from dropping stones.

At 2010 hours we removed the cotton plug. Immediately, hundreds of *M. mexicanus* workers poured out of the nest and began to forage. Shortly thereafter, more *C. bicolor* workers gathered around the nest. At 2025 hours we estimated about 100–200 *C. bicolor* workers in a circle of about 15-cm radius around the nest entrance. The number of *C. bicolor* workers being recruited to the highly active *M. mexicanus* nest considerably surpassed the numbers of those usually involved.

An important observation was that the initial presence of *C. bicolor* without stones caused the *M. mexicanus* to retreat. When most of the *M. mexicanus* workers were pushed back into the nest (2030–2035 hours), stone dropping was observed at a frequency of 30 per 5 min. Two other plugging experiments showed similar results thus confirming that the presence of ants in or around the nest entrance is important in releasing stone-dropping behavior.

Following these results we tested whether other stimuli could elicit stone-dropping behavior. Live or

dead ant workers were placed in open vials and these were buried up to the rim near a *C. bicolor* entrance to test if we could artificially release stone dropping at a place other than at a natural nest entrance. Dead and disabled *Myrmecocystus* workers proved to be effective in eliciting normal interference behavior including stone dropping. Further tests showed that even an odor such as Pine-Sol disinfectant can release stone dropping at an artificial nest entrance. Empty vials, however, did not release any reaction in *C. bicolor* even when the vials were left in position for several days.

To test whether an artificial nest entrance was necessary for interference behavior, a cotton ball soaked in Pine-Sol was placed on the surface near a *C. bicolor* nest; 6 h later the cotton was completely covered with small stones. This is evidence for a very general behavioral response in *C. bicolor* to cover certain odor-emitting sources when close to their nest entrance, possibly in an attempt to extinguish them.

The Function of Stone Dropping During Interference Behavior

To study the function of stone dropping, we had to disentangle it experimentally from other associated behaviors. We attempted to do this by trying to hit guards with small stones. Ten replications showed that being hit by a stone directly had little or no effect on *M. mexicanus*.

Some dolichoderine ants are known to produce a very potent alarm or repellent pheromone in their anal glands which sometimes repels other ant species. With this in mind we held *C. bicolor* workers with a pair of forceps and approached *M. mexicanus* guards. In all cases the immediate reaction was a quick withdrawal by the guards into their nest. Although the withdrawal can be released by approaching them with a *C. bicolor* worker, it does not reveal what happens in normal encounters. Usually the release of anal gland substance in dolichoderine ants is accompanied by a very conspicuous behavior: raising the gaster upward. This behavior can rarely be observed in *C. bicolor* when they are interfering with *Myrmecocystus*.

Although artificially dropped stones do not elicit an obvious immediate response by guards, the stones can still provide a signal which prevents the colony from leaving the nest. The following experiment was designed to clarify this question. We dropped stones of a normal size and at a normal frequency down the nest entrance of formerly unvictimized colonies and were not able to decrease the number of leaving ants. On the contrary, we observed an increase in
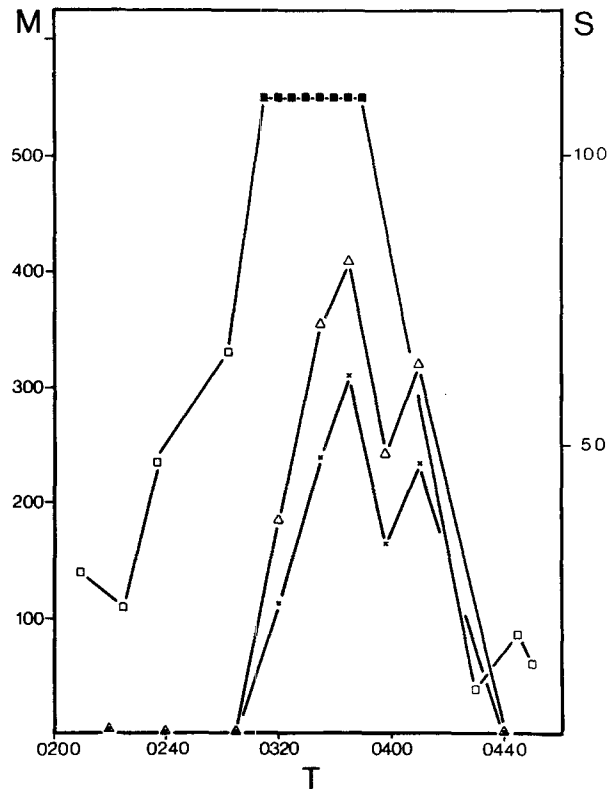

Fig. 10. Effects of artificial stone dropping at a nest of *M. mexicanus* which was victimized by *C. bicolor*. First phase, natural stone dropping (*open square*); second phase, artificial stone dropping (*closed square*), during this time all workers of *C. bicolor* approaching the nest were constantly removed with an aspirator; third phase, natural stone dropping (*open square*). M, number of *M. mexicanus* workers leaving the nest per 10 min; S, number of stones dropped per 5 min; triangle, total number of workers leaving; x, number of leaving workers carrying out stones; T, time of day

all cases, mainly due to the dropped stones being carried out of the nest.

