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RESEARCH ARTICLE

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A robust tool kit: First report of tool use in captive crested capuchin monkeys (*Sapajus robustus*)

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Abstract

Primate tool use is of great interest but has been reported only in a limited number of species. Here we report tool use in crested capuchin monkeys (*Sapajus robustus*), an almost completely unstudied robust capuchin species. Crested capuchins and their sister species, the yellow-breasted capuchin, diverged from a common ancestor over 2 million years ago, so this study fills a significant gap in understanding of tool use capacity and variation within the robust capuchin monkey radiation. Our study group was a captive population of seven individuals at the Santa Ana Zoo in California. The monkeys were given no prior training, and they were provided with a variety of enrichment items, including materials that could be used as tools as well as hard-to-access resources, for open-ended interactions. In 54 observation hours, monkeys performed eleven tool use actions: digging, hammering, probing, raking, sponging, striking, sweeping, throwing, waving, wedging, and wiping. We observed tool modification, serial tool use, and social learning opportunities, including monkeys' direct observation of tool use and tolerated scrounging of foods obtained through tool use. We also observed significant individual skew in tool use frequency, with one individual using tools daily, and two individuals never using tools during the study. While crested capuchins have never been reported to use tools in the wild, our findings provide evidence for the species' capacity and propensity for tool use, highlighting the urgent need for research on this understudied, endangered primate. By providing detailed data on clearly identified *S. robustus* individuals, this study marks an effort to counteract the overgeneralization in the captive literature in referring to any robust capuchins of unknown provenance or ancestry as *Cebus apella*, a practice that obfuscates potential differences among species in tool use performance and repertoire in one of the only species-rich tool-using genera in the world.

KEYWORDS

Cebinae, Platyrrhini, primate enrichment, robust capuchin monkeys, tool action types

Abbreviation: cm, centimeter; D.S., Danielle L. Steinberg; J.W.L., Jessica W. Lynch; m^2, meters squared; PVC, polyvinyl chloride; spp., species.

1 | INTRODUCTION

Tool use by nonhuman primates is of particular interest for primatologists, anthropologists, paleoanthropologists, psychologists, and neuroscientists because of its potential to inform understanding of both nonhuman primate ecology and cognition as well as tool use in hominin evolution (Bandini et al., 2020; Barrett et al., 2018; Haslam, 2013; Johnson-Frey, 2004; Osiurak & Reynaud, 2020). Though tool use has been observed in both the Catarrhini and Platyrrhini, only a limited number of primate species have been observed using tools, and even fewer have been documented to use tools habitually (Haslam et al., 2013; Ottoni & Izar, 2008; Wasserman & Thompson, 2017). In a widely used definition of tool use, Beck (1980, p. 10) insists that a tool must be an item "separate from that of the body of the user," must be derived from the environment, and "must be manipulated" to produce an "intentional outcome." Here we use St. Amant and Horton's (2008, p. 1203) definition that tool use is "the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment." This definition is used preferentially to that of Beck (1980) because it includes all of Beck's requirements while also including mediation of information and target alteration as potential objectives.

In wild populations, tool use has been observed in great apes, in macaques only among cercopithecoids, and in capuchin monkeys only among platyrrhines (Haslam, 2013), suggesting that the capacity for tool use evolved independently in the primate lineage at least three different times. Tool use is typically categorized by how widespread and frequent it is, from habitual tool use, in which "events are… repeated by several individuals over time" (McGrew & Marchant, 1997, p. 791) to anecdotal tool use, which are "unique or rare events" (McGrew & Marchant, 1997, p. 790).

1.1 | Robust capuchin tool use in wild populations

While most robust capuchin (*Sapajus*) species have been documented to use tools in the wild at least anecdotally, wild gracile capuchin (*Cebus*) species have been observed to do so much less frequently (Barrett et al., 2018; Boinski, 1988; Chevalier-Skolnikoff, 1990; Monteza-Moreno et al., 2020; Panger et al., 2002; Panger, 1998; Perry et al., 2017; Phillips, 1998), pointing to significant diversity in types of tool use actions and frequency of tool use performed across the capuchin radiation by different species. Of the robust capuchins, *Sapajus libidinosus*, the bearded capuchin or black-striped capuchin, is the best documented tool-using species with the most diverse tool use repertoire in the wild; some populations even exhibit habitual stone tool use for hammering (Falótico et al., 2017, 2018, 2019; Presotto et al., 2020; Visalberghi et al., 2015). In addition, a limited number of bearded capuchin populations have been documented to use tools for digging, probing, throwing as a sexual display, and for displaying aggressiveness in the wild (Falótico & Ottoni, 2014; Mannu & Ottoni, 2009; Moura & Lee, 2004, 2010; Table 1).

Highlights

- Untrained captive crested capuchin monkeys performed 11 distinct types of tool use.
- Digging and hammering were performed by the most individuals (5 of 7 and 4 of 7, respectively), and raking was the tool action most frequently performed (53 times).
- We observed tool modification, serial tool use, and tolerated scrounging of foods obtained through tool use.

While bearded capuchins (*S. libidinosus*) appear to have the most diverse repertoire of tool use, some cases of wild tool use have been reported in five of the other six *Sapajus* species (following the IUCN, 2021 classification). These other species have only been shown to use only one or two tool types, and tools are used much more infrequently than in the bearded capuchin (Table 1). Blond capuchins (*Sapajus flavius*) display both hammering (Ferreira et al., 2009) and probing (Souto et al., 2011) behavior in the wild. Black horned capuchins (*Sapajus nigritus*) use tools for hammering open seeds (Rocha et al., 1998), and for probing (Garber et al., 2012). Brown capuchins (*Sapajus apella*) also have been documented to use tools to hammer in the wild, though these instances are anecdotal (Boinski et al., 2000; Fernandes, 1991). A large-headed capuchin (*Sapajus macrocephalus*—considered a junior synonym of *S. apella* in IUCN, 2021) may have used a branch as a shovel to remove leaf litter while digging caiman eggs out of a nest, based on an interpretation of camera trap data (Torralvo et al., 2017). The Azara's capuchin, also known as the hooded capuchin (*Sapajus cay*), has been observed anecdotally to use a stick to peel back tree bark in search for insects (Smith, personal communication). Finally, there is indirect evidence for yellow-breasted capuchin (*Sapajus xanthosternos*) tool use for nut-cracking across six populations (Canale et al., 2009), as well as video documentation of *S. xanthosternos* hammering nuts with a stone tool (Martins, unpublished).

