A REVIEW OF TOOL USE IN INSECTS

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SYNOPSIS

The category of tool use, like many scientific concepts, is elusive and difficult to define precisely. This paper considers several major attempts to define tool use, discusses the problems associated with delineating this category, and advances a definition which classifies tool use as "the active external manipulation of a moveable or structurally modified inanimate environment object, not internally manufactured for this use, which, when oriented effectively, alters more efficiently the form, position, or condition of another object, another organism, or the user itself." On the basis of this definition, eight instances of insect behavior are categorized as tool use and reviewed. Problems of definitional boundaries and the resulting differences in classification are discussed.

A REVIEW OF TOOL USE IN INSECTS

A consideration of tool-using behavior must necessarily begin with the problem of defining tool use in animals. Hall (1963), in one of the initial reviews of this behavior, viewed tool use as "the use by an animal of an object or of another living organism as a means of achieving an advantage . . . The mediating object is required by definition to be something extraneous to the bodily equipment of the animal, and its use allows the animal to extend the range of its movement or to increase their efficiency" (p. 479).

van Lawick-Goodall (1970) defined tool use more narrowly: Tool use is "the use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal" (p. 105). Alcock (1972) has provided a definition most commonly accepted: Tool use is "the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the form or position of some separate object" (p. 464).

These attempts at definitions raise a few key issues involved in determining what constitutes tool use. First, should the use of "another living organism" be classified as tool use? Hall's definition includes this behavior, while van Lawick-Goodall's and Alcock's do not. At issue here are such diverse behaviors as agonistic buffering in primates (Whiten & Rusmoy 1973, Strum 1983), an ant crossing a streamlet over a bridge of linked fellow ants, or the use of conspecifics as "gluing mechanism" by weaver ants (Beck 1980). Kummer (1982) has proposed the term "social tools" to account for the use of conspecifics as tools and this terminology provides a useful distinction between social tools and mechanical tools.

Another problem concerns the nature of these tools. Hall and van Lawick-Goodall both limit tool use to the use of an external object. Alcock does similarly with his requirement that the tool be "an inanimate object, not internally manufactured". This requisite excludes the use of attached parts of the user's body as tool use and rightly so. Morphological adaptations must necessarily be excluded to preserve the meaningfulness of the category of tool use. Otherwise, valid cases could be made for any manipulation of a body part as tool use. For instance, the use of a tail by an Old World monkey

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to obtain objects otherwise out of reach is not a bona fide instance of tool use, although attempts have been made to label this behavior as such (Karrer 1970, Erwin 1974). Likewise, web construction by a spider, repulsion of an attack by the spray of a skunk, and nuptial gifts by some male empidid flies (empty silken balls composed solely of bodily secretions—Thornhill and Alcock 1983) are excluded. Again, these are physiological adaptations whose inclusion in this category makes further exclusions seem arbitrary. If these adaptations are included, why not scent marking or pheromones or even salivation (as a tool for food use)? At this point, the category of tool use becomes meaningless.

However, there are instances in which the use of internally-manufactured objects may qualify as tool use. Harcourt (1981) has proposed that washing of the hands and feet with urine may facilitate grip in galago species. Chimpanzees and other primates throw feces in an attempt to repel intruders (Beck 1980). Lochr (1983) reported "well-aimed" defecation in the fieldfare as an attack strategy against potential predators. Which of these behaviors, if any, should be classified as tool-using behaviors?

Beck (1980) has provided a rather tortuous, complex definition in an attempt to negotiate the above concerns. His definition of tool use is "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool" (p. 10). This definition allows for fine discriminations in categorizing tool-using behaviors. For instance, the definition includes the Egyptian vulture opening an egg by dropping stones on the egg, but excludes a herring gull opening a mussel by dropping the mussel on stones. Further, this definition allows for aimed throwing of feces as tool use, but not aimed defecation.

