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Why Don't All Animals Use Tools?

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Abstract – Tools give humans superpowers, so why don't all animals use them? Though technology is ubiquitous in our own species, we remain unable to predict when, why, and among whom tool use will arise elsewhere in the animal kingdom. Recent decades' research by biologists, ethologists, and archaeologists has displaced a longstanding scientific rendering of humans as the exclusive tool-using taxon. Tool users inhabit diverse bodies and environments; from ants to archerfish, crabs to cockatoos. Many of these animals engage in tool use with bodies, minds, and sensory apparatuses, in habitats, and at scales very unlike our own. Given this recent sea-change in our understanding of *who can be a tool user,* we are presented with an opportunity to return to first principles. What exactly is tool use? Who are tool users, and what unites them? Is it possible—or even useful—to identify common traits, qualities, circumstances, or conditions among phylogenetically disparate tool-users? What does tool use tell us that we need to know? Here we take a pragmatic approach and define tools as enabling objects, and tool use as attentional use of such objects, agnostic to neural and physical anatomy. In reviewing animal technologies we identify active, timely feedback loops as critical for tool use adoption. Cybernetics emerges as an appropriate analytical framework; tool-using animals are temporary natural cyborgs. Ideas from game theory and behavioral economics then inform how technological innovations stabilize or vanish. We conclude that while nearly all animals can use tools, many face prohibitive physical, sensory, and social constraints, coupled to chance events. Viewing this behavior not as a fixed trait but as contingent, dynamic and continually reliant on environmental support offers insight into captive animal tool use and the partial uptake of tools in cohabiting groups. Our approach situates the hyper-reliance of humans on tools within our evolutionary milieu, and eliminates the need for special pleading when tool use arises in nonhuman contexts.

Keywords – Tool use, Technology, Feedback, Cyborg, Umwelt, Evolutionarily stable strategy

Animals across the planet use tools in their natural habitats, including social and solitary insects, arachnids, molluscs, birds, crustaceans, fish, and mammals of the land and sea (Shumaker et al., 2024). Despite this abundance, humans still tend to consider ourselves Earth's prototypical tool users. Our complex technologies and their deep antiquity in our lineage (Harmand et al., 2015) led at times to tools—no matter the user—being proposed as special markers of human-like dexterity, flexible behavior, social learning and intelligence (Cantlon & Piantadosi, 2024; K. Gibson, 1991). Our superior status as technological creatures has been closely guarded: despite documented evidence from the 1700s onwards (Carpenter, 1887; Duerden, 1905; Gifford, 1919; Kirby, 1797; Neaf, 1923; Peal, 1879; Peckham & Peckham, 1898; Strethill Wright, 1863; Uexküll, 1909), researchers were reluctant to allow non-human animals (hereafter, animals) into our exclusive club, an embargo broken only in the 1960s by acceptance of wild chimpanzee tool making and use (Goodall, 1963). Just a few generations later, hundreds of known wild species across at least 43 orders carry out this behavior (Figure 1; Table 1) and more are discovered each year.

Figure 1

Examples of Tool-Using Animals

Note. Clockwise spiral from top left: bolas spider (*Mastophora phrynosoma*) using web sling; Californian sea otter (*Enhydra lutris*) using stone chest anvil; weaver ant (*Oecophylla smaragdina*) using silk-extruding larvae to bind leaves; coconut octopus (*Amphioctopus marginatus*) using shell shelter; tortoise beetle (*Chelymorpha cassidea*) larvae using faecal shield; sleepy sponge crab (*Tumidodromia dormia*) using sponge cover; humpback whales (*Megaptera novaeangliae*) bubble-net feeding; boxer crab (*Lybia* sp.) wielding anemones; Burrowing owls (*Athene cunicularia*) at their burrow, baited with dung. All images CC-BY, via Flickr. Credits: Judy Gallagher; Smithsonian's National Zoo; Ria Tan; Rickard Zerpe; Judy Gallagher; Bernard Dupont; Mike Freedman; Rebecca Tse; Wendy Miller.

Table 1

Wild Tool-Using Animals

Phylum	Class	Order	Genus (e.g.)	Animal (e.g.)	Tool Use (e.g.)
Arthropoda	Arachnida	Aranaea	*Ariadne*	corolla spider	prey detection
			Deinopis	ogre-faced spider	net casting
			Hyptiotes	triangle weaver spider	net launching
			Latrodectus	black widow spider	web dropping
			Mastophora	bolas spider	web slinging
			Nemesia	trapdoor spider	movable door
			Pisaura	nursery web spider	fly baiting
			Steatoda	cupboard spider	pulley system
	Insecta	Coleoptera	*Cassida*	tortoise beetle	faecal shield
		Hemiptera	*Apiomerus*	bee assassin bug	egg gluing
			Gerris	water strider	mate carrying
			Salyavata	assassin bug	termite baiting
		Hymenoptera	*Aphaenogaster*	funnel ant	sponge carrying
			Apis	honeybee	defensive smearing
			Dorymyrmex	pyramid ant	stone dropping
			Megaponera	matabele ant	wound treatment
			Melipona	stingless bee	nest plugging
			Messor	myrmicine ant	sponge carrying
			Myrmeleon	antlion	sand throwing
			Oecophylla	weaver ant	larva weaving
			Podium	thread-waisted wasp	water carrying
			Pogonomyrmex	harvester ant	sponge carrying
			Solenopsis	black fire ant	liquid siphoning
			Sphex	digger wasp	nest pounding
			Tetramorium	pavement ant	soil dropping
			Vemileo	wormlion	sand throwing
		Lepidoptera	*Synchlora*	geometer moth	debris carrying
		Neuroptera	*Chrysopa*	green lacewing	debris carrying
		Orthoptera	*Oecanthus*	tree cricket	sound amplification
		Trichoptera	*Hydroptila*	caddisfly	case carrying
	Malacostraca	Amphipoda	*Hyperiella*	amphipod	sea snail abduction
		Decapoda	*Diogenes*	hermit crab	shelter carrying
			Dromia	sponge crab	sponge carrying
			Loxorhynchus	spider crab	shell covering
			Lybia	boxer crab	anemone carrying
			Paguropsis	blanket crab	anemone carrying
			Pagurus	hermit crab	shell carrying
			Paromola	carrier crab	sponge weaponry
Chordata	Actinopterygii	Anabantiformes	*Trichogaster*	gourami	water jetting
		Carangiformes	*Toxotes*	archerfish	water jetting
		Cichliformes	*Aequidens*	Central American cichlid	leaf carrying
		Perciformes	*Pterois*	red lionfish	water jetting
		Siluriformes	*Megalechis*	brown hoopla catfish	spawn carrying
	Amphibia	Anura	*Ceratophrys*	horned frog	body covering
	Aves	Accipitriformes	*Neophron*	Egyptian vulture	stone throwing
		Apodiformes	*Chlorostilbon*	glittering-bellied emerald hummingbird	prey baiting
		Caradriiformes	*Fratercula*	Atlantic puffin	stick scratching
			Numenius	bristle-thighed curlew	coral throwing
		Ciconiiformes	*Ciconia*	white stork	sponge carrying
		Coraciiformes	*Ceryle*	pied kingfisher	bait fishing
			Eurystomus	broad-billed rollers	courtship display
		Eurypygiformes	*Eurypyga*	sunbittern	bait fishing
		Falconiformes	*Hamirostra*	black-breasted buzzard	stone dropping
		Galliformes	*Alectura*	brush turkey	debris kicking
		Passeriformes	*Artamus*	black-faced woodswallow	symbolic stick use

