Acquisition of Complex Foraging Skills in Juvenile and Adolescent Orangutans (*Pongo pygmaeus*): Developmental Influences

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Abstract

Research on primate cognition has spurred interest in developmental influences on skill acquisition, especially complex foraging skills in great apes and specifically as they relate to species' life history strategies. Survival skills are often mastered to functional levels near the onset of juvenility, for instance, this is when immatures are weaned and assume semi-independent lives. Several complications merit consideration: primate learning is lifelong; learners' situations change well beyond weaning; and individual tasks can vary such that they create rich problem spaces, mastering which entails acquiring and coordinating multifaceted skill sets. Accordingly, while skills may reach functional levels by weaning, they may be refined later. Juveniles, adolescents, and young adults, in particular, should generate such refinements given the developmental changes they experience in learning needs and opportunities, physical and cognitive abilities, and sociality. To assess acquisition beyond weaning, this study tracked the acquisition of foraging skills for extracting heart from a tree palm (*Borassodendron borneensis*) in juvenile and adolescent rehabilitant orangutans. Findings represent 744 cases of palm heart extraction, 31 rehabilitants ranging in age from older infants to young adults, and two forests in Indonesian Borneo. Data were collected observationally over 9 y and include partial longitudinal data for 14 rehabilitants. Results highlight the importance of fine-grained assessments of both behavior and problem space in understanding developmental influences on the acquisition of sophisticated foraging skills in great apes. Implications for the study of cetacean cognition are suggested.

Key Words: orangutan, great apes, cognition, foraging, development, learning, skills

Introduction

Research on primate cognition and culture has spurred interest in developmental influences on skill acquisition, especially for complex foraging skills in great apes and as they relate to ontogenetic parameters of their life history strategies (Parker & McKinney, 1999; Russon, 2003; van Noordwijk & van Schaik, 2005). Development is probably a key organizing force for cognition because it sets the pace for age-related changes to learners' needs, cognitive abilities, and learning opportunities (Parker & McKinney, 1999; Russon, 2003; and references therein). Great ape life history strategies point to the onset of juvenility as the point in development when forest skills like foraging and nesting should be functional because this is when immatures are weaned and assume a semi-independent life. In line with this view, orangutans and other great apes have been shown to master functional foraging and nesting skills by about this point in the sense of being effective enough to support semi-independent life (Byrne & Byrne, 1991; Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf et al., 2004; Sousa & Matsuzawa, 2004; van Noordwijk & van Schaik, 2005; Russon et al., in press). Several considerations suggest that for some difficult forest skills, acquisition continues beyond the onset of juvenility. This study tracked the acquisition of a very difficult foraging skill in orangutans—extracting meristem from a tree palm—to explore patterns beyond early juvenility.

Background

There are many reasons to expect the acquisition of foraging skills to extend throughout immaturity in great apes. Learning is known to be lifelong in primates. It has long been considered an important task for juveniles, and parents contribute to juvenile skills in great apes (Boesch, 1993; Parker & McKinney, 1999). Great apes change markedly with age into adulthood (Parker & McKinney, 1999; Russon, 2003; and references therein). Their cognitive capabilities, for instance, continue to develop through juvenility. Puberty, which launches adolescence, brings on dispersal, sexual maturation, and corresponding changes in size, strength, and sociality. Reproduction, the

onset of adulthood, brings further physical and social changes (e.g., altered nutritional needs, parenting, and competition). Major developmental changes like these are likely to generate new learning needs, abilities, and opportunities for foraging through to adulthood.

Second, some of the great apes' foraging problems are extremely difficult. Difficulty is commonly attributed to anti-predator food defenses like embedding matrices, protector ants, spines, toxins, or distasteful exudates. Difficulties extend to within-food variability, however. Nuts that chimpanzees crack, for instance, differ in shape, hardness, and size between species and between nuts within species, so the task of cracking them differs from one nut to the next (Boesch & Boesch-Achermann, 2000; Biro et al., 2003). Difficult foods like these are less like unitary problems and more like rich problem spaces—that is, whole sets of entities, interrelations, and constraints that are germane to solutions. While one hammer-and-anvil technique is used to crack all nuts, it must be flexible enough to handle the particulars of each nut, up to and including changing hammer and anvil materials (e.g., stone, wood).

