



Return of the Native: Cognition and Site-Specific Expertise in Orangutan Rehabilitation

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Ex-captive orangutans that have returned to free forest life in Bornean forests offer exceptional opportunities to assess the cognitive challenges facing feral great apes. They also provide opportunities to track readaptation, which requires building expertise to survive in tropical rain forests and to integrate into orangutan communities. I outline some of the foraging problems that ex-captive orangutans encounter, the cognitive processes used in their solutions, and acquisition patterns. Evidence derives primarily from observational studies of feeding behavior in free-ranging ex-captives. Discussion focuses on implications for conservation initiatives.

KEY WORDS: orangutans; great apes; cognition; conservation; rehabilitation.

Despite efforts to secure orangutan survival in the wild, prospects for Bornean orangutans are the worst they have ever been. In the early 1990s, Soemarna *et al.* (1995) estimated orangutan habitat to have declined by $\geq 80\%$ and numbers by 30–50% over the preceding 20 years. Broad surveys in the mid 1990s showed the Bornean population to be fragmented into 61 isolated subpopulations, mostly in unprotected areas (Rijksen and Meijaard, 1999). Another 20–30% of the population was probably lost because of the drought and fires that devastated Borneo in 1997–98, leaving the total as low as 15,000 (Rijksen and Meijaard, 1999). Since 1998, forest conversion, legal and illegal logging, and wildlife poaching have run rampant, reducing numbers even further (Environmental Investigation Agency, 1999; Grant, 1999).

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The situation is fulfilling predictions that orangutan conservation aimed at preserving large undisturbed areas will probably end in the near future, as remaining sites are exhausted (Clemmons and Buchholz, 1997). Orangutan survival may lie in managed populations, in designer habitat subject to sustainable use. Such conditions require conservation efforts that take behavior into account (Clemmons and Buchholz, 1997). Behavior is strongly controlled by cognition in primates, and great ape cognition may have a distinctive nature (Byrne, 1995; Russon *et al.*, 1996), so cognition should be an important factor. I discuss orangutan cognition as it is expressed in foraging and its implications for orangutan conservation efforts, especially rehabilitating ex-captives to forest life.

EVIDENCE

Evidence on orangutan foraging expertise derives from two field studies on free-ranging ex-captives in Sungai Wain Forest, East Kalimantan (Indonesian Borneo) (Peters, 1995; Russon, 1998) and published findings on wild orangutans. Primary evidence derives from systematic observational data I collected from 1995 to 1998 (6–8/95: 216 h; 3–7/96: 397 h; 6–11/97: 340 h; 5–6/98: 89 h; 5–7/99: 168 h) and Peters' (1995) findings (10/94–5/95: 923 h). My data is derived from a multiyear study on the acquisition and cognitive complexity of techniques to obtain difficult forest foods.

Sungai Wain spans 10,025 ha of lowland mixed dipterocarp forest with extensive swamp areas: habitat suitable for orangutans but devoid of a wild population (Russon and Susilo, 1999). Its resident orangutans are ex-captives reintroduced to forest life by the Wanariset Orangutan Reintroduction Project (ORP). My data represent 15 ex-captives, 4–15 yrs old, with 0–6 yrs of experience in Sungai Wain. All ranged near K3 or K5, two forest release sites located about 4 km apart in very similar habitat. Eight of the 15 subjects were from a group released in 1996 at K5; I observed 8 of them for their first 2 mo post-release and four of them again a year later. Through 1997, we saw no encounter between K3 and K5 ex-captives.

Because of their semisolitary and cryptic nature, one usually encounters orangutans individually, opportunistically, and in small numbers. In both Sungai Wain studies, we observed ex-captives while readapting to forest life via focal individual follows (Peters, 1995; Russon, 1998). We systematically identified forest foods that they consumed. Botanical experts from the Wanariset herbarium assisted with plant identification. My observations targeted three difficult food types that serve as key permanent foods for the ex-captives: palm pith (parenchyma), palm heart (apical meristem), and termites. I collected most food processing data *in vivo* and videotaped *ca.* 20% of target food bouts.

Tracking skill acquisition requires that researchers establish ex-captives' forest expertise at release, especially naïvete. Expertise must vary because prior experiences differ greatly. Most ex-captives were captured from the wild as infants and are still infants when they reach rehabilitation, e.g., 70–80% of ORP arrivals from 1991 to 1997 were <4 yrs old and only *ca.* 10% were >6 yrs old (Swan and Warren, 2000). However, some were held captive for days and others for years. Some were humanized, while others were kept in abysmal conditions. Expertise can be gauged by how skillfully or ineptly ex-captives handle forest problems immediately after release. Peters (1995) and Rijksen (1978) concluded that some ex-captives recall expertise that they had acquired in the wild before capture, while others are naive. I judged ex-captives as naive to a forest food if they consistently ignored it when it was regularly available, other ex-captives regularly ate it, and background information concurred, e.g., subjects captured <1 year old probably had no functional forest expertise.

FOOD IDENTIFICATION

Researchers who conducted long-term studies of wild orangutans at Ketambe, Sumatra, and at Tanjung Puting, Mentoko, and Ulu Segama in Borneo, each reported diets from >100 plant species (Galdikas, 1988; Leighton, 1993; MacKinnon, 1974; Rijksen, 1978). In total, orangutans ate 456 plant species in 204 genera (Rodman, 2000). Of the species/genera, orangutans ate 84%/74% of the total at only one site; they ate only 2%/5% of them at all 4 sites. The site specificity and breadth suggest that orangutan food knowledge is largely acquired experientially, and it imposes substantial memory and learning loads.

