

the few egg clutches that exhibited low mortality in the current study indicate evolution of some tolerance of acidity, it is not at all likely that the process will proceed fast enough to keep pace with the cumulative effects of acid precipitation on salamander breeding sites (2). The significance of widespread failure of salamander reproduction will extend beyond the salamanders themselves; salamanders are important predators on dipteran larvae in temporary pools (20) and an important source of energy for higher trophic levels in an ecosystem (21). Temporary ponds are also important breeding sites for many invertebrates, and changes in those ponds could have far-reaching effects.

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2. F. H. Pough and R. E. Wilson, *J. Water Air Soil Pollut.*, in press.
3. Pond pH was measured to the nearest 0.25 pH unit with Lolon pHydration paper. Laboratory comparisons with a pH meter, using dilute unbuffered solutions of sulfuric acid, confirmed the accuracy of the method.
4. Seventeen breeding sites of spotted salamanders were measured, the average pH was 5.2, range 4.5 to 8.0. Six of these sites were permanent ponds, their average pH was 6.1, range 5.5 to 8.0. Eleven breeding sites in temporary pools had an average pH of 5.0, range 4.5 to 7.0.
5. Temperature was measured beside an egg mass each time a pond was visited. Amphibian eggs absorb solar radiation and may be several degrees warmer than water temperature [D. D. Hassinger, *Herpetologica* **26**, 49 (1970); F. H. Pough, in preparation].
6. To reduce stress eggs were not lifted from the water or removed from the supports to which they were attached. Masses containing fewer than 50 eggs were counted individually; where there were more than 50 a portion (one-quarter to one-half) of the clutch was counted and the total estimated. Preliminary trials indicated that this method produced values within 10 percent of actual egg numbers.
7. Ten developmental stages could be identified under field conditions. They correspond to the Harrison stages [R. Rugh, *Experimental Embryology* (Burgess, Minneapolis, Minn., 1962), pp. 82-87] as follows.

Field stage	Harrison stage	Field stage	Harrison stage
1	1-3	6	23-29
2	4-9	7	30-32
3	10-11	8	33-34
4	12-13	9	35-39
5	14-22	10	40

8. K. L. Gosner and I. H. Black [*Ecology* **38**, 256 (1957)] observed similar shrinkage of egg membranes of several anurans at low pH.
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12. A number of mutants have been described in the axolotl (*Ambystoma mexicanum*) [G. M. Malacinski and A. J. Brothers, *Science* **184**, 1142 (1974)]. Among these mutations, those designated *f*, *g*, and *v* produce malformations that are generally similar to those seen among *A. maculatum* embryos exposed to low pH, although they differ in morphological detail and time of expression. In particular, *v* produces edema and stunted gills, is variable in its expression, and is affected by temperature [R. R. Humphrey, *Dev. Biol.* **4**, 423 (1962); R. Briggs and R. R. Humphrey; *ibid.* **5**, 127 (1962)]. It acts by producing

drastic rearrangements of cell components, especially RNA, during cleavage. Similar cytological changes are produced by exposing eggs to acid or alkaline media [J. Brachet, *The Biochemistry of Development* (Pergamon, New York, 1960)]. If a similar locus exists in *A. maculatum* acid stress may cause its expression. Alternatively, the similarity of mutant and acid-induced abnormalities may indicate only that they result from serious disruption of cellular or subcellular characteristics in early developmental stages. For example, cell surface charges are different in different germ layers of frog gastrulae and are differentially affected by acidity [H. E. Shaeffer, B. E. Shaeffer, I. Brick, *Dev. Biol.* **35**, 376 (1974)].

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14. R. E. Wilson, unpublished thesis, Cornell University (1976).
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16. Water in puddles of melted ice on the surface of ponds in April was usually 0.5 pH unit more acidic than water drawn from below the ice. In one pond melted snow and rain had collected in a small bay separated from the main pond by a dam of ice. Water in the bay was pH 4.0, in the main pond pH 5.5. A day later the ice dam had melted, allowing some pond water to flow into the bay, and its pH had risen to 5.0.
17. Analyses of water from five ponds with pH's

between 4.0 and 5.5, stored for 2 weeks in the laboratory, were made by courtesy of G. E. Likens and the Hubbard Brook Ecosystem Study. The SO_4^{2-} concentration averaged 3.9 mg/liter (range 2.9 to 4.9).

