distributions to estimate the result in the larger population. Statistical distributions use the mean and standard deviation obtained in the sample to estimate the mean and standard deviation in the population, provided certain assumptions are met. Although different statistical tests carry different sets of assumptions, all tests assume that the observed sample was selected at random from the population and assigned randomly to different treatment groups. Provided the assumptions are met, statistical distributions allow researchers to determine the likelihood that the effect observed in their sample reflects a real effect in the population. Some common types of statistical distributions include the Student's t distribution, the F distribution, and the Chi-Square distribution; these are most commonly used with the Student's t test, the F test, and the Chi-Square test, respectively.

Cross-References

► Model Fitting
► Reaction Time

References

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Stone Tools

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Synonyms

Animal tool use; Archaeology; Behavioral evolution; Lithic technology; Primate behavior

Definition

A stone tool is a single, typically moveable piece of rock that is used by an animal to effect a change on its environment. The rock may be modified before use and may be used, either attached or unattached to other objects, as one part of a multi-component tool system.

Introduction

Because of their durability and ubiquity in the human archaeological record, stone tools are the central piece of evidence available for the long-term study of human behavior. The earliest known stone implements date back 3.3 million years in Lomekwi, Kenya, and they have been used by human societies up to the present day. The hard surfaces and ability to form a cutting edge that rocks provide have made them invaluable for tasks such as pounding, slicing, scraping, and grinding and for the formation of symbolic objects.

The importance of stone tools to human evolution has increasingly made them a target for comparative observations and experiments in nonhuman animals (hereafter, animals). Particularly among primates, but also other animals such as corvids, stones have been used in studies of social transmission, behavioral ecology, and physical cognition and as analogies for the development of human behavior. In both wild and captive settings, stone tools have formed the basis for the exploration of cultural capacities in animal groups. In this entry I focus on wild activities – those observed among animals in their natural habitats rather than in zoos, laboratories, or sanctuaries – although the influence of captive studies will also be considered.

Why Use Stones?

Stones have two main qualities that render them effective tools: they are abundant and durable. Rocks are typically available on or near the surface of all parts of the planet, excluding those that

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have high levels of sediment or ice buildup, such as river floodplains and glaciers. Unlike other tool materials such as plants, they can be found from the tops of mountains to the depths of the ocean, making them accessible to all forms of animal life. Stones also naturally weather into a variety of sizes, from silt and sand to pebbles and boulders, which means that animals of all sizes can manipulate them.

Stones range in hardness from those that usually crumble under slight pressure, such as mudstones, to those that will withstand repeated impacts, such as basalt and granite. The durability of the latter means that they can be relied upon when needed as a tool, which in turn allows for tool use to become entrenched within a given animal's behavioral repertoire. An additional property of some rocks, that they can be conchoidally fractured to produce useable sharp and robust cutting edges, appears to have been discovered only by members of the human lineage (the hominins) since our split from other African apes over 6 million years ago. However, as discussed below, recent discoveries among wild capuchins suggest that production of sharp-edged stones is not unique to humans.

Stone-Tool-Using Animals

Comprehensive surveys of tool-using animals that include anecdotal accounts exist elsewhere (Shumaker et al. 2011), and the current discussion is therefore intended to be informative rather than exhaustive. Most attention has been directed toward primate use of stone tools, driven initially by observations among East African chimpanzees (*Pan troglodytes schweinfurthii*) in the latter half of the twentieth century (Goodall 1964). The Gombe Stream National Park chimpanzees threw rocks in an aggressive manner toward researchers and baboons, although they did not otherwise use stones as tools. It was only later discovered that some communities of West African chimpanzees (*P.t. verus*) habitually used unmodified stones as handheld hammers to break open encased nuts (Boesch and Boesch-Achermann 2000; Matsuzawa 2011). The fact that these communities cluster around the junction of modern-day Ivory Coast, Guinea, and Liberia, while other well-studied West African groups such as the Fongoli chimpanzees do not appear to use stone tools, suggests that stone pounding emerged independently in that region, perhaps as recently as a few hundred thousand years ago (Haslam 2014). In any case, the geographical, phylogenetic, and functional restriction of chimpanzee stone tool use to nut-cracking in *P.t. verus* indicates that it is likely a specialized, derived behavior in this subspecies. Recent reports of West African chimpanzees accumulating rocks in and around specific trees, accompanied by displays that include drumming and vocalizing, add an interesting although as yet under-explored component to this picture (Kühl et al. 2016).

