frontiers | Frontiers in Mammal Science

TYPE Perspective
PUBLISHED 09 October 2023
DOI 10.3389/fmamm.2023.1281030

OPEN ACCESS

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RECEIVED 21 August 2023
ACCEPTED 20 September 2023
PUBLISHED 09 October 2023

CITATION
Masi S (2023) Tool use, or not tool use, that is the question: is the necessity hypothesis really inconsequential for the African great apes?
Front. Mamm. Sci. 2:1281030.
doi: 10.3389/fmamm.2023.1281030

Tool use, or not tool use, that is the question: is the necessity hypothesis really inconsequential for the African great apes?

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Investigating the drivers of tool use in animals has recently received great attention because of its implication in understanding animals' cognition and the evolution of tool use in hominins. The *necessity hypothesis* posits tool use as a necessary response to food scarcity, but its role is an ongoing debate. The largest body of literature comparing animal tool use frequencies is with regard to primates, particularly comparisons between the *Pan* species. This supports the hypothesis that tool use is rarer in wild bonobos because of differential manipulation abilities of chimpanzees rather than different ecological needs. In this article, I aim to enrich the discussion concerning the *necessity hypothesis* and the ecological drivers of tool use in apes. The higher feeding flexibility of bonobos may be a key aspect to explaining the lower use of feeding tools than that observed in chimpanzees. The diet flexibility of bonobos is similar to that of the lowest level of tool users among the wild great apes: the gorilla. Gorillas can thus help to shed further light on this debate. When fruit is scarce, Western gorillas and bonobos rely more on widely available proteinaceous herbs than chimpanzees, who remain highly frugivorous. Chimpanzees may thus face a greater *necessity* to search for an alternative to obtain high-quality food: tool-assisted feeding. An indirect piece of evidence for this higher level of herbivory is that the prevalence of gut ciliates in bonobos is double that of chimpanzees. In each animal species, a different combination of necessity, opportunities, predisposition, and learning processes are likely to be at play in the emergence of flexible tool use in animals.

KEYWORDS

great apes, tool use, diet flexibility, behavioral predisposition, necessity hypothesis

Introduction

Investigating the drivers of tool use in mammals and birds has recently received much attention because of its relation to brain size, cognition, and culture (Matsuzawa, 2001; Lefebvre et al., 2004; Amodio et al., 2018). Understanding animal variation in tool use frequency has great implications for understanding the evolutionary foundations of tool use in hominins, particularly when studying primates (e.g., Luncz et al., 2019; Haslam, 2022; Lonsdorf and Sanz, 2022; Masi et al., 2022).

Over the past few years, we have witnessed an increase in the use of a more ecological approach in primate cognition studies, including tool use. However, the exploration of ecological drivers is often difficult, and subtle explanations for behavioral variants may remain hidden (Masi, 2011). Furthermore, the impact of ecological factors on a given behavior (e.g., tool use) may be dismissed because of the lack of correlation with environmental indicators (e.g., food availability), raising the question of whether or not the right association of the multiplicity of ecological variables was investigated.

The existence of ecological drivers of tool use in animals is an ongoing debate. Particularly, the *necessity hypothesis* posits tool use as a response to food scarcity, which is driven by the necessity to exploit novel food items during times of low food availability (Fox et al., 1999; Gruber et al., 2012). In this article, I aim to provide new perspectives and to enrich the discussion on the possible ecological drivers for tool-using behavior in the African apes. I underline the differences in their feeding flexibility to refine the discussion of the *necessity hypothesis* as a possible explanation for the large differences in tool use among the great apes.

Tool use and predisposition differences: the *Pan* mystery

Only 13 tool-using behaviors have been documented in wild bonobos (*Pan paniscus*, possibly 14; see Samuni et al., 2022), whereas more than 40 have been described in chimpanzees (*Pan troglodytes*; e.g., Kano, 1982; Ingmanson, 1996; Hohmann and Fruth, 2003; Sanz and Morgan, 2007; Gruber and Clay, 2016; Kalan et al., 2020; Fotang et al., 2023). Today, this difference is generally attributed to the lack of reports of tool use in wild bonobos when foraging (e.g., Samuni et al., 2022). Only one observation of a leaf sponge used to drink water has been documented in the wild (Hohmann and Fruth, 2003) despite the many zoo observations of bonobos using tools to obtain food (e.g., Gold, 2002; Shumaker et al., 2011; Boose et al., 2013). So why, despite their customary use in captivity, do bonobos use tools at a very low frequency and with poorer variety than closely related chimpanzees?