18. *Rana sylvatica* breeds simultaneously and sympatrically with *Ambystoma* in this region, but it breeds in some pools from which *Ambystoma* is absent, possibly because they are too acidic (pH 3.5 to 4.0). Laboratory experiments show that *R. sylvatica* embryos can tolerate pH's at least as low as pH 4 [F. H. Pough and R. E. Wilson, unpublished data; Gosner and Black (8)].
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22. This study was supported by Federal Hatch Funds. I am grateful to E. M. Burke, A. S. Cooke, G. E. Likens, and M. B. Pough for reading the manuscript and making helpful suggestions.

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Tool Use in a Social Insect and Its Implications for Competitive Interactions

Abstract. *Four species of myrmicine ants, Aphaenogaster rudis, A. treatae, A. tennesseensis, and A. fulva, use pieces of leaf, mud, and sand grains as tools to carry soft foods from distant sources to the colony. Tools are tended on the food and removed by colony members without regard to which individual brought the tool. Food is gathered more efficiently by tool use than by internal transport. Tool-using behavior may increase the competitive ability of A. rudis in an interspecific dominance hierarchy.*

We report here what we believe to be the first case of tool use in a social insect and discuss the importance of this behavior in terms of competitive efficiency within an interspecific dominance hierarchy. Tool use is defined (1) as the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object. Only four genera of invertebrates, solitary wasps (*Ammophila*), ant lions (*Myrmeleon*), and worm lions (*Vermilio*, *Lampromyia*) are known to use tools (1, 2). We have observed tool use in four species of myrmicine ants, *Aphaenogaster rudis*, *A. treatae*, *A. tennesseensis*, and *A. fulva*; individuals of these species use pieces of leaves, dry mud, and small sand grains to transport soft food from a distant source to the colony.

We first observed this behavior in *A. rudis* located in a woodlot in College Park, Prince George's County, Maryland. We placed small portions of jelly on index cards (7.6 by 12.7 cm) on the ground to attract ants. When individuals of *A. rudis* reached a sample of bait, they would leave after 5 to 60 seconds and return with pieces of leaves which they then

placed on the jelly. As leaf fragments accumulated, ants from the same colony tended them, adjusting the positions of the leaves or sometimes pulling the leaves off completely and repositioning them. By individually marking ants with small spots of paint, we were able to determine that a given individual may bring several leaves and that ants tend leaves brought by other ants.

After 30 to 60 minutes, ants began to remove leaves from the bait and carried them directly back to the colony, once as far as 152 cm. These leaves were visibly covered with jelly, and we suggest that the ants are using these leaves as tools to transport large quantities of food (see Fig. 1). This behavior may have evolved from the tendency shown by many ant species to cover and protect distant food sources (3) or to cover immovable, disagreeable objects near the nest with dirt or debris (4).

To determine what happens to tools taken into a colony, we set up a small colony of *A. fulva* in a transparent ant house. Ants placed tools on the jelly provided, and we observed an individual carry a tool from the jelly to the chamber containing the queen, eggs, and other workers. Several workers fed from this

tool at different times over the course of several hours by using their mandibles to scrape food from the surface. We were not able to determine if they were also able to obtain food which might have been absorbed by the tool.