Phylum	Class	Order	Genus (e.g.)	Animal (e.g.)	Tool Use (e.g.)
			Camarhynchus	woodpecker finch	stick probing
			Corvus	crow	stick probing
			Ptilonorhynchus	satin bowerbird	nest painting
			Sitta	white-breasted nuthatch	nest smearing
			Sturnus	starling	stick digging
			Ptilonorhynchus	satin bowerbird	bower painting
		Pelecaniformes	*Butorides*	green heron	bait fishing
			Nycticorax	black-crowned night heron	bait fishing
		Piciformes	*Melanerpes*	gila woodpecker	sponge carrying
		Psittaciformes	*Ara*	great green macaw	seed processing
			Cacatua	Goffin's cockatoo	seed extraction
			Nestor	kākā	branch throwing
			Probosciger	palm cockatoo	branch drumming
		Strigiformes	*Athene*	burrowing owl	prey baiting
		Suliformes	*Nannopterum*	double-breasted cormorant	feather preening
	Mammalia	Artiodactyla	*Inia*	Amazon river dolphin	object display
			Megaptera	humpback whale	bubble netting
			Tursiops	bottlenose dolphin	sponge foraging
		Carnivora	*Enhydra*	sea otter	chest anvil
			Mephitis	skunk	stone pounding
			Nasua	coati	self-anointing
			Thalarctos	polar bear	ice throwing
			Ursus	black bear	stone rubbing
		Perissodactyla	*Equus*	horse	social display
		Primates	*Alouatta*	howler monkey	stick antagonism
			Cebus	gracile capuchin	stone pounding
			Homo	human	sexual stimulation
			Lemur	lemur	scent dispersal
			Macaca	macaque	stone pounding
			Pan	chimpanzee	leaf sponging
			Papio	baboon	fluid wiping
			Pongo	orangutan	seed extraction
			Sapajus	robust capuchin	stick probing
		Proboscidea	*Elephas*	Asian elephant	fly switching
			Loxodonta	African elephant	corpse covering
		Rodentia	*Apodemus*	wood mouse	wayfinding
			Castor	Eurasian beaver	social display
			Lophiomys	African crested rat	toxin application
Echinodermata	Echinoidea	Camarodonta	*Sterechinus*	variegated urchin	body covering
			Strongylocentrotus	green sea urchin	body covering
			Tripneustes	collector urchin	body covering
Mollusca	Cephalapoda	Octopoda	*Amphioctopus*	veined octopus	coconut shelter
			Haliphron	seven-armed octopus	medusa carrying
			Tremoctopus	blanket octopus	Physalia carrying
		Sepiolida	*Rossia*	stubby squid	sand camouflage
		Octopoda	*Octopus*	gloomy octopus	debris throwing
	Gastropoda	Littorinimorpha	*Xenophora*	carrier shell	shell covering
		Trochida	*Tegula*	brown turban snail	stone leveraging

Note. Phylum, class and order of wild tool-using animals in (Shumaker et al., 2024), with selected examples of genera, common names and tool use by those genera. More genera use tools than are shown—particularly in the Passeriformes (with numerous anting species), Hymenoptera, Coleoptera, Camarodonta, and Decapoda—and some genera use multiple forms of tool. See (Shumaker et al., 2024) for full details.

The explosion of known tool-users has not, however, given us a reliable way to predict which animals will be found using tools in their natural state. No single underlying cause has been found that neatly explains and unites them, or them with us. Nor is there a settled definition of tool use behavior that

promotes cross-species investigation. Emergent links between sophisticated cognition, human-like brains and learning strategies, and tool use continue to be explored in the literature (Caspar et al., 2024; Fayet et al., 2020a; Lefebvre et al., 2004; Mangalam et al., 2022; Reader et al., 2016; Rutz & St Clair, 2012; Vaesen, 2012), including brain structure in termite-fishing great apes (Hopkins et al., 2017) and twig-probing corvids (Cabrera-Álvarez & Clayton, 2020; Ströckens et al., 2022), and social structure in sponge-wearing dolphins (Wild et al., 2019). While these trait-clusters offer valuable insights into convergent tool-use strategies, they do not help to explain why animals as far from us on the evolutionary shrub as liquid-carrying ants, coconut-carrying octopuses, sponge-wielding crabs and shell-covering sea urchins are also proficient tool users (Barrett et al., 2019; Capezzuto et al., 2012; Fellers & Fellers, 1976; Finn et al., 2009). As the undeniably sticky anthropocentric glue that initially fused the field together is washed away, where do we stand?

Recent decades have seen some major questions surrounding tool use answered, and answered conclusively. The question of whether tool use is restricted to humans, or even just primates (Leakey et al., 1964; Matsuzawa, 2008) has been well and truly answered in the negative. The follow-up question, of whether the human package of intensive brain-based modelling combined with dense social networking is essential for tool use, has also returned a negative answer (Barton & Barrett, 2025; Soley & Herberstein, 2023). A separate goal of using tool-based experiments to investigate animal cognition—including planning, causal reasoning and sociality (Boeckle et al., 2020; Fragaszy et al., 2017; Gruber et al., 2019; Jelbert et al., 2019; Sanz et al., 2013; Visalberghi et al., 2017; Whiten et al., 2007)—has been extremely productive, but it facilitates tool use as a means to an end for the scientist as much as the animal, and often focuses on animals separated from their natural environments. A search for genetic tool-use triggers has yet to bear fruit (Dussex et al., 2021). Clearly, many questions about the *why* of tool use remain. Even as it expands, the field of animal tool use risks fragmenting into separate taxon-based approaches, becoming a stamp-collecting exercise, or being subsumed within the broader field of construction behavior (Hansell & Ruxton, 2008).

In this review we offer an alternate path that re-centers questions about tool use around the experience of the animals involved—rather than the *why* of tool use, we focus on the *who* and the *what*. Tool use is a convergent phenomenon, akin to nesting or courtship, that reappears continuously across the animal kingdom. It is agnostic to underlying neural or genetic mechanisms. Further, there is now enough known variation in tool-using animal phylogenies, sizes, appendages, habitats, locomotion, perceptive arrays, and neural architecture to hypothesize that perhaps all animals are potential tool users (Bastos et al., 2025; B. Beck, 1980). Starting from that foundation, we aim to understand what processes bring animals into – and out of – tool use. This stance is centered on each animal's own specific sense-world and abilities (Uexküll, 1909), and it includes current non-tool-users and animals that may have used tools in the past, not just animals seen using tools in the past few decades. A modern theory of tool-use requires re-thinking the fundamental question being posed. Instead of asking what rare and essential gifts allow only certain animals to use tools, we ask: why don't they all?