Third, great apes' techniques for obtaining difficult foods constitute organized and flexible sets of basic skills (McGrew, 1992; Byrne & Byrne, 1993; Russon, 1998; Boesch & Boesch-Achermann, 2000). Acquisition of such techniques is understood to entail a very gradual building process extending over many years (Parker & McKinney, 1999; Langer, 2000; Matsuzawa, 2001). The typical progression suggests both learning and developmental influences: novices first acquire a kit of basic skills (as infants), next combine and organize subsets of them into effective techniques (early juvenility), and thereafter refine their techniques (mostly as juveniles and adolescents) (Inoue-Nakamura & Matsuzawa, 1997; Fox et al., 1999; Boesch & Boesch-Achermann, 2000; Biro et al., 2003; Lonsdorf et al., 2004).

Great apes' foraging situations suggest two implications for the acquisition of their foraging skills. First, techniques for obtaining the most demanding foods may not be fully acquired (i.e., mastered to adult levels) until near adulthood. Chimpanzees' techniques for hammer-and-anvil nut-cracking and cooperative hunting are prime examples (Boesch & Boesch-Achermann, 2000; Biro et al., 2003). While these techniques may reach functional levels by early juvenility, in the sense of being effective enough to support a semi-independent life, they may be refined later. Juveniles and adolescents should be prime agents of refinements given the developmental changes they continue to experience.

Further, difficult foods with marked variability present problem spaces comprised of tasks that may, in some cases, be interrelated or gradable. This is potentially significant because it may suggest avenues for inept novices to tackle foods that seem far beyond their capabilities. Related foods, such as similar foods from closely related species or foods that vary within species (e.g., new vs old leaves, unripe vs ripe vs old fruit), tend to have similar structures so they may present interrelated tasks. The advantage of interrelatedness to acquisition lies in allowing learners to transfer skills already acquired for one task to a novel but related task. Some interrelated foods may be gradable (i.e., some may be easier than others). For some foods, easier tasks may be younger ones (e.g., palm suckers vs trees), but for others, they may be older (e.g., ripe vs unripe Neesia fruits), simplified (e.g., semiprepared by others), or other species (e.g., slender vs robust rattans). The advantage of grading is allowing learners to progress step-by-step, first learning skills for easier tasks and then building upon them for more difficult ones. Wild chimpanzees suggest this in cooperative hunting skills, typically progressing from the easiest to the hardest tasks (Boesch & Boesch-Achermann, 2000).

From this perspective, the empirical record on foraging skill acquisition is weak. There has been little direct study of how foods themselves play into skill acquisition, or on acquisition of foraging skills in juveniles and adolescents—the immatures are most likely to tackle the most difficult food tasks. Available evidence suggests the following patterns.

Great ape learners make use of graded or interrelated food tasks in acquiring foraging skills. Generally, infants focus on the easiest foods or scrounge foods semi-prepared by their mothers; young juveniles focus on weaning foods (i.e., foods that help them shift from maternally assisted to adult foraging); and adolescents may focus on foods found beyond their natal range (Russon, 2003, and references therein). Scrounging simplified foods is especially important in launching skills for foods that are hidden (e.g., embedded), potentially toxic (e.g., leaf-related), or difficult to obtain (e.g., extract) (Whitehead, 1986; King, 1991; Boesch, 1993; Byrne & Byrne, 1993; Fox et al., 1999; Boesch & Boesch-Achermann, 2000; Grundmann, 2006). Individual learning typically follows scrounging, however, because foraging skills involve acting on the physical world (Inoue-Nakamura & Matsuzawa, 1997; Boesch & Boesch-Achermann, 2000; Biro et al., 2003; Marshall-Pescini & Whiten, 2004; Grundmann, 2006). Evidence suggested that grading tasks aids acquisition. After acquiring skills for extracting heart from

one palm species, rehabilitant orangutans acquired similar skills for related species much more quickly (Russon, 2002). In acquiring nut-cracking skills, chimpanzee learners succeed first with scrounged nuts, then the easiest ones, and several years later with harder ones (Boesch & Boesch-Achermann, 2000).

