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Beyond food for thought: tool use and manufacture by wild nonhuman primates in nonforaging contexts

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Tool use and manufacture by wild nonhuman primates in nonforaging contexts — an important indicator of their technical intelligence — is widespread across taxa, but is sporadic in occurrence. Such behaviors are usually displayed by one or a few individuals within a population and typically occur in four contexts: aggression, communication and sexual display, hygiene, and in the modification of the environment. The cultural transmission of such tool use is often restricted by several socio-cognitive and ecological factors. Considering the relative rarity of nonforaging tool use in the wild, we recommend the development of standardized methodologies for long-term data collection under natural conditions and the establishment of novel experimental paradigms to conduct comparative studies on captive primates.

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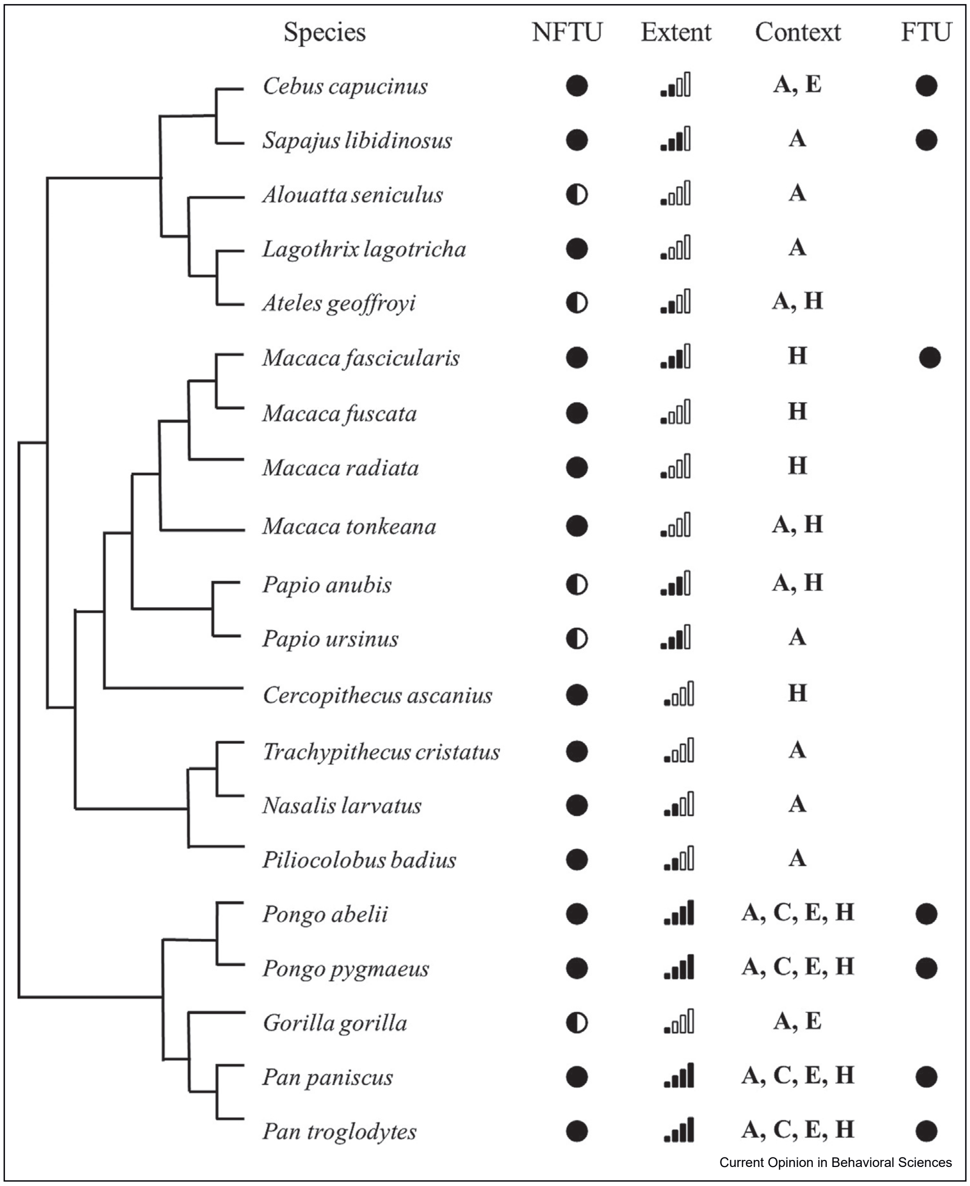
Introduction

