Primates
DOI 10.1007/s10329-016-0525-3

NEWS AND PERSPECTIVES

Complex processing of prickly pear cactus (*Opuntia* sp.) by free-ranging long-tailed macaques: preliminary analysis for hierarchical organisation

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Received: 26 January 2016 / Accepted: 12 February 2016

Abstract Complex food-processing techniques by gorillas, chimpanzees, and orangutans have allowed comparisons of complex hierarchical cognition between great apes and humans. Here, we analyse preliminary observations of free-ranging long-tailed macaques (*Macaca fascicularis*) ($n = 3$) in Thailand processing *Opuntia* sp. cactus fruits. From our observations, we suggest that there is potential to extend the analyses of hierarchical cognition to Old World monkeys. We found that the macaques used six behavioural sequences to obtain *Opuntia* fruits, remove irritant hairs from the skin of the fruits, and break open, and consume the fruits, each a unique combination of 17 action elements. Removing irritant hairs involved abrading fruits on a sand or rock substrate, and washing fruit in water. The behavioural sequences that macaques use to process *Opuntia* potentially show features of hierarchical organisation described in the leaf-processing behaviours of great apes. Our observations highlight the need for closer study of complex food-processing behaviour in monkeys to better understand the organisational capacities involved.

Keywords *Macaca fascicularis* · Hierarchically organised behaviour · Khao Sam Roi Yot National Park · Thailand

Introduction

Technically difficult foods are thought to be key selection pressures for the evolution of intelligence (Russon 1998), supporting abilities to solve extractive foraging problems, and organise multi-step processing techniques efficiently (Parker and Gibson 1979). Comparative study of primate food-processing techniques can therefore give us insight into cognitive capabilities across the primate lineage. Previous work on naturalistic tool use as an indicator of technical complexity in primate food-processing abilities has involved both monkeys and apes, in behaviours such as tool selection (e.g., Visalberghi et al. 2009; Gumert and Malaivijitnond 2013), multiple tool association (e.g., Sugiyama 1997), and coordinating actions, object affordances, and spatial relations (Lockman 2000; Visalberghi and Fragaszy 2006). Food processing without tool use, which can also be manually and cognitively complex, has to date only received attention primarily within great apes, including leaf-processing behaviours of chimpanzees (Stokes and Byrne 2001), orangutans (Russon 1998), and gorillas (Byrne and Byrne 1993). This work has facilitated comparisons between great ape and human intelligence in terms hierarchical organisation, which is the ability to construct higher level cognitive representations or behavioural sequences by building upon lower level units, rather than simply responding to external stimuli (Russon 1998; Stokes and Byrne 2001; Byrne 2005).

Here, we report new observations of free-ranging long-tailed macaques (*Macaca fascicularis*) processing *Opuntia*

Electronic supplementary material The online version of this article (doi:10.1007/s10329-016-0525-3) contains supplementary material, which is available to authorized users.

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Published online: 26 February 2016

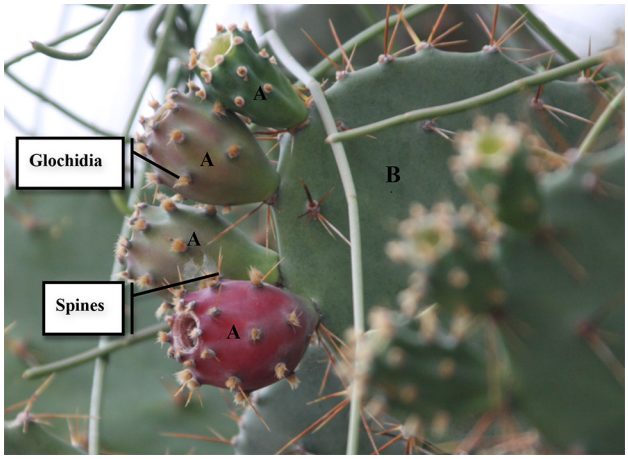


Fig. 1 Part of an *Opuntia* plant on Nom Sao Island showing fruits (A) bearing numerous clusters of glochidia and some spines, growing from its cladode (B)