Tools are Enabling Objects

Changing, expanding, and contested definitions of tools show that they are not an empirically or objectively delimited part of the natural world. This ontological ambiguity arises because tools are simply objects that are acted upon behaviorally, as part of an active process. Tools are transitive, unlike more permanent physical attributes shared between related lineages such as eyes or number of limbs. Tools are more akin to foraging patterns and strategies like social cohesion and neophobia, that can vary even between individuals and groups, let alone species. Tools, as objects, form parts of active but temporary behavioral processes that also vary between individuals, groups and species. Essentialist definitions of tool use therefore struggle to cover the many versions of object manipulation seen in the natural world (Shumaker et al., 2024), or restrict themselves only to subsets of tool use such as those involving a specific kind of mechanical force (Fragaszy & Mangalam, 2018). To avoid artificially restrictive or overdetermined definitions, here we succinctly and pragmatically define tools as *enabling objects*. A tool user may or may

not have intentions or goals that are intelligible to an observer, or themselves, but tools are always used with directed attention. We therefore define tool use as *the attentional use of enabling objects*.

Practically, and following Gibson (J. J. Gibson, 1979), tools are portable objects (see Box 1 for more on non-portable objects, or fixels). An object is a tool only while it is in use, and each individual has their own subset of suitable objects—potential tools—made up of what they can perceptively and physically separate from background environmental noise. We recognize tool use by the affordances an animal employs as it moves—where it looks, listens, smells, orients, reaches or moves—and the activities that the tool-wielding creature can perform that the solely biological one cannot. Obviously, not all environmental interactions constitute tool use. Attentionally passive environmental interactions, such as brushing through vegetation, locomoting, or even remaining at rest on a given surface are observationally distinct from directed, attentional object manipulation. A wild manik tilgnoi (or Goffin's cockatoo) grasping a branch as it rests, and one that repeatedly breaks off pieces of that branch to insert into and extract seeds from a wawai fruit, are attentionally quite different (O'Hara et al., 2021).

Box 1. Fixels

Immovable pieces of the world also can be used in tool-like ways: we term these latter objects *fixels* (note that movability is itself relative to an individual's strength and dexterity, which may change with development or injury). Fixels are attached enabling objects, used attentionally. For example, a stick held by a black bear and used to rub its muzzle is a tool, while a tree against which the same bear repeatedly rubs its back is a fixel (Reynolds-Hogland et al., 2023). A bush that a bear brushes past on its way to the river is neither. Numerous animals are skilled fixel users, for instance gulls dropping shelled prey onto hard surfaces or wrasses cracking items on coral outcrops (B. B. Beck, 1982; Tariel-Adam et al., 2025). Some species use both forms, as when an elephant uses a detached stick to swat at flies, or a stick still attached to a tree to lance an abscess inside its trunk (Hart et al., 2001; Steinbacher, 1965), or when a capuchin monkey either abrasively rubs a cashew nut on a tree branch or opens it with a handheld stone hammer (Visalberghi et al., 2016). Instead of relegating fixels to being not-quite-tools, the distinction picks up on observable differences: for example, fixels cannot be transported, combined with distant objects, and accumulated at new sites on the landscape (scaffolding further use and learning). Repeated use of fixels by default generates convergent traces of activity on a landscape—through animals' travel and in-situ material decomposition—enhancing archaeological visibility. Tools allow animals to structure activity around sites of extraction or manufacture, while fixels structure activity around the object itself.

At the simplest level, fixels are pieces of the environment that are attached to that environment and used analogously to tools. They may be partly moveable in place, like a chimpanzee poking a hyrax with a bent sapling (Hirata et al., 2001), or completely immovable by a given user, like a pathway stone used by a thrush to break open a snail (Hoskyns-Abrahall, 1891). The former covers the same territory elsewhere referred to as *freely manipulable* or *attached manipulable* objects (Shumaker et al., 2024; St Amant & Horton, 2008). The decision tree begins when we observe an animal's attentional use of a perceived object that enables new behavior. If the object is moveable around the landscape it is a tool, if not, it is a fixel. If any of those initial conditions are absent, it is something else and outside the scope of these specific concepts. As we conceive it, the conceptual role for fixels is to draw attention to and unify behaviors that in the past have been called proto-tool-use, borderline tool use, object-substrate manipulation, secondary object use, or otherwise not 'true' tool use (Bentley-Condit & Smith, 2010; Hall, 1963; Parker & Gibson, 1977; Seed & Byrne, 2010; Shumaker et al., 2024; Van Lawick-Goodall, 1971).

Separating fixels from tools in this way allows finer probing into what these behaviors mean to the animals involved. This allows us to treat fixels not as marginal or almost-tools, but as valued pieces of an animal's physical and cognitive repertoire. It gives old questions new framing: do fixels require equivalent, lesser or greater cognitive and physical flexibility than tools? Is fixel use more expedient or efficient than tool use? Does a fixel's permanent (for a given animal) location on a landscape assist or hinder its use as an enabling object? Do evolutionary trends tend to move from one kind of object use to the other, or are they separate behaviors? How often do tool and fixel use co-occur in an individual, group or species? We welcome debate around fixels, especially when they rub up against preconceptions about what animal cognition and behavior must or should entail.

Attention is bodily, directed, and energetic, resulting from the unignored intrusion of a thing into the animal's sense-world, or umwelt (Box 2). Clues to an animal's attentional focus lie in manipulative actions that use primary effectors (claws, hands, legs, beak, mouth, etc.), time spent on a task, and how the animal orients its sensory equipment (Bushnell, 1998; Fragaszy et al., 2017). For tools the foundation is attentional contact with the object, whether it is then used to hold, hit, strike at a distance, probe for a target and so on.

Box 2. Attention

Baseline data on an unaided animal's abilities are needed to fully adopt an attentional framework, similar to work on attention in human infants: what babies look at, listen to, touch and taste, and how long they do so, guides our present understanding of their worlds (Colombo, 2001). Recent developments in automatic pose and attention estimation from videos (Cheung et al., 2025; Moll et al., 2025) promise the ability to set standards of attentional focus that replicate across individuals and environments.

Social attention in the form of close 'peering' by orangutans and chimpanzees at their fellow apes has shown promise for unravelling cultural differences and tool learning based on who and what gets attention (Nodé-Langlois et al., 2025; Schuppli & Van Schaik, 2019). Methods used by field researchers to identify chimpanzee attention in the Taï National Park (Nodé-Langlois et al., 2025) offer one proven way to discern attention; for instance, 'peering events' were defined as "directly looking at the task engaged in by another individual at close range (<2 m) for >5 s), facilitating clear observations of the task". More explicit attention involved begging, included extending a hand toward the attended individual, plus "whimpers, and direct contact with the target or its items while the target was processing food". Peering is directly relevant to tool use, including when younger animals observe and then attempt tool-using actions of older role models (Bădescu et al., 2025). Visual attention by primates is easier for us (as visual primates) to recognise and interpret, but other environmental signals such as scent traces, noise cues, vibrations, and pressure waves in air or water may be more salient to the attention of other animals. The onus is on us to adapt our methods to the animals, not the other way around. Animal attention may be directed to foods, conspecifics, nests, predators, perches, hiding places, and numerous other environmental attractors outside of tool use. For more on how animals selectively attend see, for example, Zentall (2005) and Wasserman & Castro (2021).

It is the attentional focus that matters in both fixel and tool use, not the way the object is used moment to moment, or the successful achievement of an intended outcome. If a human carpenter uses a hammer to hit a nail but strikes off-center and fails in their intention to drive in the now-bent nail, or a juvenile capuchin monkey fails to crack a nut with a too-soft stone hammer (Fragaszy et al., 2023), they are still using a tool.