The possibility that chimpanzees and humans shared a common, stone-tool-using ancestor is diminished by the absence of such activities among the second *Pan* branch, bonobos (*P. paniscus*). Similarly, there is no evidence as yet of wild stone technology among the other great apes: gorillas and orangutans. Moving further out along the primate family tree, the next species that has been observed to commonly use stone tools under natural conditions is the long-tailed macaque (*Macaca fascicularis*) of Southeast Asia. Macaques in coastal areas of both Thailand and Myanmar use stones to break open a wide variety of shoreline species, particularly shellfish such as oysters and gastropods living in the intertidal zone (Gumert and Malaivijitnond 2013). While the gastropods are cracked open on an anvil using a handheld hammerstone, similar to chimpanzee nut-cracking, oysters are opened using precise strikes onto the shell, while they remain attached to a rocky substrate. This behavior requires the macaques to strike not just downward, as West African chimpanzees do, but sideways and occasionally even upward to access an oyster. Macaques do also crack nuts, especially the sea almond (Falótico et al. 2017), but their focus on animal, often mobile, prey differentiates them from other stone-tool-using primates. Their geographic and phylogenetic separation from the African great apes indicates that they too have independently converged on this behavior.

Moving across to the New World monkeys, the final species of known habitual stone-tool-using primate is the bearded capuchin (*Sapajus libidinosus*). These animals predominantly use their tools to crack open encased nuts, fruits, and seeds, including some with relatively hard shells that require full-body extension to raise a pounding stone to the required height before striking (Visalberghi et al. 2015). However, some wild capuchin groups have also developed the use of stones as aids when digging for underground foods such as arachnids and tubers and for directly percussing a handheld stone against a stationary rock, fracturing the former and releasing quartzite dust (Falótico and Ottoni 2016). The fracturing behavior, termed stone-on-stone (SoS) percussion, produces sharp-edged, conchoidally fractured pieces that possess the same technological characteristics as early human flaked tools (Proffitt et al. 2016). However, the capuchins do not use the sharp flakes, instead licking and sniffing at the dust released by their activities for reasons that are currently unclear. Female capuchins may also engage in aimed stone throwing to attract the attention of males as a form of sexual display which, along with SoS percussion, provides examples of non-foraging-related use of rock tools. Given that tool use among wild platyrrhines is very rare, the evolution of these behaviors is a further example of primate convergence on stone technology.

Outside the primates, there are few examples of habitual use of rocks as tools. However, those that have been observed offer insights into the ways that stones can be aligned with the anatomy and activities of non-primate species. In birds, for example, Egyptian vultures (*Neophron percnopterus*) have repeatedly been observed using their beaks to drop or throw stones onto ostrich eggs to access the yolk inside. This behavior has been suggested to be prompted by environmental cues rather than strongly heritable or learned (Carrete et al. 2017). Dropping as a means of opening encased foods is more widely spread among birds, although in most cases, it is the food that is dropped rather than a stone, which under current definitions does not make this activity tool use. Nevertheless, by dropping food onto stone anvils, birds make use of a specific part of their environment that requires precision and planning, much the same way that stone tool use does. For example, groups of wild New Caledonian crows (*Corvus moneduloides*) repeatedly drop candlenuts onto the same stone blocks (Hunt et al. 2002), suggesting that these stone anvils are selected for their usefulness. A similar anvil-based behavior has been reported for wild tuskfish (*Choerodon* spp.) in breaking open molluscs and other prey (Harborne and Tholan 2016).

The most prolific wild non-primate stone tool user is the sea otter (*Enhydra lutris*). Members of this species that specialize in feeding on tough-shelled prey such as marine snails and bivalves are most likely to employ rocks during foraging, partly as a result of high encounter rates with these prey (Fujii et al. 2015). The otters typically dive to collect their prey from under the water but return to the surface to feed while lying on their back. On occasion, otters also bring up a stone that they hold on their chest and strike the prey against, while stones also may be used as paw-held hammers. Genetic studies show that relatedness is not one of the main determining factors for whether an individual sea otter uses tools (Ralls et al. 2017), but instead this behavior may be a result of competition among specialized mollusc feeders.

