

Female Bearded Capuchin Monkeys (*Sapajus libidinosus*) Use Objects to Solicit the Sexual Partner

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Female wild bearded capuchins (*Sapajus libidinosus*) living at Serra da Capivara National Park (SCNP) that use stone and stick tools during foraging occasionally toss or throw stones at the male during courtship. We report similar behaviors in a different population that uses stones as tools in foraging. We video-recorded the sexual behavior of four females (27 days during nine proceptive periods) belonging to a group of wild capuchins living in Fazenda Boa Vista (FBV), 320 km from SCNP. Three females used stones or branches when they solicited the alpha male (79 episodes). The female that did not use objects was the sole female to solicit a subordinate male. The vast majority of episodes (95%) involved pushing or dropping branches, both loose and attached to the tree, toward the male. Females used objects only during the one-way courtship phase, before the male reciprocated the female's solicitations. In 93% of the episodes in which a female used objects, she performed affiliative behaviors immediately before or after using the objects. We conclude that throwing or pounding stones and pushing or dropping branches by females in SCNP and FBV in the sexual context have a clear affiliative meaning (to attract the male's attention). Given the tool-using status of both populations where these behaviors have been reported, it is important to determine whether they appear in populations that do not use tools, or are restricted to populations already primed to use objects in other contexts.

Keywords: courtship, New World monkeys, branch use, stone use

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The use of objects in the sexual context by wild nonhuman primates is rare. Orangutans use objects for auto-erotic stimulation (van Schaik et al., 2003), while chimpanzees and capuchin monkeys use objects to attract the attention of the opposite sex. Male and to a lesser extent female chimpanzees perform leaf clipping to attract the attention of the opposite sex. In this display, first

observed by Nishida (1980) in Mahale (Tanzania), typically the individual holds a single leaf by the petiole, draws it horizontally between its lips, and strips the lamina from the midrib, which produces a distinctive sound. In addition to leaf clipping, male chimpanzees in Ngogo (Uganda) and male and female chimpanzee in Mahale use branch waving to attract the attention of the partner

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(Watts, 2008). Finally, when soliciting estrous females Mahale male chimpanzees also make ground cushions (Nishida, 1997). Interestingly, these behaviors have been documented in some but not in all the studied populations of chimpanzees (Whiten et al., 1999) and they may be used in other contexts than the sexual one. For example, Ngogo chimpanzees perform branch waving to solicit a partner but also to threaten a partner, and Mahale and Bossou chimpanzees use leaf clipping to get attention of others to initiate movement (M. A. Huffman, unpublished data) and Tai National Park chimpanzees make ground cushions to solicit play (Boesch, 2012). So, the occurrence and frequency of these behaviors in the sexual context differ across sites, and the behaviors are used in different contexts within the same chimpanzee population or among populations.

Occasionally, female tufted capuchin monkeys (genus *Sapajus*) solicit the male with objects (Camargo, 2012; Carosi, Linn, & Visalberghi, 2005; Falótico & Ottoni, 2013). Carosi and Visalberghi (2002, p. 15) observed one female pushing objects toward the male, sometimes “touching the male through the object.” Falótico and Ottoni (2013) reported that in Serra da Capivara National Park, Brazil (hereafter SCNP), a minority of wild bearded capuchin females (*Sapajus libidinosus*) threw stones toward males they were soliciting, while most females did not. As use of objects in courtship is not exhibited by all individuals nor in all populations, it is a good candidate for studying the origins of group-specific behavior (Boesch, 1995; Falótico & Ottoni, 2013; Whiten et al., 1999).

Falótico and Ottoni (2013) refer to these actions by bearded capuchin monkeys as tool use, following Shumaker, Walkup, and Beck’s (2011, p. 5) functional definition of tool use as “the external employment of an unattached or manipulable attached environmental object to alter . . . another organism when the user holds and directly manipulates the tool during . . . use and is responsible for the proper and effective orientation of the tool.” The status of these actions is less clear following the biomechanically grounded definition of tool use presented by Mangalam and Frigaszy (2016). In Mangalam and Frigaszy’s definition, a tool transforms the body-only system into the body-plus-tool system; it adds at least one external degree of freedom (DoF) to the system along with reducing and/or redistributing the existing DoFs in the service of meeting the demands of the task (i.e., achieving the goal). In this definition, using an object as part of a display does not necessarily meet the requirements for tool use because the individual’s movements with the object are not necessarily constrained biomechanically by the task demands (in this case, to gain the attention of the sexual partner). Whether or not the behavior is classified as tool use, the inclusion of objects in courtship retains theoretical interest with respect to the motivational basis for the courting individual’s actions, its relation to other species-typical display behaviors, and its possible functional consequences in the courtship process.