Removing *a priori* suppositions around shared intelligence or biology has more clearly shown the specific circumstances that foment tool use, especially those that promote or prevent object attention and handling (Brebner et al., 2024). Putting it another way, we get feedback from things we pay attention to. Animal responses to feedback are valuable for both their own survival and for our ability to parse their behavior. Here we start to see underlying commonalities: tool use is enacted moment to moment as object and animal form a temporary tactile partnership. If uninterrupted, the activity continues until it reaches an endpoint that satisfices the user. At each stage from tool recognition to transport, use, and discard, the tool mediates and changes the user's perceptive range, as well as their ability set (Martel et al., 2016). Note that separating brain-based processes from attention in this way is meant to be a practical step that allows observers to recognize tool behavior. We are not suggesting that any one form of bodily focus is necessary or sufficient for tool use, nor that brains don't play a role in attention. Only that brains are not visible, and don't need to be understood, to identify technological acts.

The combination of ongoing feedback from and response to the environment, in service of reaching or maintaining an internally governed state, constitutes a cybernetic system (Wiener, 1948). The study of control systems, or cybernetics, covers actively maintained stable processes within unstable and restrictive environments. Tool use as cybernetic system has three critical sources of constraint: the user, the tool, and the local environment. The user has physical and information-processing (cognitive, perceptive, sensory) limitations derived from its evolutionary and developmental past, the tool has material properties (state, flexibility, temporal duration, texture, hardness, etc.), and the environment (physical, social) affords certain actions and precludes others (J. J. Gibson, 1979). The junctions between these three components are also potential sources of constraint, as feedback is blocked or modified. Animals using external technological support for maintaining desired biological states were first labeled 'cybernetic organisms' or Cyborgs—always capitalized—in the 1960s (Clynes & Kline, 1960), and the label remains useful today. Every tool-using animal transforms, temporarily, into a natural cyborg.

The coincidence of an unmet goal state, and a perceptible path that loops via an enabling object through the world and back to the satisficing of that state, can be enhanced or interrupted by any number of factors. Social or time pressures, predators, competing signals and demands on memory can all impinge. Tools smooth out one path, but potentially at the expense of complicating others that we as observers might not readily detect. A non-negotiable precondition for tool use is the uninterrupted, or manageable

interruption of, reliable feedback. Signal must cut through noise. Detection and use of object-mediated feedback is the difference between more passive environmental interactions, such as locomoting on, temporarily nudging against, or gripping objects, and attentional tool use (Taylor et al., 2010, 2012; Taylor & Gray, 2009). Attentional movement also separates tool-based acts from the feedback given by evolved automatic—and autonomic—environmental responses occurring to and through the body (pain, itchiness, sensations of warmth or cold, salinity, humidity, brightness, etc.). Tools add a perceptive shell beyond these body-bound sensations, and attention is the bridge between the two.

Tool use paired with the incorporation of the novel feedback it affords delivers, in a word, meaning (Ball, 2024). This is a dynamic process, in which the timing and sensitivity of external-object-derived feedback needs to match those of the animal's perceptive abilities, whether synaptic, haptic, olfactory, visual or otherwise. The bump of successful contact with a prey species at the end of a stick is valueless if the user's sensory gear fails to detect it or misinterprets the touch. If there is insufficient, mis-timed, ill-attended, or mis-perceived feedback, tool use won't happen.

Brains, and neural architecture more generally, help determine how readily and rapidly animals perceive and respond to regularities in the environment. Memories stored in brain tissue or elsewhere in the body will also improve efficiency and continuation of tool or fixel use. However, brain size and structure are not determinant of whether a species or individual animal uses tools. A tool-using animal is set on a different behavioral trajectory not by a certain kind of brain or learning style, but by the creation of novel informational loops. For example, when an animal uses tools on its own body, for comfort or relief, the user also becomes the modified environment, getting meaningful feedback not only via the grasped object but from sensations in its own scratched skin, poked tooth, or rubbed feathers. A starling rubbing wool under its wing sees, smells and feels its effects (Haslam, 2024), while a wild capuchin monkey carefully inserting a stick up her nose has exquisite information from the pressure of the object in her hand and the sensations inside her nostril (plus feedback from the involuntary sneeze that follows) (Haslam & Falótico, 2015). Recent phylogenetic modelling of self-care tooling in parrots suggests that this behavior may be much more widespread in the group than is currently known (Bastos et al., 2025). Because of this feedback richness we might hypothesize self-directed tool use as a more easily discovered form than tool activities directed at external targets. Self-directed tools exploit the stability and predictability of the self-environment and the organism-specific perception that evolved to protect and maintain it. However, starlings have efficient beaks, and capuchins fingers (Perry & Smolla, 2020), to perform the same self-maintenance tasks that these tools do, suggesting we should expect only idiosyncratic and impermanent adoption of self-directed tools as evolution works to make them redundant. If dependably available, fixels can fulfil the same role, for instance by allowing humpback whales to use specific parts of the seafloor to remove otherwise inaccessible parasites from their throat pleats (Stevenson & Werth, 2024).

Object-assisted, substrate neutral system feedback will differ from animal to animal, and between types of tool mediated actions. But the loop of *unmet goal state—external bodily response—perceptive range—local environment—functional affordance—technological action—satisficing change* underlies all. A cybernetic view moves the target for explanation from the isolated individual to the connected system. We do not dismiss brains from the equation, involved as they are in collating perceptions and coordinating bodily movements. Certain formats or sizes of brains have been found to assist with activities like primate technical innovation (Navarrete et al., 2016), or passerine vocal complexity (Audet et al., 2023). However, insufficient muscle strength or touch sensitivity, or a lack of manipulable objects, may stymy tool behavior as readily as insufficient neurons. Memory of some kind is also important for recognizing and reiterating past successful situations, whether it is encoded internally via neural circuitry or genes or externally, for instance via the crowd-sourced organizing properties of stigmergy (individual use of activity traces for social coordination, seen for instance in ant pheromone trails and paper wasp nest construction) (Collignon & Detrain, 2020; Di Pietro et al., 2022; Karsai, 1999).

Ability and Availability

Each tool-user sits at the confluence of ability and availability (see Box 3). For an object to become a tool, it has to be perceptible and manipulable at the time and place it is needed. Perception might mean discriminating a single shell or leaf, or recognizing that a useful stick exists as part of a thin branch still attached to a shrub (Hunt, 2021). Manipulation is a matter of strength and coordination: the galago and the savannah chimpanzee both have access to wood that can be made into spears, but the latter can fashion and wield larger objects than the former could ever manage; influencing who is likely to become lunchmeat (Pruetz et al., 2015). For a tool to transition from *ad hoc* use into an individual or group's repertoire, suitable objects need to be reliably re-encountered in favorable conditions, which may include build-up of past tool materials at suitable places (Fragaszy et al., 2013), or social observation and repetition of the behavior. It may also involve stochastic rediscovery among related animals and/or in similar environments.