1.2 | Robust capuchin tool use in captivity

In addition to these accounts of wild robust capuchin tool use, a body of literature catalogs tool use in captive *Sapajus*, including untrained capuchins hammering, sponging, probing, and making tools to access food rewards (see Fragaszy, Visalberghi, et al., 2004 for a thorough review of the earlier literature). Many of these studies took place before the recent and substantial taxonomic revision of the capuchin monkeys, so in many studies, all robust capuchins were labeled as *Cebus apella*, without regard for provenance or ancestry (see Lynch Alfaro et al., 2014 for discussion), a practice that continues today by

TABLE 1 Examples of spontaneous tool actions observed in untrained robust capuchins, in the wild and captivity, by species

	Sapajus									
	Wild						Captive			
	libidinosus	*flavius*	*apella*	*nigritus*	*cay*	*xantho-sternos*	*robustus* (this study)	*libidinosus*	*Cay*	*Sapajus* spp. (mixed, unknown, or hybrid)
Bait	-	-	-	-	-	-	-	1	-	-
Contact	H(2)	-	-	-	-	-	-	-	-	-
Cup	-	-	-	-	-	-	-	-	-	3, 4
Cut	A(5)	-	-	-	-	-	-	-	-	6
Drop	H(2)	-	-	-	-	-	-	-	-	-
Dig	H(5, 7, 8)	-	A(9)	-	-	-	X	-	10	11, 12
Hammer	H(5, 7, 8, 13-20)	H(19, 21)	A(22, 23)	H(24)	-	H(25)	X	-	10	12, 26, 27
Lever	-	-	-	-	-	-	-	-	10	-
Peel	-	-	-	-	A(28)	-	-	-	-	-
Probe	H(5, 7, 8, 29)	H(30)	-	Ex(31)	-	-	X	-	-	12
Pull	-	-	-	-	-	-	-	-	-	32
Push	-	-	-	-	-	-	-	-	-	33
Rake	-	-	-	-	-	-	X	-	10	-
Sponge	-	-	-	-	-	-	X	-	-	3, 26
Strike	-	-	-	-	-	-	X	-	-	33
Sweep	-	-	-	-	-	-	X	-	10?	-
Throw	H(34, 35)	-	-	-	-	-	X	-	-	36
Tweeze	-	-	-	-	-	-	-	-	10	-
Water	-	-	-	-	-	-	-	-	-	37
Wash	-	-	-	-	-	-	-	-	28	38
Wave	-	-	-	-	-	-	X	-	-	-
Weapon	-	-	-	-	-	-	-	-	10	32, 36
Wedge	-	-	-	-	-	-	X	-	-	-
Wipe	-	-	-	-	-	-	X	-	-	-

Note: Captive list includes semi-free ranging examples. Tool action types observed in the present study are defined in Table 2. Tool actions defined in the literature are as follows: bait = place or hold food in water to attract fish to catch, contact = push male by contacting with a stick, as part of courtship, cup = cup used to drink water, cut = slice through surface with sharp object, drop = drop stick on male as part of courtship, lever = wedge stick between to separate two objects, peel = use stick to peel back tree bark, Pull = put cloth over out-of-reach food and pull on cloth to retrieve food, push = push peanut out of a tube with stick, tweeze = use tiny straw from broom to remove splinter from hand, water = fill bottle with water to retrieve food stuck to bottom, wash = clean food with water prior to eating, weapon = strike, poke, club or hit with stick to do harm to another individual. Within the table the following conventions are used to demarcate frequency of tool use and whether the actions were elicited experimentally by introduced materials: A = Anecdotal, H = Habitual, Ex = experimental. X = observed in present study. Literature cited in Table 1: (1) Mendes et al. (2000), (2) Visalberghi et al. (2017), (3) Westergaard and Fragaszy (1985), (4) Westergaard and Fragaszy (1987), (5) Moura and Lee (2004), (6) Westergaard and Suomi (1994a), (7) Mannu and Ottoni (2009), (8) Moura and Lee (2010), (9) Torralvo et al. (2017), (10) Giudice and Pavé (2007), (11) Westergaard and Suomi (1995), (12) Serbena and Monteiro-Filho (2002), (13) Fragaszy, Izar, et al. (2004), (14) Mendes et al. (2015), (15) Ottoni and Mannu (2001), (16) Spagnoletti et al. (2011), (17) Waga et al. (2006), (18) Cutrim (2013), (19) Ferreira et al. (2009), (20) Santos et al. (2019), (21) Emidio and Ferreira (2012), (22) Fernandes (1991), (23) Boinski et al. (2000), (24) Rocha et al. (1998), (25) Canale et al. (2009), (26) Aguiar et al. (2014), (27) Westergaard and Suomi (1994b), (28) Smith (personal communication, 2021), (29) Falótico and Ottoni (2014), (30) Souto et al. (2011), (31) Garber et al. (2012), (32) Cooper and Harlow (1961), (33) Visalberghi and Trinca (1989), (34) Falótico and Ottoni (2013), (35) Moura (2007), (36) Hamilton and Fragaszy (2014), (37) Lessa et al. (2001), (38) Visalberghi and Fragaszy (1990).

some research groups studying captive capuchins. While these studies emphasize the ability and propensity for tool use in *Sapajus*, they do little to illuminate the diversity in tool use capacity or propensity across robust capuchin species, which have been diversifying from each other for about 3.3 million years (Lima et al., 2018). Some research groups have employed genetic analyses for species identification of the monkeys in their colonies; in one prominent lab, monkey matrilines were shown to be variously *S. apella apella*, *S. a. macrocephalus*, *S. cay*, and *S. nigritus* using mtDNA markers (Lucarelli et al., 2016). This practice should be commended, as it provides clarity about the diversity of species being studied and interacting with one another in a given laboratory. In terms of captive studies of tool use in known robust capuchin species, in Paraguayan zoos, clearly identified captive Azara's capuchins (*S. cay*) have been reported to rake in food, hammer, probe, dig and use sticks as levers (Giudice & Pavé, 2007), as well as to spontaneously dig with stones and sticks (Smith, personal communication).