The types of tools used by *A. rudis* vary somewhat from colony to colony. Partially decayed pieces of deciduous leaves and pine needles are used most commonly in the main study area. Their size is quite variable, usually 2 to 5 mm in length or diameter. In addition to leaves, we have frequently observed ants using small pieces of dry mud or sand grains (1 to 4 mm in diameter) in the same manner. When selecting an object, ants search the ground near the bait (within 4 cm of the index card) and have been observed picking up and then dropping several objects before finding one that they carry back to the bait. To investigate this selectivity in more detail, we carried out a series of 12 replicate experiments with a large laboratory colony of *A. rudis*. For each experiment, ants were presented with five potential tools of each of four types, dry mud chunks, leaf fragments, pieces of pine needles, and small sections of dry, decaying wood. All of these potential tools were approximately the same size. Of the 240 items available, the ants used 43 mud chunks, 25 pine needles, 24 wood sections, and 7 leaf fragments. Mud chunks were selected significantly more often and leaf fragments significantly less often than random (level of significance $\alpha = 0.05$; $\chi^2 = 17.46$ and $\chi^2 = 16.03$, respectively). This preference for dry mud chunks may be related to the ease of manipulation or to the amount of food that will adhere to the surface. The frequent use by *A. rudis* of leaf fragments in many field observations suggests that the relative availability of different tools may also be an important factor in some areas.

Aphaenogaster rudis feeds, in part, on dead insects (5), which could present a food source of an appropriate texture for tool use. To determine if ants would use tools to gather the body fluid of an injured animal, we squashed a large spider and placed it near a colony of *A. rudis*. The ants proceeded to put leaves on the spider's abdominal fluid in precisely the same way they had with the jelly. *Aphaenogaster treatae* also used tools on the body fluids of coleopteran larvae and rotten fruit pulp. Hence it seems that our manipulations with jelly mimic a naturally occurring phenomenon.

To determine if a significant amount of food adhered to the tools, we took 30 leaf pieces from *A. rudis* as they approached

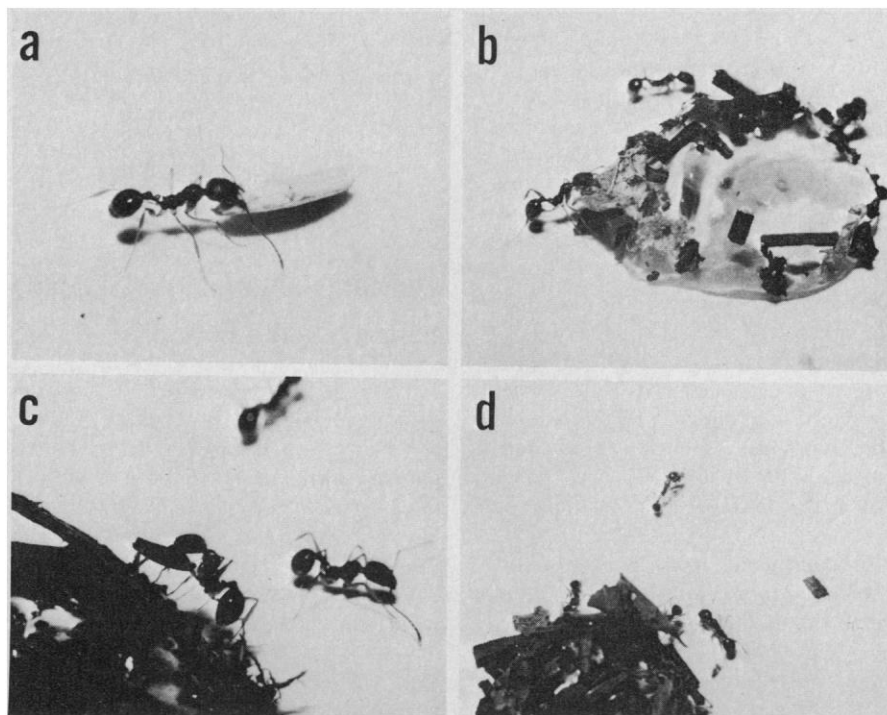


Fig. 1. (a) *Aphaenogaster rudis* carrying a tool (a piece of plant material) to the bait; (b) jelly bait with deciduous and coniferous leaf fragments (tools) in position, *A. rudis* placing another piece of leaf on the bait; (c) *A. rudis* on the bait adjusting a piece of leaf; (d) bait covered with tools and an *A. rudis* individual carrying a piece of leaf back to the colony. Scale: body length of *A. rudis*, 4.5 to 5.0 mm.