Box 3. Sponging

The intersection of ability and availability can be illustrated via six species—humans, crabs, dolphins, chimpanzees, ants and bowerbirds—united by a common tool: sponges. *Homo sapiens* has collected sea sponges since antiquity (Voultsiadou, 2007), using them in medical and hygienic settings—the god Hephaestus wipes himself with a sponge after working his forge in Book XVIII of the *Iliad*; in the Christian *New Testament* Jesus was offered a drinking sponge during his crucifixion—and as tools for crafts and painting (for example, at Minoan Knossos (Evans, 1930)). Other animals make their own absorbent 'sponge' tools: chimpanzees gather and fold together leaves or moss to collect drinking water (Lamon et al., 2018), and *Aphaenogaster* ants collect and cut pieces of soil, leaf litter and other vegetation to soak up nutrients from the forest floor (Módra et al., 2022). The purpose of both is liquid transport, to the chimpanzee's mouth or the ant nest. Male satin bowerbirds echo the Bronze Age Minoans by painting their intricate ground structures with saliva and vegetation, using a bark sponge tool to do so (Chaffer, 1945; Gannon, 1930).

Marine sponges are also a tool of dromiid crabs, which, living underwater, have less use for absorbency. Since the Jurassic, these true (brachyuran) crabs have been breaking apart sponges into suitable sizes to carry over their carapace as a form of camouflage or weapon (Capezzuto et al., 2012; Guinot & Wicksten, 2015a). Protective sponge use is similarly practiced by dolphins that carry conical marine sponges on their rostra (noses) to minimize injury while foraging in sandy substrates (Mann et al., 2008). Three of these sponging species have ready access to marine sponges either through direct contact in their habitat (crabs, dolphins) or via shoreline scavenging followed later by deliberate harvesting (humans). The other three (bowerbirds, ants, chimpanzees) fashion their own liquid-holding devices from common materials in their forest homes.

Little unites these taxa in terms of neural architecture, skeletal arrangement, number of limbs or sensory equipment, habitat, life history or social structure. Their sponges are variously made from vegetable, mineral or animal pieces, and reliance on these tools ranges from habitual (sponge crabs, chimpanzees) to occasional or locality-specific (dolphins, ants, humans, bowerbirds). The link is that in every case— insect, bird, cetacean, crustacean, primate—the user is dealing with perceptible materials of manipulable size and weight that are reliably-encountered at the point of need. Natural and manufactured sponges are scalable, offering porosity and traction. Underwater, the sponge affords grip and relatively light material, while out of water effective sponge tools depend on the cohesive forces of held liquids. Those same forces allow ants to drink, ancient Greeks to wipe away sweat, and the bowerbird to apply a charcoal/saliva mix to the inside of its seductive stick structure.

A cybernetic view offers us novel targets to query. The animal (goal state, perception, satisficing conditions), the materials and social milieu (environment) and their overlap (affordance, action) all offer points of information gathering, as well as potential weakness in the process. A non-human ape may use washed-up natural sea sponges or manufactured leaf sponges for liquid transport, just as an ant may, but the absence of marine-diving chimpanzees and ants limits the use of growing sponges to natural (dolphin, crab) or invasive (human) species. We can look to any of these points in the tool-use system to understand why different animals' tool behaviors diverge or converge.

A concept needed here is that of a high-validity learning environment. Originally posited in behavioral economics as a condition for the emergence of human skill and expertise, this idea describes the circumstances that allow an agent to get causally relevant feedback (Kahneman & Klein, 2009). A low-validity environment either has few causal links between past and future states, or those links are too complex to be discerned by the agent from the available feedback. For example, shifting desert dunes may cover and reveal resources at an apparently random rate, and returning to the same spot where you found a meal or water before is no guarantee that the same conditions and outcome will pertain. Conversely, a high-validity environment may still have some uncertainty, but it has sufficient statistical regularities that ongoing experience in those conditions can exploit feedback from those regularities, capitalizing on opportunities and avoiding disasters. High-validity environments are contexts in which we can most

confidently predict repeated tool use to emerge. A third kind of learning environment—a 'wicked' one (Hogarth et al., 2015)—gives misleading feedback, and we should not expect tool use under those conditions.

Validity is in the eye of the beholder. Regularities that we see may not be apparent to other animals, and vice versa. In effect, the only way to know whether an environment is high-validity for a given animal is to observe how they exploit it, and the effect of external disruptions on their behavior. The validity of the environment can be actively changed not only by shifts in external variables (light, tides, wind direction, predators) but by an individual's ability to sense and exploit causal links, such that environmental validity is ultimately subjective and fluid. The size of the learning environment is also relative: army ant colonies can shift their location daily in the tropical forests of eastern Nigeria, but tool-using chimpanzees roam far enough to reliably encounter them and exploit them all the same (Pascual-Garrido et al., 2013). To chimpanzees, the ants are a statistical likelihood, amenable to learning, and offering high-validity feedback. Animals with smaller ranges would find returning to the same army ant nest over and again after its abandonment unproductive, and targeting them at that site a low-validity option.

The idea that statistical regularities underpin tool recognition and adoption leads us to ask how those regularities are themselves recognized. There is a more specific role for brains here than in the whole-body feedback during active use of tools, as the brain integrates and associates sequential patterns and regularly co-occurring phenomena (Hasson, 2017; Johnston et al., 2023; Santolin & Saffran, 2018). Greater sensitivity to auditory or olfactory evidence, for example, allows for more reliable detection of any regularities in those modalities when paired with sufficiently stored and retrievable memories. This reasoning leads to a prediction that individuals or even species with better (quicker, more persistent, more flexible) ability to pick up on statistical patterns increase their chances of having accidental interactions morph into regular tool use. Whether those patterns are interpretively registered as correlations or causal links is not critical to how the animal makes use of them, although again causal reasoning will likely accelerate an animal's evaluation of tool effectiveness (Völter & Call, 2017). The potential for successful extraction of statistical regularities from an environment, without concordant comprehension, is suggested by non-biological constructions such as large language models (Dentella et al., 2024; Zador, 2019), and has been found even in newly hatched domestic chickens (Santolin et al., 2016). Pairing deep learning networks with observations of animal tool use offers one way forward for investigating how environmental regularities are experientially integrated and internalized (Johnston et al., 2025).

In every case, tool use has to start somewhere. It starts with behavior expressed by an animal in its environment. Somewhere, somewhen, an animal attentionally uses an external enabling object. If it helps, we can consider each first instance of tool use as a 'behavioral mutation.' Colloquially these one-off observations tend to be indexed as anecdotes; for example, when a lone puffin in Iceland briefly touched its chest with a beak-held stick (Fayet et al., 2020a). If this observed act was accidental—which that study's authors do not believe but others have argued (Auersperg et al., 2020; Fayet et al., 2020b)—it sets up a forking path where either the bird attentionally looks to recreate the same circumstance in future, or ignores any perceived feedback and tool use fails to spark. We suspect that most (all?) non-human tool use in natural settings initially builds on accidental actions that have sufficient salience to draw attention and therefore repetition. That first act—the accident, the mutation—is one of the boundaries between randomly touching bits of the environment and using an enabling object as a tool. Human ability to readily discern a fitness or other benefit to the action is secondary to the animal's own perception and experience. Issues of social learning, culture, and imitation are similarly downstream of the individual tool task. When a skunk uses a rock to break through frozen surface water to drink (Pesendorfer et al., 2018), a long-tailed macaque uses a stone to hunt and smash an actively defensive crab (Haslam et al., 2022), or a carrier crab pushes away a rival shark with its sponge covering (Capezzuto et al., 2012), the first step in assessing the anecdote is to track how (or whether) the individual's typical behavior is altered, before judging any outcomes from that shift.