sp. cacti, and conduct preliminary analyses of their behaviour to highlight its potential for contributing to our understanding of complex food-processing techniques in Old World monkeys. *Opuntia* cacti fruit (Fig. 1a) grow from flattened, succulent stems known as cladodes (Feugang et al. 2006) (Fig. 1b). Cladodes and fruit have two physical defenses (Fig. 1): spines which are sharp, rigid, and long, and glochidia, which are short, fine hairs that easily break off and embed painfully in a predator's skin, making the consumption of *Opuntia* potentially harmful for foragers. In regions of South America, humans rub *Opuntia* fruits on abrasive surfaces to remove glochidia prior to consumption (Feugang et al. 2006; Russel and Falkner 1987). Chacma baboons (*Papio ursinus*) (Lotter et al. 1999), Japanese macaques (*Macaca fuscata*) (Clark 1979), bonnet macaques (*M. radiata*) (Krishnamani 1994), patas monkeys (*Erythrocebus patas*) (Isbell 1998) and vervet monkeys (*Chlorocebus pygerythrus*) (Dean and Milton 2000), which are Old World monkeys, and ring-tailed lemurs (*Lemur catta*) (Kelley 2013) a strepsirrhine primate, are also known to consume *Opuntia.* Of these, Japanese macaques (Clark 1979) have been reported to rub or drag *Opuntia* along the ground, but details about the techniques are not described. It is not reported if other non-human primate species process *Opuntia* before eating them.

Methods

Study site and subjects

We observed *Opuntia* processing techniques in a group of nine free-ranging, long-tailed macaques on Nom Sao Island (NSI), in Khao Sam Roi Yot National Park, Thailand. Nom Sao Island (N 12°13′51″, E 100°0′17″) consists of karst limestone and scrub forest interior, surrounded by 1.32 km of coastline that is 0.53 km limestone cliff shores (40 %), 0.67 km rocky shore (51 %), and 0.12 km (9 %) sandy beach. There is a small shrine on NSI, located on the beach. *Opuntia* plants grow in linear patches along the forest edge on both sides of the shrine.

The NSI macaques are all habituated adult males (exact ages unknown) that forage on natural plants and marine invertebrates, but also receive limited provisioning from food offerings made at the shrine. These males are the only monkeys on NSI, and are likely displaced from a larger population of ~80 macaques on the neighbouring Koram Island, separated only by a 0.37 km-wide channel. During fights on Koram Island, losers often run into the sea to escape opponents (Tan, personal observation), and could then swim or be washed onto NSI.

Data collection

Opuntia fruit processing was observed from 20 September to 25 October 2015. We video recorded bouts of *Opuntia* processing to identify and describe stages of processing techniques, and the elements involved in each technique. We also recorded the type of substrate with which the macaques processed the fruit. We adapted definitions of techniques and elements from those used to describe leaf-processing behaviour in gorillas and chimpanzees (see Byrne and Byrne 1993; Stokes and Byrne 2001), to facilitate comparisons. Here, elements are patterns of body, hand and/or mouth actions resulting in a change to the plant or fruit, while a technique is an ordered sequence of elements, combined with substrate use, coordinated to process an *Opuntia* fruit. A bout began when contact is made with the plant, and ended upon fruit consumption.

We photographed and measured a sample of unprocessed *Opuntia* fruits on NSI, and measured the length of *Opuntia* coverage on NSI shores by taking GPS points of the starts and ends of *Opuntia* patches. A patch was defined as a line of *Opuntia* with <5 m separating individual plants. We also photographed and examined processed fruit remains to describe processing outcomes.