a bait. These leaves were weighed in groups of five and then placed on the body fluid of squashed coleopteran larvae. After 30 minutes, these leaves were removed and reweighed. The net weight gain per leaf was 1.38 ± 0.28 mg ($N = 6$). To evaluate the amount of food transported in relation to the size of *A. rudis*, ants were also weighed. The mean weight of an *A. rudis* worker was 1.28 ± 0.18 mg ($N = 24$). Thus, by using tools, an *A. rudis* worker may be able to transport an amount of food approximately equaling its body weight back to the colony. To assess the ability of *A. rudis* to carry such foods internally, we captured ten ants as they approached a bait. These individuals were weighed, allowed to feed on the jelly for 1 hour, and then reweighed. The net weight gain per individual was 0.13 ± 0.03 mg. Tool use is thus a far more efficient way for *A. rudis* to transport certain foods than internal transport.

This behavior is apparently not an isolated phenomenon in *A. rudis*. In a 50-km radius of College Park, we have observed 46 *A. rudis* colonies in which more than two workers located the bait. All of these colonies exhibited tool-using behavior. One colony of *A. treatae*, five of *A. fulva*, and one of *A. tennesseensis* have also been located. All seven of these colonies exhibited tool use similar to that of *A. rudis*.

The importance of tool use in *A. rudis* is particularly significant in light of their competitive interactions and dominance relationships with other ant species. In College Park, *A. rudis* coexists with many other ant species, the most abundant of which are *Camponotus ferrugineus*, *C. pennsylvanicus*, *Formica subsericea*, and *Prenolepis imparis*. We have observed all of these species actively chase and exclude *A. rudis* from food sources, an indication that *A. rudis* is behaviorally subordinate. A subordinate may compete with a dominant in several ways (6). One method is for the subordinate to find resources more quickly and use them before the dominant species arrives. Other strategies may include stealth and small size by which aggression from the dominant is avoided. We suggest that tool use may be another method that enables *A. rudis* to compete successfully with other species.

Ants typically obtain soft foods by drinking, filling the crop, and carrying the food back to the colony internally. This procedure necessitates spending a considerable time at the bait. For example, undisturbed *P. imparis* workers will feed for 30 to 60 minutes at a time. When *C. ferrugineus*, *C. pennsylvanicus*, or *F. subsericea* are present, they attack and chase away other ants, including *P. imparis*, thus making it infeasible for many species to utilize these food

sources. In contrast, an *A. rudis* individual can approach the bait, place a leaf, and rapidly depart before it is encountered. At a later time, it can return, quickly remove the leaf, and thus gain a portion of the resource with relatively low risk. *Aphaenogaster rudis* has been observed to place a leaf on a bait occupied by *C. ferrugineus* and later retrieve it when *C. ferrugineus* was on the opposite side of the bait. The behavior of *A. rudis* is similar when either *C. pennsylvanicus* or *F. subservicea* is present. Thus tool use allows *A. rudis* to obtain more food from such a source than it would obtain by drinking and thus increases its success in competing with these species.

Aphaenogaster rudis is also subordinate to *P. imparis* unless the latter is greatly outnumbered. However, if *A. rudis* places leaf fragments on a food before being excluded, *P. imparis* may eat all the available food but ignore the leaves. When *P. imparis* departs, *A. rudis* may retrieve the leaves. On 12 occasions, we have seen leaf-covered baits taken over by *P. imparis*. In such cases, the *P. imparis* individuals feed on the bait in their usual fashion. Occasionally, a leaf is knocked off the bait and a few individuals then glean some food from these pieces. Typically, however, the leaves are ignored and left at the bait. Presumably *A. rudis* could retrieve these at a later time, although this outcome has not been observed. Tool-covered baits have also been given to colonies of *C. pennsylvanicus* in the laboratory. Most of the food is eaten, but the tools and a moderate portion of the food under the tools are left and would thus be available for *A. rudis*.

Tool use appears to be a maximally efficient way of utilizing some food sources, regardless of dominance relationships. This behavior may be particularly adaptive for genera such as *Aphaenogaster* which have a relatively small gaster in which to carry food (7).