In this study, we report on tool use in the crested capuchin, *Sapajus robustus*, a species that has never been reported to use tools either in captivity or in the wild. One obvious reason for the absence of tool use reports might simply be the lack of research on this particular species. Thus far, there has only been a single year-long research study of wild crested capuchins, with no accounts of tool use described amongst 15 individuals in over 370 observation hours (Martins et al., 2022; Martins, 2010). Of note is that *S. robustus* diverged from its sister taxon, *S. xanthosternos*, over 2 million years ago (Lima et al., 2018)—as much or more time depth as the divergence between bonobos and chimpanzees, sister species that are extremely different in their tool use behavior (Furuichi et al., 2015). Thus, there is a significant gap of knowledge about tool use within the robust capuchin radiation.

Here we continue the project of assessing the ability and propensity for tool use behavior in captive robust capuchin monkeys clearly identified at the species level (Lynch Alfaro et al., 2014). We test whether untrained *S. robustus* individuals, when given access to substrates that could be used as tools, and food placed out of reach, will spontaneously, of their own volition, use those substrates to achieve food acquisition goals. Given that at least a limited amount of tool use has been observed in all other robust capuchin species, we predicted that captive crested capuchins would display tool use if provided with appropriate materials and observed for an adequate period of time.

2 | METHODS

2.1 | Study site and subjects

The Santa Ana Zoo's population of crested capuchin monkeys consisted of seven individuals, six of whom were born into captivity. The eldest male (Sergio) was wild-caught and subsequently rescued from the pet trade in Brazil; he was first housed in Rio de Janeiro Primate Center and came to the Brookfield Zoo in Illinois in 1999 before transferring to the Santa Ana Zoo in 2006. The monkeys were divided into two separately housed groups: a family group of five (continuous full contact—group) and a father-daughter dyad (continuous full contact—pair). The family group consisted of Matteo (male, age 12), Chloe (female, age 17), Dora (female, age 8), Sofia (female, age 7), and Maisy (female, age 1). The dyad was composed of Sergio, a male of unknown age (but at least 20+ years), and his daughter, Daisy (age 5). None of the monkeys had previously participated in any sort of scientific study or experiment and had not been given any training apart from basic station training. However, as Sergio was brought into the pet trade from the wild, it is possible he had some training early in life (though he had been living in a zoo facility for over 20 years by the time of the present study).

The group of five was housed in a large indoor-outdoor enclosure consisting of two outdoor sectors, each approximately 190.5 m^2, with chain-link fencing on all sides, wooden platforms, branches, hanging firehoses, plants, and concrete and dirt substrate on the floor connected by a smaller indoor region. In the northern sector, a raised concrete bed was filled with mulch. A few stones, smaller than a pound each, typically were scattered about the enclosure. Browse from plants on the grounds such as bamboo (*Bambusoideae* spp.) and a pomegranate tree (*Punica granatum*) were provided fresh daily. Additionally, the raised bed of mulch provided the capuchins an opportunity to dig. Thus, the enclosure provided the capuchins with "set-ups" for the opportunity to search for and process food with the aid of tools.

The dyad resided in a smaller, heated indoor enclosure, about 30 m^2, with some shelves, firehoses, and access to an outside area about 57 m^2 in size. All monkeys were provided with water ad libitum and fed twice a day, often supplemented with additional food for enrichment. Their daily diet consisted of spinach, yam, onion, commercially prepared canned primate food (ZuPreem), commercially prepared primate biscuits for platyrrhines (Mazuri Formula 5MA5), as well as other assorted fruits, vegetables, nuts, seeds, and proteins. They also received many forms of environmental enrichment as part of their weekly routine (Supporting Information: Table 1).

Zoo staff estimated that approximately 75% of the monkeys' normal diet was provided through enrichment opportunities. Occasionally, however, special treats that were not part of their normal diet (such as peanut butter, raisins, or different kinds of nuts) were provided to increase dietary diversity and to stimulate interest in enrichment.

2.2 | Enrichment during the study period

Different enrichment items were made available to the capuchins on different days of the study (Supporting Information: Table 2), to enhance the opportunities for diverse types of tool use. For the family group of five, multiple types of enrichment were made available simultaneously, to make it possible for several individuals to have the opportunity to use tools at the same time as each other. Enrichment items included probing pans; tubs of packed dirt or sand

with buried nuts; a juice tube (PVC tube filled with juice out of reach of monkeys' arms); a tree stump drilled with many holes sometimes filled with raisins; peanut butter feeder (PVC tube with holes drilled into length and smeared inside with peanut butter); boomer ball (a hard plastic ball that could be used as a hammer); various PVC pipes and hoses; metal scoops; rocks; browse and bamboo; and nuts placed both inside and outside of the enclosure. Walnuts, hazelnuts, and almonds were provided in shell, in the amount of an adult human handful. See Supporting Information: Table 3 for more detail about enrichment items.

2.3 | Data collection

Observations were made Monday through Saturday from 09.00 to 15.00 between July 13 and July 25, 2020 and then 7 days a week beginning at 08.00 between September 8 and September 20, 2020 (see Supporting Information: Table 2). D.S. spent approximately 54.25 h observing the capuchins and recorded 2.7 h of foraging behavior on a Canon Vixia HFR80 handheld camcorder. All occurrences of tool use were recorded on an *ad libitum* basis. Following data collection, videos were analyzed for tool use using the following coding system. For each video clip, we coded (1) the identity of the tool user and any conspecific observers, (2) if the tool use involved enrichment materials purposefully added to enclosure, (3) the tool type, (4) the tool action, (5) the target of the tool use, and (6) whether the tool user was successful. A tool use event was deemed a success if the target object/substance was physically obtained by the actor through the use of the tool (e.g., when a nut from outside the enclosure or in a tube was transferred into the actor's hand or mouth, when juice from a tube or bucket entered the mouth, etc.). For nonfood-related behaviors such as throwing, success was defined as hitting the presumed target with the projectile.

2.4 | Inter-rater reliability

To ensure that the videos were coded accurately, 15% of the entire collection of video clips coded by D.S. were randomly selected to be coded by J.W.L. The same coding system was used and resulted in over 95% agreement, satisfying our criteria for reliable coding.

3 | RESULTS

From the 2.7 h of video, we extracted 151 clips containing tool use. From these clips, we were able to code 169 individual events of tool use. Across these 169 events, monkeys used tools in 11 distinct actions, listed in Table 2.

Five of the seven monkeys attempted tool use during the observation period, though the frequency, diversity, and success of tool use varied dramatically between individuals despite them having similar opportunities (Table 3). We also observed tools being modified, presumably for more effective use, and occasionally tools were used serially to achieve success in a multi-step task.