Results

Characteristics of *Opuntia* on Nom Sao Island

Opuntia plants covered ~141 m of the NSI coast, along the forest edges flanking the shrine. South of the shrine, *Opuntia* grew in a 49-m-long patch, while north of the shrine, *Opuntia* grew in two patches: a 76-m patch closer to the shrine, and a 15-m patch, with a gap of 30 m between

Table 1 The 17 observed elements of *Opuntia* processing by long-tailed macaques at Nom Sao Island, which were combined into six different techniques

Elements for acquiring fruit	
Pluck	Fruit is pinched between thumb and fingers and pulled off the cladode
Pull down	Standing bipedally, one hand pinches a cladode between it's spines to pull the cladode down, then the other hand pinches further along the cladode's length to pull it lower down, repeating until fruit is within reach
Jump	The macaque jumped up off the ground to obtain fruit. We did not observe the contact made with the plant, but his action resulted in the fruit falling to the ground
Tap	Fruits on the ground are tapped around with one hand so that the base of the fruit is oriented for easy pick up
Pick up	The base of a fruit (on the ground) is grasped between the thumb and the side of the index finger, and lifted off the ground
Elements for transporting fruit	
Pinch-carry	Fruit is pinched by its base between the thumb and finger(s) of one hand, and the macaque walks tripedally with the fruit
Bite-carry	Fruit is held by its base in the mouth as the macaque travels
Elements for processing fruit on substrate	
Rub	Fruit is pushed and pulled forwards and backwards with one hand
Sweep	Fruit is pushed from side to side in sweeping motions using either one hand repeatedly, or alternating hands
Roll	Fruit is lightly pulled with one hand such that it rolls backwards on the substrate, towards the macaque
Wash	Fruit is manipulated in water in between rubbing it on rock substrate. Specific actions blocked from view
Elements for exposing pulp	
Thumb-split	Fruit is held on the ground with both hands, the thumbs are pushed down into the fruit, then pulled in opposite directions to split the skin
Bite open	Fruit is brought to the mouth and held in one or both hands. A portion of the fruit's skin is bitten off, then fruit is pulled apart by hand
Teeth-peel	Fruit is brought to the mouth and held by the base in one hand, while the skin of the fruit is peeled off in sections with the teeth, until all the skin is removed
Elements for eating fruit	
Scrape	Fruit is held open with both hands, while the pulp is scraped into the mouth with the teeth
Lollipop-feed	Fruit is held by its base in one hand, and the entire pulp is fed into the mouth like a lollipop
Eat-spit	Chunks of fruit with the skin still attached are bitten off and chewed, the pulp is consumed, and then the skin is spit out
Techniques/individual code	
T1 (Usn)	Pluck, pinch-carry, sweep + rub (sand), thumb-split, scrape
T2 (Usn)	Pluck, pinch-carry, roll + sweep (sand), bite-open, scrape
T3 (Vdm)	Pluck, pinch-carry, roll + rub (rock), bite-open, scrape
T4 (Vdm)	Jump, pick-up, bite-carry, wash + roll (rock) + rub (rock), eat-and-spit
T5 (Usn)	Pull-down, tap, pick-up, pinch-carry, sweep + rub (sand), thumb-split, scrape
T6 (Mfa)	Pluck, roll (rock), peel, lollipop-feed