We propose that tool-use mutations spark into existence all the time, across all kinds of animals (and possibly other mobile eukaryotes [Dumack et al., 2024]) but rarely are they serendipitously observed, let alone recorded. Our records are biased toward obvious examples of widespread tool use in above-

ground, land-dwelling species. These records are further shaped by research effort put into each taxon and coincidental scientific observers, as well as forms of tool use that are immediately intelligible as they mirror human-like patterns (for example, a primate probing a hole with a stick). Tool use that happens at scales, or in environments in which humans do not generally operate are commensurately less likely to be witnessed. While widespread examples alert us to the materials that draw an animal's attention: a hermit crab attending to suitable shells (Mesce, 1993), a corolla spider distinguishing quartz grains of just the right size to surround its burrow with vibration-detection tools (Henschel, 1995), finding a widespread activity should not blind us to the possibility of other technological mutations in the same species, including ephemeral or short-lived tool use. Neither should it automatically lead us to expect similar actions in similar species.

Moreover, the generation of reliable feedback may only happen in particular seasonal or prey conditions, in which case memory will also play a role in bridging the gap between one feedback report and the next. Woodpecker finches in the Galápagos archipelago use twig or cactus spine tools to pry arthropods from tree holes, but they do so significantly more often in the dry season of the island's arid zone than in the wet season (Tebbich et al., 2002). The memory of tools needs to be carried through times of little or no actual use. While isolated instances of tool use are sparked continuously across the natural world, they will remain one-off if the tool use/feedback system operates effectively only for a short period and then ceases to align. Such misaligned instances do not become fixed in the behavioral repertoire of an individual or group. Absent archaeological evidence, we have little hope of distinguishing an ex-tool-using species from one that never used tools in the first place.

Along with the ability to detect and respond to feedback, numerous tool-using ants, beetles and wasps prove that muscles scale down sufficiently to manage the task and materials at hand—in relative tool size the digger wasp tamping down its burrow with a mandible-clasped sand grain is akin to the white-faced capuchin striking a sea almond nut with a cobble (Brockmann, 1985; Goldsborough et al., 2024). Tool-using octopuses show that bones and bodily rigidity are not necessary either (Finn et al., 2009). Conversely, the availability of potential tools paired with the capacity to use them is not reliably *predictive* of tool use, as shown by the apparent current absence of nut-cracking among most wild chimpanzee groups (McGrew et al., 1997). We expect that the presence of nut-cracking in a given chimpanzee group will fluctuate over time, from decades to hundreds of thousands of years, as reliable feedback cycles are found, strengthened, lost and re-discovered. Excavation of technological primate sites in its infancy; even so we have initial evidence for tool-use fluctuations from a three millennia record of bearded capuchin stone tool use in semi-arid Brazil (Falótico et al., 2019). The present does not predict the past.

Tool Use is a Noisy Game

Like any other novel behavior, tool use cannot initially address a wider biological need for stability—it can only address a situational need for stability. To progress, we need to marry the cybernetic principles guiding probabilistic, momentary, individual actions with the wider strategies underpinning entrained behaviors shaped by the *longue durée* of evolution.

The outcomes of novel tool use can be examined through continuous-trait evolutionary game theory. Here, continuous traits constitute not only heritable phenotypes, but also learning behaviors, socio-behavioral dynamics (such as altruism), and other strategies (Abrams, 2000; Bendor & Swistak, 1997; Lehtonen & Otsuka, 2023; McGill & Brown, 2007; Roughgarden, 2016; Stephens & Clements, 1998) including tool use strategies. The landscape in which novel tool use behaviors emerge can be understood using a classical evolutionary game theory approach (Axelrod, 1990; Maynard Smith & Price, 1973) with a particular eye to Nash equilibria (Björnerstedt & Weibull, 1994; Holt & Roth, 2004; Nash, 1950). Novel behaviors arise against an existing backdrop of established behaviors within a population. Extant behaviors, settled within and enacted by the group, constitute an evolutionarily stable strategy (ESS). This ESS will naturally resist 'invasion' by a mutant activity: for example, the intrusion of incipient tool use (Maynard Smith, 1984). There must be a mechanism by which the existing strategy can be dislodged or overwritten if novel tool use is to become widely adopted (Maynard Smith & Price, 1973; McGill & Brown, 2007).

This confers a barrier-to-entry for *any* novel tool use behavior, no matter how beneficial we may imagine it to be. Crossing the ESS barrier requires a significant shift in group behavior, facilitated by strategies such as movement of the tool-using subset into a previously untapped niche, or adopting a probabilistic mixed strategy (see below).

Tool use is not inherently difficult: it is fragile. However, when the cybernetic stars align, when mutant tool use behavior is repeated, and when this mutation confers an individual, group, social, or reproductive benefit, the mutant tool use strategy may become convergently stable by crossing a minimum fitness threshold. The outcome is one of Gell-Mann's contingent outcomes, in which '[t]he treelike structure of branching histories involves a game of chance at every branching…some of those accidents become frozen as rules for the future' (Gell-Mann, 1994). Even as these opportunities repeatedly emerge, the 'successful' emergence of tool use is not deterministic, and it remains difficult to predict where tool use will arise and stick, or whether a 'failed' tool use mutation will stochastically re-emerge and lead to a different outcome.

This apparent heterogeneity in outcomes occurs, in part, because animals' adaptive landscapes change independently of the presence of new 'mutations', and in doing so, open up new opportunities for the same tactic to achieve a different outcome in evolutionary terms. Available materials, shifting needs, and changing bodies, senses, and targets can alter the reward/detriment calculus for tool use behaviors. The arrival of nutritious and oily palm nuts via human cultivation raised the value of forest-based stone hammer-and-anvil technologies for Thai long-tailed macaques on Yao Noi Island, for instance. Macaques elsewhere in the region concentrate stone tool use around island margins, exploiting tidal resources (Luncz et al., 2017).

Novel tool mutations are difficult to catch in the act: the reason we notice well-documented instances of tool use is because they have already become evolutionarily stable strategies. One-offs, anecdotes, unique or unusual observations (Bates & Byrne, 2007; Sándor et al., 2021), rather than capturing fundamentally unlikely acts or actions, signal their relatively ephemeral positions on a tool use continuum. An added wrinkle comes from the human propensity to deem certain kinds of behaviors as 'true' or 'real' tool use because of our own ways of using tools and inherent modeling biases. Despite the inbuilt checks against bias that are a critical component of scientific enquiry, *Homo sapiens* are technological animals and not a tabula rasa. Learning is an interpretive act. When we observe tool use behaviors, we interpret our observations through our own learning models, tuned to our innate and internally governed stochastic equilibria (Holt & Roth, 2004). In game theory this is deemed 'noisy introspection' (Goeree & Holt, 2001, 2004). This phenomenon explains a 'non-Nash' phenomenon in games which are played only once—as, for example, when a human observer witnesses a novel tool-use mutation; an animal doing something we haven't seen before. Noisy introspection helps explain why we anthropomorphize; why derived (human-like) but unrelated qualities such as intelligence, mental modeling and intentionality are often superimposed onto observed tool-use one-offs. In seeking to understand, to learn, we expect.