Juveniles may refine their skills in the direction of elaborating them (e.g., for a target food item), enlarging the range of complications they can handle, enhancing their technique's effectiveness, and exploring alternatives (Boesch & Boesch-Achermann, 2000). With the transition to adolescence (i.e., puberty), immatures experience range changes (at dispersal), increasingly sexualized interests, and perhaps a growth spurt (Russon, 2003, and references therein). The resulting altered ranging, shifting social interests and pressures, and increasing nutritional needs suggest they may refine foraging skills for greater efficiency—that is, to obtain a given food item more quickly and/or with less energy expended.

Current Study

To explore these possibilities, this study traced orangutans' acquisition of difficult foraging skills for extracting the meristem (heart) of one palm *Borassodendron borneensis* (locally, bandang) through adolescence. This task occurs in multiple forms, from delicate seedlings to massive adult trees, and it exemplifies a problem space that can be graded from easy to extremely difficult. Bandang heart is important in local orangutan diets as a key fallback food, especially in East Kalimantan (Leighton & Leighton, 1983; Russon, 1998, 2002). Expectations were as follows:

- Immature learners would progress by working through this problem space, from easy to more difficult forms. Palm hearts are hidden (embedded), leaf-related (potentially toxic), and sometimes difficult to extract, so novices were expected to start learning to obtain them socially (scrounging) and then to learn independently later. Early independent attempts were expected to fail because this is a physical task, so solving it requires practice. Bandang development suggests that the first skills mastered would be for younger vs mature plants, which have weaker anti-predator defenses (Jones, 1995).
- Acquisition patterns would suggest developmental scheduling. Learners were expected to master skills for obtaining heart from young bandang as infants because only infant-level cognitive abilities are required, but not for mature bandang because the

behavioral complexities involved (notably, hierarchization) require cognitive abilities that develop post-infancy (Russon, 1998; Parker & McKinney, 1999). Based on the acquisition of other difficult food processing skills in great apes, learners were expected to master bandang heart skills to functional levels by early juvenility. Skills were considered functional when they were effective enough to obtain heart from palms of all sizes.
- Acquisition would continue beyond early juvenility in juveniles and adolescents as age-appropriate refinements. Juveniles were expected to elaborate their skills for obtaining bandang heart, and adolescents were expected to hone them for greater efficiency.

Methods

Subjects

The subjects were 31 ex-captive orangutans (18 males, 13 females) that had been rehabilitated and reintroduced to free forest life by the Orangutan Reintroduction Project at Wanariset (PROW). Almost all ex-captive orangutans were captured from the wild as infants by killing their mothers; most (70 to 80%) are still infants when they reach rehabilitation (Swan & Warren, 2000). Some were captive for several years, but others for only days. Some were human-enculturated, but few compared to the numbers kept in sterile cages or worse conditions. These rehabilitants were studied once they were free-ranging in Bornean forests. Forest-living orangutans lead semi-solitary lives, so subjects were selected in the same fashion as wild orangutans are—those individuals who could be located and followed in the forest became subjects. Subjects ranged in age from older infants to near adults (est. 4 to 14 y, with 0 to 10 y experience in forests abundant in *B. borneensis* palms). Their age at release averaged 5.42 y (SD = 1.93, range 3 to 13). Ages are all estimates, based on dentition at PROW intake; they are reported in 2-y intervals to compensate for estimation errors and variation in developmental rate. Of the 31 subjects, 17 were observed in one year only and 14 over several years (3 for 2 y, 6 for 3 y, 4 for 4 y, and 1 for 8 y). The number of subjects observed at each age group was then 3 to 4 y ($n = 3$), 5 to 6 y ($n = 12$), 7 to 8 y ($n = 15$), 9 to 10 y ($n = 11$), 11 to 12 y ($n = 8$), 13 to 14 y ($n = 4$), and 15 y ($n = 1$).