To test the effect of artificial stone dropping in a more normal behavioral context, we used a colony which was regularly victimized. At a regular stone-dropping time, we removed all present and incoming *C. bicolor* workers with an aspirator from the nest area of *M. mexicanus* and started artificial stone dropping with a frequency of 110 per 5 min. During the time of artificial stone dropping, newly arriving *C. bicolor* workers were constantly removed. Thus we maintained as many factors as possible except for the presence of *C. bicolor*. The result was a striking outburst of *M. mexicanus* workers and a high cleaning-out activity (Fig. 10). After we stopped the artificial stone dropping and allowed *C. bicolor* to come in, the frequency of leaving workers decreased again, even though *C. bicolor* resumed stone dropping at low frequencies.

This leads to the question of whether the stones

themselves have a direct function during interference or whether other behaviors or signals performed by *C. bicolor* are more important. To prevent *C. bicolor* from picking up stones, we placed large sheets of fabric around the nest entrances of *Myrmecocystus* colonies in late August. The edges of the sheets (0.9–1.54 m²) had to fall short of the closest *C. bicolor* entrance and were covered with soil to prevent the ants from moving underneath the sheet. The sheets were placed during midday when neither workers of *M. mexicanus* nor *C. bicolor* were present. At night, during regular stone-dropping hours, frequency and effect of interference were recorded at experimental nests (with sheets), control nests (one, with regular stone-dropping behavior), and control nests (two, with regular foraging behavior of *M. mexicanus*).

Although the absolute numbers vary considerably among different colonies, the sheets cut down stone-dropping activity to a minimum (exp: $\bar{x}=4.2\pm1.2$, $n=27$; control: $\bar{x}=53.8\pm13.1$, $n=8$; t-test: $P<0.0001$). Some workers do carry stones from farther than the edge of the sheet. At the same moment, the number of foraging *M. mexicanus* increases significantly compared to the value of the experimental colonies before the sheets had been placed (exp: $\bar{x}=23.7\pm7.3$, $n=27$; control: $\bar{x}=0.5\pm0.2$, $n=8$; $P<0.002$).

However, other comparisons show that the number of *M. mexicanus* leaving at the sheeted nests is still significantly smaller than at the freely foraging *M. mexicanus* colonies (exp: $\bar{x}=23.7\pm7.3$, $n=27$; control: $\bar{x}=37.5\pm13.6$, $n=4$; $P<0.02$) and relative to the overall foraging activity of unaffected colonies (see Fig. 4, exp: $\bar{x}=23.7\pm7.3$, $n=27$; control: $\bar{x}=54.6\pm8.1$, $n=19$; $P<0.0001$).

Since *C. bicolor* seems to possess one or more behavioral patterns besides stone dropping to keep *M. mexicanus* colonies from foraging, more workers should make up for the loss of the stone-dropping activity. The opposite result was observed. After placing the sheets at the *M. mexicanus* colonies we recorded significantly fewer *C. bicolor* workers at those colonies.

Two explanations seem to be possible: (1) The stone-dropping behavior might be very closely linked to the complete behavioral sequence. Thus, being prevented from dropping stones, *C. bicolor* might be less able or 'willing' to continue their interference behavior. (2) The unnatural sheet situation might reduce the numbers of *C. bicolor* workers at *M. mexicanus* colonies independently from the stone-dropping behavior. We tested the latter argument by resupplying stones on top of the sheet. *C. bicolor* resumed their normal behavior including stone dropping, although the sheets were still present in those cases. Moreover, even with a numerical reduction, the numbers of *C. bicolor* workers at the *M. mexicanus*

nests still remained at levels where *C. bicolor* was perfectly able to shut down its competitor from foraging if stones were available.

Discussion

Stone-dropping behavior by *C. bicolor* has been described and analyzed in detail in an attempt to elucidate the mechanisms underlying interference competition. It turned out that it is performed regularly toward neighboring colonies if two requirements are fulfilled. The closest nest entrance of *C. bicolor* must not exceed a maximum distance and *Myrmecocystus* workers have to be present in the nest entrance.

We think that stone dropping is part of an interference behavior performed by *C. bicolor* with the effect of reducing the foraging activities of *M. mexicanus* to approximately one-eighth or normal activity.