Beck's definition, like Hall's, categorizes social manipulation of others (such as agonistic buffering) as tool use, but this allows for other social behaviors which clearly do not comprise tool-using behavior. For example, a female water strider can forage effectively "only by carrying a copulating male who apparently repels copulatory attempts by other males" (Wilcox 1984, p. 171). Female water striders foraging singly recopulated within 10 minutes and continued to forage in 61% of trials. By Beck's definition, the copulating male constitutes tool use by the female. Further, in some insect species, females copulate with a second male to replace the sperm of a genetically inferior male (e.g., a mate that fails to guard). In these cases, copulation with the second male meets Beck's criterion for tool use, although this classification is questionable at best. This problem can only be satisfactorily resolved by elimination of social manipulations from the category of "tool use". In this respect, Kummer's (1982) classification of social tools is useful as a separate but complementary class of behaviors.

Components of the above definitions can be juxtaposed and modified to form a definition which, while retaining the discriminability of Beck (1980), also excludes problematical classifications of tool use, such as social tools. Tool use can thus be defined as follows:

Tool use is the active external manipulation of a moveable or structurally modified inanimate environmental object, not internally manufactured for this use, which, when oriented effectively, alters more efficiently the form, position, or condition of another object, another organism, or the user itself.

This definition is similar to Beck's criterion but differs in two important respects. First, this definition restricts tools to inanimate objects and excludes occurrences of social tool use. Second, this definition allows for the classification of nest and burrow building (but not web building) as instances of tool use, whereas Beck's definition excludes these behaviors. This inclusion is controversial but, I argue, necessary given the elaborate construction and crucial functions served by these structures (thermoregulation, de-
fense, raising of the young, etc.). McFarland (1981), among others, has provided an argument against this inclusion:

\[ \ldots \text{to regard the nest material as a tool for making a nest would be like calling knitting-wool a tool for making a garment. Most biologists would distinguish between the material being manipulated and the means by which the material is manipulated. Knitting-needles are normally regarded as tools, but not knitting-wool. (p. 575).} \]

In defense of including nest building as tool use, I argue that another distinction is necessary—the result of the material being manipulated. A human wearing the knitted sweater (or covering himself with the knitted blanket) is using this object as a tool. Likewise, an animal using the nest as a thermoregulatory device or a defense mechanism is also employing this object as a tool. Further, field evidence clearly establishes the efficacy and necessity of these structures to the survival of the organism via reduction of energy requirements, increased protection against predators, and so on. These constructions represent adaptations in response to strong selection pressures. Thus, the use of nests and burrows will be considered as tool-using behavior, when these structures serve a necessary function and improve the efficiency of the organism's behavior in some manner.

**EXAMPLES OF TOOL USE IN INSECTS**

Documented cases of tool use in insects are rare when evaluated by the strict requirements of the present definition. These cases can be divided into eight main categories.

1) **Food Transportation**

This behavior has been reported for several species of ants. Morrill (1972), in the initial paper to report this behavior, noted that Florida harvester ants (*Pogonomyrmex badius*) when confronted with a liquid food source dropped small pellets of sand into the food and then carried the food-absorbed sand back to the nest. Tanaka and Ono (1978) noted the same behavior in Japanese ants (*Aphaenogaster famelica*), and Fellers and Fellers (1976) described a similar behavior for four species of myrmicine ants (*Aphaenogaster rudis, A. treatae, A. tennesseensis*, and *A. fulva*).

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. (p. 70).

Ants in the study preferentially used mud chunks for food transportation, but also employed pine needles, small sections of dry decaying wood, and leaf fragments. Foods transported included not only jelly, but also rotten fruit pulp and body fluids of a dead spider and coleopteran larvae. An ant worker, by using tools, can transport "an amount of food approximately equaling its body weight back to the colony" (Fellers & Fellers 1976, p 78).

McDonald (1984) questioned the veracity of labelling this behavior as tool use by
arguing that throwing soil on a liquid substance may be solely a reflexive response to a potentially nest threatening liquid. Accordingly, he placed petri dishes of water and honey water at different distances from the nest. Within 2.13 m of the nest, ants placed soil in each liquid but returned only the honey water soil to the nest. Beyond 2.13 m, only honey water produced soil-throwing behavior and transportation back to the nest. These results argue against the nest protection hypothesis and for a tool-using explanation.