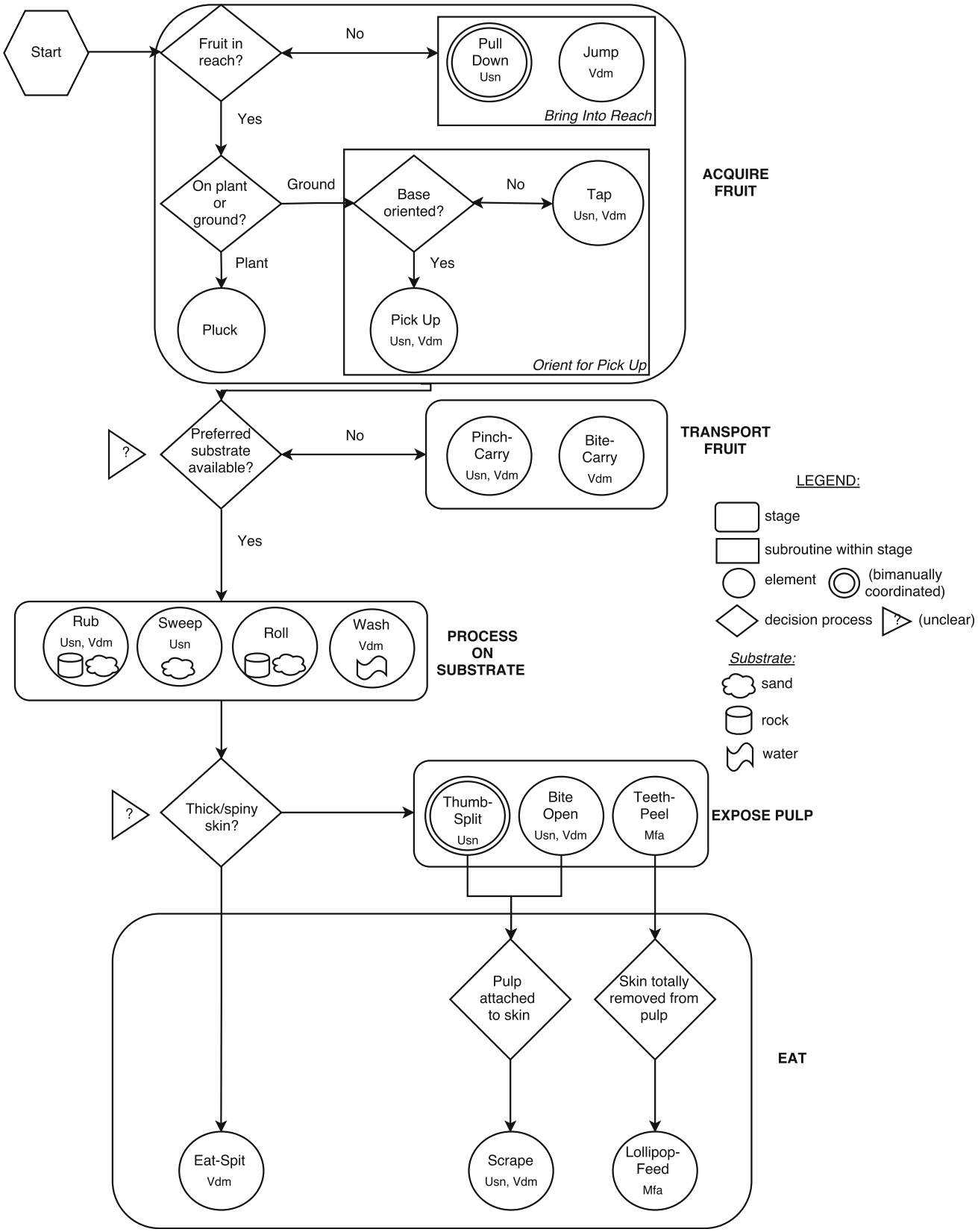
the two. Each *Opuntia* plant measured between 2 and 5 m wide, and 2 and 2.5 m tall. On average, fruits ($n = 23$) were 4–5 cm long and 2.5–3.5 cm wide. All fruits bore tight clusters of glochidia that were 0.3–0.7 cm long, and some fruits had three or four 1–2 cm-long spines that grew out of the clusters.

Processing techniques

We observed three macaques (coded as Usn, Vdm and Mfa) harvest and process one to three fruits each, a total of six processing bouts (Usn, 3; Vdm, 2; Mfa, 1). These macaques processed the fruits using three substrates: sand, rock surfaces, and water, and we observed one bout where both water and a rock surface were used by the same animal.

Stages and elements

We identified five stages of processing (1) acquire fruit; (2) transport fruit; (3) process on substrate; (4) expose pulp; and (5) eat. We observed 17 elements across the five stages (Table 1, video in Online Resource 1). Two elements, 'pull-down' and 'thumb-split' required the simultaneous use of both hands. Furthermore, when macaques proceed from 'pull-down' to 'pluck', asymmetric bimanual


