

The Nature and Evolution of Intelligence in Orangutans (*Pongo pygmaeus*)

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ABSTRACT. Orangutans share many intellectual qualities with African great apes and humans, likely because of their recent common ancestry. They may also show unique intellectual adaptations because of their long evolutionary divergence from the African lineage. This paper assesses orangutan intelligence in light of this evolutionary history. Evidence derives from observations of juvenile ex-captive orangutans reintroduced to free forest life by the Wanariset Orangutan Reintroduction Project, East Kalimantan, Indonesia. The intellectual qualities shared by great apes and humans point to a distinct “great ape” intelligence with hierarchization as a pivotal cognitive mechanism. Evolutionary reconstructions jibe with this view and suggest that technically difficult foods may have been key selection pressures. Orangutans should then show hierarchical intelligence when obtaining difficult foods. Evidence on ex-captive orangutans’ techniques for processing difficult foods concurs. Intellectual qualities distinct to orangutans may owe to arboreal travel pressures; in particular, arboreality may aggravate foraging problems. Evidence confirms that ex-captive orangutans’ techniques for accessing difficult foods located arboreally are intellectually complex—i.e. they show hierarchization. These findings suggest other factors probably important to understanding great ape and orangutan forms of intelligence and their evolutionary origins.

Key Words: Orangutans; Great ape intelligence; Hierarchical intelligence; Great ape evolution; Evolution of intelligence.

INTRODUCTION

Orangutan intelligence is critical to several active debates—the human-nonhuman intellectual boundary, the possibility of a “great ape intelligence” distinguishing great apes from other nonhuman primates, and cognitive differences among great apes. Orangutans are the sole survivors in the Asian lineage of the Hominidae, the clade including great apes and humans that issues from a common ancestor as recently as 16–19 ma (GROVES, 1989; PILBEAM, 1996). As such, they are pivotal to establishing the intellectual qualities shared by the clade. The Asian lineage was the earliest to diverge from the common ancestor and its evolutionary history independent of the African lineage is almost as long as that of the clade itself (e.g. SCHWARTZ, 1988), so orangutan intellect may deviate most strongly from the shared pattern. Knowledge of orangutan intelligence is substantial, but most of it derives from formal tests on captive subjects. Evolutionary perspectives emphasize intelligence as functional, shaped for handling species-typical pressures. Evidence on orangutan intelligence applied spontaneously to problems like those shaping its evolution is essential to establishing both shared and distinct qualities, given differences between spontaneous and elicited performances and the low ecological validity of captive-based findings. This paper attempts to characterize orangutan intelligence in light of both faces of its evolutionary history. The exercise entails five steps—characterizing great ape intelligence, inferring intellectual problems selecting for this commonality and those selecting for orangutan divergence, and assessing orangutan intellect applied to common and distinct problems. Evidence is from spontaneous problem-solving in ex-captive orangutans reintroduced to forest life.

GREAT APE INTELLIGENCE

Much evidence on living great apes points to a suite of intellectual qualities that they share with one another and humans but that distinguish them from other nonhuman primates—a “great ape intelligence” that evolved with the Hominidae, unique in its range, organization, level, and developmental foundations (e.g. BYRNE, 1995; RUSSON et al., 1996; but see TOMASELLO & CALL, 1997).

Great apes’ abilities span an exceptionally broad and flexible range, including causal and logical reasoning, counting, addition, mental maps, insight, imitation, self-awareness, ostension, pretense, role-reversal, teaching, planning, intentional deception, rudiments of mind-reading, and proto-language (RUSSON & BARD, 1996). Some, like arithmetic and proto-language, have little obvious species relevance.

These abilities seem to be organized as interconnected clusters, not isolated units (RUSSON & BARD, 1996). Interconnections include developmental dependencies, co-occurrences, and interactions. Imitation, for instance, seems to be a developmental precursor and prerequisite for self-recognition, pretense, and planning (MITCHELL, 1994; WHITEN, 1996; WHITEN & BYRNE, 1991). Co-occurrences include insight with the causal reasoning that guides tool use (KÖHLER, 1925). Interactions include language abilities enhancing analogical ones (PREMACK, 1984), logical and causal abilities combining to enhance bases for classifying and acting upon the world (e.g. classify items by causal function, identify equivalent items to serve as the same tool: LANGER, 1996; RUSSON, 1996), and imitation assisting tool use acquisition (e.g. RUSSON, in press; TOTH et al., 1993).

The distinctive great ape abilities are complex ones. They have been variously ascribed to *symbolic*, *hierarchical*, or *representational processes* (especially *meta-* and *secondary-representation*) (e.g. GIBSON, 1990, 1993; LANGER, 1993, 1996; MATSUZAWA, 1996; POVINELLI & CANT, 1995; RUSSON et al., 1998; WHITEN & BYRNE, 1991). These terms overlap in meaning; all refer to processes that construct complex cognitions in the form of higher *level* ones. Hierarchization generates complex, higher level cognitions by re-using existing cognitive units to build new cognitive structures. It operates by recursion, applying cognition to cognition rather than just to sensory and motor phenomena. In great apes, as in humans, it likely acts in conjunction with combinatorial processes that allow handling sets of cognitive units concurrently (e.g. GIBSON, 1990, 1993; LANGER, 1996; RUSSON et al., 1998). It integrates such combinations into higher level cognitive units; it can then re-use the higher level units to build further combinations, embedding them as subunits. Within higher level cognition, some work points to secondary representation as great apes’ ceiling (e.g. PARKER, 1996; PREMACK, 1988; WHITEN & BYRNE, 1991). Secondary representations are rudimentary-level hierarchical (symbolic or representational) cognitions, like those found in human children under 3–4 years of age.

Development finds great ape intelligence to the extent that some abilities appear only beyond certain ages or under certain conditions. While true of all primates, it is especially marked in great apes. The complex abilities noted develop only near the transition to juvenility, after 3–4 yr of age; some, like proto-language, develop only under special rearing conditions, like intensive teaching or enculturation (e.g. MILES et al., 1996; PARKER & GIBSON, 1990; TOMASELLO et al., 1993).