2) Soil/Stone Dropping

Two species of ants perform a similar behavior in response to potential competitors. Mgodlich and Alpert (1979) observed dolichoderine ants (Camponotus bicolor) surround the nests of ant competitors and drop small pebbles and other objects down the entrances. This stone dropping behavior produced an almost complete cessation of foraging by the competing colony and thus was an effective interfering behavior by the dolichoderine ants.

Schultz (1982) observed a similar behavior in pavement ants (Tetramorium caespitum) in response to the ground-nesting alkali bee (Nomia melanderi). Schultz describes a typical sequence:

When the ant found an entrance to a bee nest, it usually went into the hole unless the entrance was blocked by a bee. . . . Upon discovering the bee, the ant normally paused several seconds at the rim of the nest, then wandered over the surrounding area, picked up a small piece of soil, or dislodged one from the crusted soil surface. After obtaining a piece of soil, the ant headed straight back to the nest entrance, held the soil over the entrance . . . , hesitated for about 1 second, and then dropped the soil. The ant then waited there for several seconds before going quickly for another piece of soil.

Other ants usually arrived at the nest entrance and joined the first ant in dropping soil. Occasionally the bee responded to these attacks by coming near the surface and lunging at the ants with its mandibles. However, a bee was never observed successfully grasping an ant. Instead these attacks only excited the ants and intensified their soil dropping behavior. (p. 278).

This behavior was solely a function of the presence of the bee. Unoccupied holes were investigated but soil dropping behavior did not occur. Further, this behavior most frequently resulted in the death of the bee as it attempted to leave the hole. An attack ensued and typically led to the death of the bee. It is interesting to note that a different population of pavement ants used the same behavior in an attack on a halictid bee (Lasioglossum zephyrum) although the death of the bee was not a consequence (Lin 1964-1965).

3) Sand Throwing

The ant-lion, larvae of neuropteran flies, constructs a funnel-shaped pit to entrap prey (see STRUCTURE BUILDING below). Worm-lions, larvae of Vermile and Lamprophonia dipteran flies, do similarly. Prey captured in these pits are grasped, dragged beneath the soil, and consumed. Prey able to elude the initial grasp attempt to escape the pit by climbing the side, eliciting sand throwing by the ant-lion or worm-lion. Sand throwing is accomplished by quick dorsiflexion of the head and mandibles, resulting in a shower of sand aimed at the escaping prey which hinders its escape or knocks it back into the pit (Wheeler 1930). Worm-lions further throw sand at approaching prey, sometimes succeeding in knocking this prey into the pit.
4) **Nest Closure**

Female sphexine wasps of the genera *Ammophila* and *Sphex* sometimes use tools in closing the burrow or nest in which eggs and a prey have been placed. The female selects pebbles or pellets with which to close the burrow, and then

... the major pebble is placed deep in the burrow and additional, smaller objects are placed above it. Sometimes these pellets are pulverized with blows of the head, and on some occasions the female uses a pebble in the manner of a hammer to pound the fill into a compact plug. (Evans & Eberhard 1970, p. 85)

The tool is typically held in the mandibles for pounding. In addition to pebbles, “clods of earth, bits of twig, bark, seeds, and the tarsus and tibia of what appeared to be a locust have been observed to be used for pounding” (Beck 1980, p. 17).

5) **Camouflage/Bait and Capture**

McMahan (1982, 1983a, 1983b) has furnished a fascinating account of tool use in the assassin bug *Salyavata variegata* of Costa Rica. *S. variegata* nymphs feed upon termites and use tools to aid in prey capture. This bug uses tools in two ways; to provide camouflage, and to “bait” termites for capture.