Sungai Wain ex-captives fed from ≥ 111 species by 5/95 (Peters, 1995) and ≥ 241 species by 7/00 (Orangutan Reintroduction Project, 2000). The difference between the two values undoubtedly includes sampling artifacts, e.g., only Peters' study spanned a fruit season and 44 food species that she identified were not reported again and we did not formally identify rattans as eaten by ex-captives until 1997. Given their captive histories and the likelihood that orangutan food knowledge owes to learning, the difference probably reflects a true broadening of their diets in the forest. One implication is that ex-captives may not identify many potential forest foods for several years after release.

Individual behavior is consistent with the site-level finding. Some Sungai Wain ex-captives appeared to be naive about forest foods even years after release, i.e., they behaved as if they did not recognize edible items as food (Peters, 1995; Russon, 2001). I compared food knowledge of less and more experienced ex-captives within 3 dyads (one dyad compared twice), via

matched samples collected in the same season and foraging area to control for food availability and site specificity. In all dyads, the more experienced ex-captives ate more species; the sample is too small to test statistically.

Cognitive factors probably contribute to the slow acquisition of food identification skills.

Conservatism

Orangutans are conservative in food choice. Rijksen (1978) formally tested wild orangutans by offering them unfamiliar foods. Most ignored the unfamiliar foods repeatedly and the few that tasted them did so cautiously. Like other primates, orangutans probably resist exploring foliage more than fruit (Whitehead, 1986) and become more conservative with age (Pereira and Fairbanks, 1993; Rijksen, 1978).

Dietary Breadth

My data combined with findings on food conservatism suggest that ex-captives may broaden their food repertoires slowly. Evidence is clearest for common permanent foods because not eating them cannot be attributed to non-availability. Over consecutive years, several juveniles did not add important permanent foods to their diets, though they made significant advances in their techniques to obtain permanent foods they already knew (Russon, 2001).

In 1997, all 9 ex-captive subjects ate some termite species almost daily (42 of 45 follows); 4 ranged near K3 and 5 ranged near K5. During that period, I saw no K5 ex-captive eat subterranean nest-building termites (*Prohamitermes mirabilis*), though they had lived 1–1.5 years in the forest (0 of 17 follows), *Prohamitermes mirabilis* is readily available throughout the forest; all K3 ex-captives ate *P. mirabilis* daily (18 of 18 follows). K3 and K5 are very similar habitats only 4 km apart. The difference in consumption between the two groups is significant (Fisher exact test, $p < 0.001$).

Similarly, for years after ORP began releasing ex-captives into Sungai Wain in 5/92, we saw no ex-captive eat palm items that are readily available year-round. None ate heart from *Oncosperma horridum* (locally *nibung*) before 1996, or pith from *Licuala spinosa* or any item from *Pholidocarpus sp.* (locally *daun biru* and *serdang*) before forest fires struck in 2/98. In contrast, several ex-captives in the nearby Meratus forest ate *nibung* heart daily <2 years after releases began there. Of the 5 Sungai Wain ex-captives that I observed after fires subsided (5–6/98) three ate *serdang* pith and flower stalks and 2 ate *daun biru* pith; several continued to eat them one year later

(Russon and Susilo, 1999). Fire- and drought-related stress likely forced the subjects to exploit them (Russon and Susilo, 1999).

Regular ex-captive consumption of the items at some sites or at later dates shows them to be appropriate, even preferred foods. Not eating them implies ignorance, perhaps related to a reluctance to explore new foods. All 4 items could easily be neglected. Nests of *Prohamitermes mirabilis* are invisible underground, *nibung* and *serdang* palms are both very heavily defended, and other *daun biru* foods may have distracted attention from the pith.

By remaining ignorant of important food sources, ex-captives may maintain relatively narrow diets. Relying on a narrow set of core foods in the short term and searching out new foods in times of stress may be normal; wild orangutans do both (Rijksen, 1978; Suzuki, 1992). However, the distribution of orangutan foods is complex which creates irregular and sometimes extreme fluctuations in availability (Rijksen, 1978). The broad diets of wild orangutans probably buffer fluctuations in availability by allowing them to shift or to supplement their core food set. Maintaining narrow diets might jeopardize the long-term survival of ex-captives.

Socially-Mediated Learning

Orangutans may learn to identify some new foods socially, i.e., their learning may be influenced by interaction with other orangutans (Box and Gibson, 1999). Most wild orangutans that Rijksen (1978) tested first tried unfamiliar items after seeing other orangutans eat them, ate portions obtained from other orangutans, and tasted tiny bits. He concluded that observing another eat an unfamiliar item sparked the observer's interest in investigating it.

Six cases I observed plus a seventh from Grundmann *et al.* (2000) suggest a similar process in ex-captives. Initially, all 7 ex-captives acted as if naive to a food item: Five consistently ignored a readily available forest food and two refused a proffered new commercial food. Given similar opportunities, other ex-captives ate them readily. Later, 5 subjects saw another orangutan eat the item they had ignored, immediately scrounged leftovers (instead of untouched portions that were equally accessible and edible), and tasted tiny bits. Two watched a human eat the item they had refused then immediately tasted small bits when the same human offered it.

This suggests an explanation for the slowness of ex-captives to broaden their diets. In a diverse range of mammalian species, infants appear to learn to identify or to prefer many foods socially, through their mothers (Box and Gibson, 2000). Most ex-captives were orphaned as infants. Orphaning probably undermines food learning because maternal input during infancy is critical to the normal food learning process.

Categorization

Orangutans may categorize foods. Some differences between orangutan food species likely represent vicariance, i.e., specific variability within a common genus, so nominally different foods may pose similar problems. Categorization applied to a problem set characterized by vicariance would allow the identification of new food species based on their resemblance to known food categories. This could offset conservatism in developing dietary breadth. Evidence of categorization by nonhuman primates is ample (Herrnstein, 1990; Tomasello and Call, 1997).