Start
Fruit in reach?
No
Pull Down Usn
Jump Vdm
Bring Into Reach
Yes
On plant or ground?
Ground
Base oriented?
No
Tap Usn, Vdm
Plant
Yes
Pluck
Pick Up Usn, Vdm
Orient for Pick Up
ACQUIRE FRUIT
?
Preferred substrate available?
No
Pinch-Carry Usn, Vdm
Bite-Carry Vdm
TRANSPORT FRUIT
Yes
Rub Usn, Vdm
Sweep Usn
Roll
Wash Vdm
PROCESS ON SUBSTRATE
LEGEND:
stage
subroutine within stage
element
(bimanually coordinated)
decision process
? (unclear)
Substrate:
sand
rock
water
?
Thick/spiny skin?
Thumb-Split Usn
Bite Open Usn, Vdm
Teeth-Peel Mfa
EXPOSE PULP
Pulp attached to skin
Skin totally removed from pulp
EAT
Eat-Spit Vdm
Scrape Usn, Vdm
Lollipop-Feed Mfa

◀**Fig. 2** The five stages of *Opuntia* processing on Nam Sao Island. 'Transport fruit' and 'expose pulp' were sometimes omitted by the macaques. There were conditional subroutines within the 'acquire fruit' stage, alternative elements to carrying out each stage, and different substrates with which fruit were processed. When elements were not carried out by all three individuals, the individual(s) observed to carry out the element is indicated in *subscript*

coordination is needed as one hand holds the cladode in place while the other dislodges the fruit. The stages of techniques were sequential but flexible, as they could be omitted or repeated in different bouts. In one bout, the individual Vdm did not 'expose pulp', but proceeded directly from 'process on substrate' to 'eat'. In another bout, Mfa did not 'transport fruit', instead proceeding to 'process on substrate', on a rock surface located directly below the plant. And lastly, in another bout by Usn, the individual was threatened by a dominant individual several times during 'process on substrate'. In response to each interruption, he transported the fruit to a new location, then resumed 'process on substrate'.

Multiple elements were combined at each stage. Some elements were interchangeable, while others were optional and dependent on whether or not they were required by the task. For example, 'pull-down' and 'jump' were interchangeable for bringing a fruit in reach during 'acquire fruit', and both were optional, carried out only for high-growing fruit that could not be acquired using 'pluck'. In some cases, the conditions governing the macaques' usage of elements were not clearly task dependent, but we suggest possibilities (Fig. 2). For example, when Vdm proceeded directly from 'process on substrate' to 'eat', using the element 'eat-spit', we can propose that the skin of the fruit was sufficiently clean of glochidia for him to skip the 'expose pulp' stage, possibly because of the effectiveness of the substrate for removing glochidia. This suggestion is based on our examination of fruit remains, with the discarded skin of the fruit from this bout found to have the fewest glochidia remnants (Fig. 3d). The six observed techniques varied in the combinations of elements and substrates used, and therefore, all observed bouts were novel behavioural sequences (Table 1; Fig. 2).

Processing outcomes

Glochidia were worn down by the macaque processing techniques, such that <1 mm of the glochidia remained in the skins (Fig. 3b). The fruit that was processed in water had the fewest remnants of glochidia (Fig. 3d), and left numerous glochidia floating on the water's surface. Following the use of technique T5, the fruit remains still had long spines attached (Fig. 3c), but we did not find any evidence in the field (i.e., broken spines on the ground) to show that fruits processed with different techniques had spines to begin with.