As noted, rocks come in a variety of grain sizes, which has enabled some smaller invertebrates to become stone tool users. Notable among these are the corolla spiders (*Ariadna* sp.) of Namibia, which arrange a circle of usually 7–8 quartz grains around their burrow. These grains are typically less than a centimeter in width, and the spider attaches a taut thread to each of them as a means of detecting any prey that disturbs the circle (Henschel 1995). The fact that the spider first positions, and then is in remote contact with, each stone qualifies this behavior as tool use, although it differs from the percussive activities prevalent in other species. A second invertebrate example of stone use is found in the larvae of flies such as *Myrmeleon* sp., known as ant lions, who project sand grains toward prey (Pierce 1986). The result is to cause the prey to fall into a conical pit that has been previously been excavated by the ant lion, enabling capture. Habitual stone tool use for non-foraging activities has yet to be described in an invertebrate species.

Stone Tool Function

Leaving aside the symbolic and cutting functions associated with hominin lithic technology, the primary use of stone tools is force transmission and amplification. The most common targets of mammalian (primate and sea otter) rock use are encased foods, including nuts, seeds, and molluscs, that are difficult or impossible for the animal to open using only its teeth and hands or paws. For those capuchin groups that engage in the practice, digging activities also involve percussion, in that the stone is used to forcefully break up tough sediments and assist with enlarging holes. The same purpose underlies Egyptian vulture stone tool use and indirectly applies to those species such as New Caledonian crows and tuskfish that drop or throw food onto specific stone anvils. Capuchin SoS percussion does not have an intermediate target such as a nut, which means that even greater force is transmitted between the hammerstone and the underlying anvil or passive stone, contributing to the likelihood of hammerstone fracture (Proffitt et al. 2016).

Force transmission is relevant to those species that throw or project rocks toward targets. The high density of many stone materials ensures that they are less affected by air friction or winds during their flight than other materials such as leaves or grass. This characteristic means that the force imparted to the stone by the thrower is more readily transferred to the target on impact, as seen in the case of ant lions or chimpanzees. The West African chimpanzees that accumulate stones around trees may also be making use of force transmission to generate loud noises from the contact between the stone and tree trunk or buttresses. Throwing stones is therefore typically not a stealthy activity, even leaving aside direct contact with an intended target, and this feature is exploited by capuchins during sexual displays. Even a stone that misses its target will usually cause a disturbance that startles the target and draws its attention toward the thrower, which is the apparent intention of female capuchins.

The case of corolla spider stone tools is unusual in that, while it is still foraging-related, it does not involve the stone directly amplifying or transmitting a force from the user to the target. Instead, a passing prey animal causes vibrations in the arranged quartz grains, which in turn alert the spider to its direction and proximity through the attached web strands. In this manner the corolla spider incorporates stones into a multicomponent compound tool, built to serve the same vibration-based detection strategy practiced by many web-spinning spiders.

Stone Tools and Animal Cognition

The implications of stone tool use for animal cognition have been investigated for several decades, both because of its potential relevance for comparative studies with human cognition and for the study of animal behavior in its own right. One of the common features that apply to all known stone-tool-using animals is the selection of appropriate materials from a heterogenous background of available rocks. For example, both bearded capuchins and West African chimpanzees in their natural habitats have been shown to match the weight and material (and thereby density) of a hammerstone to the toughness of the nut that they need to break open (Visalberghi et al. 2015). Wild long-tailed macaques in Thailand also select larger stone tools to open larger prey items (Gumert and Malaivijitnond 2013), and Egyptian vultures preferentially throw smooth over jagged pebbles at ostrich eggs (Thouless et al. 1989). Such selection does not necessarily require complex brains, as the width of the quartz grains arranged by a corolla spider also closely tracks the spider's body size and the diameter of its burrow (Henschel 1995). This universal selection process derives from the fact that not all stone materials are suitable for all tasks. Tool selection is therefore often likely to be driven by the functional fit between a rock's affordances, an animal's physical capability, and the required outcome, rather than a conscious decision-making process.

