American Journal of Primatology

RESEARCH ARTICLE

Cup Tool Use by Squirrel Monkeys

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Captive-born male and female squirrel monkeys spontaneously 'invented' a cup tool use technique to *Contain* (i.e., hold and control) food they reduced into fragments for consumption and to *Contain* water collected from a valve to drink. Food cup use was observed more frequently than water cup use. Observations indicate that 68% ($n = 39/57$) of monkeys in this population used a cup (a plastic slip cap) to *Contain* food, and a subset of these monkeys, 10% ($n = 4/39$), also used a cup to *Contain* water. Cup use was optional and did not replace, but supplemented, the hand/arm-to-mouth eating and direct valve drinking exhibited by all members of the population. Strategies monkeys used to bring food and cups together for food processing activity at preferred upper-level perching areas, in the arboreal-like environment in which they lived, provides evidence that monkeys may plan food processing activity with the cups. Specifically, prior to cup use monkeys obtained a cup first before food, or obtained food and a cup from the floor simultaneously, before transporting both items to upper-level perching areas. After food processing activity with cups monkeys rarely dropped the cups and more often placed the cups onto perching. Monkeys subsequently returned to use cups that they previously placed on perching after food processing activity. The latter behavior is consistent with the possibility that monkeys may keep cups at preferred perching sites for future food processing activity and merits experimental investigation. Reports of spontaneous tool use by squirrel monkeys are rare and this is the first report of population-level tool use. These findings offer insights into the cognitive abilities of squirrel monkeys and provide a new context for behavior studies with this genus and for comparative studies with other primates. Am. J. Primatol. © 2015 Wiley Periodicals, Inc.

Key words: Saimiri; squirrel monkey; tool use; tool transport; planning

INTRODUCTION

Tool use is rare and is estimated to occur in less than 1% of nonhuman animal genera [Biro et al., 2013]. Among nonhuman primates there are a handful of taxa with populations that use tools regularly in the wild and include two apes, orangutans, *Pongo* sp., chimpanzees, *Pan troglodytes*, one Old World monkey species, the Burmese long-tailed macaque, *Macaca fascicularis aurea*, and one Neotropical monkey species, the bearded capuchin, *Sapajus (Cebus) libidinosus* [Meulman et al., 2013; Shumaker et al., 2011; Spagnoletti et al., 2012]. There are also anecdotal reports of tool use by other captive and wild-living primates [for a comprehensive review see Bentley-Condit & Smith, 2010 and Shumaker et al., 2011] including wild squirrel monkeys (*Saimiri* spp.). The latter, described in Kortlandt and Kooij [1963], includes one observation of an agonistic display by a squirrel monkey defined as deliberate flinging down/dropping of a stick (pg. 78), and another observation states "a squirrel monkey used a stick, in a sweeping movement, to move fruit along the ground, dislodging the ants on it" (pg. 80).

The rarity of observed tool behavior emphasizes the contribution that each discovery of it in captive or wild primate populations can offer towards understanding what aspects of species' ecologies may be associated with the evolution of these cognitive abilities and the evolutionary emergence of these abilities across taxa.

To *Contain* is a mode of tool use that functions to provide "effective control of fluids and solid objects" and is defined as to "place fluids or objects into or on

Contract grant sponsor: National Institutes of Mental Health; contract grant sponsor: Pritzker Family Foundation

Conflicts of interest: None.

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Received 22 February 2015; revised 15 August 2015; revision accepted 13 September 2015

DOI: 10.1002/ajp.22486
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

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top of another object (the tool) to control and/or transport them" [Shumaker et al., 2011]. The use of objects as containers is ubiquitous and so deeply embedded in nearly every aspect of modern humans' daily lives it is easily forgotten that *Containing* is a mode of tool use that is viewed as an adaptive behavior important throughout the evolutionary history of the human lineage. The use of natural items as containers (e.g., animal parts, shells, bark, etc.) is proposed to have emerged alongside other early hominid technologies such as stone flaking and stick sharpening during the period ~2.6 -1 MYA [Toth & Schick, 2009]. Across time container use is thought to have offered a means to efficiently accumulate and transport particulate food items, e.g., seeds and insect larvae, which would have otherwise been too energetically costly to obtain in sufficient quantity [Henry et al., 2014; McGrew, 2014].