The ability to use and manufacture tools is often considered a hallmark of cognitive sophistication in nonhuman primates, although the complexity of the tools used in the wild ranges from simple stereotypes to those more flexible in their structure and function [1,2]. Most reports of habitual tool-use behaviors by nonhuman primates, however, appear to be confined to various contexts of food acquisition, particularly extractive foraging, while those in nonforaging situations continue to remain sporadic and limited [3]. Consequently, our understanding of nonhuman primate material cultures and the evolution of technical intelligence in these lineages has been primarily derived from the available empirical data on tool use in foraging contexts [4,5]. In such a scenario, a systemic review of the rare and possibly neglected records of tool use and manufacture in nonforaging situations is crucially required to understand the limitations of innovation and transmission of material cultural traditions in nonhuman primates. We attempt such a review here in the hope that this brief, but comprehensive, account of the use and manufacture of tools by wild primates in nonforaging contexts will help us locate these behavioral capabilities within the contemporary theories of technical intelligence and its evolution in nonhuman primates. Although not reviewed here, we also draw attention to the observed cases of such tool use and manufacture by primates in captivity, as these can additionally contribute to our understandings of technical intelligence across primate lineages as well.

Tool use and manufacture in nonforaging contexts

An extensive search that we conducted on Google Scholar, using keywords, such as nonhuman primate, monkey, tool use, tooling, tool manufacture, and nonforaging, other than foraging, wild, and their various combinations, yielded more than 500 reports of tool use and manufacture by wild primates. Of these, 20 species used tools in nonforaging contexts, while 15 of these species also manufactured tools. Seven of these species displayed the use of tools in foraging contexts as well (Figure 1). Tool use in nonforaging contexts appears to be rarely and sporadically performed by primates and typically by a single or a few individuals within a population. Our review also indicates that such nonforaging tool use is primarily displayed in four major contexts, which we characterize as (1) agonistic interactions, (2) communication and sexual display, (3) hygienic behavior, and (4) modifications of the immediate environment. We would like to point out here that we have not included object-play by nonhuman primates in this review, as it has traditionally not been considered goal-oriented behavior, and hence, outside the purview of tool use. A novel conceptualization has, however, argued for dynamic mechanical interactions, potentially mediating the flow of information, between a subject and their environment as being constitutive of tool use [33]. Accordingly, we argue for future reconsiderations of object-play as viable exemplars of tool use.

Figure 1



Tool use by wild nonhuman primates in nonforaging contexts. NFTU: records of tool use in nonforaging contexts, ◐: Tool use alone, ●: Tool use and manufacture. Extent: The nonforaging tool-use behavior performed with the highest propensity, : Present, : Rare, : Habitual, : Customary, after van Schaik et al. [6]. Context: A: Agonistic Interactions, C: Communication and Sexual Display, H: Hygienic Behavior, E: Modification of the Immediate Environment. References: *Cebus capucinus* [7–9]; *Sapajus libidinosus* [10–13]; *Alouatta seniculus* [14]; *Lagothrix lagotricha* [12]; *Ateles geoffroyi* [15,16]; *Macaca fascicularis* [17–19]; *Macaca fuscata* [20]; *Macaca radiata* [21]; *M. tonkeana* [22]; *Papio anubis* [23,24]; *Papio ursinus* [25]; *Cercopithecus ascanius* [26]; *Trachypithecus cristatus* [3]; *Nasalis larvatus* [27]; *Piliocolobus badius* [28]; *Pongo abelii* [29]; *Pongo pygmaeus* [29]; *Gorilla gorilla* [30]; *Pan paniscus* [31]; *Pan troglodytes* [32].

Tool use during Agonistic Interactions, which is relatively simple and more widespread across apes, Old World- and New World monkeys, commonly involves the dropping or throwing of detached objects, such as branches, sticks, or stones on conspecific or heterospecific individuals, or clubbing them with such tools (reviewed in Ref. [34]). Aimed throwing, both underarm and overarm, however, appears to be restricted to capuchin monkeys and apes, who seem particularly adept at and commonly use tools to acquire and modify foods. Whether the acquisition of these capabilities for essential foraging purposes provided the schemata for and facilitated the later appearance of such tool use during agonistic interactions remains to be explored.

The use of tools for Communication and Sexual Display is customarily displayed by female capuchin monkeys in Serra da Capivara National Park and in Fazenda Boa Vista, both in Brazil, who respectively throw stones at or push attached or detached branches toward males as part of their regular repertoire of sexual behaviors [35,36], Bornean orangutans, who emit leaf-modified kiss squeaks in response to disturbance and/or fear toward potential predators or other orangutans [37], and by adult or adolescent male and estrous female chimpanzees, who perform leaf-clipping as courtship display or as solicitation of copulation [38,39].