From the current taxonomic and geographical distribution of tool using species, and the lack of unifying qualities among them, we hypothesize that a multitude of individual animals over hundreds of millions of years have attentionally used enabling objects. Few will develop species- or genus-wide technologies. The dominant outcome will be that early stage tool use fizzles out sooner or later, through misaligned or low-validity environmental feedback, leaving what we today see as 'non-tool-using' species. Assessments of cognitive thresholds do not enter into this hypothesis. An apt analog is construction behavior: a form of world-manipulation that adds and subtracts materials to improve an animal's niche (Hansell & Ruxton, 2008). Complex animal constructions like weaver bird and termite nests, mammal burrows and beehives have been observed since before humans were humans, which we suggest as the reason that these activities rarely accumulated the same expectations of cognitive sophistication or planning directed at animal tool use. Constructions therefore provide a salient corrective for searches for human-like intelligence as a prerequisite for manifestations of 'complex' behavior (Street et al., 2025). Finding out that extinct animals from any time period constructed nests or burrows would not immediately require rethinking their intelligence or brain structure, and the same should apply to tool use.

A Faunocentric View

If tool use is not about intelligence, necessity, or the opportunities and utility that the tool-using life brings—see (Hunt et al., 2013) for a thorough summary of these perspectives—what can our alternate framework offer? First, we stress the individual living within its umwelt as the unit of tool use. Everything perceived, given directed attention, manipulable and returning salient feedback in a high-validity environment is game for tool use. Everything else is not. There may be forces outside an animal's ken that we humans can recognise as influencing them—genetic inheritance, climate shifts, diseases, and invasive competitors, for example—but those are not the primary causes of tool behavior. Tool use is caused every time anew by a match between unsatisficed needs, remembered or evoked feedback, perceived affordances, and the physical ability and time to resolve those needs using something outside their own body; that is, via enabling objects. It is important to remember that most animals' needs can be met by using their bodies alone; via internal regulation by evolved endocrine, immunological, digestive, waste management, thermoregulatory, and other bodily systems that do not involve a behavioral response to which a tool could be appended. *Homo sapiens'* hyper-reliance on tools is an extreme outlier in this regard, to the extent of being evolutionarily distinctive. Tool use among other species should never be assumed or explained away by presupposing or superimposing derived hominin technological patterns where they do not belong. By removing these frameworks, our questions become more pertinent and compelling; why *that* animal and *that* object, right then and there? What would they have done if the object was not available? What would their neighbor of a different sex, life-stage, and disposition (read: personality) have done? What might they do if that object is available again next time? A focus on individuals prioritises the physical cyborg doing the work (Barton & Barrett, 2025; Boogert et al., 2018), not abstract notions of cognition or a species-level label. This redrawing also opens up avenues for exploring the effects of individual personality differences, as posited for tool-using ants and chimpanzees (Maák et al., 2020; Massen et al., 2013).

Second, an ESS grounding helps explain why tool use seems to be optional in several species. Where tool use behaviors persist, game theory posits that populations can evolve to branching points. These branches may then prompt a probabilistic mixed ESS to evolve, where tools are used only in certain conditions that depend on what others in the group are doing. We can see this scenario indirectly played out in female digger wasps that use hammer tools during nest building (Brockmann et al., 1979). For these wasps the costs of digging a new nest are higher than entering and exploiting an abandoned one dug by another wasp, although they risk attack if the latter turns out not to have been actually abandoned. The result is that both *dig* and *enter* strategies persist, not just across the species but in individual wasps, who switch back and forth between the two behaviors over time.

We may also find that branching points prompt populations to diverge into separate cliques with distinct strategies. We see this, for example, in dolphin foraging in Shark Bay, Australia, in which sponge tool-use is practiced by only 11% of adult females, and an even lower percentage of males (Mann et al., 2008; Sargeant & Mann, 2009). As yet, there is no clear reproductive fitness benefit conferred by tool use; indeed, evidence suggests that using sponge tools interferes with echolocation (Jacobs et al., 2025). A sex divide also characterizes foraging stick tool use in bearded capuchins in Serra da Capivara National Park, with 97% of this behavior performed by adult and juvenile males, and none by adult females (Falótico et al., 2021). White-faced capuchins on Coiba island in Panama have a similarly skewed but island-specific bias towards male stone tool use (Goldsborough et al., 2024). Californian sea otter use of stone tools to break shelled food is closely tied to individual dietary preferences under maternal influence (Fujii et al., 2017), with variation in when and how tools are used arising within single populations (Law et al., 2024). If young woodpecker finches in the Galápagos islands do not learn to use probe tools to access invertebrates through trial and error they may never do so, despite growing into healthy adult birds (Tebbich et al., 2001), a sensitive learning period reported also for wild western chimpanzee nut-cracking behavior (Biro et al., 2003).

Third, a cybernetic framework helps explain our own effect on animal technologies. In captive settings such as laboratories and zoos, humans construct controlled interventions that iteratively scrape away constraints for other animals. Animals are given limited and different materials to interact with

compared to their natural homes, and can be guided towards projects that explicitly encourage object interactions (Hopper et al., 2015; Motes-Rodrigo & Tennie, 2022; Zhou et al., 2025), while at the same time removing pressures around sourcing food and shelter and avoiding predators. Captive conditions create artificial high-validity learning environments. Here, the progressive removal of inhibiting factors and/or promotion of stable feedback allow or elicit tool use in species that currently show no such behavior in their wild habitats, from naked mole rats to stingrays and more (Bird & Emery, 2009; Haslam, 2013; Kuba et al., 2010; Nagano & Aoyama, 2017; Okanoya et al., 2008; Rutz et al., 2016; Shuster & Sherman, 1998; Stoinski & Beck, 2001; Teschke et al., 2011; Tomonaga et al., 2023). This work permits researchers to target specific fine-grained aspects of tool selection and use, but the idea that the human-controlled animals being tested are direct stand-ins for their wild brethren is one that requires closer scrutiny (Bandini et al., 2025). From a cybernetic stance, the default expectation is that captive conditions will give different results to those found in nature, owing to the construction of predictable environments, trustworthy information, and objects deliberately provided for attentional use. If natural and captive behaviors match, the likelihood of equifinality can be assessed to determine if the two patterns are being achieved in the same way.

Even when species successfully bring tool strategies into their ESS, they may still subsequently fade as the animal evolves behavioral or physical solutions (e.g., longer limbs, harder teeth, commensalism, more effective camouflage) that render the technology obsolete. That process is much slower than the vanished spark of tool use coming from mis-timed feedback in a single animal, but it is a loss nonetheless, leading to an equifinality that again makes it hard to distinguish an ex-tool-using species from one that never used tools in the first place. The other end of the spectrum also exists: rather than evolving away tool use through anatomical refinement, some animals have made long-term investments in bodies that actively support and depend on tool use. The water-jetting archerfish is a clear example. This fish brings down aerial prey while remaining underwater at the surface, using its evolved grooved palate and enlarged, compressive basihyal to form and release streams that coalesce at their target (Girard et al., 2022). The reduced, dorsal fifth pereopods of carrying crabs are another unambiguous case of physical adaptation to tool use (Guinot & Wicksten, 2015b), as is the uncommon form and arrangement of hominin and human fingers (Kivell et al., 2023). These changes force a hyper-reliance on tools that can only remain effective if the tool materials are ubiquitous at point of use—as water is to a fish.