Using both an ecological and a cognitive approach, one recent study directly compared several possible hypotheses in the two *Pan* species for explaining differences in tool use frequency (Furuichi et al., 2014). The differences in tool use repertoires could not be explained by ecological variables (e.g., climate, habitat use, and availability of fruit, social insects, and nuts) investigated in the habitat of two communities representing the two species: the *necessity hypothesis* was thus considered unlikely (Furuichi et al., 2014). Because the comparison did not support the other hypotheses, the authors concluded that differential propensities for tool use between *Pan* species (in the wild) may reflect a divergent behavioral predisposition.

Follow-up studies investigated hypotheses such as the *intrinsic predisposition hypothesis*, which suggested that wild chimpanzees were more inclined to manipulate objects than wild bonobos (Koops et al., 2015a; Koops et al., 2015b). Based on the availability of tools or insect prey, bonobos did not have fewer ecological opportunities to fish for termites, leaving the different *intrinsic* motivation for tool use as the only candidate for explaining the variation between *Pan* species (Koops et al., 2015a). However, given the similar tool use abilities observed in captivity for *Pan* species, a different intrinsic manipulative capacity between them seems implausible. Similarly, such higher tool use in captive bonobos is not explicable by the higher opportunity for social learning in captivity, i.e., proximity to conspecifics, predator absence, and food provision, as suggested for some animal species (Amodio et al., 2018). Indeed, wild bonobos are also highly sociable during feeding (Kano, 1980; Kuroda, 1984; Hohmann and Fruth, 1993; White, 1994; Hohmann and Fruth, 2002; Surbeck and Hohmann, 2008), and experience similar predation pressure to chimpanzees. Furthermore, bonobos, but not chimpanzees, possess a tendon similar to the human flexor pollicis longus, which is responsible for our exceptional tool manufacture/use capacities (Susman et al., 1999; Diogo, 2018).

Having more tool-using models, may young chimpanzees be simply more used to observing individuals grabbing tools/objects than young bonobos, rather than having an intrinsic predisposition? However, this seems unluckily the result of social learning, because the objects manipulated by immature chimpanzees did not include adult tools and the behavior was present already in < 1-year-old infants (Koops et al., 2015b). Therefore, it was suggested that bonobos lost their predisposition for tool use as a trade-off between tool use motivation and social attention (Koops et al., 2015b), in contrast to chimpanzees who focus more on objects (e.g., tools; Kano et al., 2015). If we compare the manipulation data available from different wild chimpanzee communities, manipulation frequencies between the low-tool-using communities (Lamon et al., 2018) and the high-tool-using communities (Koops et al., 2015a; Koops et al., 2015b) indeed seems comparable. However, the most intriguing question is rather, why bonobos could afford to lose such a predisposition? As nutrition is a main driving factor for animal survival, why were social aspects privileged over nutritional ones? One overlooked hypothesis could be that bonobos may meet their nutritional requirements more easily than chimpanzees, particularly when fruit is scarce (Kano and Mulavwa, 1984; but see Yamakoshi, 2004). On the other hand, by engaging in the alternative feeding strategy of tool-assisted feeding, chimpanzees offer youngsters more opportunity for social learning. This could, *per se*, explain the different object manipulation rates found in *Pan* species.

Discussion

Reconsideration of the *necessity hypothesis* for *Pan*

In this framework, do bonobos really need to engage in energetic and cognitively demanding tool use to forage? If the *necessity hypothesis* is not a valid one, then the two *Pan* species should have similar feeding choices given the similar environmental conditions (i.e., food availability).