Records in the literature and our own observations revealed that the *C. bicolor* and *Myrmecocystus* species involved share major food sources and our investigation demonstrated that foraging area and foraging times largely overlap. The stone dropping and its associated behaviors are a technique of interference competition, leaving *C. bicolor* as the highly dominant species in this relationship. Since the interference occurs daily or nightly, respectively, throughout the summer season, one must wonder how the affected *Myrmecocystus* colonies satisfy their food requirements. There may be a seasonal change in degree of interference behavior starting in the second half of August, although our observations in this regard are very preliminary. It is conceivable that storing enough food by means of a replete storage caste allows *Myrmecocystus* colonies to overcome periods of strong interference competition, provided they can forage more extensively during other periods of the year. However, even if this is the case, it remains to be explained why *Myrmecocystus* does not employ any counter strategy, especially since the workers which manage to get out do not experience any direct aggression.

Although the complete interference behavior shown by *C. bicolor* kept *Myrmecocystus* colonies from foraging, the effective mechanisms, particularly the function of stone dropping, cannot be explained completely. Our experiments showed that artificial stone dropping without *C. bicolor* being present did not keep the *Myrmecocystus* colonies from leaving the nest. If the stones have any effect during the interference process, then their properties must be different if dropped by *C. bicolor* or they reinforce another signal associated with the presence of *C. bicolor*. For example, the stone properties could be altered by contaminating them with a chemical repellent. Preliminary observations and experiments make this possibility very unlikely.

However, we would like to present here the hypothesis that the stones provide an additional mechanical communication signal, one which serves to reduce 'other expenses' of the colony. One possibility is to reduce the number of *C. bicolor* workers necessary to keep workers of a *Myrmecocystus* colony from leaving the nest. In the 'plugging experiment' (Fig. 9) as well as during the 'natural experiment' (Fig. 6), the *C. bicolor* colonies recruited high numbers of workers to push the *Myrmecocystus* colonies back at the beginning of the interference. Only after this had been achieved was stone-dropping behavior initiated. We should expect that as more stones are dropped, fewer *C. bicolor* workers are needed. Instead, analysis of our records shows a positive correlation between the number of *C. bicolor* workers at a given moment around the colony of *M. mexicanus* and the number of stones dropped ($r = +0.67$). The distribution of the data gives no indication of an increase in workers at low stone-dropping frequencies.

Another 'expense' which might be reduced by stone dropping is the application of chemical repellent substances, generally emitted from the anal gland by dolichoderine ants. In the same desert area another dolichoderine, *Iridomyrmex pruinosum*, also performs an interference behavior at the nest entrance of other ant species (Hölldobler, personal communication). Workers approach the nest entrances, turn around, and display their raised gasters to the resident ants. Sometimes the discharge of a strong-smelling repellent from the anal gland can be detected. This behavior seems to serve as in *C. bicolor* to keep workers from leaving the nest. However, stone dropping was never observed in *I. pruinosum*. On the other hand, gaster flicking could rarely be detected in *C. bicolor*. Nevertheless, it was sometimes seen in those experiments where large numbers of *C. bicolor* workers arrived to push many *Myrmecocystus* workers back into the nest. After this had been achieved, stone dropping started and the numbers of *C. bicolor* workers around the nest entrances declined.

The comparison of the interference behaviors of *I. pruinosum* and *C. bicolor* supports our hypothesis that in *C. bicolor* the stone dropping assumes a signal function to reduce the necessity of chemical display and the number of workers needed. The chemical repellent might only be used occasionally.

Lin (1964) reported a behavior where workers of *Tetramorium caespitum* dropped sand grains into the nest entrance of a halictine bee, *Lasioglossum zephyrum*. The author assumes the interaction 'to be an aggressive one' where the ants use the grains 'as weapons'. Unfortunately, the statements are only based on a few observations and there is no evidence for the true function of this behavior. An experimental analysis of this interaction would be of considerable interest to possibly uncover a similar mechanism of interference competition. Furthermore it would be valuable to determine whether *T. caespitum* might even use the same behavior in interactions with other ant species analogous to *C. bicolor*.

The stone-dropping response of *C. bicolor* was very general. We were able to release stone dropping with artificial nest entrances containing different species of ants and even unrelated chemical odors. Even without providing an artificial nest entrance, objects were carried and released on an odor source placed close to the nest entrance. It has been widely observed that different ant species cover disagreeable objects or odor sources close to their nest with material (Wheeler, 1910). This general response could have served as a preadaptation for the development of interference using stone dropping.

If the stones dropped by *C. bicolor* truly provide a signal, then this is the first recognized example in ants where communication signals are produced using an object taken from the environment, rather than mechanical, acoustical, or chemical signals which are generated by organs of the ant. However, more experiments are needed before this question can be resolved unequivocally; it has to be demonstrated that stone dropping is not an epiphenomenon associated with interference behavior.

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