Implications of these qualities for models of great ape intelligence are not yet resolved, including what cognitive processes generate it—generalized ones, an aggregate of independent ones, or something in between. This issue is critical given long-standing dispute over the generality versus modularity of human mentality itself, but little debate has yet occurred. TOMASELLO and CALL’s (1997) volume on primate cognition devotes barely 3 of over 500 pages to it;

POVINELLI (1996) opens the issue but offers no resolution. Most researchers to date have assumed the traditional model of nonhuman mentality, an aggregate of special-purpose, isolated cognitive structures (e.g. CHENEY & SEYFARTH, 1990; DAVEY, 1989; HIRSCHFIELD & GELMAN, 1994)—often tacitly, by studying intelligence in terms of single, narrowly-defined abilities (RUSSON & BARD, 1996). Those who have addressed the issue squarely advocate either processes for interconnecting relatively independent abilities, in view of the clusters and linkages found (e.g. MITCHELL, 1994; PARKER, 1996; RUMBAUGH & PATE, 1984a, b; WHITEN, 1996; WHITEN & BYRNE, 1991; TOMASELLO & CALL, 1997, promote this for all primates), or centralized generative processes, in view of the openness of great apes' repertoires to abilities without evident species relevance and the similar levels achieved across their top abilities (e.g. BYRNE, 1997; GIBSON, 1993; LANGER, 1996; POVINELLI & CANT, 1995; RUSSON et al., 1998). Both positions posit overarching or generalized processes capable of building and integrating special purpose abilities.

Hierarchization is a good candidate for one of these generalized processes. It is recognized as essential to many complex abilities (e.g. language, symbolic-level problem-solving, planning: CHOMSKY, 1957; NEWELL et al., 1958; MILLER et al., 1960) and their development (e.g. CASE, 1985; LANGER, 1986; PIAGET, 1954)—abilities found in great apes' repertoire. Hierarchical cognition has been detected in great apes' feral problem-solving, including mountain gorilla food manipulation, chimpanzee and rehabilitant orangutan tool use and object manipulation, and mountain gorilla and rehabilitant orangutan imitation (BYRNE & BYRNE, 1991; BYRNE & RUSSON, in press; LANGER, 1996; MATSUZAWA, 1996; RUSSON & GALDIKAS, 1994). Its contributions to cognition include economy (a relatively small repertoire of basic cognitive units generates a wide range of complex cognitive structures, by combining and recombining them), flexibility (structures are relatively easily modified and corrected) and perhaps most importantly, bringing the cognitive structures that organize complex behavior under voluntary control (BYRNE, 1997; BYRNE & RUSSON, in press; DAWKINS, 1976; GIBSON, 1990, 1993).

THE EVOLUTION OF GREAT APE INTELLIGENCE

Evolutionary pressures that shaped great ape intelligence should point to natural problems in which that intelligence is optimally expressed. These pressures and the cognitive gains they induce are not well established but several proposals have been advanced (for a review, see BYRNE, 1997).

Current candidates as selection pressures are diet, prolonged ontogeny, arboreal travel, and large size. (Social complexity is currently excluded: it correlates with enhanced intelligence in haplorhines and great apes show enhanced social cognition, but great apes do not differ as a group from other haplorhines on social complexity indices: BYRNE, 1997; DUNBAR, 1992). Great apes' *large size*, the extreme for primates, aggravates dietary and arboreal travel problems (BYRNE, 1997). Great apes' *diet* is considered distinct in its reliance on foods that are hard to obtain and prepare for ingestion: embedded foods may have favored abilities specific to extractive foraging problems (e.g. intelligent tool use: PARKER & GIBSON, 1977, 1979) or a broad range of "technically difficult" foods may have favored generalized hierarchization for its greater efficiency and flexibility, affecting cognition overall (BYRNE, 1997). Great apes undergo a *prolonged ontogeny* plausibly linked with extended learning, especially mastering complex feeding skills, and a correspondingly prolonged dependency that could retard maternal reproduction; both pressures could be addressed by enhanced knowledge transfer abilities (e.g. demonstration teaching, imitation: PARKER, 1996; PARKER & GIBSON, 1977, 1979). *Arboreal travel* exacts a high toll due to great apes' large size, requiring enhanced capacities for

managing the self; this may have favored the evolution of generalized representational cognition, which enhances cognition overall (POVINELLI & CANT, 1995). Extant reconstructions recognize these four pressures as interdependent and propose that intellectual bottlenecks resulted from interactions among them—diet with ontogeny (PARKER, 1996; PARKER & GIBSON, 1977, 1979), arboreal travel with size (POVINELLI & CANT, 1995), arboreal travel and diet with size (BYRNE, 1997).

Problems remain. Only arboreal travel and difficult diet models propose cognitive gains that span great apes' ability range. The arboreal travel model dovetails with what may be *the* locomotor adaptation of the Hominidae, suspensory arboreal locomotion, but this adaptation characterizes small hominoids as well (MORBECK & ZIHLMAN, 1988). It is also moot whether early Hominidae faced such arboreal travel pressures; among living great apes, only orangutans travel arboreally and their locomotor adaptations for arboreal travel appear recent (MARTIN & ANDREWS, 1993; MOYÀ-SOLÀ & KÖHLER, 1993; PILBEAM, 1996; TUTTLE & CORTRIGHT, 1988). Further, the large ancestral hominoid that POVINELLI and CANT (1995) suggest to have faced cognitively challenging arboreal travel problems, *Oreopithecus bambolii*, had a relatively small brain (HARRISON, 1989)—not the large one found in modern great apes and entailed in complex problem-solving.

This leaves large size, prolonged ontogeny, and dietary difficulty as a set of interrelated cognitive pressures selecting for cognitive gains, probably generalized gains like hierarchization. Novel implications of this view include: hierarchization is tied to ontogenetic as well as food pressures (i.e. it would have to have become available for the juvenile period) and ontogeny-size interactions may be important.

The prediction for orangutans examined here is that their techniques for processing difficult foods, in juvenile and older individuals, show hierarchical cognition. These techniques are known to be complex (MACKINNON, 1974; RIJKSEN, 1978; RODMAN, 1977) but have not been probed for cognitive information.