The previous comparative study investigating ecological correlates for differences in *Pan* tool repertoires excluded the *necessity hypothesis* because fruit availability revealed similar patterns for both species (Furuichi et al., 2014). However, this phenological comparison may be considered with caution as, first, the monthly proportion of trees with ripe fruit provides only a rough estimate of fruit availability in comparison to the estimation of crop abundance (e.g., score 0–4; Chapman et al., 1994). Second, because bonobos and chimpanzees respond differently to fruit scarcity, with bonobos relying less on fallback fruit (see below; Wrangham, 1986; Wrangham et al., 1996; Yamakoshi, 2004), considering the overall forest fruit productivity as opposed to only the species consumed by the apes may lead to an overestimation of fruit availability for bonobos. Finally, the comparison of food spatial distribution included trees of smaller sizes for bonobos (tree diameter: > 5 cm vs. > 10 cm; Furuichi et al., 2014) possibly leads, again, to an overestimation for bonobos. Considering this, and that the results of other previous studies, indicates differences in feeding choices between the two *Pan* species (Wrangham, 1986; Wrangham et al., 1996; Yamakoshi, 2004; Hohmann et al., 2010), a deeper re-examination of these differences in the context of tool use may be worthwhile for reconsidering the *necessity hypothesis*, for which bonobos may have a lower necessity than chimpanzees for tool-assisted feeding.

Both bonobos and chimpanzees are frugivorous and inhabit tropical forests, which are characterized by large seasonal variations in fruit availability (Brockman and van Schaik, 2005). Chimpanzees remain mainly frugivorous throughout the year by continuing to search for fruit when fruit is scarce, concurrently increasing the consumption of leaves and herbs as a secondary fallback strategy (Table 1; Wrangham et al., 1991; Tutin and Fernandez, 1993; Malenky and Wrangham, 1994; Kuroda et al., 1996; Wrangham et al., 1998; Basabose, 2002; Morgan and Sanz, 2006; N'guessan et al., 2009; Koops et al., 2013; Sanz and Morgan, 2013). During the low fruit season, chimpanzees may be more stimulated to search for highly nutritious (tool-needing) food (e.g., honey, ants, termites) to meet their daily nutritional and energetic needs.

Bonobos feed more on high-quality herbs (terrestrial herbaceous vegetation, THV) than chimpanzees do (Malenky and Wrangham, 1994; Wrangham et al., 1996; Yamakoshi, 2004). To feed on herbs (Terada et al., 2015), bonobos visit inundated swamps more often than chimpanzees do (Hashimoto et al., 1998; Morgan et al., 2006; Mulavwa et al., 2010). Because bonobos rely more on vegetative food, they are said to occupy the Western gorillas' (*Gorilla gorilla*) niche in a forest where gorillas are absent (Table 1; Wrangham et al., 1996; Yamakoshi, 2004; see below for more details on the Western gorillas' diet). THV is not only more widely available than fruit, but it also provides high concentrations of nutrients such as proteins, non-structural carbohydrates, and lipids (e.g., Conklin-Brittain et al., 1998; Chapman and Chapman, 2002; Rode et al., 2003; Rothman et al., 2006; Masi et al., 2015). When fruit is scarce, bonobos feed more on herbs and reach nutritional intakes similar to that of chimpanzees (Kano and Mulavwa, 1984; Wrangham et al., 1991; Kuroda et al., 1996; Wrangham et al., 1996; Yamakoshi, 2004; Hohmann et al., 2010). Therefore, each year bonobos show greater flexibility than chimpanzees by consuming more herbaceous plants (Wrangham, 1986; for debate see Yamakoshi, 2004). This is also likely why bonobos have larger party sizes than chimpanzees (Furuichi et al., 2014).

In summary, as they remain mainly frugivorous year-round, during low-fruit periods chimpanzees may have different incentives than bonobos do, thus in turn use different strategies. The different rate of tool use may be the result of different feeding necessities, or a different response to a similar nutritional problem. In this view, chimpanzees are likely to be more constrained by their nutritional needs than bonobos, which may also explain why bonobos use fewer tools, specifically in feeding contexts (Furuichi et al., 2014; compare Sanz and Morgan, 2007 and Hohmann and Fruth, 2003). In addition, given the lower rate of feeding tolerance and food sharing in chimpanzees than in bonobos (Hare et al., 2007; Hare and Kwetuenda, 2010; Wobber et al., 2010; Lucchesi et al., 2021), they may be more likely to rely on alternative feeding strategies to decrease feeding competition.