In the sections below, we describe each of the tool use actions in detail, starting with the actions that were attempted by the greatest number of individuals. Figure 1 shows examples of each of the 11 actions taken from the video in our corpus, and Supporting Information: Video 1 includes video examples of each of these tool action types.

3.1 | Digging

The tool action performed by the largest number of capuchins (5 of 7) during the observation period was digging. The two males, Matteo and Sergio, were responsible for 22 of the 30 total observed attempts, but Sofia, Dora, and Maisy also dug. Apart from one instance of digging with a stick, all occurrences involved the use of a metal scoop in a tub filled with either dirt or sand, with buried nuts and/or mealworms (Supporting Information: Video 1). Sergio had the longest digging events, which sometimes would last for several minutes. All other monkeys dug for less than a minute.

3.2 | Hammering

The tool action hammering was attempted by four of the seven capuchins. To hammer, a hard object such as a stone, boomer ball (a thick plastic ball with a six-inch diameter and a few holes drilled into it), or metal scoop would be grasped with both hands, lifted up, and brought down on a target object with force (Supporting Information: Video 1). Fifteen of the 18 observed hammer events were attempts at cracking open nuts. Matteo, using a stone, and Sergio, using a boomer ball, both regularly and successfully opened hard-shelled nuts using this technique. Dora and Maisy attempted cracking nuts but were not successful.

3.3 | Probing

Matteo performed probing in several different contexts. In all cases, probing involved his inserting a tool, such as a piece of bamboo, through an opening in order for the end of the tool to come in contact with a target object such as viscous food or liquid (Supporting Information: Video 1). Matteo successfully obtained yogurt from an aluminum pie dish placed outside of his enclosure during a “probing” enrichment activity and peanut butter from inside the peanut-butter feeder by probing with bamboo, sticks, and strips of bark. On two occasions, we also observed Sergio using a piece of bamboo to probe and slightly reposition a heat lamp hanging above his enclosure.

The first time the capuchins were presented with the peanut butter feeder, there were no end caps secured on it, so the monkeys could reach through the mesh and into the sides of the tube to retrieve the reward without using tools. Despite being able to obtain

TABLE 2 Tool actions observed during the study

Tool action	Definition	Observed tool(s)
Dig	Grasping an object with one or both hands, lifting it above substrate, and then bringing down into substrate with enough force to disturb substrate; motor patterns are dynamic and sometimes very similar to "hammer," but can also include scooping, sifting, and sweeping motions; the behavior seems to be used both to disrupt the dirt/sand to uncover objects, and also to make contact with hard objects under the surface, for subsequent retrieval; often exploratory and used in combination with digging with hands; digging can also occur with stick, using finer motor control and less force.	Metal scoop, stick
Hammer	Grasping an object (usually a rock) with both hands, lifting it up, and then bringing it down onto a target object with force.	Rock, boomer ball, scoop
Probe	Inserting a tool through an opening such that the end of the tool makes contact with a target food or object; holding a tool above a liquid or viscous target and lowering it until contact is made between the tool and the target such that the target adheres to the tool.	Bamboo, strip of bark, branch, stick, newspaper
Rake	Using a tool as an extension of the hand/arm by extending the tool to the target object or just past the target object and then retracting the tool back towards the body while attempting to maintain contact with target.	Bamboo, strip of bark, branch, stick
Sponge	Used exclusively with a liquid target, compacting and pushing the tool into a container to reach a liquid target; requires two hands, one to guide the material and the other to compact the material; the tool must be able to absorb the liquid; uses both hands in various positions to direct the tool toward the target. (see *absorb* in Shumaker et al., 2011).	Newspaper
Strike	Grasping a stick-like object near one end and then propelling it forward on the horizontal plane using the elbow as the fulcrum point to strike an object so that it is propelled forward away from the body (a more forceful variant of "*push*" as described in Visalberghi & Trinca, 1989).	Stick
Sweep	Grasping a tool and flicking the wrist such that the tool moves back and forth over the horizontal plane on a substrate, disturbing the top layer.	Bamboo, strip of bark, branch, stick
Throw	Propelling an object through the air by taking it in hand and releasing it as the arm moves forward from the fulcrum of the elbow.	Green bean, bamboo, stick, branch
Wave	Grasping a tool (usually a stick or branch) and moving it back and forth through the air in the direction and view of a target individual or target individuals.	Stick, bamboo, branch
Wedge	Inserting a tool through an opening, placing the far end past the object and wedging it between the top and bottom of the enclosed space, and then using the top of the enclosure as a lever, retracting the tool back towards the body to drag a target object back out with it through maintaining pressure that forces the object against the substrate (may be considered a variant of *rake*, but utilizes the stick like a lever wedged between the two sides of the enclosed space to force the target object closer).	Stick, strip of bark
Wipe	Holding the tool with flat open hand facing downwards, and sliding the tool back and forth against the substrate; using this motion to pull up items (e.g., ants) from the surface onto the tool for consumption.	Newspaper

peanut butter with his hands alone, Matteo still used a strip of bark to probe into the side of the tube to reach the peanut butter. Five days later, when the peanut butter feeder was reintroduced to the group with end caps on it, Matteo quickly solved the foraging task by using a thin, straight piece of bamboo to probe the apparatus through the holes drilled through the front.

Matteo also probed for liquid. On July 18, a small plastic bucket filled almost to the top with diluted juice was placed outside the enclosure, against the mesh so that the monkeys could reach it. While Maisy and Dora opted to dunk their hands into the juice to lick it off their fingers, Matteo selected a branch from the pile of browse and placed the tip into the bucket and then licked the juice from it (Supporting Information: Video 1). Matteo's second probing for liquid attempt occurred after 9 min of unsuccessful interaction with the novel juice tube enrichment device. He probed with a thin, bent stick, approximately 10 cm in length, into the juice tube, removed it, and moved away. Due to the poor quality of the video, it was unclear if Matteo succeeded in obtaining any juice.