Future research can forge productive paths linking animal technologies by focusing on information flow between the components of the cyborg system (St Amant & Horton, 2008). It can also help us recognize deviance in our own technological strategies. Tool-using primates such as chimpanzees, capuchins and macaques help build high-validity environments by accumulating materials at particular locations, handing off tools to other group members at tool-use sites, and providing opportunities for imitation and emulation of tool collection, manufacture and use (Haslam et al., 2017). New Caledonian crows similarly leave both tools and the negative impression or 'counterpart' of removed leaf tools in locations near food sources (Hunt & Gray, 2003). Our own species has taken this strategy to an extreme by investing heavily in moving materials across large distances and deforming local environments to maintain tool-target co-presence and compatibility. From handbags to server farms, humans and our hominin forebears have buffered against uncertainty by putting massive effort into making conditions stable for the tools themselves as valued partners (Haslam, 2023).

We recognize the inherent risks in proposing a broad definition of tool use. More inclusive definitions allow for greater breadth of comparison at the risk of becoming unworkable. To reiterate, then, 'enabling objects' are separate pieces of the environment that an animal uses to do things in a way it otherwise could not. Where those objects come from does not matter: it could be a spider picking up and wielding its own silk net (Stafstrom et al., 2020), a sea urchin collecting shells and stones as cover (Barrett et al., 2019), or a squirrel applying rattlesnake scent to its fur (Clucas et al., 2008). The cognitive and physical effort that the task requires is also irrelevant, including whether we see it as closer to reasoning and planning or more of an automatic response to environmental cues. The *enabling* part is critical—the animal is doing something that gives it new powers to operate within and act on its world, including on itself. Whether it be an octopus waving a stinging jellyfish tentacle (defense), a human child putting on a

sock (thermoregulation), or a humpback whale casting a fishing net made of bubbles (feeding), each is transformed into a natural cyborg during the act of tool use.

To dispute or falsify a claim that some behavior is tool use, you need to show that the object does not enable any kind of meaningful outcome for the animal, or that the animal pays it no attention. This might seem a high bar, and for poorly studied behaviors that likely will be the case. We intend for this definition to elicit precisely these kinds of investigations; to prompt questions around *why* we might want to accept or deny something as tool use, rather than simply adding or subtracting a trading card from the tool use deck. Upon examination, initial designations of tool use may come to be recategorized. A squirrel rubbing itself with discarded rattlesnake skin to disguise its scent may come to be deemed a medicinal behavior; a human using a refrigerator or washing machine may be engaging in habitat construction as well as fixel use. Perhaps counter-intuitively for a paper containing definitions, our interest is less in policing the boundaries of the idea than in asking what kinds of motivation and outcome tool use engenders for the animals and for us as interested observers. Shorn of automatic links between intelligence and tools, what do we want tool use to be for?

Conclusions

Why don't all animals use tools? Members of all species are capable of doing so, but usable objects, unsatisficed needs and salient feedback do not co-occur reliably enough and without interruption to augment bodily functions in most taxa. Barriers to tool use are raised at various levels, from individual personalities and propensities, to environmental and affordance constraints. These barriers are augmented by existing evolutionarily stable strategies in a population that either stamp out innovative behaviors, or cause branching into tool-users and non-tool-users. The diversity of animal forms, life histories and habitats means that no single explanatory driver exists for tool use, whether opportunity, necessity, cost/benefit or fitness calculations, or the shape of mind or muscle. Like a tower of nested sieves, technology is susceptible to forces that combine to keep it out of the adjacent possibility space (Kauffman, 2014) for different species. To continue the analogy, however, it may only take a seemingly small and innocuous twist of one sieve (altered material availability, social assistance, prey habits, perceptive range, limb length, ectoparasites, and so on) to open up stable tool use in a currently non-technological species. Or to shut a currently tool-using group down.

Like much behavior, tool use works on partial information in a probabilistic way. No one outcome is predetermined, even for 'species-typical' activities. Unmoored from humans as a high-water mark, tool use is no longer considered a tale of gifted beings crossing a cognitive threshold to achieve mastery of their world. Instead, it happens everywhere, all the time, sputtering into existence and then vanishing again largely unremarked. Occasionally one of countless little object-use accidents survives and becomes routine by slipping through the cracks in the constraints that all species face, each in their own umwelt. Every technology's lifespan is uncertain and contingent on much more than a given species' biology. When constraints return, or new ones arise, the behaviour either ends or transforms.

Removing anthropocentrism has opened up the field of animal tool use, and undercut one of its core motivations. We believe that a more ecologically relevant and individually centred framework will help the field regain its footing. Tool users have little in common other than physical responses to changing natural constraints, which is where cybernetic loops come in. This conceptual coherence is valuable for investigation, documentation, conservation and welfare outcomes, even if ultimately tool-using animals are an amorphous group similar to lumping those that scent, sleep, build, fly, or play. Interspecies comparisons may reveal unexpected convergence, but at points the technological similarity cannot sustain the comparison: if stone pounding tools help us understand a capuchin monkey's sociality and reasoning processes (Falótico, 2022), it is largely irrelevant whether or not a digger wasp's stone pounding is psychologically or conceptually similar.

The growing diversity of known tool users and tool functions continues to throw stumbling blocks in the path of an orderly, cleanly bounded definition of tool behavior. In response we have suggested an observable, process- and system-based alternative that we believe is flexible enough to capture the essence

of what tools are (enabling objects) and what they require (attention) without overspecifying what the resulting actions may look like or relying on intuiting an animal's intent. In the absence of neural data—which is impossible to retrieve for most observed tool use bouts—we offer a way forward through the identification of feedback loops from the actions of the animal itself. Our framework is intended to complement, not replace, efforts to drill into brains, social transmission chains, ontogeny and experimental capacity for tool use; the results of those efforts over the past 50 years form the basis for our confidence in the present framework.

Tool use will always be interesting *to humans* because it is a key part of our evolutionary legacy. We have evolved to pay attention to tool use. Naturally our oversized brains led us towards complex neuronal patterns being *the* pathway along which tool use arises (once the idea of humans simply being gifted technologies by gods faded from preference). But brains do not use tools. Bodies do. Brains are ineluctably embedded in bodies, but an isolated brain is a wet mess, not a successful technologist. Cognition in its broader sense as information management is essential to tool use, but the extent to which technological cognition is based in a controlling brain across the wide swathe of non-human tool-using animals—including numerous invertebrates—is an empirical question that has yet to be resolved. Whether or not the brains of non-tool-using individuals in so-called 'tool-using species' are deficient or abnormal in predictable ways is also an open question—our cybernetic, ecological framework predicts no such differences will be found. Empirical research assisted, for instance, by high-resolution positional tracking, will increasingly allow us to tease apart the components of the cybernetic cycle, and to see technological activities more from the perceptive viewpoint of the acting animal. Once those gears are determined they can be evaluated for necessity and sufficiency, testing predictions of which parts of the information loop require social information or practical experience of material properties or landscape regularities to produce long-lasting tool behaviors.

A cyborg, game-theoretic view of tool use systems takes pressure off the search for human-like characteristics in tool-using animals. From this standpoint, we encounter animal tool users not as archetypes but as active agents creating meaning in their worlds. Natural cyborgs surround us and have likely been features of Earth since the emergence of animal life, blinking in and out of existence. Getting to know them better will assist our understanding of how deeply entwined animate life is with its environment, and aid in our search for similar behavior in the past, or even—as for the original Cyborg conception—beyond our own planet.

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