Nymphal *S. variegata* coats itself with carton crumbs scraped from the termite nest and thus camouflages itself. “The crumbs are patted onto the body surface, which is covered with glue-secreting setae . . . The camouflage effectively conceals the bug from would-be predators that hunt visually, as well as preventing its detection during tactile and olfactory examination by its blind prey” (McMahan 1983b, p. 483). Use of this camouflage enables the bug to capture a termite prey, which is then killed by a paralytic toxin and consumed by a sucking behavior, leaving only a hollowed carcass. The hollowed carcass is then used to lure other termites closer, a tactic McMahan labeled as a “bait and capture” strategy.

The bug, still holding the carcass in front of its head with its forelegs, moves back to the breach which is being repaired. It slowly pushes the carcass into the opening, jiggling it slightly in a movement that may be described as “tantalizing”, while remaining effectively insulated from the termites. Usually one or more of the workers will try to seize the carcass with their mandibles and pull it into the hole. Occasionally a worker succeeds in wresting the carcass from the bug and carries it into the nest interior. Usually, however, the bug pulls the grasping worker steadily backward, and draws it slowly from the nest. When the worker’s head is in an accessible position, the bug grasps it quickly with its forelegs and continues to back away from the hole. Insertion of the beak and ingestion of the body fluids soon follow. The carcass that had been used in baiting is dropped as soon as the fresh prey has been seized. (McMahan 1982, p. 249).

In one episode, McMahan witnessed one nymph successfully bait and capture 31 worker termites within three hours, finally quitting with a distinctly distended abdomen!

6) **Defense By a Fecal Shield**

The larva of the *Cassida rubiginosa* beetle carries a “fecal shield” above its back and uses this tool in defense against potential predators (Eisner et al. 1967). This shield is a packet consisting of “the molted skins previously shed by the larva, together with the dried remains of its accumulated fecal wastes” (p. 1471) and held in a raised position above the back by a two-pronged fork projecting from the tip of the abdomen. Immediate defensive positioning of the shield was elicited by experimental prodding of the larva. In tests of larvae exposed to ant attacks, the shield was maneuvered in the
direction of the attacking ant and was successful in repelling the ant attack in all but one of "several dozen encounters" (p. 1473). The lone exception occurred when a larva was fatally bitten before the shield was mobilized. Experimental removal of the fecal shield left a defenseless larva, one highly vulnerable to attacking ants.

7) Sound Baffle

Tree crickets of the Oecanthus species employ a calling song to attract mates. O. burmeisteri are able to increase the effectiveness of this behavior through the construction and use of a tool. O. burmeisteri males gnaw a small hole in a leaf, then orient so that the front of the body and the front legs rest on the upper surface of the leaf. Stridulation in this position results in a greater sound amplitude than stridulation without this tool (Prozesky-Schulze et al. 1975). The leaf acts as a baffle to prevent destructive interference of the signal (Forrest 1982) and, consequently, to increase the sound amplitude produced by stridulation. It should be noted that this behavior, the effective use of a tool, would not be so classified under Beck's (1980) definition because the leaf is neither "unattached" nor held or carried by the user. Yet this behavior is effective in attracting females through sound amplitude and used by virtually all male singers (Prozesky-Schulze et al. 1975).

8) Structure Building

Many insect species fashion structures (burrows, nests, etc.) that serve a multiplicity of function. An exhaustive review of this behavior is beyond the scope of this paper, but a few examples merit mention. Evans and Eberhard (1970) classified wasps’ nests into certain types and noted that nests of these species range from minor modifications of pre-existing cavities to constructions composed of mud or plant materials. Their use as a subterranean birthplace for the young has already been noted. Eumenid wasps, in nest construction, often carry water to the nesting site which is used to soften the earth before digging (Evans & Eberhard 1970). Further, an Australian eumenid of the genus Paralastor builds a complex funnel as the opening to the nest. The funnel apparently functions to keep out parasitic wasps while the nest is constructed. The funnel is destroyed following nest closure (Burnett 1981).

Worm-lions and ant-lions, as discussed above, excavate a funnel-shaped pit in which prey are captured. Lucas (1982) performed a biophysical analysis of pit construction by ant-lion larvae (specifically Myrmeleon crudenii) and found that both the physical properties of the sand (the angle of repose and Stoke's drag force) and ant-lion behavior (trajectory angle of throw, regulation of particle velocity) increase the number of fine particles on the pit walls and therefore enhance the prey capture efficiency of the structure by making escape more difficult.