3.4 | Raking

The most common tool action Matteo performed throughout the observation period was raking (Supporting Information: Video 1). It occurred on 8 of 11 days of observation and was attempted a total of 50 times by Matteo. Sofia also attempted raking three times. Unlike many of the other examples of tool use, raking often occurred spontaneously without the stimulus of enrichment designed to

TABLE 3 Tool use actions used by each individual during the study

	$Matteo_g$ male age 12	$Sergio_d$ male age 20+	$Maisy_g$ female age 1	$Dora_g$ female age 8	$Sofia_g$ female age 7	$Chloe_g$ female age 17	$Daisy_d$ female age 5
Dig	X	X	X	X	X	-	-
Hammer	X	X	X	X	-	-	-
Probe	X	X	-	-	-	-	-
Rake	X	-	-	-	X	-	-
Sponge	X	-	-	-	-	-	-
Strike	-	X	-	-	-	-	-
Sweep	X	X	-	-	-	-	-
Throw	X	-	-	-	-	-	-
Wave	X	-	-	-	-	-	-
Wedge	X	-	-	-	-	-	-
Wipe	-	X	-	-	-	-	-

Note: The subscript g or d indicates whether the monkey was part of the group or the dyad, and sex and age are indicated for each individual.

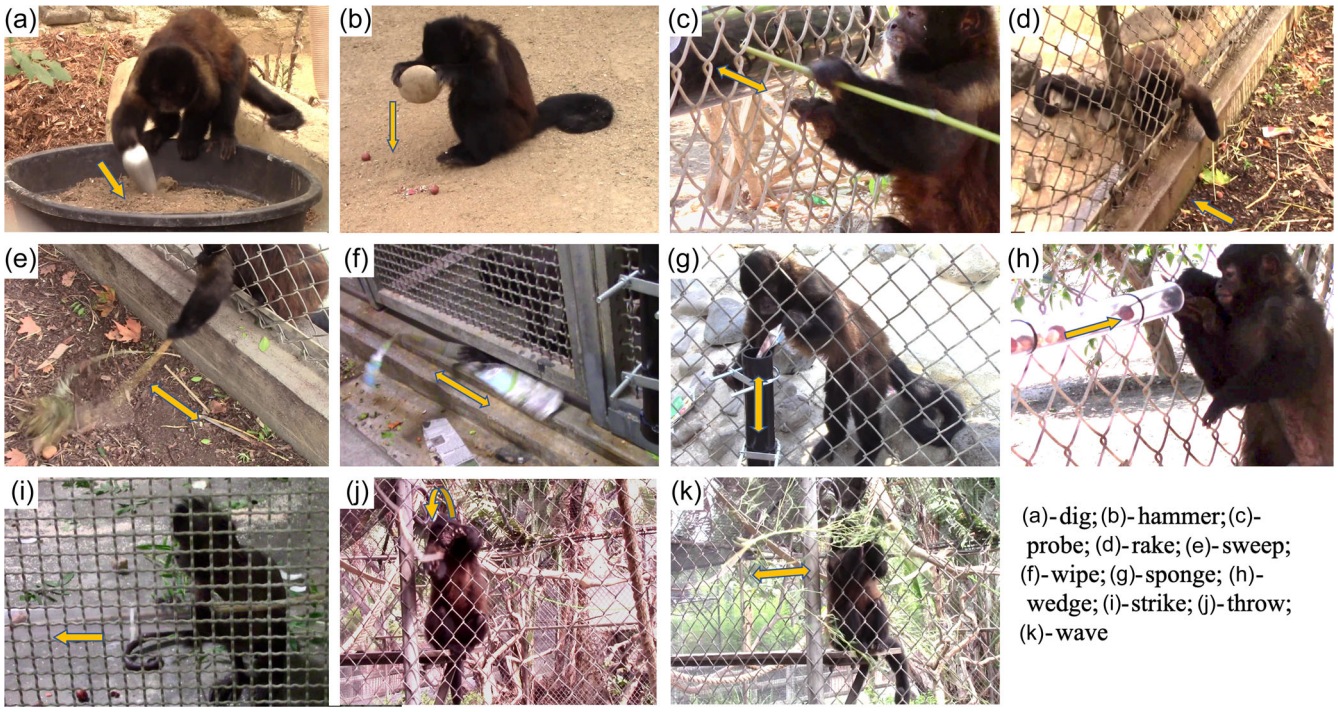

FIGURE 1 Tool use actions observed in the study. (a) Dig; (b) hammer; (c) probe; (d) rake; (e) sweep; (f) wipe; (g) sponge; (h) wedge; (i) strike; (j) throw; (k) wave

require tools. Forty-seven of Matteo's 50 attempts at raking took place on the floor of the enclosure against the mesh where he would attempt to bring objects on the ground outside of the enclosure within hand's reach. His other three attempts and Sofia's three attempts took place on a branch high up near the northern side of the southern sector of the enclosure where they attempted to rake in unidentified objects from the roof of the indoor area. On September 12, Matteo held a stick while standing on a branch close to the indoor enclosure. He had his arm through the mesh to the elbow and was moving the stick back and forth as if to rake something in. Soon after Matteo appeared to lose interest and walked away, Sofia approached and used the same stick to perform the same behavior, albeit briefly and unsuccessfully. She soon returned again with a longer, thinner stick and tried again two more times to no apparent avail.

Matteo repeated this behavior 6 days later, but it was unclear if he succeeded in retrieving anything from the roof.

3.5 | Sweeping

Matteo spontaneously performed sweeping 14 times. This action differs from raking as raking is directed towards a specific target, while sweeping is not. The purpose of sweeping seems to be exploratory rather than target-directed. Because of this, defining "success" for this tool action is challenging. Like raking, however, sweeping was performed on the dirt substrate outside of the enclosure (Supporting Information: Video 1). Sweeping events were brief—once he had disturbed the substrate, Matteo often would attempt to rake in an object uncovered by his sweeping.

3.6 | Sponging

Matteo was the only capuchin to perform sponging. Sponging is used exclusively with a liquid target and a tool that must be able to absorb the liquid. The action of sponging requires dexterity as both hands are used for different purposes simultaneously. One hour and four minutes after first encountering the juice tube, Matteo succeeded in sponging up juice to drink using a folded strip of newspaper (Supporting Information: Video 1). In total, Matteo attempted to use newspaper to sponge juice from the juice tube three times on the same day but was only successful in obtaining juice twice.

3.7 | Wedging

On July 21, the capuchin family group was given transparent hose and opaque PVC tube enrichment items. Both items contained a handful of nuts, unshelled, placed far enough into the tube or hose so that the adult monkeys could not reach in from either side to obtain the food. Matteo tried to procure the nuts in the transparent hose first by shaking the hose and then by attempting to reach in but was unsuccessful. He then picked up a thin, straight stick, approximately 30 cm long from the ground and inserted it into one end of the hose until it was wedged between the top of the hose and a nut, and then repeatedly retracted it back toward his body to drag a nut out with the tool (Supporting Information: Video 1). The following day, Matteo successfully repeated the same action, but with a strip of bark that he wedged under the nut rather than over it. In sum, Matteo was recorded performing this action four times and three of these times were successful in obtaining the nut.