The most diverse form — typically self-directed — of nonforaging tool-use behavioral repertoires among nonhuman primates has been recorded for Hygienic Behavior. Such behaviors could include simple forms, ranging from employing leaves to wipe blood or semen off fur by chimpanzees or using leaf napkins to wipe off sticky latex by orangutans to object-assisted scratching of the body by chimpanzees and orangutans [6,32], as well as more complex acts, such as wound inspection or nasal and dental probing with sticks or twigs by bonnet macaques, who often modify these tools appropriately ([21], Pal et al., abstract, 57th Annual Conference of the Animal Behavior Society, July 2020). It is important to note here that most of these self-directed tool-use behaviors appear to remain restricted to the innovators themselves, disappear from the population, or have been reinvented [37]. Tool use for cleaning purposes — wiping and dabbing — has, however, spread and continues to be persistently performed by certain populations of orangutans and chimpanzees [6,32]. Dental flossing, however, seems to be the only tool-use behavior performed customarily by Old World monkeys — two subspecies of the long-tailed macaque [17,18] — while genital probing by a female bonnet macaque using variously modified tools continues to remain the only case of active tool manufacture in any context — foraging or nonforaging — by a wild-monkey species [21].

Finally, wild primates have been observed to occasionally use tools to modify their immediate environments for the comfort and ease of their daily activities. These include chimpanzees and orangutans using branches as swatters to ward off insects or arranging a bundle of leaves for sleeping comfort [6,32], chimpanzees creating leaf-cushions on wet ground [32], and gorillas using sticks to measure the depth of water and for constructing a bridge to cross a pool of water [30]. From this brief review, it would appear that, as compared with foraging contexts, instances of nonforaging tool use and modification are more sporadic, often restricted to one or a few individuals, constrained in their spread within a population and rarely encountered across communities.

Innovation in tool use and manufacture

Almost all our understanding of tool use in nonhuman primates, ranging from empirical evidence used to test hypotheses and make predictions of technical intelligence in primate lineages to their anthropocentric extrapolations to understand trajectories of hominid evolution, is based on our knowledge of tool-assisted foraging behaviors [2,5,40,41•]. In stark contrast, however, tool use in other-than-foraging contexts has remained largely neglected, possibly due to the relatively fewer records documenting these instances and the absence of statistically comparable quantitative information. Our review, nevertheless, indicates that nonforaging tool use and manufacture is indeed widespread, displayed — albeit sporadically — by a great diversity of primate taxa, performed to accomplish various goal-oriented purposes, and demand appropriate, often unique, cognitive capacities for their successful performance. It may also be important, in the future, we believe, to qualitatively compare the evolution of tool use and modification in foraging and nonforaging contexts, both within and across primate lineages, in efforts to understand their ontogenetic and phylogenetic origins, and whether their underlying cognitive mechanisms have occasionally facilitated their mutual appearance and sustenance, both within individuals and across communities.

Several socioecological and cognitive hypotheses have been proposed and tested, based on the empirical data on nonhuman primate tool use in foraging contexts, to understand the innovations in and the cultural propagation of tool-aided behaviors [5,42••,43]. One such is the ecological necessity hypothesis, which suggests that innovations arise in tool-assisted extractive foraging behaviors when there is a scarcity of preferred or ready-to-access food items and it becomes essential for an individual to exploit alternative, hard-to-access, food resources [44]. While some studies have indeed suggested a correlation between tool-aided foraging and seasonal food scarcities in capuchin monkeys [45], macaques [19], or apes [46], it must be noted that there continues to be ambivalence about whether such generalizations hold across sites and even across tool-using practices. Another proposed hypothesis — the ecological opportunity hypothesis — is not mutually exclusive to the ecological necessity hypothesis and, in fact, proposes that the simultaneous availability of instrumentally relevant objects as well as food materials that can be extracted by such objects may promote the emergence of tool use [44] in such situations. This view has been supported by cross-population studies on tool-assisted foraging behaviors in capuchin monkeys [47], orangutans [44], and chimpanzees [48].