Each sex plays a role to achieve mating. The general rule in primates is that males court females, who signal their fertile status in a variety of ways, especially with morphological changes and olfactory signals (Dixson, 1998). For instance, cycling female chimpanzees exhibit evident perineal swelling, and there is a temporal relation between the period of maximum swelling and ovulation (Deschner, Heistermann, Hodges, & Boesch, 2003). Tufted capuchins are an outstanding exception

to the general rule. Apparently, females seem to lack morphological or olfactory cues signaling ovulation, and they extensively court the male by using a rich set of proceptive behaviors (Carosi & Visalberghi, 2002; Carosi et al., 2005; Janson, 1984; Tiddi, Wheeler, & Heistermann, 2015). In the days preceding ovulation, the female closely follows the male and actively tries to attract his attention; in this phase of one-way courtship, the female solicits the male, but he is disinterested, annoyed, and sometimes even mildly aggressive toward her (Carosi & Visalberghi, 2002). Typically, the female performs “touching and running,” a behavior in which she approaches the male, briefly contacts his body or tail, and immediately runs away to avoid his possible negative response (Carosi & Visalberghi, 2002). Only hours or days later, the initially reluctant male begins to reciprocate the female’s solicitations (Lynch, Ziegler, & Strier, 2002; Tiddi et al., 2015). In this two-way reciprocal phase that corresponds to the time of ovulation, mating occurs (Carosi, Heistermann, & Visalberghi, 1999).

As part of a pilot study of sexual behavior in wild bearded capuchins, we assessed the frequency, form, and context in which females in one group of *Sapajus libidinosus* living in Fazenda Boa Vista, a site located about 320 km from SCNP, to verify whether they use stones or other objects to solicit males, as do females at SCNP. Field assistants and researchers at Fazenda Boa Vista have informally noticed that females throw stones and wave branches to solicit males. The behavior was filmed by Noemi Spagnoletti in 2010 and included in a documentary (Visalberghi & Albani, 2014). In this article, we quantify this behavior. On the basis of Carosi and Visalberghi (2002), who described the striking proceptive behavior of female capuchins, we predicted that these behaviors occur only in the one-way phase of courtship when the female wants to approach the male and tries to attract his attention and to contact him. We compare our findings with those of Falótico and Ottoni (2013) for females at SCNP.

Chimpanzees exhibit leaf clipping and stone/branch throwing in contexts other than courtship. Among Tai chimpanzees, leaf clipping is regularly observed as part of the drumming sequence of adult males and precedes hand and feet drumming on buttress roots of trees (Boesch, 1995; see also Kuhl et al., 2016) and throwing stones/branches during encounters with predators (Boesch, 1991). Similarly, capuchins use branches in contexts other than courtship. Capuchins throw branches during aggressive inter- and intraspecific encounters (e.g., Boinski, 1988; Moura, 2006), to explore locations, and to elicit a response from a prey (Falótico & Ottoni, 2014; Vitale, Visalberghi, & De Lillo, 1991). A female tufted capuchin made “open-mouth threat face” and alarm vocalizations, indicating an aggressive defensive context, immediately before she tossed a branch and then a stone toward a tortoise (Hamilton & Frigaszy, 2014). Hence, different populations, different individuals within the same population, and even the same individual may use the same behavior (leaf clipping in the case of chimpanzees and stone/branch throwing in the case of capuchins) in different contexts and for different purposes. We predicted that while using an object to contact the male during courtship, the female performs affiliative behaviors and facial expressions toward the male and not threatening or aggressive behaviors.

Method

Location

The study was carried out at Fazenda Boa Vista (FBV), in the northeastern Brazilian State of Piauí (9°39'S, 45°25'W). The physical geography of the field site is a sandy plain at approximately 420 m above sea level, punctuated by sandstone ridges, pinnacles and plateaus, and surrounded by cliffs (Visalberghi et al., 2007).

Study Group

We followed and observed a fully habituated group of 23 bearded capuchin monkeys, including 8 adult females, 1 dominant male, another 4 adult males, and 10 youngsters (7 females and 3 males).