3.8 | Wiping

Sergio performed a wiping tool action on the cement substrate outside of his cage. On September 12, he was provided with newspaper strips to be used with the juice tube enrichment. After approximately 5 min of unsuccessful attempts at obtaining juice, Sergio took two long strips of newspaper that were folded in half and wiped them back and forth under the enclosure's door over an area covered in ants, clearing the floor of the insects (Supporting Information: Video 1). He subsequently ate several ants off of the newspaper strips. Sergio's single wiping event lasted 5 s.

3.9 | Striking

When presented with the opportunity to retrieve nuts from inside a horizontal tube, Sergio used a different action than Matteo to obtain the food reward. In contrast to Matteo's technique of wedging, in which he pulled the nut towards his body, Sergio used a stick to strike the nut like a billiards player striking the cue ball with a cue stick, so the nut would roll toward the far end of the tube (Supporting Information: Video 1). Sergio was the only capuchin to perform this action and did so twice, successfully retrieving nuts on both attempts.

3.10 | Throwing

Throwing was unrelated to enrichment or food. Matteo was the only individual to perform this action and did so a total of 12 times with various objects including pieces of bamboo, sticks, and even a green bean on one occasion (Supporting Information: Video 1). Matteo spontaneously threw objects on six of the observation days. The first 10 attempts were all unsuccessful in hitting his assumed target (D.S. or keeper). Despite missing his target, Matteo did succeed in directing the attention of the target to him, a possible goal of this behavior. In the two cases in which he did succeed in hitting a human with a projectile, Matteo's response was not noticeably different than when he missed.

3.11 | Waving

Like throwing, Matteo occasionally waved an object around outside the enclosure, presumably to gain attention and/or make physical contact with a target individual (Supporting Information: Video 1). Before the observation period and the zoo's closure due to the COVID-19 pandemic, Matteo would grasp a tool (usually a stick or branch), insert his arm and tool through the mesh, and move it all around through the air in the direction and view of zoo visitors daily. During the observation period, Matteo performed this action five times. This is a less clear example of tool use, due to the lack of confirmed goal-oriented behavior, but should be studied further.

3.11.1 | Modifying tools

Before or while using branches, sticks, and bamboo as tools, Matteo occasionally would modify them, presumably to improve their

functionality or efficiency. During the observation period, 14 instances of tool modification were recorded. Matteo stripped the leaves and/or bark off of branches on seven confirmed occasions. He also shortened a tool by breaking or biting it on four occasions (Supporting Information: Video 2). In three additional instances, Matteo both stripped and trimmed his tool. Stripping branches of their leaves and offshooting twigs was often done in congruence with probing and raking behavior and allowed the tool of choice to fit more easily through the opening required to obtain the food reward. Shortening tools was seen in conjunction with throwing, waving, and raking behaviors.

Not all modifications had a clear function or goal, and sometimes modification led to reduced efficiency. In one of the instances of tool-shortening, Matteo attempted to rake a nut into hand's reach using a stick but was not successful after a few seconds. He then pulled the stick back in, bit it to shorten it to about two-thirds of its original length, and proceeded to try to rake the nut in again. On his first attempt, the stick was long enough to reach the nut, but after shortening it, Matteo could not reach the target nut with the modified tool.

3.11.2 | Serial tool use

On three recorded occasions, Matteo serially used more than one tool action type (Supporting Information: Video 2). Two recorded events of serial tool use (*sensu* Shumaker et al., 2011, p. 19: "two or more tools used sequentially, usually each in a different mode to achieve a single outcome, when the first tool is not used to manufacture the second") involved him using a branch or stick to rake in a piece of bamboo that he subsequently used as a different rake and/or as a projectile. During the other recorded case and on a few (fewer than five) unrecorded occasions, Matteo would obtain a nut by either digging with a metal scoop or raking it in from outside the enclosure and then would immediately proceed to crack open that nut using a stone hammer. In two recorded instances in which Sergio had access to unshelled nuts and a boomer ball, he immediately used his boomer ball to crack the nuts he had acquired through digging.

3.11.3 | Tool use observation and tolerated scrounging

While collecting data on tool use behavior, D.S. noticed that monkeys not engaged in tool use behavior would frequently observe the tool user, meaning that they would direct their full attention to watching the tool user perform a task involving tools. Furthermore, when Matteo used tools, he often tolerated scrounging from Maisy and occasionally from the other females, allowing them to access bits of the food reward that he had worked to obtain (Supporting Information: Video 2).

Of all 151 videos involving tool use (encompassing 169 distinct tool use events), 67 videos (~44%) showed at least one monkey observing the focal tool user. It is likely that this is an underestimation, due to the fact that observers could have been out of frame as the tool use itself was the focal activity being documented. All of the videos showing observations of tool use were from the family group of five.

Of the 67 videos containing tool use observation, 66 of them had Matteo as the focal tool user, while one clip showed Dora watching Maisy dig with a metal scoop. Chloe and Sofia were recorded once each as observing Matteo using tools, Dora was seen observing 26 tool use events, and Maisy was recorded observing at least 50 instances of tool use, often situating herself right next to Matteo and even placing her hands on the tools occasionally. There were two additional instances in which it was clear that Matteo was being observed by at least two females while performing a raking behavior, but the identities of the females could not be determined from the video. Within the dyad group, Daisy was never coded as observing Sergio's tool use behavior.

In seven videos, Matteo tolerated scrounging from either Maisy or Dora, and in seven more, he allowed both females to eat some of his food acquired through tool use (Supporting Information: Video 2). In addition, on five different occasions, after Matteo left a tool use site, females were able to collect "leftovers" such as remains of smashed nuts.