Among nonhuman primates, examples of container use have been reported for apes, rarely for Old World monkeys, and for some New World monkeys, specifically, capuchin monkeys [for a review see Bentley-Condit & Smith, 2010 and Shumaker et al., 2011]. An example of *Containing* by a wild ape population (as categorized by Shumaker et al., 2011) comes from the chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea and involves folding leaves in the mouth such that the leaves emerge with regular folds (pleats) at about 3cm intervals and are used to manually obtain water from tree cavities to drink [Tonooka, 2001]. Reports of container use by Neotropical primates include observations of captive capuchin monkeys using a plastic container to collect water from a spigot to drink (*Sapajus* (*Cebus*) *apella*) [Westergaard & Fragaszy, 1985] and Phillips [1998] reported that wild capuchin monkeys (*Cebus albifrons trinitatis*) used leaves like cups to extract water from within tree cavities to drink.

Aside from our previously reported preliminary observations that captive-born squirrel monkeys (*Saimiri sciureus sciureus*) were observed using an object provided for environmental enrichment, plastic slip caps, as containers (henceforth cups) to *Contain* food or water [Buckmaster et al., 2012; Shumaker et al., 2011, pgs. 86,88] we found no other reports of *Containing* behavior by squirrel monkeys. However, captive-born squirrel monkeys (*Saimiri* spp.) at a fellow institution have been observed using an object provided for enrichment (i.e., toy tea cups) to collect water from a valve to drink (pers. comm. Dr. Lawrence Williams, University of Texas-MD Anderson Cancer Center).

Here we extend our preliminary observations of cup tool use by captive-born squirrel monkeys by investigating this behavior further. The specific aims of this study was to estimate the number of individuals in the population that use a cup to *Contain* food or water, describe how monkeys use a cup, describe the function of cup use, and characterize the logistics involved in accomplishing cup use in the arboreal-like environment in which this population lived.

METHODS

Subjects and Housing

A captive population ($n = 57$) of socially housed male ($n = 19$) and female ($n = 38$) squirrel monkeys aged 6–14 years were the subjects of this study. All monkeys were born and continuously housed at Stanford University. Monkeys lived indoors in same gender groups in one of fifteen artificial arboreal housing environments comprised of large interconnecting compartments. Each compartment measured $0.92 \times 1.22 \times 1.83\,m^3$ and had six levels of linear perching that spanned the height and width of each. Various affixed and unaffixed manipulatable objects were continuously present for environmental enrichment. Fresh standard primate chow (Lab Diet New World 5040) and water was available ad libitum and supplemented daily with fresh fruits or vegetables. Rooms were climate-controlled with an ambient temperature of 26°C and had a 12:12 light-dark cycle with lights on at 0700. The Research Animal Facility at Stanford University is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care International. This study was conducted in compliance with protocols approved by Stanford's Administrative Panel for Laboratory Animal Care and adhered to the legal requirements of the United States and the Society for Primatologists guidelines for the ethical use of primates in research.

Procedure

Food cup use was defined as the act of *Containing* food in a cup and consuming the food from the cup. Water cup use was defined as the act of *Containing* water in a cup and drinking the water from the cup. Food or water cup use may or may not have involved transporting the *Contained* food or water. Each food or water cup use act ended when the *Contained* food or water was ingested from the cup and the cup was disposed. The object serving as a cup was a schedule 40, 1.9 cm, plastic polyvinylchloride (PVC) irrigation pipe slip cap (LASCO Fittings Inc., Brownsville, TN). These were provided as species-appropriate manipulatable environmental enrichment objects because of the small size, light weight (16 g), and durability. Multiple cups (4–8) and other enrichment objects, e.g., balls, tubes, hoops (4–8 of each kind of object) were continuously available in each home environment and to all monkeys.

Cup tool use was unpredictable, therefore, we used *Ad Libitum* behavior sampling (Altmann, 1974) to monitor for it during any visit to monkeys' rooms and by video-recording monkeys in their home environment. All monkeys were visited daily and observed routinely in the mornings and afternoons for approximately 10–15 min at least twice daily during the week and at least once daily on weekends, generally in the afternoons. Additional opportunistic observations were made during visits to rooms for any other purpose. Cup use was logged, and video-recorded when possible, during room visits. In addition to room visits, video-recordings of monkeys in the home environment, in the absence of humans, were obtained by placing a camera (Sony DCR-HC52) at the front of each home environment on multiple occasions for 1 hr recording sessions. These sessions occurred in the afternoons when husbandry routines were completed and food enrichments (e.g., fruits, vegetables, nuts, mealworms) were provided. Each home environment was filmed for 2–9 hr for a total of 59 hr. Multi-compartment home environments housing large social groups were filmed more often to capture all monkeys on film than single compartment environments housing fewer individuals. Cup use activity was captured on video when monkeys entered the field of view of the camera during cup use and was logged in the same manner as direct observations. Together, these observation methods captured the spontaneous behavior of all 57 monkeys in the population.