METHODS

Subjects were six ex-captive orangutans reintroduced to free life in Sungai Wain Protection Forest, E. Kalimantan, Indonesia, by the Wanariset Reintroduction Project; this forest is devoid of wild orangutans (see Table 1 & Fig. 1). All had access to daily supplemental provisions at two forest sites. They were chosen as regularly locatable (near feeding sites) and experienced (1.5–4.5 yrs' in this forest).

Data on subjects' food processing techniques were collected by event sampling within focal

Table 1. Ex-captive orangutan subjects.

Name	Sex (M/F)	Age ¹⁾ (yr)	Forest experience (years)	Hours observed (N)	Palm leaf food bouts (N)
<i>Charlie</i>	M	10	>4	55	10
<i>Bento</i>	M	7	>3	37.5	18
<i>Enggong</i>	M	6	>2*	61	51
<i>Paul</i>	M	6	1.5	85	36
<i>Aming</i>	M	9	>4	43	7
<i>Imelda</i>	F	8	>4	23	1

¹⁾ Approximate age at start of study (03/96) based on intake and medical records; * *Enggong* had forest experience beyond 2 years in Sungai Wain through a prior rehabilitation program.

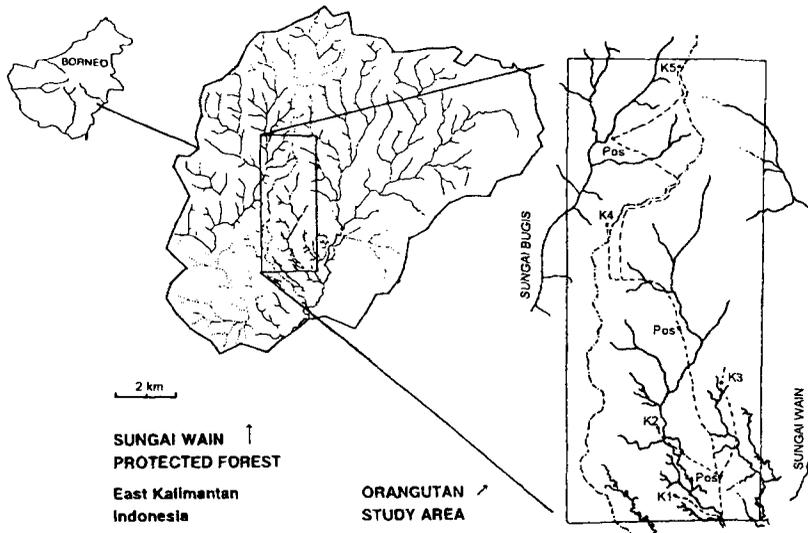


Fig. 1. Orangutan study area, Sungai Wain Protected Forest (East Kalimantan, Indonesia).

individual follows. Each follow aimed to span three successive days; most spanned 08:00–17:00, some covered rising to nesting or half days. The target event was a food bout, the period invested in obtaining one food item. A bout started when I could predict the target food (often, as the orangutan climbed toward its source) and ended when that food was abandoned (the orangutan was finishing eating and leaving the food source). For each bout, I recorded subject name, food item and species, bout onset and offset (to nearest min), height above ground (m), and the technique used to obtain the food. Described for the technique were the subtasks involved in obtaining the food (e.g. enter tree, extract palm leaf), the strategy for each subtask (e.g. extract palm leaf—repeatedly, subdivide leaf then pull out each section), and the actions used to carry out each strategy (e.g. subdivide leaf—separate several leaf lamina into a small section with lips/fingers, bend the section’s tip, bite over bent section tip, pull section). Conditions permitting, I videotaped bouts for more detailed coding.

Empirical criteria exist for hierarchical organization in behavior (e.g. DAWKINS, 1976; MILLER et al., 1960) but hierarchical organization characterizes many behaviors not governed by cognition. For hierarchically organized behavior to signal hierarchical cognition, it must first be established that the target behavior is cognitively governed (e.g. BYRNE & BYRNE, 1993). In humans, simple, voluntary motor actions like reaching or grasping are among the simplest behaviors governed by cognition—the *schemata* or *primary representations* of infant cognition (CASE, 1985; LANGER, 1996; OLSON & CAMPBELL, 1993). Comparative studies suggest this applies to great apes as well (e.g. DORÉ & DUMAS, 1987; LANGER, 1996). Great ape behavior composed of multiple motor actions that also shows hierarchical features then implies hierarchical organization in the governing cognition.

Hierarchical cognition in great apes then entails, minimally, combinations of schemata that generate combinations of motor actions, or behavior complexes. Associative cognition also builds combinations of schemata that generate behavior complexes, however, so the empirical problem includes distinguishing hierarchically from associatively organized behavior. It has been argued that the two organize behavior in distinguishable ways (e.g. DAWKINS, 1976;

LASHLEY, 1951; MILLER et al., 1960; for primates, see LANGER, 1996; VISALBERGHI & LIMONGELLI, 1996); associative processes build behavior complexes by chaining actions sequentially, with actions triggered by local contingencies, whereas hierarchical processes do so by generating higher-level cognitive structures, called routines or programs, that subordinate component actions and direct their scheduling. Several behavioral indices have been identified that mark the key distinction, subordination versus chaining.

Routines, revealed by behavior complexes **iterated to criterion**—re-enacted in their entirety until some predetermined criterion is achieved (BYRNE & BYRNE, 1991; Miller et al., 1960). Iteration of a whole behavior complex implies that individual motor actions operate as part of a larger behavioral unit, not independently. Its iteration to criterion indicates that enactment of the behavioral complex is subordinated to some predetermined condition rather than local contingencies (BRUNER, 1973; DAWKINS, 1976; CASE, 1985).

Subroutines, routines that themselves serve as components of higher-level routines (e.g. CASE, 1985; GREENFIELD, 1991; LANGER, 1996). Subroutines point to hierarchical organization because they likewise reveal subordination of some behavioral structures to others.

Intercoordination, modifications to subroutines that accommodate linkages between them in line with superordinate programs (e.g. CASE, 1985). Such intercoordination shows that subroutines are not isolated units linked serially but units integrated within and subordinated to broader structures: they can be altered in line with considerations *beyond their own bounds, relative to other subroutines and the larger strategy*.