Rocks that are suitable for use as tools are not always available in the immediate vicinity of the site where they are needed, so all wild stone tool users also transport materials. Transport distances can range from centimeters in the case of the corolla spider to tens or hundreds of meters for monkeys and vultures, to kilometers for chimpanzees (Luncz et al. 2016), although in each case the cumulative effect of multiple movements through time may increase the overall distance that a given tool travels. Transport costs can also affect stone selection, for example, wild capuchins have been experimentally shown to transport lighter stones when the subsequent travel distance to an anvil is extended (Visalberghi et al. 2015). Both hammer and anvil stones are transported by wild capuchins cracking cashew nuts in Brazil, chimpanzees breaking palm nuts in Guinea, and sea otters in the eastern Pacific (Haslam et al. 2017). Anvil transport has yet to be documented in wild macaques, although its future discovery by researchers or innovation by the macaques cannot be ruled out. In the case of both selection and transport, an animal needs to be able to recognize technically salient aspects of the available rocks, including characteristics such as density that may not be immediately visually obvious. The solution employed by most animals is haptic, by touching, moving, and sometimes lifting a potential tool in order to assess its suitability.

Collectively, the selection and transport of rock material to tool use sites is part of a process by which these materials are incorporated into what has been described as a body-plus-tool system (Mangalam and Fragaszy 2016). In this scheme, tools become an embodied part of the animal's perception of itself, in effect meaning that feedback (such as vibrations and shifts in tool weight distribution) is experienced by the animal as occurring to a part of its own body. This kind of material cognition may even extend to the environmental niches created by tool-using animals, as they repeatedly bring objects and the targets of tool use together in specific locations on the landscape (Mosley and Haslam 2016). The long-term durability of stone tools and anvils means that such collection points both lower the costs of assembling such sites for future tool users and provide a scaffold for the more rapid learning or adoption of tool use by juvenile group members. In wild stone-tool-using primates, this learning process typically involves years of play and practice before full proficiency is achieved, while in corolla spiders and Egyptian vultures, the behavior appears to occur spontaneously.

Stone Tools and Social Behavior

Beyond documenting the development of individual skills, stone tools have assisted with investigations into the emergence and spread of group-specific behaviors. Where these behaviors extend in time and across multiple individuals in an interacting group, they can be considered traditions, and sets of traditions that differentiate one group or community from another may be labeled animal cultures. Experiments with captive animals, particularly chimpanzees (although not necessarily of the West African subspecies), have repeatedly demonstrated how social transmission of novel behaviors can occur (Whiten 2017). Cultures and traditions can involve any aspect of shared, learned behavior, from vocalizations to social interactions (McGrew 2004) but of relevance to the current instance are those involving rocks.

Wild West African chimpanzees confronted with natural and artificial stone tool selection tasks have demonstrated an ability to learn by observing the actions of others. This spread of social knowledge has involved both the foods suitable for targeting with such tools (Biro et al. 2003) and the materials suitable for use at a given time (Luncz and Boesch 2014). Use of digging rocks by wild capuchins at Serra da Capivara National Park (SCNP), Brazil, but not by groups of the same species at the Fazenda Boa Vista site (which instead dig using their hands), may also be a result of social traditions within these communities. When combined with other differentiating activities that have no clear ecological drivers, such as stick tool use among the SCNP capuchins (Cardoso and Ottoni 2016), the collected suite of distinguishing behaviors suggest that bearded capuchins also exhibit cultural norms. The cultural mechanisms and patterning of New Caledonian crow tool use are subjects of a currently unresolved debate, although these discussions concentrate on plant tool manufacture and use, and stone anvil use has yet to be examined in this light.

Research into sea otter stone tool use has not found social learning to be an important component of this behavior. Instead, individual learning tied to familiarity with prey species that require or benefit from technological processing seems to be more important determinants. Given that feeding preferences can be transmitted from mother sea otters to their children, tool use may also be indirectly transmitted within specific lineages, but clear evidence for such technological transmission is currently lacking, and group-specific tool use traditions have yet to be identified in this species (Fujii et al. 2015). Vulture rock throwing has seen less research intensity, but both individual and social learning strategies are unlikely explanations for this activity (Carrete et al. 2017). Instead, personality traits that differ between individuals may result in reinforcement of stone tool use in some vultures but not in others, building on a natural propensity for dropping smooth objects. Neither corolla spider nor ant lion tool use has been studied in sufficient detail to discern traditional or cultural patterns, and at present these are assumed to be expressed with little variation by naïve individuals.