Use of palm foods by Sungai Wain ex-captives suggests food categorization. Palms form a complex family of *ca.* 2600 species in 215 genera (Jones, 1995). Over 40 species occur in Sungai Wain. For 5 consecutive years, Sungai Wain ex-captives ate regularly from palm species that they had not been observed to eat in previous years. The circumstances involved suggest that they may have relied on categorization to identify new palm food species.

All palms share a few basic features; they are perennial, woody, reproduce by seeds, and grow from a single apex embedded atop a stem (Jones, 1995). Otherwise, palms vary widely. Most have a trunk but some are trunkless or climb. Some have a single stem, others have several. Some distribute leaves in a crown, others along a stem. Many are edible, some are toxic. Some grow to 0.3 m, others to 100 m. Some have spines, others do not. This variability makes it unlikely that orangutans identify palms as strictly individual species or as one undifferentiated group.

Based on consistent differences in techniques for extracting palm heart, Sungai Wain ex-captives appear to classify palms into 4 categories linked to structural constraints (meristem location relative to other plant parts, robustness). They extract the shoot from a young slender rosette centers with a single pull then bite the meristem off its base. They tear open robust non-climbing rosettes at the base from the side, then bite out the meristem. They pull the shoot from a crowned palm center via complex techniques, e.g., subdivide and fold the shoot, then bite the meristem off its base. They tear open the sheath of sheathed palms near the apex from the side, then bite out the meristem. Ex-captives also distinguish species within categories because technical details vary according to whether, for example, a sheath is tough or tender or a climber's stem is spiny or smooth.

Categories are probably due partly to perceptual similarities—different categories simply look different—but palms are so dissimilar perceptually that this does not account fully for how orangutans classify them. The techniques that ex-captives use to obtain invisible palm parts, like meristem or fruit pulp, suggest that categories may be based on structural similarities that are not directly perceptible. For example, in climbing palms like rattans, the

meristem is hidden beneath the stem's sheath *ca.* three leaf nodes below the newest shoot. Biting much higher or lower fails to expose the meristem. Experienced ex-captives regularly bite the stem at the correct location so they must be applying accurate structural information.

If the categories of ex-captives are based on structural principles, they could be governed by cognition rather than perception. Great apes as young as 4.5–5.5 years old show the cognitive capacity to classify at second-order levels, like 2–3 year old children (Parker and McKinney, 1999). Achievements include abstract logical categories like all versus some/none/one (Premack, 1983), classifying by multiple features (Braggio *et al.*, 1979; Matsuzawa, 1990), and matching relations among relations (Thompson, Boysen, and Oden, 1997). Cognitively-governed classification could facilitate identifying new foods because it may allow rapid identification of unfamiliar category members by generalization (Herrnstein, 1990).

Consistent with this possibility is the speed with which ex-captive knowledge of palm species broadened. Ex-captives fed on ≥ 4 palm species by 5/95 and ≥ 26 palm species by 7/00 (Table I). Over the same period, they increased the number of other species in their diet from 107 to 215 (Peters, 1995; Orangutan Reintroduction Project, 2000). It is unlikely that ex-captives released after 5/95 brought the knowledge because palms are minor food resources at other locations (Rodman, 2000). However, the increase in palm species is probably inflated because rattan species were not systematically identified until 1997. Nonetheless, all rattan species from which ex-captives obtained meristem were clearly added after 5/95. Accordingly, even allowing for identification biases, ex-captive knowledge of palm species appears to have grown faster than their knowledge of other food species.

Orangutans may then learn new foods by generalization, based on their structural and/or processing similarity to an established food category. If the argument holds, high-level classification abilities may play a role in orangutan forest life.

FOOD PROCESSING

Food processing refers to readying food items for consumption after they have been located. It may rank among the most challenging cognitive problems for great apes because they rely on foods that are difficult to process (Parker and Gibson, 1977; Byrne, 1997). Their difficult foods are commonly protected by physical or chemical defenses like embedding matrices, spines, protector ants, distasteful exudates, or toxins, several of which may protect a single food (Russon, 2001). Accordingly, great ape techniques for obtaining difficult foods can be highly complex, involving flexible, lengthy manipulative sequences and sophisticated tool use (Byrne and Byrne, 1991; McGrew, 1992;

Table I. Changes in palm food consumption from 5/95 to 7/00

Genus	Species	Fr	Fl	YL	L	M	P	Fl-St
<i>Borassodendron</i>	<i>Borneensis</i>	Fr ^a	Fl	YL	L	M	P	Fl-St
<i>Licuala</i>	<i>Spinosa</i>	Fr	Fl			M^b	P	Fl-St
<i>Pholidocarpus</i>	<i>Sp.</i>		Fl				P	Fl-St
<i>Oncosperma</i>	<i>Horridum</i>	Fr				M	P	
<i>Pinanga</i>	<i>Sp. a & b</i>					M		
<i>Rattans (unident.)</i>	<i>Sp.</i>				L			
<i>Calamus</i>	<i>Caesius</i>					M		
	<i>Fimbriatus</i>	Fr				M		
	<i>Flabellatus</i>					M		
	<i>Javensis</i>					M		
	<i>Marginatus</i>	Fr				M		
	<i>Nigricans</i>					M		
	<i>Ornatus</i>	Fr				M	P	
	<i>Sarawakensis</i>					M		
	<i>Concolor</i>					M		
<i>Ceratolobus</i>	<i>Didymophylla</i>	Fr				M		
<i>Daemonorops</i>	<i>Fissa</i>					M		
	<i>Sabut</i>	Fr				M		
<i>Korthalsia</i>	<i>Echinometra</i>					M		
	<i>Ferox</i>					M		
	<i>Flagellaris</i>	Fr						
	<i>Furtadoana</i>					M		
	<i>Rigida</i>					M		
<i>Plectocopiopsis</i>	<i>Sp.</i>				L			
	<i>Geminaflora</i>					M		

Note. Entries indicate food parts eaten by 7/00 (Orangutan Reintroduction Project, 2000); Bold entries highlights food parts also eaten by 5/95 (Peters, 1995); Fr (fruit), Fl (flower), YL (young leaf), L (leaf), M (meristem), P (parenchyma), and Fl-St (flower stem).