Ethical Note

We adhered to the guidelines of the American Society of Primatologists and the Association for the Study of Animal Behavior for the treatment of animals in behavioral research and teaching and to the American Society of Primatologists' principles for the ethical treatment of primates. Permits to Elisabetta Visalberghi, Patricia Izar and Dorothy Fragaszy were given by IBAMA SISBIO (Sistema de Autorização e Informação em Biodiversidade of the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, n. 28689-3) and CNPq (National Council for Scientific and Technological Development, n. 002547/2011-2). The land where the study was conducted was privately owned; no threatened species was sampled.

Data Collection

Behavioral observations were carried out opportunistically while Luca A. Marino and one field assistant collected data on food processing (on average six days a week, seven hours per day, from May 21 to August 16, 2014). Because of previous direct experience with capuchins and the detailed descriptions of their sexual behaviors (Carosi & Visalberghi, 2002), the observers could easily detect when a nearby female was courting a male. If this was the case and they were not already filming food processing, one or both observers filmed the female (ad libitum sampling, Martin & Bateson, 1993) with a Canon EOS 600D and/or a JVC GC-PX100 camera. Filming was done at relatively close distance (3–20 m) from the female, and whenever possible, both partners were filmed.

We scored from video clips the instances in which proceptive females moved objects in a manner that would contact the male, or move close to the male. We also noted when the object involved was unattached or attached and the type of object used (stone or branch). As in Falótico and Ottoni (2013), a single episode of object use consisted of one or more events occurring between the same individuals, in the same location, and less than 10 min apart. For Falótico and Ottoni the number of events corresponded to the number of stone throws (whether or not throws involved different stones is not specified). In our study, the number of events corresponds to the number of stone throws/pushes/pounds performed with different stones. Since a branch is used over a longer period

of time and it may occur on trees where leaves prevent full view (making it impossible to determine whether the female is holding the same branch throughout the episode), we did not count the events of branch use, but estimated its occurrence on the basis of the number of 30-s intervals in which the behavior was scored.

In addition, we scored the occurrence of affiliative behaviors typical of courtship (eyebrow raising with or without grin, touching and running, pulling tail or contacting body, vocalizing, following, nuzzling; see Carosi & Visalberghi, 2002 for detailed descriptions) and aggressive behaviors (open-mouth threat face, and aggression; De Marco & Visalberghi, 2007) occurring in the 20 s before and after the female used the object.

Data Analysis

During 525 contact hours with the group, we collected six hours of video clips of sexual behavior which were suitable for behavioral coding (e.g., the subject(s) was/were in view and in focus). Coding was done on slow motion by Cecilia Di Bernardi; the interobserver agreement with Elisabetta Visalberghi on all the video-clips was 100% for subjects' identity and tool use episodes and 95% for the occurrence of affiliative behaviors.

Results

Females used the rich repertoire of solicitations typical of tufted capuchins, though some differences were evident. For example, in FBV females did not perform chest rubbing and backing into lap (behaviors commonly observed by Carosi & Visalberghi, 2002), but often touched the male's genitals during reciprocal courtship and after mating, a behavior not described before.

Four adult females (out of the five females belonging to the group) showed proceptive behavior. We observed 27 proceptive days distributed over nine proceptive periods. Three females used objects while soliciting the alpha male (see Table 1), while the fourth female did not and solicited the beta male. Females pushed branches (with or without leaves, hereafter branches) attached to a tree in 31 episodes, branches already detached from the tree in four episodes, and branches they detached from a tree in seven episodes. Females threw or pushed stones toward the male in two episodes and pounded stones on the ground while watching the

Table 1
Number of Observed Proceptive Periods (and Days), Number of Branch and Stone Use Episodes

Female	# proceptive periods (# days)	Number of branch use episodes (number of 30 s intervals)			Number of stone use episodes (number of events)	
		B-A	B-fD	B-aD	S-T/P	S-PO
Piassava	2 (8)	9 (20)	1 (1)	3 (3)	1 (3)	0
Pamonha	2 (8)	4 (6)	3 (3)	0	1 (1)	0
Chuchu	1 (1)	0	0	0	0	0
Doree	4 (10)	18 (37)	3 (4)	1 (1)	0	1 (4)
Total	9 (27)	31 (63)	7 (8)	4 (4)	2 (4)	1 (4)

Note. B-A = Branch attached to the tree; B-fD = Branch detached from the tree by the female; B-aD = Branch already detached from the tree; S-T/P = Stone thrown or pushed; S-PO = Stone pounded.

male in one episode. Stones were used on the ground, whereas branches were used both on the ground and in trees. Below we describe in some detail the behaviors observed.