Optional or alternative subroutines, subroutines enacted facultatively or several subroutines used interchangeably (DAWKINS, 1976). Flexibly incorporating, eliminating, or swapping whole subroutines points to governing structures that transcend sequential patterns and cues. These two indices also manifest another characteristic of hierarchically organized behavior, stability at the level of behavioral strategy coupled with variability at the level of behavioral components. Both suggest that the actor is operating with multi-level structures for behavior.

Disruption handling, in the sense of coping with events disturbing the normal flow of action without losing original direction and organization (e.g. BYRNE & RUSSON, in press). In hierarchically organized behavior, the normal flow of action can be interrupted to correct errors or respond to interruptions as they occur, then resumed from the point of disruption; sequentially organized behavior tends to be derailed by such interfering stimuli. Maintaining control of behavior despite misleading contingencies points to cognitive structures that represent overarching behavioral plans as well as local event detail and that can distinguish events that serve high-level plans from those that do not (e.g. PREMACK & DASSER, 1991).

HIERARCHICAL COGNITION IN ORANGUTAN FOOD PROCESSING

I assessed orangutans' food processing techniques for these indices. Reported are preliminary analyses of techniques for obtaining one of their most difficult food items, the meristem of new leaves of a fan-leaf palm, *Borassodendron borneensis* (Fig. 2). *B. borneensis* is a permanent food source to Sungai Wain orangutans; the new leaf's meristem is a preferred food. Each new leaf grows from the palm's heart, in the center of its crown, emerging as a spear-like, tightly closed fan of many lamina. Its meristem is embedded in the heart so obtaining it entails pulling



Fig. 2. *Enggong* entering a wild fan-leaf coconut palm (*Borassodendron borneensis*) by vehicle tree.

the leaf out. Mature palms grow to 7–10 m, however, and their new leaf spear is massive and surrounded by a fence of razor-sharp mature leaf petioles, so obtaining it can entail more than a simple pull. There is little question that orangutans' techniques for obtaining the meristem are cognitively governed: many ex-captives know nothing of the technique when newly released and take years to fully acquire it (PETERS, unpubl.; RUSSON, pers. obs.).

I observed 123 feeding bouts on this food in 306 hr observation, March–July 1996 (Table 1). Descriptive data for some bouts were poorly detailed due to poor visibility, notably when feeding was arboreal. The usual problem was loss of motor action detail (e.g. if a leaf was pulled by mouth, hand, or both) while retaining gross behavior (e.g. the leaf was pulled). This does not invalidate assessments because it weakens data for lower- but not higher-level behavior units. Weaker data still represent cognitively governed behavior and loss of detail induces conservative estimates of hierarchical complexity, because routines could be mistaken for single, unified actions.

I assessed each orangutan's technique separately because hierarchization concerns mental processes within individuals. Detailed analyses are offered for one orangutan, *Enggong*, the most devoted consumer of this food (51 bouts) with others discussed relative to him. Assessments also value one-time behavioral improvisation within stable behavioral structures. Improvisation offers substantial insights into complex cognition because flexibility is a major feature of hierarchical cognition (e.g. POVINELLI & CANT, 1995); stability should hold across performances in high-level structures, but variability in low-level ones.

Figure 3 shows a composite version of *Enggong's* technique for obtaining the new leaf meristem from tall palms, based on all 51 bouts. The left column shows his technique in broad outline; the center column expands on selected subroutines from the left column (those in bold print and boxed) to show their organizational structure; the right column expands on selected subroutines from the center column (those underlined) to illustrate motor action detail. Only selected motor action detail is shown because variation is too extensive to show in full (in one 3-day follow, *Enggong* performed 19 bouts, averaging 12.6 min ($sd=5.56$) of highly variable manipulation each). Components representing behavior complexes serving clear subtasks is shown in *ITALIC CAPITALS*.

Enggong's technique comprised four major behavior complexes, across all 51 bouts: (1)

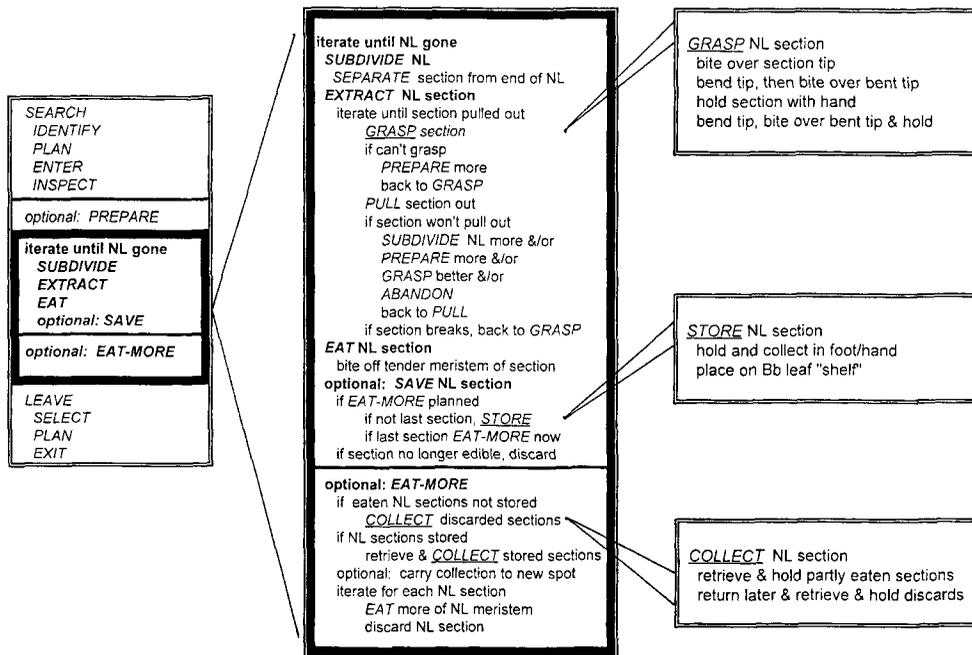


Fig. 3. Food processing technique for *Borassodendron borneensis* (Bb) and new leaf (NL).