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anonymous reviewers who kindly offered criticisms of the manuscript, although the conclusions remain our own. We thank S. Mann and S. Lilien who assisted in the initial observations, and D. R. Smith, U.S. National Museum, who kindly identified the ants.

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Oroville Earthquakes: Normal Faulting in the Sierra Nevada Foothills

Abstract. *Aftershocks of the Oroville, California, earthquake of 1 August 1975 define a 16- by 12-kilometer fault plane striking north-south and dipping 60 degrees to the west to a depth of 10 kilometers. Focal mechanisms from P-wave first motions indicate normal faulting with the western, Great Valley side downdropped relative to the Sierra Nevada block. The northward projection of the fault plane passes beneath Oroville Dam and crops out under the reservoir.*

On 1 August 1975, at 2020 Greenwich mean time, an earthquake of magnitude $M_L = 5.7$ (University of California, Berkeley), $M_L = 6.1$ (California Institute of Technology, Pasadena), and $m_b = 5.9$ (USGS National Earthquake Information Service) occurred in the Sierra Nevada foothills southeast of Oroville, California. The earthquake was felt strongly in Sacramento and was noticeable in Menlo Park, at a distance of 225 km. Taken together with the aftershocks, the Oroville earthquake is the most significant strain release episode in California since the 1971 San Fernando earthquake. The main shock epicenter (star in Fig. 1) was near the town of Palermo, 7 km south of Oroville and 11 km from the 235 m high Oroville Dam.

Because of the proximity of the earthquake to the dam and the possibility that

the seismicity was induced by the 4.3 billion cubic meter reservoir, the U.S. Geological Survey (USGS) began deployment of 16 high-gain telemetered seismographs in the area on 2 August. The network was completed by 11 August and was augmented by data from a tripartite array of local stations, telemetered to Menlo Park through a data exchange with the California Department of Water Resources (CDWR). Ten strong-motion accelerographs were installed in the epicentral region within 48 hours of the occurrence of the main shock. The locations of the five instruments installed by personnel of the California Institute of Technology and the USGS are shown in Fig. 1. Five additional instruments were installed by the California Division of Mines and Geology. One hundred seventy strong-motion accelerograms of

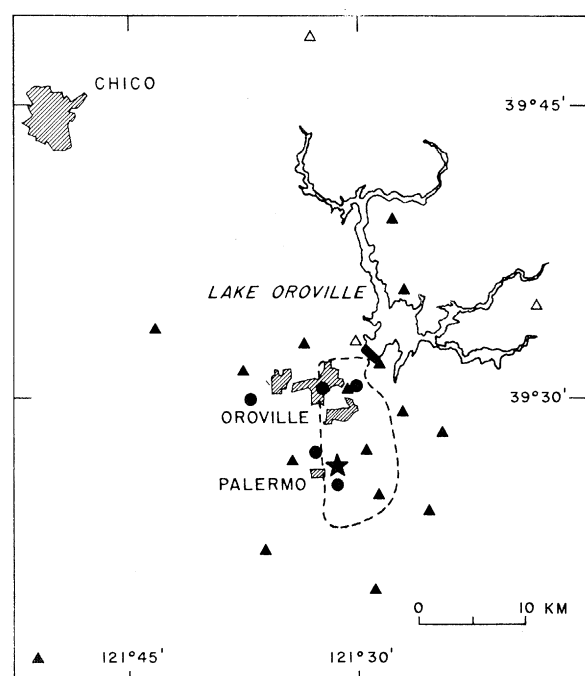


Fig. 1. Seismographic stations used in this study. Closed circles are strong-motion seismographs. Closed triangles are telemetered short-period seismographs installed by the U.S. Geological Survey after the 1 August 1975 earthquake. Open triangles are seismographs operated since 1964 by the California Department of Water Resources. The approximate epicenter of the main shock is indicated by a star. Distribution of aftershocks (August to October 1975) is indicated by the dashed line. The Oroville Dam is shown by the bar at the southwest corner of the reservoir.