It must, however, be realized, in this connection, that the ecological necessity hypothesis will possibly never be able to explain the evolution of tool use in nonforaging contexts, as situations, such as food particles stuck in one's teeth or sticky substances adhering to the body, may not be important driving factors for innovations to appear and spread across populations. Additionally, the presence of strong, species-specific, behavioral norms that could mediate agonistic exchanges or facilitate sexual communication may not require the development of alternative, culturally spread, repertoires of such behaviors in most species populations. Many individual primates, nevertheless, occasionally confront specific problems of the nature outlined above, and if certain naturally abounding objects, including various plant parts or stones could, through trial-and-error learning, be innovatively used as tools to solve some of these other-than-foraging problems, such experiential learning could quickly establish certain forms of tool use within the lifetime of these tool-employing individuals. Regular interactions with these objects, especially in case of persistent, even if individual-specific, needs could then provide opportunities for the tool-user not only to grasp the affordances of the physical and action-relevant properties of the tools, but also allow them to modify the tools in an appropriate manner and thus, finally contribute to the determination of the object's potential use for a definitive, goal-oriented purpose [21,49••]. Moreover, the relative profitability hypothesis [50] suggests that the relatively higher profitability of a problem being solved through the use of a tool than by its nontool-assisted alternatives will promote tool-use behavior, and this may also be applicable for primates confronting comparatively restricted, nonforaging problems of a personal nature. Consider, for example, the sole female bonnet macaque, who investigated a possible infection in her genitalia with a variety of modified tools; such innovative behaviors, given their individual-specific application, may not, of course, diffuse any further within the community.

Moving from the ecological factors that potentially promote the origin and spread of tool-use behaviors in populations and individual-specific factors that lead to their appearance only in certain individuals, let us now turn to a psycho-cognitive perspective, wherein we examine how psychological predispositions could provide the motivation for an individual to engage in object-assisted behavior, especially when they face specific problems. It has been suggested that certain pre-existing schemata, which could be innately present within an individual, could motivate and allow their everyday interactions and experiences with action-relevant objects to be transformed into individual-specific, affordances, to be used over one's lifetime [51,52•]. Mangalam and Fragaszy [53], for example, propose an embodied theory of tool use, based on the premise that a tool transforms a body-only system into a body-plus-tool system, which could now be employed across situations and tools. We have also discussed earlier how individual experiences of playing with objects during the early part of one's life or using an object as a tool for foraging purposes could also later be used to solve nonforaging problems, when required (see also Refs. [49••,51,52•]).

It should be noted that certain species-specific limitations in limb morphology and consequently, their functional capacities and dexterity during manipulative behavior could also constrain the kind and complexity of tool-use behaviors observed within a species, despite, arguably, the extensive distribution of natural objects that could potentially be used as tools. The conceivably simple acts of dropping or throwing objects, directed at conspecific or heterospecific individuals, for example, have only been recorded in a few populations of Old World monkeys and apes [3]. What must also be remembered is that although there does exist occasional empirical evidence that independently supports some of the hypotheses proposed to explain innovative tool-use behavior, such evidence is often neither explicit nor unambiguous in its applicability. Moreover, some studies show that the various factors driving such innovation are not mutually exclusive but could have mixed effects on the emergence of tool-use behavior [43]. It is thus conceivable that a more comprehensive framework, as, for example, the Comparative Socioecological and Developmental Approach (CSDA), with its combination of socioecological, cognitive, ontogenetic, and phylogenetic perspectives, could be applied more effectively to examine and explain the evolution of tool use in primates, not only within an individual's lifetime but also possibly across generations as well [42••].

Cultural propagation of tool use

We have now shown that the individual nature of the problems that could potentially be solved by tool use in nonforaging contexts often restricts the applicability of such object use to the innovators themselves or rarely among a few others, who may be psychologically motivated to either directly use or have the ability and/or opportunities to recognize the use of such tools within certain domains of need. Are there, however, factors that otherwise hinder the social propagation of tool use in nonforaging contexts and would it be possible to unravel these by examining the available theories on the culturally mediated spread of tool-aided foraging behaviors?

Social and individual learning have been considered as two major pathways for the cultural transmission of behavior, while other factors, such as local ecologies, innately pre-existing schemata, psychological motivation, motor dexterity, and a host of genetic influences, could also play substantial roles in the individual acquisition of behavior, in this case, object manipulation in nonforaging contexts [54•]. Nonforaging tool-use behavior can be broadly categorized into those that are self-directed and those directed toward others. Is it possible that most of the self-directed behaviors fail to be learnt by conspecific individuals, unlike the use of tools directed toward others? Interestingly, although tool use for foraging purposes is also self-directed behavior, many of these appear to effectively spread through the community in due course of time. It can be argued here that it is likely that primate-group members individually possess critically important information on edible and nonedible food items in their environment, having socially learnt their usability in the early days of their lives. Many of these food items could subsequently stimulate and motivate individual primates, especially immature individuals, to not only experiment with ways of obtaining them, even, if need be, with the help of tools, but also observe proficient, tool-assisted, extractive foragers, and practice such behavior, if opportunities arise. These explorations could be mediated, we suggest, by a variety of underlying mechanisms, including, more directly, an intrinsic motivation to use tools [51] or indirectly, by increasing the likelihood of prolonged site presence and interaction with objects, potentially leading to the discovery of various affordances by stimulus enhancement [55•].