SEARCH for a palm with a likely new leaf; (2) *PREPARE* to extract the leaf, (3) *EXTRACT-AND-EAT* the leaf meristem; and (4) *LEAVE* the palm. YAMAKOSHI and SUGIYAMA (1995) reported similar stages in chimpanzee palm-leaf processing. Subroutines were largely, but not totally, dictated by problem constraints. *SEARCH* involved identifying a likely palm, planning a route to its crown, entering, and checking for a desirable new leaf. *PREPARE* entailed varied subsets of making a "workseat" (a place to sit while extracting the new leaf), removing obstacles (e.g. blocking mature leaf petioles or debris). *EXTRACT-AND-EAT* was the most complex package, amalgamating two other behavior complexes, *EXTRACT* new leaf spear and *EAT* meristem, into one broader, integrated one. It involved extracting a small piece of the spear then eating from its meristem, and repeating this sequence until the whole spear was gone (i.e. iterate the sequence—*SUBDIVIDE* spear by separating a few adjacent lamina from one side to make a "section," *EXTRACT* the section, and *EAT* the section's meristem—until the whole spear was removed and eaten). *Enggong* sometimes divided *EAT* the meristem in two stages, like two courses of a meal, in which case he inserted a third, optional subroutine, *SAVE*, between the two stages. After he had *SUBDIVIDED* and *EXTRACTED* each section, he would *EAT* just the most tender parts of its meristem then *SAVE* the remains by storing them at a safe spot. After finishing the first *EAT* and *SAVE* for all sections, he would *COLLECT* his stored remains, then iteratively *EAT-MORE* of each (less tender parts). *LEAVE* involved choosing an exit direction (often continuing his prior travel direction), planning an exit route, and executing the plan.

Bento and *Charlie* used techniques virtually identical to *Enggong's*; *Paul's* differed. *Aming's* and *Imelda's* samples were too small to characterize their techniques. *Paul's* technique was simply grasping then pulling the whole spear, from the ground. It was comparatively primitive (typical of younger/naive vs older/experienced orangutans), narrowly effective (only for short palms with crowns accessible from the ground) and showed little understanding (e.g. he did not subdivide the leaf, which reduces the extraction force needed). Differences probably owed to

his limited forest experience (1.5 years). At the level of subtasks, there were similarities and differences between orangutans; *Charlie* and *Imelda*, for instance, used methods for storing leaf sections that *Enggong* was not observed to use and *Charlie*'s extraction technique was more efficient than *Enggong*'s, probably because of his larger size.

Enggong's technique shows all indices of hierarchical organization. The first three appear at the strategy level so they apply to *Charlie* and *Bento* as well (Fig. 3, center column). Three others appear in motor action detail, so they are more idiosyncratic (Fig. 3, right column).

Iteration to criterion: *Enggong* iterated several behavior complexes to criterion. *EXTRACT* involved repeatedly performing the behavior complex—bend section tip with lips, *GRASP* section (bite over its bent tip), *GRASP* section again (hold lamina with hand), pull section with teeth and hand—until the section came out. *EXTRACT-AND-EAT* involved repeatedly enacting the behavior complex—*SUBDIVIDE* leaf, *EXTRACT* section, *EAT* meristem—until the leaf was completely removed and its meristem eaten. Both *EXTRACT* and *EXTRACT-AND-EAT* then qualify as routines. Other behavior complexes (*GRASP*, *SUBDIVIDE*, *EAT*, *STORE*, *EAT-MORE*) qualify as routines in similar fashion.

Subroutine: Several of *Enggong*'s routines were used as components within other routines, e.g. *GRASP* was used in both *EXTRACT* and *COLLECT*, *EXTRACT* was a component within *EXTRACT-AND-EAT*. This shows his use of subroutine structures.

Optional subroutines: *Enggong* used certain subroutines in some but not all bouts, e.g. *STORE* partly-eaten leaf section, *EAT-MORE* of section's meristem.

Alternative subroutines: *Enggong* had at least two distinct subroutines for *STORING* partly-eaten leaf sections—*COLLECT* and hold sections in hand, or place and secure sections on vegetation "shelf." Other orangutans also used varied *STORE* subroutines but some of their alternatives differed from *Enggong*'s; *Imelda*, for instance, stored sections by draping them over branches.

Intercoordination: In bouts when *Enggong* used *EAT-MORE*, he did not *STORE* his final leaf section after *EATING* it even though he had *STORED* all previous ones. Instead he would *EAT* more meristem of the final section than he had of previous sections, immediately discard it, *COLLECT* the other stored sections, and *EAT-MORE* of them. For the final section only, he integrated *EAT* with *EAT-MORE* by deleting *STORE*. *Charlie* showed this same efficiency. All orangutans might intercoordinate *EAT* or *EAT-MORE* with *LEAVE*, by moving out of a palm while still eating.

Disruption: *Enggong*'s most common error was breaking a section's tip when pulling. He corrected this by *GRASPING* the broken section again, using a variety of motor actions to improve his hold (e.g. hold with hand closer to the leaf base) and/or strengthen the section (e.g. add several more lamina to the section, fold new lamina tips over broken tips, bite over new folded tip), then resumed his pulling. A common interruption was rain; if rain started while *Enggong* was working on a new palm leaf, he might pause his work, *MAKE A RAINHAT*, put it on his head, then pick up his work from the point at which he had paused. Other orangutans handled disruption in similar fashion. *Bento* made the most insightful error correction I observed. A leaf section broke at the tip when he pulled it. His first simply bit the section farther down the lamina then pulled again. The section broke again, so he added a few adjacent

lamina to his original section and bent their tips over the broken ones, making his section thicker and stronger, then bit over the folded tips and pulled again. This thicker section still broke so he let the whole thing go and separated a completely new section—from the untouched, opposite side of the leaf fan.

These indices show hierarchical organization in orangutan food processing techniques, based on the motor actions that are accepted as governed by cognition. It follows that the cognition governing them is hierarchically organized. This evidence of hierarchization was common and easily identified.

ORANGUTANS AS ARBOREAL FORAGING SPECIALISTS

Of pressures distinguishing orangutans from other great apes intellectually, arboreality stands out. POVINELLI and CANT's (1995) arguments on the complexities of arboreal travel for large-bodied primates fit orangutans well, if they are less applicable to other great apes. Evidence on cognition in orangutan arboreality is limited to travel problems like navigation and locomotor techniques; it does show a role for cognition in terms of lower level or highly specific processes, like advanced sensorimotor intelligence and self-concept (BARD, 1993; CHEVALIER-SKOLNIKOFF et al., 1982; POVINELLI & CANT, 1995).