In the initial stages of this study we logged food cup use acts only as defined above. As observations of food cup use accumulated, the options for accomplishing it in the spatially complex arboreal-like environment became evident and these logistical options were also logged. These logistics included how monkeys brought food and a cup together, where in the environment cup use occurred, and what monkeys did with the cup after using it. However, the logistics logged for these cup use acts vary because observation conditions sometimes prevented full logistics to be discerned. For example, if cup use was observed live in progress the logistics preceding it, i.e., where the cup was obtained, could not be known. Similarly, if cup use was captured on video the logistics preceding or following it could be observed only if it occurred within the field of view of the camera.

All food cup use acts comprising the data in this report were observed between October 2013 and July 2014 ($n = 195$ acts). Water cup use acts were observed across a broader time span between April 2009 and June 2014 ($n = 6$ acts between April 2009 and July 2012; and $n = 11$ acts between March 2013 and June 2014). All cup use activity by the squirrel monkeys reflects spontaneous behavior that occurred in their home environment without experimental or observation prompting. Together, these observations comprise the descriptive data set reported here.

RESULTS

Cup tool use was first observed by chance during routine husbandry rounds. The monkeys in this population 'invented' this cup use technique. That is, it is an untrained behavior that emerged in the population spontaneously. Specifically, aside from providing the cups (empty PVC caps) and other objects continuously to enrich the home environment, none of the monkeys in this population were given cups with food or water in them; none were trained to choose, hold, or manipulate the cups or other objects; and none were exposed to experiments designed to test knowledge about objects or tool use ability thereby training or fostering this behavior. Cup use was optional. It was not necessary that monkeys used a cup to eat the food provided to them or to obtain and drink water. Cup use did not replace, but supplemented, the hand/arm-to-mouth eating and direct valve drinking exhibited by all members of this population.

Population-Level Cup Use

With *Ad Libitum* behavior sampling 212 cup use acts were collected of which 195 involved food cup use and 17 involved water cup use. Food cup use was observed more frequently than water cup use. We determined that 68% ($n = 39/57$) of the monkeys in this population, including males and females, use a cup to *Contain* food and 10% ($n = 4/39$) of these individuals also use a cup to *Contain* water (Table I).

Of the 39 monkeys in this population observed using a cup to *Contain* food, 79% ($n = 31/39$) were observed doing so on multiple occasions (mean acts/monkey = 5, median = 5, range = 1–17). The four monkeys that also used a cup to *Contain* and drink water were also observed doing so on multiple occasions

TABLE I. Overview of Squirrel Monkey Population-level Cup Use

Gender	Population	# Monkeys *Contain* food	# Monkeys *Contain* water	# Food cup acts	# Water cup acts	Total cup acts
Female	38	26	2	135	9	144
Male	19	13	2	60	8	68
Total	57	39/57	4/39	195	17	212

(mean acts/monkey = 4.25, median = 4, range = 2–6). The eighteen monkeys in the population that were not observed using a cup to *Contain* food or water were adults that lived with cup-users and had no obvious impediment preventing the behavior. However, because our *Ad Libitum* sampling techniques depended on monkeys either performing cup use when an observer was in the room with them or entering the field of view of the video camera during home environment filming we do not know with certainty that these monkeys do not *Contain* food or water with the cups.

Cup Use

Figure 1 depicts a representative example of food cup use. It was observed in progress. An adult female squirrel monkey (Meg) was first seen holding a cup she was using to *Contain* food (standard monkey chow) that she began reducing into chewable fragments moments earlier and was transporting to a new location in the home environment (Fig. 1A). Next, she resumed reducing the chow by first manually extracting it from the cup and placing it into her mouth (Fig. 1B, C). To *Contain* the chow as she processed it into fragments she held the cup next to her mouth as she bit down on the chow with her teeth (Fig. 1D). She then manually removed the chow fragment(s) from the cup (Fig. 1E) and placed it in her mouth and consumed it (Fig. 1F). Note the competent bimanual coordination as she held the cup in one hand and manually extracted the food from it with the other hand as well as the sustained correct orientation of the cup held vertically upright as it is effectively used as a container.

Figure 2 depicts a representative example of water cup use. Here, an adult male squirrel monkey (Isaac) obtained a cup from the floor and transported it ~1.95 m to the water valve. Isaac first *Applied* (see definition below) the cup horizontally over the valve (Fig. 2A, B) causing release of water into the cup. He then removed the cup from the valve to a vertically upright position and looked into the cup, putatively monitoring progress collecting the water (Fig. 2C). Next, he again *Applied* the cup horizontally over the valve (Fig. 2D, E), removed the cup again and looked into it (Fig. 2F), then transported the cup with the *Contained* water to the back of the cage ~0.8 m away from the valve (Fig. 2G–I) where he inverted the cup and sipped the water from it (Fig. 2J). Note that two tool use modes are used simultaneously to obtain water from the valve, *Apply* and *Contain*. Shumaker et al., [2011] define one form of *Apply* as the tool use mode whereby "an object is *Applied* to an inanimate object".