What could, however, restrict the self-directed, nonforaging, use of tools to particular individuals within certain situations of need is the failure of other individuals to recognize the applicability of such object-handling, especially if they do not themselves personally experience that specific need at that point of time [Pal et al., abstract, 57th Annual Conference of the Animal Behavior Society, July 2020]. It is also generally true that nonforaging problems tend to be rarer and more individual-specific, with their solutions often being realized in nonsocial contexts than are food-related problems. Conspecific individuals thus tend to have fewer opportunities to observe and learn tool-based behavioral solutions to such problems (but see Refs. [6,31] for a greater diversity of tool use in nonforaging rather than foraging contexts in wild orangutan and bonobo tool repertoires, respectively). In situations, where foraging and nonforaging tool use are both successfully propagated across communities, they may be of comparable necessity, but is it also likely that similar learning pathways coexist for such object manipulation and use?

Table 1

Recommendations for future studies on primate tool use in nonforaging contexts.

1. Opportunistically observed, sporadic behavioral events that constitute tool use by nonhuman primates in nonforaging contexts should not be neglected but documented in as much detail as possible to build up exhaustive databases, which can then be shared across research communities.
2. Once identified, the performance of such behaviors should be followed in the long term and natural experiments designed, if possible, to examine the mechanistic, cognitive, communicative, and cultural processes that may be involved in their further manifestation and propagation.
3. It is imperative that peer-reviewed publications of anecdotal records of tool-assisted and manipulative behaviors, especially in nonforaging contexts, be encouraged and promoted in relevant journals and at suitable conferences.
4. The available qualitative and quantitative information on tool use in nonforaging contexts must be considered while proposing, testing, and validating the various theories and hypotheses on the evolution of technical intelligence in primates.
5. All efforts should be made for comprehensive, comparative studies on the structural, functional, cognitive, and cultural aspects of tool use in foraging and nonforaging contexts.
6. Tool use, displayed in other-than-foraging contexts by nonhuman primates in captivity, needs to be analyzed within an evolutionary framework of technical intelligence, which could also incorporate insights from studies in the wild. Novel experimental paradigms of object manipulation by captive nonhuman primates in nonforaging situations should be developed to examine the processes underlying their emergence, manifestation, and learning under captive conditions.

Concluding remarks

Although it is possible that the innovation and propagation of object use in foraging and nonforaging contexts broadly follow the same evolutionary pathways in primate lineages, certain individual factors, both biological and ecological, may restrict the use of tools in most nonforaging contexts and hinder their social spread within populations. The relative rarity and restricted application of such tools may have also been instrumental in limiting our observations of such tool use and hence, of our knowledge of such phenomena. If we then need to examine the evolution of technical intelligence in nonhuman and human primates, and explore the contributions of tool use in other-than-foraging contexts to these processes, we must develop innovative approaches that can allow us to unravel and understand the cognitive mechanisms underlying such object manipulation. Relatively long-term observations should be conducted on the rare individuals, who perform innovative tool use in nonforaging situations and the pathways that promote or constrain the learning of such techniques by conspecific individuals examined in detail. Moreover, long-term studies across multiple populations will increase the possibility of our encountering similar, even if infrequent, tool-use behaviors in these populations, thus allowing us to comparatively examine their underlying cognitive processes. We could also envisage addressing long-debated questions on the evolution of primate material culture through the design of novel, quasi-environmental, empirical studies at these study sites [56••], while considering, of course, the ethical challenges that may arise with such experimentation, even in natural contexts. We end this brief review with the observation that although tool use in nonforaging contexts may be extremely important for the lives of individual primates, it continues to be one of the least-understood aspects of primate material cultures. We thus make an urgent plea for the future development of innovative studies that would explore the cognitive differences underlying the use of foraging- and nonforaging tools, especially in wild populations of species, such as orangutans or bonobos, which tend to have complex repertoires of other-than-foraging tools. Such more-than-human studies will not only provide insights into the origins and evolution of technical intelligence in nonhuman primates, but also on human cultural evolution, wherein tools may have been increasingly used by our hominoid ancestors in nonforaging contexts, simultaneously with the appearance of complex sociality and rapid intellectual development (Table 1).

Author contributions

The order of authors is arbitrary, as their contributions were equivalent.

Conflict of interest statement

The authors declare no conflict of interest.

Data Availability

No data were used for the research described in the article.

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