^aOnly young fruit eaten before 5/95, mature fruit also eaten by 7/00.

^bOnly from small shoots before 5/95, also from mature shoots by 7/00.

Russon, 1998; van Schaik, Fox, and Sitompul, 1996). Some techniques are so complex that immature individuals master them only near adolescence, and mothers assist by teaching them (Boesch, 1993; Matsuzawa, 1994).

How Orangutans Obtain Foods

Cognitively, interest lies in the mental processes governing processing techniques. My data show that orangutans use various operations to process food. An operation is a type of food manipulation (Russon, 1998). Some operations consist of simple actions, e.g., bite, pull, suck, while others involve complex principles, e.g., sponge, or a combination of several actions, e.g., lather. Lathering is wetting chewed food, usually with saliva, grabbing a hank of hair, usually from the back of the forearm, spitting and sucking the food-saliva mix through the hair, and picking out and eating desired bits.

Usage reveals greater complexities. One operation may be used to process several foods. For example, ex-captives use lathering to process some *Diospyros sp.* fruits, some leaves, and soap. Wild orangutans use a similar operation—hair sucking—on some astringent-tasting fruits (Rijksen, 1978). Operations may also be combined to create complex techniques governed by overarching strategies (Russon, 1998). For example, to remove bark some ex-captives use a strategy that coordinates two operations: score a length of bark, i.e., repeatedly, bite along the length to loosen a long strip, then tear off the loosened strip. Finally, alternative strategies exist for one food. Some wild orangutans have two different strategies for fruit of *Neesia sp.* one tool-based and another manipulative (van Schaik *et al.*, 1999).

Obtaining Difficult Foods

The most difficult foods in Sungai Wain often pose two types of serious problems: heavy defenses and arboreal location.

Heavily Defended Foods

Many heavily defended foods in Sungai Wain are permanent foods that sustain ex-captives through periods of food scarcity, e.g., rattans and termites. Nest-building termites illustrate the complexities involved. Ex-captives regularly forage nests that resemble small basketballs (*Bulbitermes sp.*), mounds with drooping lobes (*Dicuspitermes sp.*), or lumpy footballs (*Prohamitermes mirabilis*). Their basic strategy for obtaining termites is to find a chunk of a nest, to crack it open, and to suck termites from exposed cells (Peters, 1995).

This basic strategy is the foundation for a complex strategy that I observed with 3 adolescent ex-captives with 2.5–4.5 years of forest experience. Each subject collected several nest chunks, examined them, discarded some, presumably empty ones, and retained others, presumably with termites. Having selected 2–3 chunks, each subject held one chunk manually and held the remainder pedally. They cracked a small fragment from the working chunk, picked it up with lips or fingers, sucked newly exposed cells, and ate the contents. They sometimes rotated a fragment to find more open cells, flicked debris from its surface digitally, picked out small edible items with thumb and forefinger, or spit out unwanted items. If a fragment contained closed cells, two of the adolescents sometimes broke it down recursively into smaller and smaller fragments and sucked each cell individually. They held fragments until they were emptied of food, probably to avoid confusing them

with discarded fragments and to mark progress. When finished the working chunk, they transferred another chunk from foot to hand and repeated the process. A nest could take over an hour to process.

One of the 3 ex-captives, Paul, used an ordered system of holding fragments. He held all fragments from his working chunk in one hand: the first fragment between the tips of his thumb and one finger, fragments of the first pinned to the base of his palm by a third fingertip, fragments of the second balanced on his wrist, and (once) fragments of the third balanced higher on his wrist. He processed the fragments in order, from smallest to largest, discarding the smallest when he had exhausted it then resuming work on its direct parent. Paul's use of body parts to order fragments resembles rudiments of the body part counting systems used by some human groups (Saxe, 1981).

Food processing invokes recognized cognitive abilities, including causality or means-ends reasoning, e.g., applying forces, logic, e.g., equivalent problem-solving alternatives, and socially mediated learning. However, no one ability explains orangutan food processing because obtaining a food may require using several abilities in concert (Russon, 1998). Construing cognition in terms of abilities also neglects the levels of complexity involved. For example, causal and logical abilities can operate at multiple levels in humans and great apes (Langer, 1996). Cognitive analyses of great ape food processing techniques have therefore focused more on centralized processes that construct expertise, notably hierarchization. Hierarchization is a generalized cognitive process that builds complex cognitions in the form of higher-level structures, commonly by intercoordinating several lower-level structures (Byrne and Byrne, 1991; Gibson, 1993; Langer, 1996). Hierarchical cognition consists of programs that generate sets of behaviors organized at multiple levels, not just sensorimotor schemes that generate simple actions organized in string-like chains.

Some orangutan food operations represent simple hierarchical programs as well as subprograms within strategies, so orangutan food processing techniques can represent complex hierarchical programs (Russon, 1998). The levels of cognitive complexity shown in orangutan techniques for accessing heavily defended foods resemble those achieved by other great apes and 2–3.5 yr old children (Byrne, 1995; Russon *et al.*, 1996).

Arboreally Located Foods

Arboreality is a cognitive challenge for orangutans in relation to arboreal travel (Chevalier-Skolnikoff, Galdikas, and Skolnikoff, 1982; Povinelli and Cant, 1995). However, food is the main reason that primates are in the trees and the major influence on their locomotor habits (Fleagle, 1984).