Orangutans' arboreal problems may, however, entail higher level and more generalized cognitive processes and they may extend beyond travel. POVINELLI and CANT's (1995) descriptions of orangutan arboreal travel suggest hierarchical cognition: they describe error correction, behavioral complexes resembling routines, solutions improvised to handle disruptions and errors, and flexible behavioral detail. Arboreal difficulties can plague foraging as well as travel because most orangutan feeding is arboreal—notably, it complicates food access and embedding problems.

Food access problems for arboreal foragers extend beyond the well known fruit-on-flimsy-terminal-branches. Orangutans also eat arboreal parts of plants like lianas and rattans that obtain support from other plants. Their location then depends on the host's as well as their own species' habits, increasing the variability in their distribution. Liana and rattan supports also tend to be flimsy so, for large-bodied foragers, access routes and processing sites tend to be indirect. It is virtually impossible, for instance, for orangutans to access a mature rattan's heart, a preferred food item that grows near the plant's tip, by climbing the rattan itself or by sitting in the rattan while extracting it. Both distribution variability and difficult access increase foraging complexity, and so further tax cognition.

Embedding problems also worsen for arboreal foods because processing requires extraction, which often requires force. For arboreal embedded foods, sites that offer access are not necessarily sites from which extraction force can be applied (CANT, 1987; REMIS, 1995). An important technique that enables applying force terrestrially, anchoring or bracing against a solid substrate, can be unmanageable arboreally. Arboreal extraction likely requires independently creating a more complex set of interrelated force vectors (extracting, counterbalancing, absorbing). Difficulties are further aggravated because several manipulators tend to be occupied supporting the body (e.g. CANT, 1987). In arboreal feeding, CANT's (1987) adult female subjects used at least three limbs to support and anchor their bodies almost 60% of the time and two limbs, 98%—leaving only one limb and the mouth to create the multiple forces needed to extract food. If embeddedness alone is a cognition-enhancing evolutionary pressure in the Hominidae, embeddedness interacting with arboreality should exert pressures for even more complex cognition.

I assessed whether arboreal foraging poses exacting cognitive problems by assessing arboreal foraging techniques for indices of hierarchical cognition. My focus was techniques for handling access rather than embeddedness; all great apes forage arboreally, so arboreal embeddedness is a shared rather than a unique problem, and access problems tie more closely to the arboreal locomotion distinct to orangutans. Data on ex-captive juveniles' food processing provide a basis for assessments because feeding bouts include approaching food items prior to processing, with two important caveats. First, access data are less systematic than food processing data because observation focused on processing; I noticed access problems and began recording the associated techniques about half way through the study. Second, assessments cannot establish whether arboreality affected cognitive evolution in the orangutan lineage through its impact on foraging; they offer, as a first step, indications of whether it is a plausible source of cognition-enhancing pressures.

Enggong's technique for accessing new palm leaves again serves to illustrate. Access problems span two subtasks, *ENTER* and *PREPARE*. Figure 4 is a composite of his technique, like Figure 3 but highlighting his access strategy with its organization and behavioral detail.

Enggong commonly *ENTERED* the palm's crown indirectly. The palm's trunk is encircled with stumps of dead leaf stalks with sharp edges, making it perilous and punishing to climb, so he commonly entered by climbing vegetation adjacent to the palm—a liana, a tree with connecting lateral branches, or a pole-like “vehicle” tree than could be swayed near the palm. *PREPARE* involved a subset of: make a “workseat” from which to extract the new leaf, move obstructing leaf stalks out of the way, and remove debris. *Charlie* and *Bento* shared these strategies; *Paul* showed similar *PREPARE* but not *ENTER* strategies (he did not access tall palms). *Enggong's* technique showed all indices of hierarchization.

Iteration to criterion: *Enggong* and other orangutans use nearby pole-like trees as vehicles to

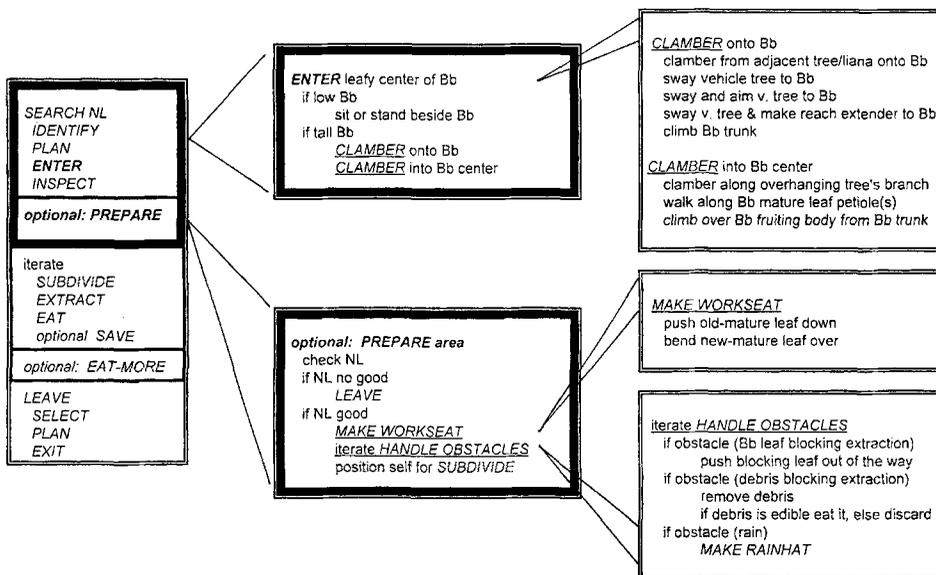


Fig. 4. Search and preparation techniques for *Borassodendron borneensis* (Bb) and new leaf (NL).

enter target trees (e.g. BARD, 1993). For palms, they climb a selected vehicle tree, take a position slightly higher than an accessible entry point to the palm, then *SWAY* the vehicle tree back and forth until they can grab the palm. *SWAY* represents a behavior complex. *Enggong's SWAY* was a variable combination of behavior units, including lean out from the vehicle tree to bend it, "pump" the tree to make it swing back and forth (i.e. as in pumping a swing, dynamically change position, posture, and/or degree of lean to induce and modulate the tree's bending), and remove vegetation restricting the swing. *Enggong* iterated this behavior complex *until* he attained the palm, qualifying his *SWAY* as a routine.