Function of Food Cup Use

Of 195 food cup use acts collected 192 (98%) involved standard monkey chow and only three acts involved other foods (dried cranberry, piece of walnut meat, grape). The base diet provided *ad libitum* to this population was a dry, semi-hard, extruded rectangular chow formulated for Neotropical primates (8794 Teklad New World Primate Diet formulation, Harlan Laboratories, Indianapolis, IN). This chow was too large for the monkeys to eat whole and they first had to reduce it in size into chewable fragments for consumption. All monkeys in the population processed chow into fragments by holding a whole piece in the hand(s) and biting it. When biting the chow, fragments that remained in the mouth were eaten, whereas those that fell from the mouth were lost to the environment, a scrounging peer, or were collected onto the hand(s), or the forearm(s) held supinated at about chest height and then consumed. The latter method used by squirrel monkeys to collect food pieces on the forearm(s) has been described as "table-making" by Hopf et al., [1974]). When monkeys used a cup to *Contain* chow that they were processing into fragments they held the cup in a vertically upright orientation close to their mouths so that the chow fragments fell into the cup. To consume the processed chow the fragments were removed from the cup in a bimanually coordinated manner and placed in the mouth as in Figure 1, or the cup was inverted at the mouth so that the fragments fell directly into the mouth. Thus, the

Fig. 1. Food cup use by an adult female squirrel monkey (Meg) in her home environment (**A**) Transporting a cup that she began using moments earlier to *Contain* chow (**B**) Removing the chow from the cup (**C**) Placing the chow in her mouth (**D**) Holding the cup next to her mouth to *Contain* chow fragments as she crushes the chow with her teeth (**E**) Removing the food fragments from the cup (**F**) Eating the food fragments. See Supplementary movie.

Fig. 2. Water cup use by an adult male squirrel monkey (Isaac) in his home environment (**A**) Approaching water valve with a cup in hand (**B**) *Applying* the cup horizontally onto the valve (**C**) Removing the cup from the valve and looking into it, putatively monitoring progress collecting water (**D**, **E**) *Applying* the cup horizontally onto valve again (**F**) Removing the cup from the valve again and looking into it, putatively monitoring for collected water (**G**) Transporting the cup with the *Contained* water to the back of the home environment (**H**, **I**) Preparing to sip water from the cup (**J**) Inverting the cup at the mouth and sipping the water from it. See Supplementary movie.

cup served as a means to *Contain* food, primarily standard monkey chow, when it is being reduced into chewable fragments for consumption and may serve as an alternative to using hands or forearms to control these fragments. Examples of cups that contain chow that monkeys reduced into consumable fragments are provided in Figure 3.

Function of Water Cup Use

Water valves are the source of hydration for this population and are located at the front of each home environment. Operation requires depression of a central stem. All monkeys in the population obtain water from the valves by various manipulations. Lips/teeth are pressed onto the valve expressing water directly into the mouth; one hand or both are used to depress the valve creating a mid-air stream of water that can be caught into the mouth; one hand is used to depress the valve so that water collects onto the palm of the opposite hand that is licked. When the cup is used to *Contain* water it is first *Applied* horizontally over the valve. This causes the interior bottom of the cup to depress the central stem and release water into the cup. To sip the water from the cup monkeys manually lifted it to their mouths and inverted the cup so that the water fell directly into the mouth. Before sipping the water monkeys most often transported the cup to the back of the cage. Thus, one function of water cup use may be to consume water away from the cage front. Why this might be desirable is unclear. One possibility is privacy. The back area of the caging offers some privacy from adjacent monkey groups. Monkeys