Studying behavior in animals removed from their natural environmental and social settings is problematic, especially when the overwhelming influence of human captors is taken into account (Haslam 2013). However, studying animals in laboratory contexts can, at times, allow for researchers to investigate variables that might influence stone technology in a more controlled manner. For example, caged capuchin monkeys spontaneously broke stones that were provided to them by experimenters in a laboratory, in the absence of any immediate need for such broken pieces (Westergaard and Suomi 1994). One of these captive animals also used stones to cut through an acetate barrier to reach a food reward, on occasion breaking the stones to reduce them to a useable size. Similarly, captive bonobos raised as members of an ape-human collective also were encouraged to break stones in order to obtain a cutting edge and get a food reward (Whiten et al. 2009). With practice, these animals were able to remove small, sharp-edged flakes from a larger stone core, although the total assemblage of broken stones that this activity produced were readily distinguishable from those produced by ancient hominins. A juvenile zoo-housed orangutan was also successfully encouraged to break and use stones to cut a cord and retrieve food (Wright 1972). No captive or wild animal of any species is known to have spontaneously flaked and then used cutting stones without human intervention and encouragement, although judging by attempts to date, it is likely that an individual could eventually be trained to produce and use simple stone assemblages that mimic hominin flaking.

Using captive animals to investigate the development of behaviors that naturally occur within their own species, rather than attempting to get them to imitate hominins, adds a level of ecological veracity. For example, chimpanzee social learning of nut-cracking with stone tools has been demonstrated under captive, sanctuary conditions (Whiten 2017). This work showed that, provided individuals had reached a similar age to that seen among proficient wild West African chimpanzees, socially observing nut-cracking increased an individual's own nut-cracking activities. The East African chimpanzee subspecies (*P. t. schweinfurthii*) studied in this experiment does not presently use stone tools in the wild, which lends further weight to the conclusion that wild chimpanzee nut-cracking in West Africa is derived and cultural rather than solely genetically mediated.

Social transport and use of rocks results in the nonrandom accumulation of durable materials across a landscape. While the actions of a single individual may be difficult to identify and interpret, the repeated activities of a social group build up an often unintended but distinctive assemblage of related tools. This basic principle underlies the search for and analysis of sites created by hominins over the past few million years (see below), enabling their archaeological investigation. However, since the start of the twenty-first century, archaeologists have increasingly turned their attention to the stone assemblages left by wild animals, building on prior work that recognized the value of reconstructing chimpanzee behavior from widespread and patterned activities such as nest building (Stewart et al. 2011). Initially conceived of as chimpanzee or primate archaeology, and at present still dominated by excavations and analysis of primate stone pounding behavior, this work is growing to encompass other stone tool using species (Haslam et al. 2017). Although in its early stages, this practice adds an extended temporal dimension to the behavioral work on wild primates conducted over the past 50 years, enabling direct investigation of topics such as the longevity and geographical spread of stone tool traditions and the identification of tool use in vanished animal populations.

Human Stone Tools in Animal Context

This section summarizes the major trends in hominin lithic technology, as currently understood, in order to contextualize the preceding discussion of animal stone tool use. The key difference between the two is that members of the human lineage developed a reliance on breaking stone tools to form either useful edges or intentional shapes. While hominins have also likely used pounding tools for force amplification throughout our technological history, those tools are often difficult for archaeologists to distinguish from naturally occurring rocks. Advances in the study of use-damage patterns on pounding tools hold promise but are in their infancy when detecting early percussive stones (Haslam et al. 2017). The story of human stone tool use is therefore almost exclusively derived from flaked stones, including assessments of cognitive and manual abilities and social information transmission.

As noted, the earliest known flaked stone tools come from the 3.3 million-year-old Lomekwi 3 site in Kenya (Harmand et al. 2015). These tools were accompanied by large rocks that were interpreted as anvils, suggesting that the flakes were broken against those anvils rather than being made by striking one handheld rock against another. The site predates evidence for members of the *Homo* genus by half a million years, leaving a species of *Australopithecus* or *Kenyanthropus* as the most likely creators. A 3.4 million-year-old site in Ethiopia also has evidence for animal butchery using stone tools, although in that case the cut-marked bones, rather than the tools themselves, were recovered (McPherron et al. 2010).