Branch Use

Typically, the female pushed an attached branch in the male's direction, shaking the proximal end of the branch so that the distal end moved toward the male (Figure 1 and supplemental video S1). Sometimes the movement of the branch attracted his attention, though briefly. The female watched the male closely as she moved the branch toward him. Sometimes the female detached a branch (supplemental video S2), or grasped an already detached branch/stick (supplemental video S3) and then moved it in the male's direction. This occurred while the female was level with the male, or on a branch above the male.

Stone Use

One episode consisted of three events involving different sandstones (supplemental video S4). Piassava threw a sandstone toward the male, then pushed a larger sandstone (estimated weight more than 1 kg), and finally she threw a smaller sandstone toward him. In another episode, consisting of one event, Pamonha pushed a large quartzite stone (about 1 kg) a few centimeters toward the male (supplemental video S5). In a third episode, (supplemental video S6), Doree looked at the male and pounded a siltstone on the stone anvil where he was seated. Immediately afterward, she climbed up a nearby tree and monitored him from a distance, and then she moved back and twice pounded the same stone she had used previously. One min later she pounded a sandstone on another nearby anvil (that rolled down), a very small sandstone (twice), and another small sandstone (once). Finally, she recovered the initial sandstone and pounded it again. Given the number of different stones used, this episode consisted of four events. Since there were no nuts or nut debris on the anvil where she struck the stone, nor did she eat anything afterward, her behavior could not be interpreted as using a tool to crack nuts, as these monkeys

typically do (Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011).

Phase of Courtship and Occurrence of Object Use

All the observed episodes of object use occurred during the one-way phase of courtship when the female was actively courting the male and the male did not reciprocate her behaviors.

Female's Behavior While Using Objects and Male's Response to Her

In 93% of the episodes (40 out of the 43 in which it was possible to score these behaviors) the female performed one or more affiliative behaviors (see list in the "Methods" section) typically observed during the one-way phase of courtship. In contrast, the female never performed aggressive behaviors toward the target male when using a stone or a branch. The target male never responded to her solicitations as if he had perceived a threat, nor did he threaten the soliciting female. Interestingly, the four instances in which the male threatened or mildly aggressed the female occurred when she solicited him without using an object at close distance, as illustrated in the supplemental video S7.

Discussion

During a three-month period, we observed several episodes in which proceptive female bearded capuchins at Fazenda Boa Vista used stones, loose branches, or attached branches to reach toward or to touch the male that was the target of their sexual solicitations. When not proceptive, females were never observed to perform these behaviors (Luca A. Marino, Elisabetta Visalberghi, & Valentina Truppa, unpublished data). The capuchins at our study site do not use branches as foraging tools. They did not use branches even when an experimental apparatus was set up to elicit dipping (Cardoso & Ottoni, 2016). Nevertheless, and despite the fact that in this site both sexes habitually use stone tools to crack open palm



Figure 1. Pamonha (above) courts Jatobà (below). The female's hand (in the circle) holds an attached branch (left), moves it toward the male (center), and contacts his body (right).

nuts (Spagnoletti et al., 2012), the use of branches in courtship was far more frequent than the use of stones.

Using Objects in the Sexual Context in FBV: A Comparison With SCNP

Table 2 presents a summary of the data from Falótico and Ottoni (2013) and the current study. During a 23-month study in SCNP, Falótico and Ottoni (2013) observed 17 proceptive females (out of the 23 present) for 49 proceptive periods. During three months of data collection in FBV, we observed four proceptive females (out of the eight present) for nine proceptive periods. The percentage of proceptive periods in which the female used stones was higher in FBV than in SCNP (33% vs. 8%), and the percentage of proceptive females using stones in courtship was higher in FBV than in SCNP (at least 50% vs. 18%) (see Table 2). Females in FBV used branches to contact the male relatively often as well. Although Falótico and Ottoni (2013) did not report females waving branches toward the male during courtship, Falótico (pers. comm.) indicates this behavior occurs in SCNP. Overall, it appears that females at FBV and SCNP use similar objects in courtship in similar ways, although females at FBV seem to do so at a higher rate than do females at SCNP. Since FBV and SCNP data were collected in different ways the comparisons of quantitative descriptors should be considered preliminary and further data are necessary to confirm these findings.

