White-Faced Capuchin, *Cebus capucinus imitator*, Hammerstone and Anvil Tool Use in Riparian Habitats on Coiba Island, Panama

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Introduction

Tool-aided extractive foraging is an important element of the success of many dietary generalists in resource-limited ecosystems. The study of primate tool use offers insight into the possible form and function of tool use in early hominins, as well as related ecological pressures. It informs us about instances of tool use where raw materials or sites may not be preserved due to site degradation. It helps us map observable behavior onto site accumulation and increases our understanding of taphonomic biases and site formation. While habitual tool use has been reported in all great apes and many robust capuchins, it is rarer in other primates. Recently, island-living populations of long-tailed macaques (Matrivijonod *et al.* 2007) and gracile capuchins (Barrett *et al.* 2018) have been discovered to habitually use stone tools. The contrast of these tool-using insular populations relative to their mainland counterparts, and the heavy reliance on tool use in many island-living birds (Tebich *et al.* 2002), suggests that some aspect of island ecology such as reduced predation, increased terrestriality, decreased dietary richness, increased ecological stress, or increased niche breadth due to reduced heterospecific competition may be conducive to the innovation, maintenance, and cultural transmission of tool use.

Although robust capuchins (*Sapajus* sp.) are well documented tool users, gracile capuchins (*Cebus* sp.), which diverged from their sister taxa *ca.* 6.5 mya, show little to no reliance on tool use, despite well-documented evidence of other types of socially learned traditions. The only known exception is a population of white-faced capuchins, *Cebus capucinus imitator*, foraging on fruits and structurally protected gastropods and crustaceans in coastal ecosystems on the Pacific island of Jicarón in Coiba National

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Park (CNP), Panama. Here we report a second population of stone-tool using white-faced capuchins living on Coiba, the largest island in CNP.

Site Description

Coiba (53,582 ha) lies 30 km west of mainland Panama in the Pacific Ocean. This biodiversity hotspot possesses a unique floristic composition, distributed among varied habitat types. Islands in the Coiban archipelago have been isolated from the mainland since the last glacial maximum 12,000–18,000 years ago.

We first observed evidence of hammerstone and anvil tool use by capuchins on the northwest of Coiba in March 2019. During an ongoing survey of tool use across the archipelago, we observed river cobbles that had been used as hammerstones resting upon stone anvils in shallow riffles in the middle of the river and along the river bank. At nine tool sites, we observed remains of freshwater snails under hammerstones and lying on and alongside stone anvils (Fig. 1a). Tool sites were found in clusters (two or three sites separated by <5 m) as well as in isolated sites. Distances between tool sites ranged from *ca.* 25 to 100 m. In April 2019, we counted 10 tool sites on a *ca.* 1-km transect of riverbank that lies 620–1000 m from the coast. In July 2019, we observed evidence of capuchins using hammerstones to process *Bactris* sp. palm fruits *ca.* 800 m

Fig. 1 (a) Hammerstone resting on anvil. Fragments of *Pomacea* shells lie on top of the anvil and alongside it in the river and riverbank. (b) Fragments of *Bactris* palm fruits under and around a hammerstone on a stone anvil in a stream bed. (c) Adult male capuchin ingesting food he processed with hammerstone on stone anvil while conspecifics observe intently. (d) Adult male capuchin using a hammerstone on a wooden anvil to process unidentified food items on the coast. Photo credits: (a) Christian Ziegler; (b) CMM; (c, d) ZMR.

from the coast (Fig. 1b). Later we observed from a boat an adult male capuchin using hammerstones to process unidentified coastal resources accompanied by two conspecifics *ca.* 1300 m from the riparian site (Fig. 1c, d).

Conclusions

This is only the second description of hammerstone and anvil tool use in *Cebus* despite numerous decades-long habituated studies across their range. The only other known tool-using population is a single group 39 km southwest on Jicarón, the second largest island within CNP (Barrett *et al.* 2018). Our discovery of another population of stone-tool using capuchins on a second island in the Coiba Archipelago suggests that at least two independent innovations of this behavior presumably occurred on the islands of Coiba and Jicarón since their isolation from each other and the mainland 12,000–18,000 years ago. Although no dispersal events are known between the islands, this should be interpreted cautiously; Coiba and Jicarón are separated by 6.5 km at their closest point. This observation also supports the hypothesis that some aforementioned aspect(s) of island ecology favor the evolution and spread of tool use.

Despite significant camera trap surveys since March 2017 (see Barrett *et al.* 2018), we have observed stone tool use only in two geographically restricted areas of Coiba and Jicarón. The vast majority of capuchins on these islands do not appear to use stone tools, despite having access to all of the materials required to do so. Different groups across CNP in similar ecological conditions process identical resources with (Barrett *et al.* 2018) and without (Méndez-Carvajal and Valdés-Díaz 2017) hammerstone and anvil tool use; this is consistent with stone tool use being a localized cultural tradition. Further targeted surveys on ecologically plausible sites for tool use in Coiba, and an understanding of intra- and intergroup social interactions, are necessary to explain the absence of tool use in the majority of capuchin groups in CNP.

The presence of primate stone tool use along streambeds is comparable to early hominin tool use locations in river beds or streams. In Jicarón, seasonal flooding affects site preservation in stream beds. Understanding formation of primate tool-use sites in conditions in which preservation is unlikely can provide us with testable hypotheses about the early hominin tool-use behavior and the visibility and preservation of the associated archeological record (Panger *et al.* 2002).

Unlike on Jicarón, we have observed tool use up to 1 km inland on Coiba. This new description on Coiba suggests that shallow, fast-moving streams further inland might be ideal areas to target when searching for new populations of tool-using primates. Both stone materials made available by stream flow and structurally protected invertebrates are abundant in tumultuous, riparian environments. This discovery also suggests that structurally protected resources found in streambeds and along rocky intertidal areas are equally important areas to further explore the breadth and patterning of *Cebus* tool use. Currently, we do not know if these coastal and riparian hammerstone and anvil tool sites on Coiba have been used by single or multiple capuchin groups. Future explorations to the site and camera trapping will be important to resolve if this tradition is confined to a single group or more widely spread.

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Ethical Note No animal care and use protocol was required for this study. The authors declare that they have no conflict of interest.

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