There is no reason to assume that, once Lomekwian technology was invented, all hominins used flaked stones for the subsequent 3.5 million years. The early stone record is very patchy, and the next identifiable flaked stone tools after Lomekwi date from much later at 2.6 million years ago. These simple broken cobbles are part of the Oldowan tradition, named after the early archaeological site of Olduvai Gorge in Tanzania. *Homo habilis* is assumed to have produced at least some of the Oldowan, although contributions from contemporaneous australopiths cannot be ruled out. Humans continue to make and use simple flaked stones right up to the present day, with additional, more complex, stages added onto this foundation.

The second major step in hominin lithic technology was the deliberate shaping of large tools to produce cutting and chopping edges, sometimes with symmetrical shapes. This tradition is called the Acheulean, after the French site of Saint-Acheul, and it emerged around 1.7 million years ago. This timing roughly coincides with early records of *Homo erectus*, who had a much enlarged brain compared to prior hominins, and there are strong associations between this species and the Acheulean at a number of sites. Like the Oldowan, much of the Acheulean is assumed to have been targeted at carcass processing, as meat increasingly entered hominin diets. *H. erectus* was the first hominin to range widely across the Old World, and its enhanced technological skills would have been a crucial part of that process.

The final major step in hominin stone technology starts at different times in different places but was underway by around half a million years ago.

At that point a number of *Homo* species were emerging in Africa and Eurasia, including *H. neanderthalensis* and the Denisovans, and the complexity and interbreeding revealed by recent genetic studies suggests that we should be cautious in assigning any one tool tradition to a given species without direct fossil association (Stringer 2016). Variously known as the Middle Stone Age or Middle Paleolithic, this stage involved creating smaller, more complex stone tools that were likely combined into composite tools such as spears and hafted scrapers. In some parts of the world, such as Europe, the more recent parts of this tradition involved long stone blades and tiny microliths (these form part of the European "Upper Paleolithic"), but these are not universal developments and cannot be generalized to other regions.

The overall trend in human lithic technology is the development of tool forms that require more precision and more planning in their manufacture and the development of a toolkit that joins stones to other materials using adhesives and binding. Force transmission remains a central part of the function of these tools, including through the focusing of human strength into small surface areas such as a thin cutting edge or the tip of a spear. However, tasks such as scraping and shaping require more precision and modulation of force than simple percussion. It is also clear that humans began imbuing their tools with symbolic meaning, that is, the stones played a role in a wider worldview that was not solely determined by tool shape, material, or usefulness. The origins of symbolic thought are debated, but they were present at least 100,000 years ago.

The human lineage has converged on the same role for stone tools as each of the other animals discussed above. They are used to change human muscular force into an amplified, concentrated, or spatially transmitted form, and they are used as parts of multicomponent tools. Human tendency toward tool use appears to be innate, as in the other species, except that humans rely on object manipulation and combination to a much greater degree than in other species, and they bolster this process with knowledge storage mechanisms underpinned by language. That said, modern humans do not automatically develop the ability to make even simple Oldowan tools, and like the other tool-using primates, they have to go through a learning period involving repeated trial and error in a social context. It is therefore most likely that earlier humans required the same learning process, during which skills such as the ability to select and transport the correct raw materials were honed.

In this light, the essential difference between human stone tools and those of the mammals, birds, and invertebrates is an ability to derive seemingly innumerable novel technological solutions to risky problems. Humans developed a toolkit that combined stone-, plant-, and animal-derived tools and became reliant on that toolkit to survive in the varied environments into which they dispersed. Animal tool use is, on the other hand, built on specific tools for specific tasks, with little to no flexibility in how those tasks are performed. The animal approach ensures a high degree of success in tool use activities, but it limits those activities to locations with appropriate materials for practice and performance. Human cooperation and reliance on social information enhances the speed and efficiency with which we learn about the affordances of objects around us, although again this is likely to be a difference of degree and not kind, at least when compared with other mammalian stone tool users.