The hive of the honey bee (Apis mellifera), in addition to maintaining group cohesion and keeping out enemies, provides thermoregulatory aid as well. The honeybee hive retains heat and moisture and, during winter, can maintain a temperature differential as great as +50°C (Wilson 1975). This differential is maintained by the construction and position of the nest and the body heat and behavior of the workers (Wilson 1971). During the summer, bees cool and provide moisture in the hive by bringing in water in response to high temperatures.

The thermoregulatory properties of the insect nest is well illustrated by the mosaic nests of termites. The complexity of the nests of Macrotermes termites of Africa in particular attest to this function:

The labyrinthine internal structure of these termite colonies has been designed in the course of evolution to guide a regular flow of air from the central fungus gardens, where it is heated and rises by convection, upward and outward to a flat,
peripheral system of capillarylike chambers, where it is cooled and freshened by proximity to the outside air. In *M. natalensis* the architecture is so efficient that the temperature within the fungus garden remains within one degree of 30°C and the carbon dioxide concentration varies only slightly, around 2.6 percent. (Wilson 1975, pp. 11-12).

The burrows of male mole crickets (*Gryllotalpa* species) serve a unique function: Their design increases the calling male's acoustical output (Bennet-Clark 1970). *G. vireae*. In particular, constructs a shallow two-exit burrow which acts like an acoustic horn, increasing the conversion of muscle action into sound by over 30%. The design also acts to provide directionality as well. The burrows of two *Scapteriscus* species of mole crickets perform a similar role with acoustical output increased as a result of calling from the entrance of the burrow (Nickerson et al. 1979).

**DISCUSSION**

At the onset of this paper, problems of defining tool-use behavior and attempts to satisfy these intricacies were presented and critiqued. I recognize that the definitions put forth currently may not hurdle all obstacles to the satisfaction of every reader. Accordingly, Table 1 lists the behavioral examples presented in this paper and their classification based on other definitions. Readers are invited to judge for themselves which definition best encapsulates their view of tool-using behavior.

As Table 1 indicates, there is general agreement of the classification of tool-using

**TABLE 1. CLASSIFICATION OF TOOL USE BY FOUR DEFINITIONS**

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<td>Weaver ants using conspecifics as gluing mechanisms</td>
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<td>Ants crossing a streamlet over a bridge of linked fellow ants</td>
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<td>Nuptial gifts by male empidid flies (composed of bodily secretions)</td>
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<td>Foraging female water striders while copulating</td>
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<td>N</td>
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<td>Use of sand/soil for food transportation by ant</td>
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<td>Soil/stone dropping behavior by <em>Conomyrma</em> and <em>Tetramorium</em> ants</td>
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<td>Sand throwing by ant-lion and worm-lion</td>
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<td>Nest Closure by <em>Ammophila</em> and <em>Sphex</em> wasps</td>
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<td>Camouflage/Bait and capture by the assassin bug</td>
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<td>Fecal shield defense by <em>Cassida rubignosa</em></td>
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<td>Sound baffle use by <em>Oecanthus</em> crickets</td>
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<td>Structure building by many species</td>
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behavior with exceptions primarily resulting from subtleties of definition. Distinctions
established may appear trivial at times, and boundaries of definition may be perceived
as artificial. The claim of artificiality of boundaries may be true to a certain extent.
However, it is also true that, as Mason undoubtedly said to Dixon, we've got to draw
the line somewhere. Boundaries must be established to make the category a valid one;
i.e., to restrict "tool use" to a meaningful subset of the behaviors performed by
organisms. The restrictions placed by the current definition represent an endeavor to
isolate tool use to a restricted set of behavioral adaptations. Social manipulations of
others are excluded because these actions expand the range of the definition to an
increasingly widening set of behaviors and produce fuzziness in the boundaries of this
category. Likewise, adaptations such as the spider's web and the skunk's spray are
excluded to preserve the requirement that tool use represent behavioral adaptations
that compensate for the restrictions of morphology. In this respect, the classification of
structure building as tool-using behavior fits well. Functionally, the behavior acts to
compensate for morphological restrictions. Structurally, the behavioral components are
comparable to the manipulations associated with other tool-using behaviors (selecting,
carrying, orienting, etc.).