Settings

Rehabilitant subjects were observed as they ranged in their normal habitat, one of two forest blocks in East Kalimantan (Sungai Wain, Meratus) that PROW used for reintroduction. Sungai Wain is a

protected forest gazetted as ca 9,800 ha of lowland mixed dipterocarp rainforest with extensive swamp areas (Smits et al., 1994). Meratus is a more remote block of partly logged state-protected forest, ca 30 km NW of Sungai Wain, of which ca 28,000 ha of good quality lowland to hill rainforest with some swamp were allocated for orangutan reintroduction. Both forests provide habitat suitable for orangutans and have been devoid of wild orangutans for over 50 y (Russon & Susilo, 1999). For this study, rehabilitants were observed in Sungai Wain from 1995 to 1998 and in Meratus from 1999 to 2003.

Sampling and Data Collection

Sampling—Data were obtained via event sampling within full-day focal individual follows conducted during annual field seasons from 1995 through 2003. The events sampled were bouts—that is, the whole of an orangutan's attempt to extract meristematic tissue (heart, cabbage) from a *B. borneensis* (bandang) palm. Seasonal variation in availability is not important for this food. In both forests, it is available year-round, and orangutans consumed it in all periods sampled.

The Task—Bandang is a fan-leaf tree palm endemic to Borneo. Its meristem is a preferred and a fallback food for rehabilitants in both forests. Obtaining bandang meristem is among the most difficult foraging tasks for these rehabilitants (Russon, 1998). Bandang meristem is apical (i.e., located at the tip of the stem) as it is in all palms. As the plant's only growing point, it is well-defended against would-be predators (Jones, 1995). For orangutans, the task of obtaining palm meristem varies between species. In tree palms with crown shafts, for instance, meristem may be accessible through the side of the shaft. In tree palms like bandang, however, with crowns but no shafts, it may be accessible only from the top, via the leaves growing at the palm's tip. Bandang leaves grow one by one from the meristem, emerging as unfurled spears up through the center of the crown, so extracting the new leaf gives access to the meristem.

Bandang development also alters the task of obtaining bandang meristem. Bandang develop initially on the forest floor, from slender suckers shaped like small rosettes to increasingly robust rosettes. Once rosettes produce adult-sized leaves, they begin to develop trunks and ultimately mature into trees 15 to 20 m tall with massive crowns. The new leaves change in size from slender grass-like shoots (small rosettes) to sturdy spears as thick as a women's wrist (robust rosettes and trees). Meristem defenses also change, from a light stem sheath at ground level (suckers) to a crown of ca 50 giant leaves with razor-sharp petioles that surround the tip of the trunk (trees).

Data Collection—Most bandang heart bouts were coded in the field; ca 20% (clearly visible) were videotaped for detailed coding. Coders were the author and trained field assistants. Observers coded each bout (i.e., each attempt to obtain heart from one bandang palm) for the technique used. A technique refers to an organized set of several basic or component skills; each technique was coded in terms of the skill components used.

Repertoires of techniques and skill components used to obtain bandang heart were identified during early observations of the rehabilitants (Table 1; see Russon, 1998, for details). Briefly, rehabilitants used one overarching approach to obtain bandang meristem—pull the new leaf upwards, out of its socket, as it emerges up through the center of the crown. With care, the spear can be extracted with some meristematic tissue adhering to its base (pulled too roughly, it snaps above the meristem). Meristematic tissue is then simply bitten off the base of the spear. Techniques differed, however, for small vs robust bandang. They used a basic technique for small to mid-sized rosettes—simply grab the whole new leaf spear and pull it out all at once. They used a mature technique for robust rosettes and trees—essential steps are to subsection a few laminae from the spear, pull out the section, eat meristem from the section's base, and then repeat this set of steps until the spear is exhausted. Alternative or optional operations beyond these essential ones might be used depending on circumstances.