TABLE 1 Diet comparison among the two *Pan* species and Western gorillas in terms of (annual average) percentage of feeding time spent on each food type.

Species	% fruit	% seeds	% flowers	% leaves	% THV	% bark	% prey
Pan paniscus	55	0	2	14	25	2	2
	(0–100)		(0–7)	(0–28)	(0–100)	(0–11)	(0–3)
Pan troglodytes	64	3	2	16	7	4	4
	(19–99)	(0–30)	(0–14)	(0–56)	(0–27)	(0–41)	(0–28)
Gorilla gorilla	39	–*	1	37**	11	3	7***
	(4–70)		(0–2)	(0–75)	(5–19)	(0–5)	(0–13)

In parenthesis, the minimum and maximum monthly average of the percentage are provided.
THV, terrestrial herbaceous vegetation; % prey includes vertebrates and invertebrates unless specified.
The table was adapted from Conklin-Brittain et al. (2001) for the *Pan* species and from Masi (2008) for the Western gorillas.
* = included in fruit; ** = young leaves only; and *** = insectivory only.

Contribution to the debate of the lowest level tool user: the gorillas

Further support for the *necessity hypothesis* explaining the different tool use rate in *Pan* may be found in the lowest-level tool user among the great apes: the gorilla. However, although only a small amount of tool use was observed in wild gorillas (Breuer et al., 2005; Wittiger and Sunderland-Groves, 2007; Grueter et al., 2013; Kinani and Zimmerman, 2014; Masi et al., 2022), captive gorillas' use of tools is similar to orangutans, bonobos, and even chimpanzees (e.g., Parker et al., 1999; Shumaker et al., 2011). The low tool use has been considered as being linked to the absence of food requiring extractive foraging in a wild diet, rather than to low cognitive and manipulative capacities (McGrew, 1989; van Schaik et al., 1999). However, Western gorillas do rely on extractive foraging to ingest insects or spiny foods (Masi et al., 2012a; Masi et al., 2015; Masi et al., 2022; Auger et al., 2023). Another hypothesis for explaining this low rate of tool use in gorillas is their lower social tolerance and complexity than chimpanzees (Masi et al., 2009, Masi et al., 2012a; Goodall, 1986; Watts, 2003). In orangutans more sociable populations show higher variety of tool use, by providing more opportunities for social learning (Schuppli et al., 2017). The higher sociability and terrestriality of chimpanzees seem also responsible for the greater variety of tool use in comparison to orangutans (Meulman et al., 2012). As gorillas are the most terrestrial apes, sociability and terrestriality together cannot explain the observed differences in ape tool use. Therefore, are there ecological reasons why wild gorillas should not use tools?

If the *necessity hypothesis* explains the low level of tool use in bonobos and gorillas, they should have similar feeding choices. Western gorillas are seasonal frugivores with highly flexible diet (Remis, 1997; Doran-Sheehy et al., 2009; Masi et al., 2015). They change from being highly (70% of feeding time) frugivorous when fruit is available, to highly herbivorous when fruit is scarce (Doran-Sheehy et al., 2009; Masi et al., 2009; Masi et al., 2015; Masi and Breuer, 2018). In contrast to chimpanzees who consume THV as fallback food (Tutin et al., 1991; Wrangham et al., 1991; Kuroda et al., 1996; Wrangham et al., 1998; Koops et al., 2013), Western gorillas consistently consume highly proteinaceous herbs year-round and rely mainly on them and young leaves when fruit is scarce, like bonobos (Table 1; Remis, 1997; Doran-Sheehy et al., 2009; Masi et al., 2015). The presence of symbiotic ciliates in the gorilla gut and their enlarged hindgut (due to its large size) enables them to extract energy from fiber fermentation (Chivers and Hladik, 1980; Lambert, 1998). In the altitude forests, where fruit is scarce, mountain gorillas (*Gorilla beringei beringei*) rely almost entirely on herbaceous plants, thus experiencing even more annual stability in terms of food provision (Watts, 1984; Ganas et al., 2004). Under the *necessity hypothesis*, such higher stability should not stimulate a high rate of tool use, as is the case in the well-studied mountain gorillas.