What does animal tool use have to do with intelligence? At one time, a strong
relationship between tool use and intelligence was postulated, even assumed. Pioneers
in this field often considered tool use the exclusive domain of man and some even took
tool use (and later, tool making) as one of the defining characteristics of man (e.g.,
Oakley 1964, Gruber 1969). However, Hall (1963) argued that tool use behavior is not
an index of intelligence, but rather, indicative of behavioral adaptations to the environment.
Alcock (1972) proposed that current instances of tool use originated by "the novel
use of a pre-existing behavior pattern" (p. 466). Once established, selection acts on the
new behavior pattern if this new pattern provides an adaptive advantage. Alcock's
example for insects was the sand-throwing behavior performed by ant-lions and worm-
lions. These larvae remove sand from their prey pits by the characteristic head dorsif-
lexion. According to Alcock,

All that would be required for the origin of sand throwing at prey is an individual
with a low threshold for the performance of the action. A passing prey or a
struggling one which dislodged some sand grains might trigger sand throwing,
be struck by some particles, and be captured by the pioneer tool-users in ant-lion
and worm-lion populations. (p. 466).

This pre-adaptation hypothesis is a plausible explanation for other instances of tool
use. For instance, McDonald (1984—see above) demonstrated that soil dropping is a
response elicited by liquids near the nest. Given that carrying foods back to the nest is
an elicited response to a food stimulus, a liquid food source near the nest might have
produced both behaviors as a response. Tool use then results from pre-existing behavior
patterns. As another example, Moglich and Alpert (1979) noted that C. bicolor, like
many different ant species, cover odor sources and other objects (like liquids—see above)
with soil or other materials. This initial behavior pattern could have served as the
preadaptation for the specific stone dropping behavior in response to competitor nests.
As final examples, the two uses of tools to increase acoustical effectiveness (sound
baffles in leaves and acoustical burrows) may have arisen from the simultaneous execu-
tion of two separate behavior patterns. In the case of acoustic burrows, an advantage
would have arisen when a male called while constructing the burrow if this behavior
produced a louder signal. As evidence for this point, males call from the front of the
burrow while facing inward (Nickerson et al. 1979). In the case of sound baffling by use
of a leaf, the fortuitous production of this effect could have arisen when a cricket stridu-
lated while feeding. Prozesky-Schulze et al. (1975) noted that the pear-shaped hole used
for baffling differs from the "irregularly shaped feeding holes" (p. 142), but this per se
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does not rule out a preadaptation explanation. Thus, to answer the question posed earlier, tool use, at least in insects, has nothing to do with intelligence. Of the eight main categories of tool use described, each instance enables the animal to increase the efficiency or effectiveness with which it obtains a goal and thus gain a selective advantage over individuals who do not perform this behavior. Rather than indices of intelligence, tool-using behaviors are adaptations to compensate for morphological restrictions; adaptations which are shaped by selection pressures and guided by evolutionary processes.

Postscript: A Request

This review was intended to be an exhaustive survey of tool use by insects, but its comprehensiveness is limited to the scope of the reference tools used. I fully expect that I have missed some (few, I hope) examples of insect tool use. Readers aware of any references overlooked are invited to chastise me at the address given at the front of this article, so that a complete catalogue, if warranted, can be composed at a later date.

Acknowledgments

The helpful comments and suggestions of James E. Lloyd, Donald A. Dewsbury, Bruce Fergusson, and D. Kim Sawrey are gratefully acknowledged. Also, thanks go to Thomas J. Walker and John H. Kaufmann for critical readings of earlier forms of this article.

Literature Cited