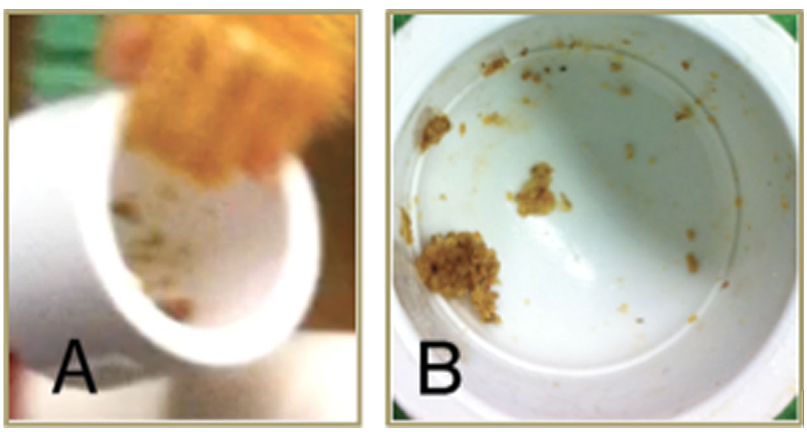

Fig. 3. Cups that adult female squirrel monkeys used to *Contain* chow processed into fragments for consumption. (**A**) 'Ingrid' holding a cup in her left hand with processed chow fragments in it (**B**) A cup with leftover chow fragments that was placed onto high-level perching by 'Greta' after she finished using the cup to *Contain* the chow.

transported the cup with *Contained* water by traversing the linear perching bipedally when the cup was held in both hands and tripedally if the cup was held in one hand. Often, a combination of bipedal and tripedal locomotion occurred during cup transport (e.g., see Fig. 2 movie). We have observed monkeys *Containing* only small amounts of water from the valve, enough for what appears to be 1–3 sips (based on the number of inversions of the cup to the mouth) and have not observed any monkeys filling the cups completely. Water cup use was observed infrequently relative to food cup use. This could be due in part to the greater cognitive/physical demand presumably required to simultaneously *Apply* the cup to depress the valve, *Contain* the water, and manage the cups orientation. Alternatively, water cup use may simply have less overall value to squirrel monkeys than food cup use. As water cup use was infrequent we limit further discussion of it.

Logistics of Food Cup Use in the Artificial Arboreal Environment

The spatial complexity of the arboreal-like home environment in which these monkeys lived contributed to the logistics of food cup use. Each environment had linear spans of perching (single and double or triplet side-by-side plastic tubes) across the width and depth of it. The low-level spans began 0.35 m above the floor, the middle-level span was 1.0 m above the floor, and the high-level spans ended just below the enclosure ceiling at 1.6 m. In keeping with this species' arboreality, the upper perching levels, i.e., the middle-level and high-level perching, were most frequently used and was where the monkeys ate, slept, and socialized, whereas the lower levels generally served as steps to-and-from the floor. Another factor involved in the logistics of food cup use was the dispersion of food and cups throughout the environment (largely due to monkeys activities) that provided various logistical options for organizing cup use. Chow could be obtained from hoppers hung at the cage fronts, the floor (monkeys pulled chow from the hoppers), or a peer. Cups could be obtained from the floor, a peer, or perching. The key difference where cups and chow could be obtained was that some spans of perching at each level had suitable surface area (e.g., groove between side-by-side tubes) where monkeys could place cups, whereas there was no suitable surface area on perching at any level where monkeys could place chow.

The various options for organizing food cup use are illustrated by a subset of food cup acts, 54% (106/195) in which the full logistics surrounding each could be discerned, i.e., it was evident how monkeys brought food and cups together, where cup use occurred, and what monkeys did with the cups after use. This subset of cup use acts includes logistical data from 34 monkeys (acts = 106, mean acts/monkey = 3.12, median = 3, range = 1–8) and are provided in Table II.

Together, these data provide an overview how monkeys accomplished food cup use and revealed

TABLE II. Logistical data for Food Cup Use by Squirrel Monkeys Living in an Artificial Arboreal Environment

Logistics (106 food cup acts)	# Cup use acts (%)	Monkeys (#)	Acts per monkey (mean)	Median (acts)	Range
Preparing for cup use					
-Cup obtained from peer	15 (14.1)	9	1.67	1	1–7
-Food and cup obtained from floor	18 (17.0)	12	1.5	1	1–2
-Cup obtained from perching	73 (68.9)	33	2.21	1	1–6
-Self-placed cup	24 (32.9)	13	1.85	1	1–6
-Cup placed before use	2 (8.00)	2	1.00	1	1
-Subsequent return and use	22 (92.0)	11	2.00	1	1–6
-Peer-placed cup	28 (38.4)	19	1.47	1	1–3
-Unknown if self or peer placed	21 (28.8)	16	1.31	1	1–3
-Perch level of placed cup					
-Low level	11 (15.1)	5	2.20	1	1–6
-Middle level	38 (52.1)	22	1.73	1	1–6
-High level	24 (32.8)	17	1.41	1	1–3
Perch level of cup use act					
-Low level	11 (10.4)	5	2.20	1	1–6
-Middle level	43 (40.5)	22	1.95	2	1–5
-High level	52 (49.1)	28	1.86	1	1–4
Disposition of cup after use					
-Drop cup	6 (5.7)	5	1.20	1	1–2
-Transfer cup to peer	23 (21.7)	15	1.53	1	1–5
-Cup placed on perch	77 (72.6)	29	2.66	2	1–8
-Low level	12 (15.6)	6	2.00	1	1–6
-Middle level	38 (49.4)	22	1.73	1	1–6
-High level	27 (35.0)	16	1.69	1	1–3