However, all this raises the question of how bonobos can metabolize energy from fiber vegetation (THV, leaves) if they do not possess the same fermenting abilities of gorillas (i.e., a shorter hindgut tract)? Comparing studies using the same coproscopic method (Masi et al., 2012b; Narat et al., 2015), surprisingly, bonobos are shown to have a much higher density of gut symbiotic ciliates than chimpanzees and Western gorillas do (Figure 1; although study site differences cannot be excluded). Doubling ciliate density likely increases bonobo fermenting abilities (Landsoud-Soukate et al., 1995) in comparison to chimpanzees. Because *Pan* species share the same gut morphophysiology, this provides further indirect evidence of a more herbivorous diet in bonobos. These ciliates are highly present in both chimpanzees' (80%) and bonobos' (94%) feces thus witnessing their biological need for help in fermenting fibers, when compared to gorillas (31%; Masi et al., 2012b; Narat et al., 2015) that do so primarily with the enlarged hindgut.

Lower frugivorous diet and necessity as driver for tool use in primates

In summary, during periods of fruit scarcity, chimpanzees may experience greater nutritional constraints than bonobos and Western gorillas, who generally rely more on a high-quality diet

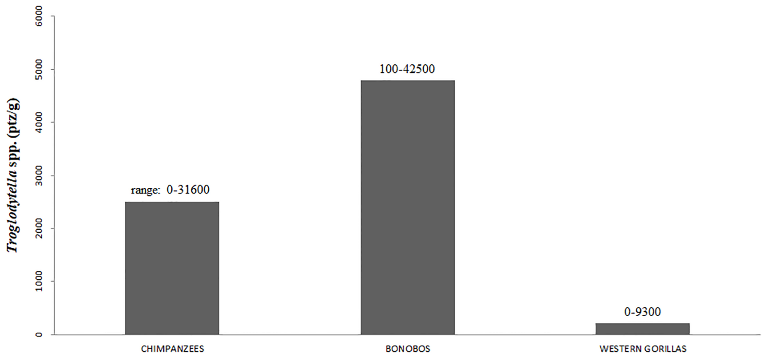

FIGURE 1
Mean corrected abundance of *Troglodytella* spp. (ptz/g) in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and Western gorillas (*Gorilla gorilla*). Ptz is the abbreviation for protozoa. The data were compiled from Masi et al. (2012b; chimpanzees and Western gorillas) and Narat et al. (2015; bonobos) using the same methods. Up on the bar is displayed the range of the corrected ciliate abundance.

by feeding on THV and young leaves (e.g., Wrangham et al., 1991; Kuroda et al., 1996; Wrangham et al., 1996; White, 1998; Doran-Sheehy et al., 2009; Hohmann et al., 2010; Masi et al., 2015). A more herbivorous diet may thus elicit a lower tendency of tool use. Studies on different chimpanzee communities and other primates corroborate this.

In some chimpanzee communities, tool use is negatively correlated with fruit abundance and more leafy diets, leading to lower levels of tool use (Yamakoshi, 1998; Gruber et al., 2016). In savannah chimpanzees, tool use seems a necessary response to lower overall food abundance in comparison to forest habitats (Hernandez-Aguilar et al., 2007; Bogart and Pruetz, 2011). As chimpanzees use tools more after periods of fruit scarcity, necessity is seen as a major factor in the emergence of tool use (Gruber et al., 2012, Gruber et al., 2016; but see Sanz and Morgan, 2013). The largest-scale study on 144 chimpanzee communities showed that environmental variability, such as larger seasonality in rainfall and presence of savannah woodland habitats, fosters within-species behavioral diversification, including tool use (Kalan et al., 2020).