3.11.4 | Failed attempts

In addition to the numerous successful tool use events, we also observed many failed tool use attempts. For example, on two occasions, Matteo performed the hammering action, but not in the context of nut cracking. On July 23, Matteo used a metal scoop in an apparent attempt to hammer raisins out of the tree stump enrichment but was unsuccessful. That same day, Matteo used a large, flat stone, like the ones he generally used on nuts, to hammer a transparent, empty hose that was secured on the metal mesh of the enclosure, as well as to hit the mesh itself. The purpose of this particular behavior was undetermined, as no food reward was present. Maisy used a metal scoop twice in an attempt to strike a piece of monkey chow in a hammer-like motion, but missed the food and hit the concrete instead. Dora attempted to use a metal scoop to hammer open a walnut but was unsuccessful as the walnut was in a soft, dirt substrate that absorbed some of the force.

4 | DISCUSSION

By providing detailed data on clearly identified *S. robustus* individuals, this study marks an effort to counteract the overgeneralization in the captive literature in referring to any robust capuchins of unknown provenance or ancestry as *C. apella*, a practice that obfuscates potential differences between species in tool use performance and repertoire in one of the only species-rich tool-using genera in the world. When provided with materials and opportunities, the crested

capuchins we observed used a variety of tools. We predicted that this species would display tool use, given the presence of tool use in other robust capuchin species. What surprised us, however, was the diversity of the tool use repertoire we observed (Table 1). We predicted that the crested capuchins would show tool use behavior comparable to what had been observed in the wild in the majority of other robust capuchin species—that is, a few anecdotal cases of one or two tool use actions. Alternatively, they might display some subset of tool use actions already observed in other robust capuchins in captive or free-ranging situations. However, we observed a total of 11 distinct tool action types, spanning and exceeding the tool use actions seen within any of the other robust capuchin species in the wild, including *S. libidinosus* and including new action types that had not been described formally for captive robust capuchins. We suspect that one reason why we observed such a diversity of tool use is because the monkeys were regularly given a variety of raw materials and diverse enrichment items on different days, resulting in ample opportunity for "open-ended" tool use, meaning they were free to explore and manipulate objects at their leisure as opposed to under experimental constraints (e.g., Glickman & Sroges, 1966).

Another framework to explain this variety and frequency of tool use we observed could be the *captivity bias* (Haslam, 2013). In captivity, animals do not need to forage for food nor be vigilant for predators, giving them spare free time and energy. Having spare free time and energy is one of the conditions outlined by Kummer and Goodall (1985) as allowing for innovation, a precursor to tool use. In addition to Kummer and Goodall's spare time hypothesis, Haslam also pointed to increased contact between individuals allowing for observation and social learning of tool use as contributing to the captivity bias. Additionally, exposure to human tool use may also influence the captivity bias phenomenon (Haslam, 2013). However, a recent study on wild Barbary macaques (*Macaca sylvanus*) found that neither "social facilitation" nor "reaction to humans" had an effect on individuals' abilities to innovate (Amici et al., 2020). Our data are consistent with the captivity bias in that we observed diverse and frequent tool use in captive crested capuchins, while such behavior has never been reported in wild populations. However, if spare time and energy were the primary contributing factors to tool use in these monkeys, then we would have expected that tool use might be observed more equally across all individuals exposed to the same conditions; in fact, there was a significant skew in individual tool use and success across individuals in our captive study population.

Our results are also congruent with the opportunity hypothesis (Fox et al., 1999), which has been used to explain the increased tool use in wild *S. libidinosus* when compared to the other robust capuchins (Spagnoletti et al., 2012). The opportunity hypothesis also proved to be a useful framework when comparing tool use presence or absence in wild capuchin populations across species and habitats; the availability of resources to allow a given task, rather than food availability or social organization (such as group cohesion or intra-group tolerance), best predicted tool use across populations (Izar et al., 2018). In our study, when captive crested capuchins were given objects containing foods that were not accessible without the use of tools, and objects that could be used as tools to obtain the foods—what Fox et al. (1999) call "propitious circumstances for tool invention" (p. 112)—five of seven individuals attempted tool use, with 11 different types of tool use observed.

The crested capuchins at the Santa Ana Zoo did not need to use tools, since they were provided with ample food that does not require processing. Yet some individuals performed tool use regularly, and most individuals attempted tool use at least once during the study. Additionally, not all of the tool use behaviors were directed towards acquiring food. Similar to bearded capuchins (Falótico & Ottoni, 2013) and chimpanzees (Hopkins et al., 2012; Russell et al., 2005; Tomasello et al., 1989), some behaviors like throwing and waving seemed to be used for communication in crested capuchins, a use of tools beyond the domain of food acquisition.

4.1 | Other notable findings

In addition to the large number of tool use action types observed, our study also identified several tool use actions which we would like to highlight, as they have not been clearly delineated in previous literature. In Sergio's *strike* tool action, he used a stick to hit a nut along a horizontal hose with a billiards-like action. Wild experiments with both robust and gracile capuchins have demonstrated that these animals have a hard time performing *pushing* actions to retrieve a reward, and are much more likely to perform *pulling* actions (Garber & Brown, 2004; Garber et al., 2012). However, in a captive experiment *Sapajus* spp. individuals did successfully *push* a peanut reward out of a tube using a variety of different techniques (Visalberghi & Trinca, 1989). One individual in that study may have used the action we called *strike*; the action was described as "extremely effective; when he was pushing the peanut out of the tube his style was rash and the strength of his movements often caused the reward to shoot out of the opening" (Visalberghi & Trinca, 1989, p. 516). Here we explicitly split the more forceful *strike* action from the gentler *push*, in which the user maintains contact between tool and object to obtain the desired movement of the object. Sergio used *strike* successfully to solve a foraging task that Matteo had independently solved using a different, pulling-toward action (*wedging*). While we separate *wedging* as an action different than *raking*, because *wedging* uses the stick like a lever to force the object in a tube towards the actor, *raking* and *wedging* are similar action patterns that pull to bring the object nearer.

To our knowledge, the actions we label as *sweeping*, *waving*, and *wiping* have not been clearly defined in the literature, although they may have been observed in other capuchin populations and described in more general terms. The most similar published description to *sweeping* seems to be captive Azara's capuchins using sticks and leaves "to explore the soil or the grass growing outside the enclosures" (Giudice & Pavé, 2007, p. 67). Chevalier-Skolnikoff (1989) described a capuchin *waving* a long leaf as a threat to zoo visitors; apparently, the same waving action as observed in our study, but used in a context of aggression rather than simply attention-seeking. While a *wiping* motion has been reported in a captive

capuchin using a cloth to sweep debris out of its cage (Gibson, 1990; as described in Shumaker et al., 2011) we have not found previous reports in the literature of capuchins wiping a substrate with paper or cloth to pick up ants or other potential food to eat.