how monkeys most often organized it. Prior to cup use monkeys more often obtained cups for use that were previously placed on perching by themselves or by peers and these cups were most often obtained at upper-level perching. Cup use most often occurred on upper-level perching. After cup use, monkeys rarely dropped the cups and more often placed the cups onto perching. It is important to note that the surface area available to place cups on upper-level perch spans is minimal, compared to the area in which the cups could be dropped, and required some effort and precision to place the cups onto the grooves between the perch tubes. Thus, the placement of cups on perching is most accurately described as deliberate and motorically appears to be so.

Monkeys' actions that preceded cup use were consistent with the possibility that various degrees of planning were involved in preparing for cup use activity. Specifically, when monkeys obtained a cup from a peer or obtained a cup that a peer left on perching it suggests cup use was opportunistic. In contrast, actions consistent with the possibility that cup use was planned and monkeys took action toward this goal included obtaining a cup first before collecting chow and then transporting both to upper-level perching ($n = 2$ acts, Table II) or gathering chow and a cup from the floor simultaneously and then transporting both to upper-level perching ($n = 18$ acts, Table II). In the latter cup use acts in which food and cups were gathered from the floor and carried simultaneously, the cups and chow were transported ~1.0 m from the floor to middle-level perching ($n = 2$ acts) and ~1.6 m to high-level perching ($n = 16$ acts). These measures are minimum distances traveled and reflect straight-line distances from the floor to each respective perch level. Monkeys' slightly meandering routes (e.g., to avoid peers) to sites where cup use took place would increase actual travel distances.

Interestingly, 53% ($n = 18/34$) of the monkeys only obtained cups for use that were previously placed on perching either by themselves or their peers; however, 47% ($n = 16/34$) prepared for cup use flexibly, i.e., they obtained cups previously placed on perching, but also obtained cups for use directly from a peer, and/or obtained cups from the floor simultaneously with food and transported both to upper perching.

Finally, after cup use monkeys more often placed cups onto perching. In a subset of cup use acts ($n = 22$, Table II) we could discern that monkeys subsequently returned to use these cups again to *Contain* chow. This behavior is consistent with the possibility that monkeys may place cups on perching for future use. However, with our descriptive dataset we cannot conclude this.

The following real-life cases illustrate the different degrees of planning that may be involved in food cup use.

Case 1- Immediate use of self-placed cup obtained before chow. Adult female 'Thea' entered the cage compartment from an adjacent compartment, picked up a cup that was midway on middle-level perching, carried it to the end of the same perching (~0.6 m), placed it within the wall bracket that attached the perch tubes to the cage wall, left it, went directly to the floor below (~0.4 m), stood quadrupedal and scanned the chow on the floor, chose a piece, returned directly to the cup (~45 sec elapsed from the time she left the cup in the bracket to when she returned to it), grabbed the cup from the bracket, and transported the chow and cup simultaneously to high-level perching (~1.6 m) and used the cup to *Contain* the chow she processed into fragments and ate from the cup.

Case 2- Immediate use of food and cup gathered from the floor simultaneously. Adult female 'Ruby' traveled from middle-level perching to the floor (~1.0 m), stood bipedal and scanned the chow on the floor, chose a piece, moved to obtain a cup that was on the floor, and then transported both to upper-level perching (1.6 m) and used the cup to *Contain* the chow she processed into fragments and ate from the cup.

Case 3- Subsequent use of self-placed cup. Adult male 'Rio' moved a cup on the middle of a high-level perch to the end of the same perch and left the cup there. Approximately 2 minutes later he returned to the cup with chow and used it to *Contain* the chow he processed into fragments and ate from the cup. After he ate the chow from the cup he placed the cup back onto the perching where he retrieved it and left the area. Approximately 3 minutes later he subsequently returned to the cup with chow, used it again to *Contain* chow to eat, and then transported the cup to middle-level perching and left it. The second episode begins 20 minutes later. He retrieved the cup that he previously placed on middle-level perching in the first episode, and repeatedly used it to *Contain* chow to eat, 3-min, 11-min, 5-min, and 3-min later, respectively, each time leaving the cup at the same spot on middle-level perching. During intervals between cup use in both episodes he investigated the home environment, interacted with peers, ate chow without using the cup, and drank water directly from the valve.