In SCNP females succeeded in hitting the male in 10 out of 52 cases (Falótico & Ottoni, 2013). In FBV, females used stones without hitting the male, however they did touch the male's body with branches. This behavioral difference could be related to different factors. In SCNP females threw stones while close to the male (cf. the video clips of the supplemental material in Falótico & Ottoni, 2013), making hitting relatively easy. In fact, though Falótico and Ottoni (2013) Figure 1a suggests that the female threw a pebble from a distance of at least a few meters to the male, the video, from

which the still image was taken, shows that in that frame the female was simply holding the pebble while moving closer to the male toward whom she eventually threw the stone from a distance of about 1 m. The stones thrown by females in SCNP were easily maneuvered with one hand because they were relatively light (average weight 52 g, range 19–84). In FBV the stones thrown or pushed required both hands to be maneuvered and were estimated to weigh more than 800 g. Another difference in the females' behavior was evident between the two sites. In FBV the females using objects were always targeting the dominant male, whereas in SCNP females targeted another high-ranking individual in 78% of episodes, and the alpha male only in 22% of the episodes (Falótico & Ottoni, 2013); this difference might be due to the fact that in SCNP the group was larger (eight adult males and 16 adult females).

In FBV the stone episodes occurred in different locations such as on anvil sites often used to crack open palm nuts and on the ground never used for this purpose. Most of the stone episodes filmed in SCNP occurred in the provisioned area where small stones are extremely common. It would be interesting to know whether being in a location where stone tools are often used to forage has prompted the females to use stones on the same location also for the purpose of soliciting a male. Dubois, Gerard, Sampaio, de Faria Galvão, and Guilhem (2001) found that capuchins used sticks as probing tools more frequently at sites where they had previously manipulated objects than at other sites where they did so to a lesser extent. It is as if using a particular kind of object as a tool in a given place were dependent on previous experience acting with other objects in that place. By extending this line of thinking, we predict that the monkeys are more likely to use stones to solicit a male in a location in which they commonly use stones as foraging tools. Recently, Falótico and Ottoni (2016) predicted that capuchin monkey populations that have wide availability of raw stone material, as seems to be the case in SCNP, would exhibit more diversity in stone tool use than capuchins in areas with a lower abundance of adequate lithic material, such as FBV (Visalberghi et al., 2007; Visalberghi et al., 2009). Both these predictions should be properly tested in the field.

Table 2

Object Use by Wild Female Bearded Capuchin Monkeys During Courtship at Fazenda Boa Vista (FBV) and Serra Da Capivara National Park (SCNP)

	FBV	SCNP
Contact time (hours)	525	1716
# proceptive females	4	17 [^]
# proceptive periods	9	48 [§]
# proceptive periods with stone use	3	4
# proceptive females using stones	3	3
# proceptive females using branches	3	n.a.*
# episodes using stones	3	7 [@]
# episodes using branches	42	n.a.*
% of proceptive periods with use of stones	33	8.3
% of proceptive females using stones	75	18 [^]
% of proceptive females using branches	75	n.a.*

[^]Falótico & Ottoni (2013) wrote "18" in Table 1 and "at least 17" in p. 2; according to Falótico (personal communication) they were "at least 17" because at the beginning of their study unidentified females could be among those already identified. Thus, we use the value 17. [§] Falótico & Ottoni (2013) wrote "49" in p. 2 and "48" in Table 1; according to Falótico (personal communication) the correct value is 48. * Data not available, although the behavior has been seen. [@] Falótico (personal communication) clarified that each line of their Table 2 corresponds to one episode.

Behaviors Performed While Using Objects in the Sexual Context

While using an object to contact the male or to gain his attention, the females almost always performed affiliative behaviors and/or affiliative facial expressions; they never threatened the male. The male never performed agonistic behaviors toward the female following an episode in which she used an object. On the basis of our pilot study, we suggest that in the sexual context objects are used by the female capuchin to solicit and gain the male's attention in a period when he is largely indifferent to her advances, and not to threaten or keep him away, as it occurs during aggressive encounters (Boinski, 1988; Hamilton & Frigaszy, 2014; Moura, 2006; Vitale et al., 1991). In other words, capuchins use the same behaviors with objects in different contexts to communicate distinctive meanings.