The *necessity hypothesis* seems plausible also when looking at tool-using monkeys. In capuchin monkeys, only groups inhabiting harsh (dryer) environments and experiencing extreme seasonal variation in intakes, use tools at a high frequency (Moura and Lee, 2004; Canale et al., 2009; Lee and Moura, 2015). When compared to the wet season, capuchins show higher tool use rates during the dry season (although no support for the *necessity hypothesis* was found; Spagnoletti et al., 2012; Falótico and Ottoni, 2023). Necessity has thus been suggested to foster tool use in primates (Lee and Moura, 2015). Interestingly, the other monkeys that possess a highly diverse repertoire of feeding tool techniques are the macaques (e.g., Carpenter, 1887; Gumert et al., 2009; Gumert and Malaivijitnond, 2012; Haslam et al., 2016; Falótico et al., 2017; Luncz et al., 2017; Pal et al., 2018). Macaques show advanced ecological flexibility by having adapted to various landscapes, tolerating wide climate fluctuations, often harsh ones (Fa, 1989). To cope with this, unsurprisingly, they show different alternative strategies, such as highly flexible diets and tool use (e.g., using stones to access seafood, Malaivijitnond et al., 2007).

Multifactorial influence on the emergence of tool using behavior

Suggesting that different tool use rates may reflect different diet flexibility highlights that the *necessity hypothesis* deserves further consideration. This view does not exclude the possible contribution of other factors to explain such differences.

In mammals, ecology is thought to be important in shaping the emergence of behavioral flexibility and a feeding-related culture, although the precise impact remains poorly understood (e.g., dolphins: Patterson and Mann, 2011; great apes: Gruber and Clay, 2016; Gruber, 2016; Grund et al., 2019; Kalan et al., 2020). Indeed, the *necessity hypothesis* is difficult to test as it depends on the correlations between tool use rates and multiple variables that may differ according to species habitat and sociality, and past and present environment.

Current directions investigating tool use in different animals underlines the importance of the species' psychological predispositions in flexible tool use (Amodio et al., 2018). An example could be the wadging behavior and leaf sponging in chimpanzees, the latter being the absorption of water with leaves after depriving them of their juice (e.g., Goodall, 1964; McGrew, 1992; Sugiyama, 1995). Although Western gorillas ingest (digest) the whole fig fruit or *Aframomum* piths, chimpanzees make "wadges" out of them by extracting the juice and discarding indigestible fibers (personal observation). The gut's inability to process fibers predisposes chimpanzees to extract juices from plants (wadging), like when they use leaf fibers to adsorb water (*latent solution*, Tennie et al., 2009).

In animals, environment, sociality, and cognition have been identified as main factors influencing the emergence of tool use, invention, and the transmission and retention of culture (Koops et al., 2014). It is likely that the specific behavioral propensity of a species also has its place here. A combination of ecological necessity and opportunities, propensity and learning processes may interplay in different ways in the emergence and maintenance of tool use in wild animals.

Finally, stimulating the discussion at the ecological level for interpreting behavioral differences in tool use will hopefully encourage future work in investigating in greater detail the interacting roles of environment (diet) with the cognitive abilities and behavioral predisposition of the study species.

Author contributions

SM: conceptualization; investigation; writing—original draft; and writing—review and editing.

Funding

Funding was received from the Muséum Nationale d'Histoire Naturelle. The author declares that financial support was received for the research, authorship, and/or publication of this article.

Acknowledgments

I thank Claudio Tennie, Victor Narat, Thomas Breuer, Laura Muniz, and Antonio Sanna for useful comments. I thank the relevant institutions that supported and granted me my long-term work: WWF Central African Republic (CAR), Dzanga-Ndoki National Park, Ministries of Education and Water and Forests of the CAR, University of Rome La Sapienza, Max Planck Institute, Muséum national d'Histoire naturelle (MNHN), Cleveland Metro Park Zoo, Action Transversal du Muséum, Federative Projects of the Department of "Homme et Environnement" of MNHN, LabEx BCDiv, ANR SAFEAPE, and CNRS. Lastly, I thank very much Steven Emilio Churchill for his review work.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author SM declares that they were an editorial board member of Frontiers at the time of submission. This had no impact on the peer-review process and the final decision.

Publisher's note

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