In cases 1 and 2 monkeys' behavior appeared planned toward immediate food processing activity with the cup. In contrast, Case 3 provides an example of behavior that is consistent with the possibility that the cup was placed at favored perching sites for future food *Containing* activity with it.

GENERAL DISCUSSION

Captive-born male and female squirrel monkeys spontaneously 'invented' a cup tool use technique to *Contain* food they reduced into fragments for consumption and to *Contain* water collected from a valve to drink.

The ways in which squirrel monkeys organized cup use provides evidence of planning ability in this tool use context. Planning is generally agreed to be an ability that involves representing (mentally/cognitively) and preparing for a future goal [Atance & Jackson, 2009] as well as the ability to choose among alternatives prior to action [Tecwyn et al., 2013]. *Containing* food in a cup and eating the food from the cup, or *Containing* water from a valve into a cup and drinking it, are conditions not present to external perception. As such, cup use by squirrel monkeys presumably involves cognitive representation of the activity prior to taking actions toward it. Cup use was optional. When eating or drinking monkeys chose between taking action toward cup use or not, and individual monkeys organized cup use flexibly, i.e., they used two or more alternative logistics to bring the food and a cup together for cup use activity. The act of tool selection indicates an individual anticipates using the tool and transporting items involved in tool use presents cognitive challenges such as planning the course of action [Visalberghi et al., 2009]. Logistics prior to cup use that involved choosing the cup first before the chow, or gathering the food and cup from the floor simultaneously, before transporting both items to upper-level perching, suggests monkeys may have planned cup use activity and took action toward it. The distance that food and cups were transported in these cases was typically 1.6 m (the distance from the floor to high-level perching). For a brief comparative, wild chimpanzees (Pan troglodytes verus) often transported stone hammers and nuts to anvils distances of 200 m and 5–15 m, respectively [Boesch & Boesch, 1982] and wild adult bearded capuchin monkeys (Sapajus (Cebus) libidinosus) transported stone hammers to anvils, to crack nuts and other encased foods, a median distance of 3 m and 5.5 m, respectively, and nuts or other encased foods to anvils a median distance of 16m by males and 10m by females [Visalberghi et al., 2009]. Food and cup transport distances by the squirrel monkeys, constrained by cage size, was far less than the above examples. Nonetheless, cup transport by squirrel monkeys prior to food cup use activity is consistent with the possibility that cup use was planned. One aspect of cup transport conducive to experimentation would be to test how far squirrel monkeys would transport cups to food, or food to cups, given unconstrained space.

Planning is also conceptualized on a spectrum of complexity where planning for an immediate need/event is considered less complex than planning for a future need/event [Osvath & Osvath, 2008; Suddendorf & Corballis, 2007]. Considered in this context, all cup use activity by squirrel monkeys would fall under the category of planning for an immediate need/event, i.e., immediate food cup use, with one exception. The act of placing cups on perching after food cup use and subsequently returning to use the cups again is consistent with the possibility that monkeys placed cups on perching for future use. However, with descriptive data alone we cannot conclude that monkeys place cups on perching for future use. Cup placement could reflect processes other than anticipatory behavior, for example, an innate predisposition to store items or a propensity to place items where they were used, and subsequent cup retrieval could reflect memory for location of placed items (not associated with earlier anticipatory behavior) or simply the act of searching the environment for cups after obtaining chow.

We found no reports of food or object storing behavior by wild squirrel monkeys; however, one example of food-storing behavior has been reported for captive-living squirrel monkeys (*S. sciureus*) [Marriot & Salzen, 1979]. In this case, monkeys stored food out of sight in various cage crannies but within reach for future retrieval. The investigators concluded that monkeys were hiding food to prevent stealing by group members. Informally, we have only occasionally observed members of our population place food into cage crannies. As no wild squirrel monkeys are reported to store food or objects the food-storing behavior reported for squirrel monkeys in the latter study may reflect the expression of cognitive flexibility fostered by the captive environment rather than an innate biological predisposition.

Experimental studies that were conducted to determine if squirrel monkeys could plan for the future report positive evidence for this ability. Here, monkeys made choices in the present, in the context of current motivational states [McKenzie et al., 2004] and independent of current motivational states [Naqshbandi & Roberts, 2006], and the investigators propose that the monkeys choices suggested they anticipated the future consequences of those choices. However, the latter study met with criticism by Shettleworth [2007] and Suddendorf and Corballis [2008] who suggested that associative learning could explain the findings. Raby and Clayton [2009] on the other hand suggest that it is questionable whether associative learning could have occurred given the consequences of the choices were 30 min and 3 hr later. Importantly, whether nonhuman animals are able to plan for the future, how to assess it, and what cognitive mechanisms may support this ability, continues to be one of the most debated topics in the field of animal cognition [Osvath & Martin-Ordas, 2014].