Subroutines: *Enggong* and others also use *SWAY* in play, with the same behavior complex. When they *SWAY* to enter a palm, then, they use the routine as one component of the broader *ENTER* routine—that is, as a subroutine.

Disruptions-errors: A common error in *SWAY*, one *Enggong* and many orangutans make, is not swinging the vehicle tree *toward* the target. They often correct this by pausing their *SWAY* routine (usually the set of pumping actions), fixing the error by pulling on adjacent vegetation to alter the direction of the vehicle tree's swing so that it is better aimed at the target, then resuming *SWAY*. Another of *Enggong's* errors was a poor choice of vehicle tree—one his *SWAY* could not swing far enough to reach the palm. Once, after repeatedly failing with *SWAY*, *Enggong* paused *SWAY* and inserted a whole new behavior complex within it—*MAKE A REACH EXTENDER*. He cracked a branch growing from his vehicle tree's trunk until it dangled loosely, shifted position, then shifted his hold from the trunk to the dangling branch a few cm out from the trunk (thereby leaning closer to the palm). He resumed *SWAY* and tried to reach the palm but failed—his branch was too low. To fix this error, he *MADE A REACH EXTENDER* a second time, from a higher branch. He shifted his hold to the new reach extender, resumed *SWAY*, and succeeded in grabbing the palm on the next swing (Fig. 5).

Optional subroutines: *Enggong's MAKE A REACH EXTENDER* qualifies as routine and subroutine: it comprises a behavior complex, he iterated that behavior complex *until* he had a device that allowed him to seize his target palm (i.e. it is a routine), and he embedded that routine in a broader routine, *ENTER* palm (i.e. it is a subroutine). He used this subroutine optionally. I observed him use it only twice, in a single feeding bout, although it was feasible on numerous other occasions.

Intercoordination: In the same food bout, after using his vehicle tree to enter the palm, *Enggong* retained and re-used it to *MAKE A RAINHAT* (it was raining heavily). *MAKE A RAINHAT* is a well-known orangutan routine. Its behavior complex involves locating a leafy branch, breaking it off, and putting it on the head; this complex is iterated *until* the 'hat' offers protection; alternatively, several branches may be broken in succession, collected together, then put on the head all at once. *Enggong* inserted *MAKE A RAINHAT* as he completed *ENTER*. While clambering to the palm's crown, he retained hold of the vehicle tree; once at the crown he sat, pulled down the vehicle tree's leafy top, and *MADE A RAINHAT* from some of its leafy branches (Figs. 6 & 7). Orangutans normally release vehicle trees as soon as they secure their hold on target trees. Altering *ENTER* by retaining the vehicle tree longer than usual, then using that vehicle tree to *MAKE A RAINHAT*, shows inter-coordination: one subroutine (*ENTER*) was altered to facilitate another (*MAKE A RAINHAT*).

Disruptions—interruption: *MAKE A RAINHAT* can be construed as handling an interruption—



Fig. 5. *Enggong* makes and uses a reach extender to transfer from a vehicle tree into a palm tree.



Fig. 6. *Enggong* clambers into a palm's crown while retaining hold of his vehicle tree.



Fig. 7. *Enggong* makes a rainhat (from his vehicle tree's leafy branches) and then resumes his routine for accessing the palm crown.

heavy rain—that disrupted *Enggong*'s *SEARCH* subroutine for palm hearts. He interrupted his *SEARCH* subroutine just as he reached the palm's crown (end of *ENTER*), inserted a subroutine to handle the interruption (*MAKE A RAINHAT*), then resumed *SEARCH* from the point of interruption (start *INSPECT*).

Alternative subroutines: *Enggong* used alternative subroutines within *PREPARE*, for *MAKING*



Fig. 8. *Enggong* uses an alternative method of making a workseat.

A WORKSEAT. *Enggong* and other experienced orangutans commonly *MAKE A WORKSEAT* on which to sit while extracting the palm's new leaf. The common method all use is to push the petiole of a mature leaf from its normal position, vertical to diagonal, to a horizontal position; they then sit on the base of the horizontally-positioned petiole beside the desired new leaf (as in Fig. 7). This involved a behavior complex: move behind the chosen petiole and move it from the palm center (this rotates the petiole downwards) until it sits diagonally; shift position and move it farther downwards, via diverse actions, until it sits horizontally; walk back to the center of the crown along the repositioned petiole; then sit on it. This complex involves iteration to criterion—repeat (move self then move leaf) until leaf is horizontal, so it qualifies as a routine; its use within *PREPARE* renders it a subroutine. *Enggong* had a second method for *MAKING A WORKSEAT*, one that allowed sitting directly above the new leaf rather than to its side (Fig. 8). He used the second method if the palm had a young leaf just opening its fan, likely because only young petioles are sufficiently flexible. The second method likewise included a behavior complex iterated to criterion: move behind the young leaf, grasp its petiole near the fan, move it inwards across the crown (versus out and away) until it starts to rotate downwards; shift position and move the petiole downwards until it sits horizontally; sit on it above the desired new leaf. The first subroutine is always possible so he used the second by choice—i.e. as an alternative.

As with food processing, orangutans' techniques for accessing arboreal foods readily show up indices of hierarchical cognition.

DISCUSSION

Established views portray nonhuman primate cognition as compartmentalized, claiming the evolution of generalized cognition for the human lineage. Current views and evidence point farther back, to the common great ape/human ancestor, for this evolutionary move. They point to interrelated problems associated with size, foraging, and ontogeny, but not arboreal travel, as critical selection pressures; to cognitive enhancements accruing from centrally reorganizing cognition hierarchically; and to the ontogenetic scheduling of hierarchical cognition to support foraging independence in juveniles. Juvenile rehabilitant orangutans' food processing techniques were then predicted to show indices diagnostic of hierarchical cognition. Arboreal movement appears to entail similarly complex cognition, in orangutans if not other great apes, so juvenile orangutans' techniques for accessing arboreal foods were also predicted to show hierarchical cognition. Evidence is consistent with both predictions. It strengthens support for centralized hierarchization as a key underpinning for great ape cognition; for technically

difficult foods and, in orangutans, foraging-related arboreal movement, as problems eliciting high level cognition; and for juvenility as a developmental period revealing of sophisticated cognition. It also points to a number of further issues.