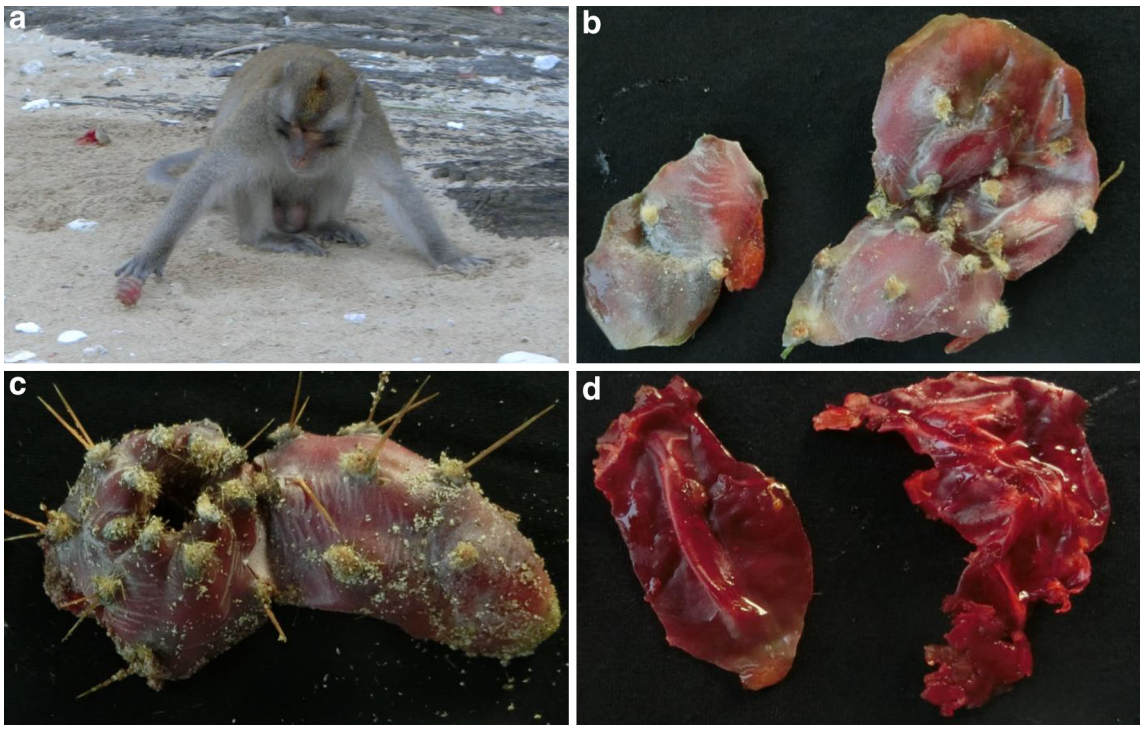


Fig. 3 Macaque processing of *Opuntia* fruit, Nom Sao Island. **a** A macaque processing *Opuntia* on sand with the 'sweep' element. **b** After processing, glochidia are rubbed off leaving only the bases, but **c** spines remain. **d** Washed fruit had the fewest remnants of glochidia

Discussion

Our report of free-ranging long-tailed macaques processing *Opuntia* fruits adds to the sparse record of complex food-processing behaviour by Old World monkeys. The macaques harvested the fruit, sometimes from difficult-to-reach areas of the plants, and carried the fruit via the base (i.e., the part of the fruit where it attaches to the cladode) where there are less glochidia and therefore is safer to handle, to a suitable substrate for processing. The macaques then processed *Opuntia* by pushing, sweeping, or rolling them on sand or rock substrates, or by washing them in seawater. The actions of pushing and sweeping, and the pinching of the fruits by their bases could minimise contact with glochidia while acquiring, transporting, and processing the fruits on substrate. Processing the fruit on substrate appears to be aimed at removing the fine glochidia of the fruit, rather than the longer and more rigid spines. Spines are more prominent, less numerous, and do not break off easily, and can be avoided with careful handling. On the other hand, glochidia grow in multiple dense clusters over the surface of the fruit. Each glochidium readily becomes embedded in the skin, an injury that can be avoided by first breaking off the glochidia upon a substrate. Based on these initial observations, processing the fruit in water may be particularly effective, because it helps to separate broken glochidia from the fruit surface.

Macaques demonstrate manual dexterity in *Opuntia* processing, and our observations have identified at least two action elements that involve the simultaneous use of both hands, one of which further involves asymmetric bimanual coordination, or the simultaneous coordination of both hands for different roles. Study of macaque stone-tool use has provided separate evidence that they use a variety of precision and power grips in food processing and are capable of bimanual role-differentiation; for example, holding a food item steady with one hand and striking at it accurately with a tool held in their other hand (Tan et al. 2015). Analyses of gorilla and chimpanzee leaf-processing has documented their use of different hand grips and action elements involving bimanual role-differentiation in great detail, which has both enabled finer scrutiny of individual variation in processing techniques, and contributed to the understanding of the dextrous manual capabilities in these species (Byrne and Byrne 1993; Stokes and Byrne 2001). Future research can do the same for macaques, which would also facilitate further cross-species comparisons.