Coded for each bout were orangutan ID, date, start and end times, palm size (small/large rosette, tree), skill components used, outcome, and number of sections pulled to extract the new spear. Enactment details (e.g., motor details, performance variation, flow of behavior, noteworthy features) and novel patterns were recorded as descriptive field notes. Outcome was coded as success small/robust palm (eat heart extracted independently from a small/robust palm), scrounge (eat heart another orangutan obtained), or try-fail (try to extract heart independently but leave without eating heart). Success was distinguished for small vs robust bandang because this size difference corresponded to a skill difference (basic vs mature technique).

Results

Results represent 744 cases of bandang heart extraction over 9 y. Data include partial longitudinal data on 14 orangutans. Only full bouts were analyzed (i.e., an orangutan's complete attempt to extract meristematic tissue); bouts that terminated because of conspecific or other interference were dropped as incomplete attempts. Statistical

Table 1. Skill components coded in attempts to extract bandang heart

Skill component	Definition
Check new spear	Manipulate a bandang new leaf spear for 2 to 3 seconds (typically, lightly finger or mouth laminae tips) then leave, making no attempt to extract it.
Move obstructions	Force central petioles that are obstructing the work zone away from the center of the palm (push, pull, or stand on them).
Make workseat	Bend a petiole to a horizontal position so that it lies beside or above the new shoot. The orangutan then sits on it while extracting the shoot.
Subsection spear	Separate a few laminae from the tip of a new shoot, by hand/fingers or mouth, then manipulate these laminae as a unit (section).
Bend section tip	Holding a section, bend the tip of its laminae double, then bite or hold the section over its doubled tip (strengthens against snapping).
Consecutive pulls	Pull several sections in a row, not eating heart from any between pulls (more common is biting heart from each section when it is pulled).
Self-correct errors	Spontaneously self-correct behavior "online" to achieve predefined criteria when the current performance failed to do so (i.e., when failure occurred, then resume). Examples: pull section so hard that it snaps—correct by bending the broken section tip over for more strength; make a section too large to pull out (too many laminae)—correct by removing some laminae from the section.
Store section remains	Deliberately "park" sections/section remains on a support (e.g., nearby petiole, branch, log) for later retrieval, instead of discarding them.
Collect sections	Retrieve, in a bunch, several sections previously discarded or stored.
Re-eat sections in palm	While still in the palm, retrieve one/multiple section remains and eat more heart tissue from their base.
Re-eat sections after leaving palm	After having left the palm, retrieve one/multiple section remains and eat more heart tissue from the base.

analyses of categorical data used logistic models (see individual analyses for details). Developmental periods were defined by the biological events that mark transitions; approximate age ranges were taken from published research on development in wild Bornean orangutans (Table 2).

Acquisition Sequence
My best estimate of an orangutan's progress in acquiring functional bandang heart skills was the date on which I first observed each landmark outcome. The rank order of each landmark's date of first observation then estimates an orangutan's acquisition sequence. Days which produced no attempts to obtain bandang heart were coded as

no try. Of the 31 subjects, 26 ate bandang heart at least once, by whatever means. Four subjects (3 male, 1 female) provided enough longitudinal data to test the order quantitatively. The order of achieving landmarks was predicted as no try, scrounge, try-fail, success-small palm (small rosette), and success-robust palm (large rosettes, trees). A non-linear mixed effects (exponential) model fitted to rank data showed that the order in which skills advanced was common across these four subjects and consistent with this prediction ($p < 0.001$).