Arboreal location adds two tasks to the problem of obtaining a food: positioning for access and positioning for manipulation. For orangutans, arboreal positioning can be cognitively complex in its own right (Povinelli and Cant, 1995; Russon, 1998). It likely challenges all great apes. For instance, cracking nuts with stones and hunting are more challenging to chimpanzees arboreally than terrestrially (Boesch and Boesch, 1981, 1984; Boesch and Boesch-Achermann, 2000).

The cognitive difficulties posed by arboreal location go beyond adding tasks. First, food processing and arboreal positioning require different abilities. Processing food mainly requires causal abilities because it involves changing the physical world. Arboreal positioning relies mainly on spatial abilities because it involves assessing relative positions of self, supports, and food. Consequently obtaining arboreal foods requires multiple abilities.

Second, arboreal positioning and food processing tasks may be interdependent. Food processing operations can affect arboreal positioning and arboreal positioning can constrain food processing operations. An ex-captive once applied so much force to crack a termite nest that he almost fell off a branch. Others change processing operations to suit their current positions or shift position to perform specific food processing operations. Examples are picking fruit by pulling in a fruiting branch rather than reaching out to its tip when sitting versus standing or taking one position to pick a coconut then shifting to a different position to open it. Wild orangutans similarly shift positions in processing fruits of *Neesia* (Fox *et al.*, 1999).

Third, orangutans have too few manipulators to handle both tasks independently. They allocate three manipulators to secure an arboreal feeding position >60% of time (Cant, 1987). They may also allocate ≥ 3 manipulators to difficult force-based food operations, as do humans (Reynolds, 1991). Examples from ex-captives include cracking termite nests via all 4 manipulators or tearing open palm petioles using a hand, a foot, and the mouth. In the 1997 sample of difficult food bouts (269 bouts, 6 ex-captives, 52 hrs processing time), orangutans allocated ≥ 3 manipulators to food processing in 54% of bouts (114/269) and on average 4.76 times per bout. Because each task alone can require 3 manipulators, solving the 2 tasks independently of one another can require 6 manipulators in total.

Orangutans have 5 manipulators available, given that they use the mouth to obtain food (Fox *et al.*, 1999; O'Malley and McGrew, 2000). Oral use may relate to arboreality when other limbs are needed for support (O'Malley and McGrew, 2000). In my 1999 video sample (44 food bouts, 8 ex-captives, 11 foods), the mouth contributed to processing for 50% of the duration of bouts on average. Teeth held, pulled, scored, tore, scraped, cut, punctured, crushed, and cracked; lips picked and folded; inside the mouth, fruit skins and seeds were removed.

Five manipulators are still to few. Nonetheless, orangutans obtain difficult arboreal foods; they may handle the two tasks in combination rather than independently. Two behavior patterns suggest how. Ex-captives sometimes share one manipulator between two tasks. For example, to process *bandang* pith arboreally, ex-captives tear the petiole sheath open then pull out lengths of pith, while hanging in a nearby tree. The two tasks periodically share one foot. One foot may contribute to food processing by holding the lower half of the torn petiole sheath away from the pith and simultaneously contribute to arboreal positioning by leaning on the lower half of the petiole sheath, i.e., using it for support. One task may also borrow a manipulator from the other, typically for a few seconds. Using the same *bandang* pith example, a foot contributing to a hanging position in a nearby tree may let go, swing up to help the hand and mouth tear pith for a few seconds, then swing back to its positioning role.

Foods vary in the problems they pose, and food problems vary in difficulty with orangutan size and strength. Accordingly, share and borrow rates should vary across foods and orangutans. I compared share and borrow rates in arboreal and terrestrial bouts for *bandang* pith, for 3 ex-captives (Table II). Borrow and share rates were higher in arboreal bouts. Siti, the smallest, showed the highest borrow and share rates per min, perhaps reflecting her greater need for 3–4 manipulators to generate enough force to tear the petiole sheath. *Bandang* processed arboreally are normally more robust, i.e., more difficult, than those processed terrestrially, so higher rates may simply reflect the longer duration of arboreal bouts. If bout duration effects are removed by using rates per min, arboreal-terrestrial differences are less consistent. The ex-captives juggled manipulators between positioning

Table II. Borrow and share rates for arboreal vs. terrestrial *bandang* pith bouts

Ht ID	Age (yrs)	No. of bouts	Av. bout duration (min)	Per bout		Per minute	
				Share	Borrow	Share	Borrow
Terr							
Panjul	11	3	3	0	0.3	0	0.07
Judi	15	5	7	1.4	1.2	0.17	0.1
Siti	6	8	3	1.1	2.3	0.38	0.82
Arb							
Panjul	11	7	9	2.3	2.4	0.21	0.45
Judi	15	5	44	2.4	7.4	0.04	0.24
Siti	6	22	11	2.5	6.6	0.57	0.76

Note. Ht: Height at which food was processed; Terr: processed terrestrially; Arb: processed arboreally, 3–5 m above ground; based on 1997 data on manipulator use in food processing. Subjects were included if data were available for ≥ 3 *bandang* pith bouts in both terrestrial and arboreal conditions. Bouts were excluded at 1–2 m (ambiguous), at >6 m (insufficient comparable cases), or if both arboreal and terrestrial processing occurred.

and processing for difficult arboreal foods, as often as every 1.5–2 min, i.e., they interconnected their solutions to the two tasks.

Such interconnections suggest that an additional generalized cognitive process may be operating in orangutan arboreal food processing: cognitive integration, i.e., interconnecting different cognitive abilities. Cognitive integration is a highly sophisticated process that operates only in hierarchical cognitive systems. It is valuable because some problems are solved best or only by several abilities interactively (Langer, 1996). It has been considered to be exclusively human, but evidence from other species is meager (Langer, 1996; Premack, 1984; Russon *et al.*, 1998). Sungai Wain ex-captives' strategies for processing difficult arboreal foods involve behavioral integration, so the cognition that governs them must be integrated as well. Orangutans therefore offer evidence of cognitive processes beyond those conventionally credited to great apes.