Possible limits to the generality of findings concern differences between wild and rehabilitant orangutans' techniques. Rehabilitants are ex-captives, orphaned early in life and deprived of the normal input that builds skills—some so naive on return to forest life that they show neither recognition that this palm offer *any* food, let alone its meristem, nor skills for obtaining it. With reduced and delayed experience on which to build these skills and little expert social input from kin, wild orangutans (reintroduction forests harbor none, by law), or fellow rehabilitants (their community, established in 1992, held only five years' knowledge), rehabilitants' skills should be less sophisticated and more idiosyncratic than wild ones'. Whether wild and rehabilitant orangutans *do* differ remains largely unanswerable because wild data are sparse. The palm studied here is endemic to Borneo and eaten by only some populations, e.g. Sengatta (RODMAN, 1977) and Gunung Palung (LEIGHTON & LEIGHTON, 1983) but not Tanjung Puting (GALDIKAS, 1978). The only report of wild orangutans' techniques for obtaining its meristem is for adult males (RODMAN, 1988, pers. comm.). They differ so greatly from juveniles in weight, strength, and ability that differences cannot be attributed to rehabilitant-wild backgrounds. Differences are worth exploring, especially with current interest in social transmission of expertise. For this paper, which aimed to establish whether orangutans express high-level cognition similar to that which other great apes show in their ecological problem-solving, the differences predicted would strengthen findings.

Ontogeny-size interactions warrant investigation. In great apes, this hierarchical cognition emerges around 3–4 yr of age and may continue to develop until 8–10 yr old. My subjects were mostly mid-range juveniles, 6–8 yr old. Taken alone, this suggests older subjects may express yet more complex cognition. However, a second factor enters into play, size. Size (large) has been portrayed as a constant pressure in great ape cognitive evolution but it varies greatly with age. Its impact on arboreal or dietary problems should then vary ontogenetically. In particular, access problems for arboreal foods should worsen for mature (large) but lessen for immature (small) individuals while processing problems should lessen for mature (large, strong) individuals but worsen for immature (small, weak) ones, given the large, tough foods on which great apes rely (JANSON & VAN SCHAİK, 1993). The few existing data suggest this pattern. RODMAN's (pers. comm.) adult males ate only the meristem of palms accessible from the ground or large over-hanging branches whereas my juveniles accessed and ate from virtually any palm; adult males simply ripped the whole new leaf from the palm's crown whereas juveniles used a complex, multi-staged technique that involved subdividing the new leaf into smaller sections their strength could handle. That juvenile great apes are *small* may then be significant for cognition: their small size combined with immature skills, growth needs, and an ecological niche largely determined by adults may converge to induce maximum cognitive difficulty and performance (JANSON & VAN SCHAİK, 1993). Changes in problem-solving from juvenile to adolescent should be especially revealing of this convergence.

These assessments do not show what hierarchical levels or structures operate. Hierarchical cognition covers a broad span of increasingly complex cognitive processes; the empirical indices detect hierarchical organization but not specific levels or structures. For great apes' manual versus tool-assisted food processing techniques, hierarchical levels and structures have not been assessed (BYRNE & RUSSON, in press). The levels operating are predictable from work on other great ape abilities; this points to secondary representation as the level of juvenile functioning (LANGER, 1996; WHITEN & BYRNE, 1991; WHITEN, 1996). Predictability may be limited because the ontogenetic processes that generate great apes' cognition likely induce vari-

ation in hierarchical cognitive structures across individuals, as a function of age and experience. As to structures, hierarchical models do not alter existing views of a suite of relatively independent, special-purpose cognitive structures (e.g. abilities, modules) geared to particular types of problems (e.g. logical, causal). Techniques for obtaining difficult foods probably rely heavily on means-end cognition (i.e. manipulating energy/force relations to induce physical change) so the hierarchical structures used by juvenile orangutans may be secondary-level means-ends ones. Work on human cognitive development suggests that such structures manage operations on simple physical relations, such as removing *barriers*, exploring *inside* or *under* logs, or pulling stems *apart* (see CASE, 1985; LANGER, 1996; PIAGET, 1954; RUSSON & GALDIKAS, 1994). Rehabilitants used such operations in their food processing, but verifying the cognitive structures involved requires closer analysis. Hierarchization adds two main notions to views of great apes' cognitive structures—abilities may be products of generating processes that are hierarchical, and centralized. Broadly, it helps account for the multiple levels at which great apes' abilities may operate, developmental change, generativity, and interconnectedness (e.g. GIBSON, 1993; GREENFIELD, 1991; LANGER, 1996; RUSSON et al., 1998).

Findings also leave obscure what processes account for great apes' full cognitive potential. Hierarchization may be a generalized foundation of a great ape intelligence but great apes' abilities extend beyond the threshold of hierarchical cognition. This makes it likely that the processes supporting their greatest potential are additional ones that build upon hierarchical foundations. Not only do we still need conceptual structures for characterizing these processes, we are by no means certain that we have in hand the evidence of great apes' highest performance that is needed to make assessments.

Finally, this exercise suggests another look at the role of arboreal pressures in the evolution of great ape intelligence. Evidence does not support arboreal *travel* as a cognitive pressure acting on the common great ape ancestor but it does point to arboreal *foraging* for difficult foods. Food is deemed the main reason primates are in the trees and the major influence on their locomotor habits (FLEAGLE, 1984), and all great apes feed arboreally (REMIS, 1995; RODMAN & MCHENRY, 1980). Arboreal versus terrestrial location should aggravate obtaining technically difficult foods, especially embedded ones. Cognitive studies of great apes' food processing have favored terrestrial problems (e.g. BOESCH, 1991; BYRNE & BYRNE, 1991; MATSUZAWA, 1994; but see YAMAKOSHI & SUGIYAMA, 1995; REMIS, 1995). This points to the study of arboreal foraging as an untapped source of valuable data on complex great ape cognition.

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