Taken together, experiments designed to explore the boundaries of planning ability by squirrel monkeys in a tool use context would be valuable. Studies designed to investigate anticipatory planning, that control for motivational states and associative learning, similar to those used to assess the ability of apes to plan for the future in a tool use context [e.g., Mulcahy & Call, 2006; Osvath & Osvath, 2008] are in order.

Certain aspects of cup use offer opportunity to consider more broadly why squirrel monkeys engaged in this activity. Cup use was optional, i.e., it was not necessary to use a cup to obtain food or water, it was voluntary, i.e., monkeys chose whether and when to use a cup, and cup use did not replace, but supplemented, hand/arm-to-mouth eating and direct valve drinking. Tool use is generally considered to be cognitively demanding [Teschke et al., 2013] and is proposed to occur when it benefits the user through nutritional energy gains [see Sanz & Morgan 2013]. Given that cup use was optional, presumably created cognitive demand, and occurred in a captive condition with abundant resources, it is not obvious that monkeys engaged in cup use solely as a means to increase energy or water intake. We therefore suggest alternative explanations why squirrel monkeys engaged in cup use and raise the possibility of cognitive mechanisms involved in subjective hedonic experience and voluntary action. Neuroimaging studies in humans and other primates have identified specific brain regions, e.g., orbitofrontal cortex, as candidate areas for cognitive processing of food-related subjective hedonic experiences, the pleasurable aspects of eating food independent of homeostatic needs [Kringelbach, 2005] and neuroimaging studies in humans indicate voluntary actions have intrinsic hedonic value apart from the rewarding consequences the actions generate [Parkinson & Haggard 2013]. Thus, squirrel monkeys may engage in cup use because it is a voluntary activity and a pleasurable way to eat food or drink water.

Finally, in a broader context, the ability of squirrel monkeys to spontaneously 'invent' an activity that involves tool use offers a new framework for comparative studies among primates and in particular with capuchin monkeys (*Cebus spp.* and *Sapajus spp.*) the only Neotropical primates known to use tools regularly in the wild. Capuchin monkeys (*Cebus ssp.* and *Sapajus spp*.) are proposed as sole sister genera to *Saimiri spp*. in the subfamily *Cebinae* (Schneider & Sampaio, 2015). *Containing* behavior has been observed in captive-living capuchins [*Sapajus (Cebus) apella*, Westergaard & Fragaszy, 1985] as well as wild capuchin monkeys [*Cebus albifrons trinitatis*, Phillips, 1998]. *S. apella* and *S. sciureus sciureus* form semi-permanent foraging associations throughout their ranges indicating shared ecological pressures [Levi et al., 2013]. Additionally, some populations of wild capuchins monkeys (*Sapajus (Cebus) libidinosus*) regularly use stones with anvils to crack open nuts [Fragaszy et al., 2004; Ottoni & Izar, 2008] and sticks to probe for small prey, honey from wasp nests, and to poke toads and poisonous snakes [Falotico & Ottoni, 2014]. That a squirrel monkey population unrelated to ours has been observed *Containing* (water) offers convergent evidence that *Containing* behavior may reflect a species or genus level cognitive ability rather than a behavioral idiosyncrasy of either population. Taken together, two implications arise. First, the ability of squirrel monkeys to spontaneously 'invent' cup tool use and engage in it regularly implies greater cognitive continuity with capuchin monkeys (*Cebus* spp. and *Sapajus* spp.) in general and in this tool use context. Second, in keeping with parsimony, the last common ancestor to this subfamily, estimated to have lived prior to 13.8 MYA [Chiou et al., 2011; Perelman et al., 2011], may have had similar cognitive abilities.

In conclusion, an anecdotal report more than fifty years ago hinted at tool use ability by wild squirrel monkeys [Kortlandt & Kooij, 1963]. Here we describe a cup tool use activity by captive-born male and female squirrel monkeys that occurred regularly and at the population-level. This finding offers insights about the cognitive abilities of squirrel monkeys and provides a new context for behavioral studies with this genus and for comparative studies with other primates.

ACKNOWLEDGMENTS

We are grateful to Dr. Alan F. Schatzberg for continued support of behavior research with this population and thank Mr. Elias Godoy and Mr. Cesar Veloz for providing excellent daily care for the monkeys. This study was conducted in compliance with protocols approved by Stanford's Administrative Panel for Laboratory Animal Care and adhered to guidelines in the Guide for the Care and Use of Laboratory Animals (National Research Council, 2011). This population was funded by grants from the National Institutes of Mental Health and The Pritzker Family Foundation.

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