We found substantial individual variation in both the propensity to use tools and in the likelihood of success. Matteo, a capuchin born at this zoo and never trained in using tools, successfully used tools on every day of observation. In contrast, two of the seven capuchins never attempted tool use. In previous studies with similar individual skew in tool use performance, the bias was attributed to unequal access to enrichment and tool materials, with some individuals monopolizing tool use opportunities (e.g., Garber et al., 2012). However, we found no evidence for lack of access in our study because enrichment items were distributed so that a single monkey could not monopolize all available tool activities. All monkeys had the opportunity to use tools daily. Nevertheless, tool use was much more frequent in the two males (the most dominant individuals). This finding is in contrast to predictions from the *necessity hypothesis*, according to which low-ranking individuals would be likely to use tools more frequently than higher-ranking individuals due to necessity (food deprivation resulting from competition for resources) (Fox et al., 1999). Other possible explanations for this individual variation could be sex differences or individual personality differences. Some tool use studies note that male capuchin monkeys are more prone to tool use than females (Falótico & Ottoni, 2014; Garber et al., 2012). Our data, though consistent with this reported bias, are from too small a sample to conclude that sex differences are driving individual differences. It is also important to note that due to the diversity of age and sex classes represented in our study population, that physical abilities to solve specific tasks could be constrained by the morphological characteristics of a particular monkey; one must consider size, body mass, and proportions when determining what are feasible actions for an individual to perform with a given object.

We also observed serial tool use by both Matteo and Sergio. Both individuals first used a metal scoop to shovel nuts from a dirt or sand substrate, then immediately cracked open nuts using a hammer. Serial tool use may signal higher cognition as it can require planning and flexibility (Hihara et al., 2003; Martin-Ordas et al., 2012; Parker & Gibson, 1977). The implications of serial tool use in this species should be explored more in future work.

4.2 | Failed attempts and individual learning

Failed tool use attempts may indicate trial-and-error learning and point to the array of object manipulation actions made possible by the open-ended tool use possibilities afforded by our study design. When we presented Matteo with an enrichment item he had not seen before (transparent hose), he first attempted to retrieve its contents through brute force, but when that did not work, he adjusted his approach and used a completely different method (tool use through "wedging" action), resulting in success. Following his introduction to the transparent hose, a subsequent encounter with the same enrichment item quickly resulted in success as Matteo immediately selected the appropriate raw material to wedge nuts out from within. Learning about objects and the environment with repeated exposure is described as perception-action developmental learning for human children, and may be similar to what occurred in this example with capuchin monkeys (Lockman, 2000; Lockman et al., 2020).

4.3 | Opportunities for social learning

We recorded high rates of tool use observation and tolerated scrounging by some individuals, suggesting the potential for social learning. Ottoni et al. (2005) showed in a semi-free ranging robust capuchin group, that young, less proficient individuals would often watch skilled individuals as they cracked nuts with hammers, and these young individuals often gained food through tolerated scrounging. In our study, the two capuchins that never attempted tool use (Chloe and Daisy) expressed very little to no interest in observing other monkeys using tools. In contrast, Maisy (age 1) and Dora (age 8) both observed Matteo for nearly half (at least 44%) of his tool use events and they were successful in scrounging food from his successful actions in about 29% of the events when they observed him using tools. Ottoni and Izar (2008) hypothesize that scrounging is a proximate motivation that catalyzes social learning. Though crested capuchins can use tools spontaneously, social learning may work to further enhance and diversify tool using behaviors as is the case in New Caledonian Crows (Holzhaider et al., 2010). Multiple studies of *S. libidinosus* populations have noted that adults tend to be tolerant of inexperienced group members closely observing and even scrounging food bits from tool use and that this tolerance is what allows for social learning and, thus, the spread of various tool use behaviors (Mannu & Ottoni, 2009; Mendes et al., 2015; Spagnoletti et al., 2011).

4.4 | Should we expect to see tool use in wild *S. robustus*?

We predict that at least some wild crested capuchins use tools. Due to their Atlantic Forest habitat, crested capuchins are surrounded with raw materials and likely experience marked seasonal variation in fruit availability (Martins et al., 2022; Spagnoletti et al., 2012), both of which contribute to the opportunity to create tools for solving foraging challenges. Furthermore, as a gregarious primate, the ample raw materials allow for the opportunity of tool-mediated social interaction such as throwing and waving. In our study, 71% of tool use events (120 of 169) involved plant material (e.g., branches and leaves) that could be easily accessed in the animals' natural habitat, thus the opportunity for tool use exists even without stones.

Since it has not been observed before, tool use in wild populations of *S. robustus* is likely not ubiquitous; rather, it may be a social tradition in some groups, but not others (Perry, 2011).

This phenomenon of intergroup variation in tool use can be seen in *S. xanthosternos* (Canale et al., 2009), the species most closely related to *S. robustus* (Lima et al., 2018; Lynch Alfaro et al., 2012). The single-year-long research study to date of wild crested capuchins (Martins, 2010; Martins et al., 2022) may have simply observed by chance a group that did not use tools, and the species remains severely understudied. Even in populations where tool use does not occur, individuals in this species may be using their manual and cognitive skills to deal with other complex challenges. As the human population increases, crested capuchins, an endangered species whose population is declining (Martins et al., 2017, 2021), find themselves in novel anthropogenic environments subject to fragmentation (Martins et al., 2022; Mota et al., 2018). Studies examining how crested capuchins respond and adapt to these novel environments, and documenting diversity in behaviors such as tool use across different populations, are sorely needed for this understudied and endangered species.

AUTHOR CONTRIBUTIONS

Danielle L. Steinberg: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Writing—original draft (lead); Writing—review & editing (supporting). **Jessica W. Lynch**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Supervision (lead); Writing—original draft (supporting); Writing—review & editing (lead). **Erica A. Cartmill**: Conceptualization (supporting); Methodology (equal); Supervision (supporting); Writing—original draft (supporting); Writing—review & editing (supporting).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All video clips are available from the corresponding author Danielle L. Steinberg upon reasonable request.

ETHICS STATEMENT

This study was carried out at the Santa Ana Zoo in Orange County, California with all permissions approved by the zoo manager, Ethan Fisher. The study required no invasive data collection and no direct interaction with the animals, exempting the study from the need for an ARC protocol approval as described by UCLA's policy 990: Use of Animals in Research, Teaching, and Testing. The methods adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

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