ACQUISITION OF FOOD PROCESSING EXPERTISE

Several findings on acquiring food processing expertise, including two cognitive factors that affect the acquisition process, have implications for conservation.

Orangutan complex foraging techniques are acquired slowly. Ex-captives judged naive to a difficult forest food when newly released have taken ≤ 2 yr to master generally effective strategies for obtaining it, after discovering it (Russon, 2001).

Development constrains acquisition. For what may be the most difficult orangutan food in Sungai Wain, *bandang* heart, the youngest individuals to master the generally effective strategy of dividing the job into smaller sub-tasks were juveniles > 5 yrs old (Peters, 1995; Russon, 1999). Orangutans likely resemble other great apes in this regard, i.e., their most complex expertise is mastered after infancy (Boesch and Boesch-Achermann, 2000).

Dead-end and inefficient techniques can develop, and persist, despite their ineffectiveness. For over a year, one juvenile ex-captive banged chunks of termite nest against hard surfaces to open them, though it never worked. An adolescent ate ants one by one, though it is more efficient to scoop up handfuls. Paul, 5–6 yrs old, devised a dead-end tactic to enhance his simple technique to obtain heart from *bandang* rosettes: he braced himself against a nearby tree to increase his pulling force. This allowed him to pull shoots from some *bandang* otherwise beyond his strength (mid-sized rosettes) but not large rosettes or trees. Paul used this tactic for ≥ 6 mo before shifting to a strategy effective for all *bandang*, subdividing the shoot and pulling each section in succession. Clearly ex-captives can retard progress by failing to

abandon poor strategies. They can devise better strategies only once they abandon poor ones.

Some ex-captives acquired a technique independently, while others appeared to have benefitted from social input. Socially mediated learning has been documented in wild orangutans by Fox *et al.* (1999) and van Schaik *et al.* (1999) and in other great apes by Boesch (1993) and Byrne and Byrne (1993). Several ex-captives illustrate the role that social input may play in acquiring food processing techniques (Russon, 2001): Of 9 ex-captives naive to *bandang* heart when I first observed them, the 3 that later mastered effective processing techniques did so after traveling with knowledgeable ex-captives. Two pairs of regular traveling companions shared techniques that no other ex-captives used and that appeared after the pair began to travel together. In three cases when naive ex-captives first tried to obtain a novel food after observing a conspecific obtain it, they used the technique they had observed with partial success. Two of them involved experienced ex-captives translocated to unfamiliar areas; they ate 2 readily available species of bark that systematically monitored residents had not eaten in the previous 1.5 yr. In both cases, residents noticed the newcomer eating bark, approached, watched him work and did not try to obtain bark themselves. As soon as the newcomer left, the observant residents took the vacated position and foraged bark via the same technique, but succeeded only partially.

IMPLICATIONS FOR CONSERVATION

Orangutan rehabilitation and other great ape conservation efforts could benefit from considering several cognitive factors. Food processing can pose highly challenging cognitive problems. Orangutans are highly intelligent, but like other great apes, they may need years to develop expertise. Based on Sungai Wain ex-captives, techniques for processing some permanent foods can be especially difficult to acquire. This expertise can be critical to survival in times of severe food scarcity, so understanding the systems and structures that foster its acquisition is essential to provide effective protection. Socially mediated learning is likely involved, so social structures and processes are probably essential underpinnings.

Researchers who evaluate potential orangutan habitat should assess the availability of permanent foods in addition to fruit, the dominant dietary item. Permanent foods may be difficult to locate and to obtain, so the problem of discovering them and the potentially slow acquisition of processing techniques should also be considered.

For orangutans, forest life exacts cognition at the same high levels shown by human-reared great apes, and perhaps even higher level ones. Rehabilitation programs could take advantage of high-level learning processes like

classification, imitation, or insight, not just simple ones like imprinting and conditioning (MacLean, 1997). Orangutan high-level learning is powerful enough that conservation programs could promote the acquisition of principles or strategies rather than behavioral details, for instance, or valuable innovations, e.g., identifying new foods.

The importance of sociality to orangutan cognitively governed expertise is gaining appreciation, including social learning, traditions, and cultural processes (Russon, 2001; van Schaik *et al.*, 1999). Implications are that disturbing communities risks destroying expertise critical to local survival, especially expertise that is not readily reinvented. Further, newcomers may have difficulty adapting to new habitats because of difficulties entering the resident community, which could interfere with acquiring locally important expertise (Rijksen, 1978). Rehabilitation programs could manage sociality to minimize its interference with readaptation or even to promote readaptation. For instance, social factors should be assessed when considering translocations and communities might be seeded with expertise by promoting the acquisition of critical skills or knowledge in selected members (Beissinger, 1997; Rijksen, 1978).

Although orangutans can function at high cognitive levels, they may acquire expertise slowly. The ecological and social experiences that found their expertise must also occur at the appropriate point in development. Offered too early, they cannot be assimilated; offered too late, they may meet reduced readiness for change (MacLean, 1997; Russon, 2001). Chances for successful rehabilitation should improve to the extent that key experiences, e.g., exposure to foods, social introductions and release, are synchronized with species-typical developmental patterns in social tolerance, cognitive capacities, and readiness to learn.

Orangutan rehabilitation has been criticized because of uncertainties over whether it achieves feralization (MacKinnon, 1977; Peters, 1995; Rijksen, 1982; Yeager, 1997). Critics often focus on behavioral deficiencies of ex-captives and attribute them to ineptitude. From a cognitive viewpoint, it is equally likely that deficiencies owe to poor programing and unreasonable expectations, e.g., low management of human contact, low appreciation of the social, ecological, and developmental conditions that foster readaptation and of the learning problems caused by human contact, and underestimation of the time needed to acquire feral skills (MacKinnon, 1977; Rijksen, 1978, 1982). These problems all concern learning, so better consideration of learning processes would likely enhance program effectiveness. If programs have been ineffective, part of the reason may be that behavioral and cognitive experts have not become actively involved. Given how much they have to offer conservation programs for great apes, their involvement should be actively encouraged.