Opuntia processing by macaques potentially shows two features of hierarchical organisation (criteria outlined by Russon 1998) that are also present in great ape leaf-processing behaviours. The first is the presence of "optional or alternative" behavioural components. There is evidence that the macaques omit unnecessary stages, and that there is flexibility in their use of different stages, elements and substrates for the one task of processing *Opuntia* fruits. The second feature of hierarchical organisation that we possibly see in *Opuntia* processing is "disruption handling". One individual (Usn) was interrupted by a dominant individual, but picked up from where he left off in the processing technique, without disruption to the overall goal of processing and consuming the fruit. These observations suggest the presence of overall behavioural plans, and abilities to distinguish between actions and events that fall into these plans (Byrne and Russon 1998; Russon 1998). Many more observations will be needed to determine if the macaques truly and consistently demonstrate these features of hierarchical organisation in their *Opuntia* processing behaviour.

More data will also be needed to identify if the macaques exhibit any other features of hierarchical organisation seen in great apes' food-processing behaviours. The great apes demonstrate routines and subroutines, which are behavioural complexes nested within larger sequences, that they reiterate until the task is achieved, or to maximise efficiency (Russon 1998). For example, gorillas repeated elements involved in gathering leaves until a handful was obtained before folding leaves (Byrne and Byrne 1993), and chimpanzees stripped multiple leaves and accumulated them in the hand before biting off the inedible petioles (Stokes and Byrne 2001). We did not observe the macaques repeating element sequences within any stage of *Opuntia* processing, and they only processed single fruits at a time. We suggest, however, that this does not exclude their potential capability for doing so. In the case of *Opuntia* processing, the properties of the fruits (i.e., being round and large), could constrain the macaques from gathering and effectively handling more than one at a time. Furthermore, macaques demonstrate reiteration of element sequences to maximise efficiency during their use of stone tools on marine gastropods, as they often search for and collect several gastropods, before taking them to an anvil for processing (Gumert and Malaivijitnond 2012; Tan, personal observation).

In conclusion, *Opuntia* processing consists of multiple, manually challenging elements that macaques deal with flexibly, using these elements in various combinations. Our findings provide preliminary evidence for at least some features of hierarchical organisation in macaque *Opuntia* processing. Hierarchical organisation of behavioural programs is currently known to be a shared capability unique to the great apes and humans, while being absent in other nonhuman primates (Russon 1998; Stokes and Byrne 2001; Byrne 2005). Our early observations, however, highlight the value of reporting and further scrutinizing complex

food-processing behaviour in monkeys, to better understand what features of hierarchical cognition may be shared amongst different members of the primate lineage. Given the small sample size of these opportunistic observations, we likely have not yet fully discovered the breadth of diversity and complexity of this food-processing technique employed by long-tailed macaques. Closer study of how macaques collect and process crabs, caterpillars, buried shellfish, and other technically difficult to access foods, could also be explored to assess if macaques exhibit any forms of hierarchically organised sequences of behaviour.

Acknowledgments We thank the National Research Council of Thailand (NRCT) for permitting Amanda W. Y. Tan, Lydia Luncz, Michael Haslam, and Michael D. Gumert to conduct research in the Kingdom of Thailand, and the Department of National Parks, Wildlife, and Plant Conservation (DNP) for allowing our team to conduct research in Khao Sam Roi Yot National Park (KSRY). We thank Mr Runjroj Atsawakultarin, the superintendent of KSRY for administrative help, and the community of Phu Noi Village for logistical support and hospitality during our project. Thank you also to Ms Lauren O'Boyle for her field research assistance, and Mr Felix Merklinger for information on *Opuntia* cacti. The project has been funded by the Visiting Professor Scheme at the Department of Biology, Chulalongkorn University, the College of Humanities, Arts and Social Sciences (HASS) Incentive Grant Scheme, a Leakey Foundation Doctoral Research Grant, and a European Research Council Starting Grant No. 283959 (PRIMARCH).

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