Boesch (1995) argued that the changes in the context of leaf clipping among Tai chimpanzees over time suggest that leaf clipping is a cultural behavior for which the context of use is arbitrarily fixed by group members and that social convention is the best explanation to account both for the different functions of this

behavior across chimpanzee populations and for the new function it acquired in Tai chimpanzees. Along the same lines, Falótico and Ottoni (2013) suggested that, since stone throwing was repeatedly shown only by some members of just one of the groups of monkeys at SCNP, and the number of females observed to throw stones increased after the completion of their study, this sexual display “was independently invented” by one or more females of the PF group. They also suggested that it was socially transmitted since in 2012 three additional females of the PF group “copied” this “enhanced display” (p. 5). However, we show that females in at least one other group of bearded capuchin monkeys use objects in courtship, and have done so for several years at least. Thus it seems unlikely that this behavior is a recent invention among the females at SCNP. As for the use of stones to crack nuts and seeds, which is geographically widespread among bearded capuchins (Ottoni & Izar, 2008; see also De Moraes, Souto, & Schiel, 2014; Ferreira, Emidio, & Jerusalinsky, 2010; Mendes et al., 2015), the use of stones and branches by females during courtship may be a widespread phenomenon in this species.

Capuchin monkeys occasionally throw, drop, or push objects to threaten individuals of other species (Boinski, 1988; Fragaszy, Visalberghi, & Fedigan, 2004; Hamilton & Fragaszy, 2014; Moura, 2006; Vitale et al., 1991). Captive capuchins are easily trained to perform aimed throwing (Westergaard, Liv, Haynie, & Suomi, 2000). Hence, it can be argued that throwing and pushing objects is part of the capuchins’ species-typical behavioral repertoire and that capuchins perform these behaviors in aggressive as well as affiliative contexts. What prompts the female capuchin to use an object to solicit the male? Systematic behavioral data indicate that during the one-way phase of courtship the female seeks to contact the target male but is also afraid of his response (Carosi & Visalberghi, 2002). Typical of this phase is “touching and running,” in which the female quickly approaches and briefly contacts the male, and immediately runs away (Carosi & Visalberghi, 2002; Carosi et al., 2005). In our view, the object affords the female the means to be somehow closer to the male. By using an object as an extension of her arm, the female maintains some distance between her body and the male’s body, but still indirectly contacts him. It is possible that in this way, the female reduces the risk of reprisal by the male (such as slapping or biting) for her actions, especially by the dominant male who is more aggressive than the subordinate males (Mendonça-Furtado et al., 2014). This interpretation is consistent with the finding that all three females that solicited the dominant male used objects whereas the one female that solicited the subordinate male did not use objects. The females of SCNP always directed stone throwing toward high-ranking males (Falótico & Ottoni, 2013), although not predominantly the alpha male. The bias to contact high-ranking males more often than subordinate males with objects may be because the former are less ready to reciprocate the females’ sexual interest than the latter (Carosi et al., 2005). Alternatively, it may reflect the proportion of all courtship directed to high-ranking males.

Since FBV females use both stones and branches to solicit males, even if no members of their group use branches or sticks as foraging tools, it seems that the use of specific objects in courtship does not require the same objects to be used as foraging tools. Capuchins use in courtship the same behavioral patterns and objects they commonly employ against intruders and predators (Fragaszy et al., 2004; Moura, 2006). Interestingly, by examining

the cases of dropping, throwing, and rolling objects against intruders and predators present in Shumaker et al.’s (2011) review it appears evident that arboreal monkeys (e.g., colobus, guenons) use branches whereas terrestrial ones (e.g., macaques and baboons) use stones. Capuchins are arboreal monkeys that decrease the amount of time spent on trees when living in less forested habitats (as the Cerrado, the Caatinga and the mangrove swamps). Branches are ubiquitous in the habitats of arboreal and semiarboreal primates whereas stones are available only to those that spend time on the ground. Thus, we expect *Sapajus* females’ solicitations with branches are more widespread across habitats than solicitations with stones. In particular, we expect that (a) the use of stones in courtship is present only in populations with terrestrial habits and living in landscapes where loose stones are plentiful, and (b) the likelihood of using stones in courtship is impacted by degree of terrestriality, as already argued for stone tool use (Meulman, Sanz, Visalberghi, & van Schaik, 2012). Observations of wild populations that differ in time spent on the ground and of captive individuals that often spend much of their time on the ground (such as those observed by Carosi and Visalberghi (2002) who first noticed object use in courtship) can contribute to testing these hypotheses.

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