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REFERENCES

- Beissinger, S. R. (1997). Integrating behavior into conservation biology: Potentials and limitation. In Clemmons, J. R., and Buchholz, R. (eds.), *Behavioral Approaches to Conservation in the Wild*. Cambridge University Press, Cambridge, UK, pp. 23–47.
- Boesch, C. (1993). Aspects of transmission of tool use in wild chimpanzees. In Gibson, K. R., and Ingold, T. (eds.), *Tools, Language and Cognition in Human Evolution*, Cambridge University Press, Cambridge, UK, pp. 171–183.
- Boesch, C., and Boesch, H. (1981). Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. *J. Hum. Evol.* 10: 585–593.
- Boesch, C., and Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *J. Hum. Evol.* 13: 415–440.
- Boesch, C., and Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*, Oxford University Press, Oxford, UK.
- Braggio, J. P., Hall, A. D., Buchanan, J. P., and Nadler, R. D. (1979). Cognitive capacities of juvenile chimpanzee on a Piagetian-type multiple-classification task? *Psychol. Rep.* 44: 1087–1097.
- Byrne, R. W. (1995). *The Thinking Ape*, Oxford University Press, Oxford.
- Byrne, R. W. (1997). The technical intelligence hypothesis: An additional evolutionary stimulus to intelligence? In Whiten, A., and Byrne, R. W. (eds.), *Machiavellian Intelligence II*, Cambridge University Press, Cambridge, UK, pp. 289–311.
- Byrne, R. W., and Byrne, J. M. E. (1991). Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. beringei*). *Cortex* 27: 521–546.
- Byrne, R. W., and Byrne, J. M. E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardization. *Am. J. Primatol.* 31: 241–261.
- Cant, J. G. H. (1987). Positional behavior of female Bornean orangutans (*Pongo pygmaeus*). *Am. J. Primatol.* 12: 71–90.
- Chevalier-Skolnikoff, S., Galdikas, B. M. F., and Skolnikoff, A. (1982). The adaptive significance of higher intelligence in orangutans: A preliminary report. *J. Hum. Evol.* 11: 639–652.
- Clemmons, J. R., and Buchholz, R. (eds.). (1997). *Behavioral Approaches to Conservation in the Wild*. Cambridge University Press, Cambridge, UK.
- Environmental Investigation Agency (1999). Environmental investigators expose rampant illegal logging in Indonesia's national parks. Retrieved Aug. 24, 1999, from <http://eia-international.org>.
- Fleagle, J. (1984). Primate locomotion and diet. In Chivers, D. J., Wood, B. A., and Bilsborough, A. (eds.), *Food Acquisition and Processing in Primates*, Plenum, New York, pp. 105–117.
- Fox, E. A., Sitompul, A. F., and van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In Parker, S. T., Miles, H. L., and Mitchell, R. W. (eds.), *The Mentalities of Gorillas and Orangutans*. Cambridge University Press, Cambridge, UK, pp. 99–116.
- Galdikas, B. M. F. (1988). Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *Int. J. Primatol.* 9: 1–35.

- Gibson, K. R. (1993). Animal minds, human minds. In Gibson, K. R., and Ingold, T. (eds.), *Tools, Language, and Cognition in Human Evolution*, Cambridge University Press, Cambridge, UK, pp. 3–19.
- Grant, J. (1999). Trade in endangered species thrives on fringe of animal markets. *South China Morning Post*, Jan. 18, 1999, p. 11.
- Grundmann, E., Lestel, D., Boestani, A. N., and Bomsel, M.-C. (2000). Learning to survive in the forest: What every orangutan should know. Presented at *The Apes: Challenges for the 21st Century*, Brookfield Zoo, Chicago, May 10–13.
- Herrnstein, R. J. (1990). Levels of stimulus control: A functional approach. *Cognition* 37(1/2): 133–166.
- Jones, D. L. (1995). *Palms Throughout the World*, Smithsonian Institute, Washington.
- Langer, J. (1996). Heterochrony and the evolution of primate cognitive development. In Russon, A. E., Bard, K. A., and Parker, S. T. (eds.), *Reaching into Thought: The Minds of the Great Apes*, Cambridge University Press, Cambridge, UK, pp. 257–277.
- Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *Int. J. Primatol.* 14: 257–313.
- MacKinnon, J. R. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.* 22: 3–74.
- MacKinnon, J. R. (1977). Rehabilitation and orangutan conservation. *New Scientist* 74: 697–699.
- MacLean, I. G. (1997). Conservation and the ontogeny of behavior. In Clemmons, J. R., and Buchholz, R. (eds.), *Behavioral Approaches to Conservation in the Wild*, Cambridge University Press, Cambridge, UK, pp. 132–156.
- Matsuzawa, T. (1990). Spontaneous sorting in human and chimpanzee. In Parker, S. T., and Gibson, K. R. (eds.), *“Language” and Intelligence in Monkeys and Apes*, Cambridge University Press, New York.
- Matsuzawa, T. (1994). Field experiments on the use of stone tools in the wild. In Wrangham, R., McGrew, W. C., de Waal, F. B. M., Heltne, P., and Marquardt, L. A. (eds.), *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, pp. 351–370.
- McGrew, W. C. (1992). *Chimpanzee Material Culture*. Cambridge University Press, New York.
- O'Malley, R. C., and McGrew, W. C. (2000). Oral tool use by captive orangutans (*Pongo pygmaeus*). *Folia Primatol.* 71(5): 334–341.
- Orangutan Reintroduction Project (2000). Orangutan food repertoire: Sungai wain protection forest, E. Kalimantan, Unpublished Wanariset report.
- Parker, S. T., and Gibson, K. R. (1977). Object manipulation, tool use, and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J. Hum. Evol.* 6: 623–641.
- Parker, S. T., and McKinney, M. L. (1999). *Origins of Intelligence: The Evolution of Cognitive Development in Monkeys, Apes, and Humans*. Johns Hopkins, Baltimore.
- Pereira, M. E., and Fairbanks, L. A. (eds.). (1993). *Juvenile Primates: Life History, Development, and Behavior*. Oxford University Press, New York.
- Peters, H. H. (1995). *Orangutan Reintroduction? Development, Use and Evaluation of a New Method: Reintroduction*, MSc Thesis, Groningen University, Netherlands.
- Povinelli, D., and Cant, J. G. H. (1995). Arboreal clambering and the evolution of self conception. *Q. Rev. Biol.* 70(4): 393–421.
- Premack, D. (1983). The codes of man and beast. *Behav. Brain Sci.* 6: 123–167.
- Premack, D. (1984). Possible general effects of language training on the chimpanzee. *Hum. Dev.* 27: 268–281.
- Reynolds, P. C. (1991). Structural differences in intentional action between humans and chimpanzees—and their implications for theories of handedness and bipedalism. In Anderson, M., and Merrell, F. (eds.), *Semiotic Modeling*, Walter Gruyter & Co, Berlin, pp. 19–46.
- Rijksen, H. D. (1978). *A Field Study on Sumatran Orang Utans (Pongo pygmaeus abelii Lesson 1827)*. H. Veenman & Zonen B. V., Wageningen.
- Rijksen, H. D. (1982). How to save the mysterious “man of the forest”? In de Boer, L. E. M. (ed.), *The Orang Utan: Its Biology and Conservation*, Dr W. Junk Publishers, The Hague, pp. 317–341.