Conclusion

The usefulness of rocks for force amplification has been discovered multiple times among the primates and in a small number of other taxa. Considering the ubiquity of stones at all time periods, it is probable that the pounding, throwing, and force transmission behaviors seen among living animals were also present in extinct species and in prior members of extant lineages that no longer use such tools. However, recovering evidence of such activities will require further investigation into the use-damage patterns that they would leave on the tools. Where we might currently expect stone tool use but find none – in East African and Central African chimpanzees, for instance – then archaeological research may well turn up evidence for such use in ancestors of those species living thousands or millions of years ago. Loss of stone technology, which may have happened several times among various early hominins, needs investigation just as much as its innovation and spread.

Inventive, non-primate taxa such as wild octopuses, elephants, cetaceans, and corvids are targets for further research into possible stone use. Given the addition in the past decade of well-studied taxa such as wild capuchins and macaques to the known stone-tool-users club, and the comparatively limited investigation of such behavior among invertebrates and aquatic animals, we can be certain that additional wild species will be found using stone tools in future. Of particular relevance to that search will be those animals that consume encased foods or whose foraging can be performed more efficiently by forcefully breaking down barriers. Animal stone tool use has probably always been a rare behavior, with its associated costs of tool selection and handling, but the variety of living species that have converged on it indicates a solution that will have emerged time and again throughout the history of animal life.

Cross-References

▶ Bill McGrew
▶ Catarrhine Cognition
▶ Comparative Cognition
▶ Convergent Evolution
▶ Cultural Transmission
▶ Culture
▶ Cumulative Culture
▶ Dorothy Fragaszy
▶ Elisabetta Visalberghi
▶ Embodied Cognition
▶ *Homo erectus*
▶ *Homo ergaster*
▶ *Homo heidelbergensis*
▶ *Homo sapiens*
▶ Jane Goodall
▶ Kanzi
▶ Louis Leakey
▶ Lucy
▶ Mustelidae Cognition
▶ Nut-Cracking
▶ Perception-Action Theory
▶ Platyrrhine Cognition
▶ Primate Cognition
▶ Social Learning
▶ Taï Chimpanzees
▶ Teaching
▶ Technical Intelligence Hypothesis
▶ Tool Use

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Stop-Signal Task

► Go/No-Go Procedure

Storage Site of Nuclear Material

► Nucleus

Strategy Reversibility

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Synonyms

Behavior plasticity; Phenotypic reversibility; Reversible plasticity

Definition

Concept that behavioral and phenotypic adaptations are plastic, or flexible, in the environment and can induce or retract their expression.

Introduction

For every adaptation or strategy developed to maximize an animal's fitness in the wild, there is also the capacity for the reversal of these traits. Strategy reversibility is a phenomenon that can occur on different temporal scales and via different mechanisms. Depending on the context, reversibility can be morphologically or behaviorally phenotypic, can involve temporal scales from seconds to thousands of years, and can be responsive to environmental conditions.

Reversal of Traits in Response to Environment

To fully understand the scope of phenotypic plasticity, and therefore strategy reversibility, organisms must be exposed to and observed in environments with changing factors. An experiment that tested predator-induced plasticity in gray tree frog (*Hyla versicolor*) tadpoles revealed that the differences in development were considerable depending on whether or not tadpoles were exposed to predation in their early developmental stages (Relyea 2003). The phenotypic differences observed were both behavioral and morphological in nature as the tadpoles adapted to potential predators in their environment. Differences included responses in activity level, whereby tadpoles that were exposed to predation during early development reduced their activity level considerably and spent a greater amount of time hiding compared to their counterparts without predator exposure. Tadpoles that changed their behavioral strategies in response to predation were more likely to survive to adulthood than tadpoles that did not adapt different behavioral strategies. Upon removal of the threat of predation in their environment, tadpoles were most likely to return to normal patterns of behavior.

Morphological adaptations were less plastic in that the deeper tail fins, shorter bodies, and greater mass developed by tadpoles exposed to predation were not as quickly reversed as behavioral adaptations were. Animals will also respond with plasticity to an environment that has had a new prey item introduced, but in different ways than those exposed to predation (Gabriel et al. 2005).

Reversibility of traits in the natural habitat of these tadpoles would most likely not only affect the individuals of the species but would also have an effect on the ecological community as well.

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