- Rijksen, H. D., and Meijaard, E. (1999). *Our Vanishing Relative: The Status of Wild Orangutans at the Close of the Twentieth Century*. Kluwer Academic, Dordrecht.
- Rodman, P. S. (2000). Great ape models for the evolution of human diet. Retrieved Dec. 2000, from www.cast.uark.edu/local/icaes/conferences/wburg/posters/psrodman/GAMHD.htm.
- Russon, A. E. (1998). The nature and evolution of orangutan intelligence. *Primates* 39: 485–503.
- Russon, A. E. (1999). Acquisition of food processing expertise in free-ranging orangutans. Presented at *Gesellschaft für Primatologie*, Utrecht, Aug. 17–22.
- Russon, A. E. (in press). Comparative developmental perspectives on culture: The great apes. In Keller, H., Poortinga, Y., and Schoelmerich, H. (eds.), *Between Biology and Culture: Perspectives on Ontogenetic Development*, Cambridge University Press, Cambridge, UK.
- Russon, A. E., Bard, K. A., and Parker, S. T. (eds.). (1996). *Reaching into Thought: The Minds of the Great Apes*, Cambridge University Press, Cambridge, UK.
- Russon, A. E., Mitchell, R. W., Lefebvre, L., and Abravanel, E. (1998). The comparative evolution of imitation. In Langer, J., and Killen, M. (eds.), *Piaget, Evolution, and Development*, Erlbaum, Hillsdale, NJ, pp. 103–143.
- Russon, A. E., and Susilo, A. (1999). The effects of drought and fire on the orangutans reintroduced into Sungai Wain Forest, East Kalimantan. In Suhartoyo, H., and Toma, T. (eds.), *Impacts of Fire and Human Activities on Forest Ecosystems in the Tropics*, Tropical Forest Research Center, Mulawarman University and Japan International Cooperation Agency, Samarinda, Indonesia, pp. 348–372.
- Saxe, G. B. (1981). Body parts as numerals: A developmental analysis of numeration among the Oksapmin of Papua New Guinea. *Child Dev.* 52: 306–316.
- Soemarna, K., Ramono, K., and Tilson, R. (1995). Introduction to the Orangutan Population and Habitat Viability Analysis Workshop. In Nadler, R., Galdikas, B., Sheeran, L., and Rosen, N. (eds.), *The Neglected Ape*, Plenum, New York, pp. 81–83.
- Suzuki, A. (1992). The population of orangutans and other non-human primates and the forest conditions after the 1982–83 fires and droughts in Kutai National Park, East Kalimantan, Indonesia. In Ismail, G., Mohamed, M., and Omar, S. (eds.), *Forest Biology and Conservation in Borneo*, Yayasan Sabah, Centre for Bornean Studies, Publ. 2, Kota Kinabalu, Sabah, pp. 190–205.
- Swan, R. A., and Warren, K. S. (2000). Health, management, and disease factors affecting orang-utans in a reintroduction centre in Indonesia. Presented at *The Apes: Challenges for the 21st Century*, Chicago, May 10–13.
- Thompson, R. K. R., Boysen, S. T., and Oden, D. L. (1997). Language-naïve chimpanzees (*Pan troglodytes*) judge relations between relations in a conceptual matching-to-sample task. *J. Exp. Psychol.* 23(1): 31–43.
- Tomasello, M., and Call, J. (1997). *Primate Cognition*. Oxford University Press, New York.
- van Schaik, C. P., Deaner, R. O., and Merrill, M. (1999). The conditions for tool use in primates: Implications for the evolution of material culture. *J. Hum. Evol.* 36: 719–741.
- van Schaik, C. P., Fox, E. A., and Sitompul, A. F. (1996). Manufacture and use of tools in wild Sumatran orangutans: Implications for human evolution. *Naturwissenschaften* 83: 186–188.
- Yeager, C. P. (1997). Orangutan rehabilitation in Tanjung Puting National Park, Indonesia. *Conserv. Biol.* 11(3): 802–805.