I explored the range of acquisition patterns in all 26 orangutans. Data indicated no additional landmarks; they suggested other orders for only 3

Table 2. Developmental periods in orangutans

Period	Definition	Age range [3, 5, 6]
Infant	Pre-weaned immature too young to survive independently [1]	0-4/5
Juvenile	Pre-pubertal immature who can survive losing adult caregivers[1]	4/5-7/8
Adolescent	Post-pubertal immature not yet fertile [2, 7]	7/8-10/15
Sub-adult (male)	Post-adolescent male lacking adult secondary sexual characteristics (SSCs) but otherwise sexually mature[4, 7]	9/11-??
Adult	Reproductively mature females at first birth and males with SSCs and adult reproductive roles[7]	11/20-40+

Sources: [1]Pereira, 1993; [2]Pereira & Altmann, 1985; [3]Galdikas, 1995; [4]Utami, 2000; [5]Rijksen, 1978; [6]Watts, 1985; [7]van Schaik & van Hooff, 1996

of the 26 subjects. For two subjects, scrounging occurred later in the sequence. For one of them, the time lag between the first observed scrounging and other landmarks was two years; this subject was followed rarely in the earlier year, so this pattern is probably a sampling artifact. For the second subject, the same time lag was just over two weeks; this difference is negligible and suggests sampling limitations. For the third subject, all landmarks except no try were observed in the reverse order to that predicted. Time lags differed by at least a year for all these landmarks, and this subject was followed rarely in all years, so these differences too are probably sampling artifacts. The overwhelming pattern was a very consistent order of acquisition.

Developmental Scheduling

Progress from small to robust palms involved a change in technique from basic to mature. The youngest subjects to master the basic technique (succeed with small palms) were ca 4 y old; the youngest to master the mature technique (succeed with robust palms) were 5 to 6 y old. This is consistent with the prediction that developing from infant to juvenile would afford this progress because the hierarchical cognition needed for the mature technique does not develop until juvenility.

Some additional evidence suggests this age difference may reflect development more than experience. For juveniles and adolescents, advancing from the basic to the mature technique appeared rapid. Based on first observed success, the lag between mastering basic and mature techniques was 2 to 47 d for 8 of the 10 subjects observed using both (lags for the final 2 of the 10 were 2 to 3 y, so they most likely reflect sampling limitations). Grundmann (2006) found similarly rapid progress, 1 mo, in an adolescent female. The only 4-y-old to master the basic technique was not observed to master the mature technique within a similar period of time. The only juvenile with both techniques at 5 y old had neither technique at 4 y old, although he already scrounged bandang heart at 4 y old. This sample included only three infants; all were older (ca 4 y old), and only two of the three tried to obtain bandang heart, so these patterns are suggestive at best.

I considered bandang heart skills functional when they enabled the orangutan to obtain heart from any bandang palm. I equated this with mastering the mature technique because this allowed even small orangutans to extract spears from adult palms. The youngest to achieve functional skills in this sense were 5 to 6 y old—as predicted, young juveniles.

Acquisition in Juveniles and Adolescents

Analyses tested for changes in both the skill components incorporated into the techniques used and the relative frequency of different techniques beyond early juvenility.

Quantitative Changes—Figure 1 shows the distribution of outcomes at all age levels observed. Failure rates and success rates on small rosettes leveled off beyond the early juvenile period (6 y). Success rates on robust palms (large rosettes, trees) increased monotonically through adolescence (to 14 y), and scrounging rates decreased monotonically from their peak early in juvenility (5 to 6 y) through adolescence (to 14 y). The sharp and continuous drop in scrounging levels is significantly related to age ($p < 0.0008$; logistic, generalized linear mixed model).

I also assessed age-related changes in the number of sections pulled to extract an entire new leaf, using only the hardest cases (tree palms) and bouts that resulted in complete extraction (i.e., no interruption). A logistic linear regression model (log [age] x sex on section) was used to test for effects of age and sex on number of sections. Results were significant for both factors. Number of sections pulled decreased with age regardless of sex ($t = -1.156$, $p < 0.0000$), but males uniformly used fewer sections than females ($t = -3.06$, $p = 0.0026$). Averages at 6 vs 12 y were ca 7 vs 3 sections for males and ca 9 vs 5.5 sections for females. Both age and sex differences probably reflect size and strength differences.

Both analyses show quantitative change in skills through adolescence, with some sex differences. Success levels but not sectioning efficiency appeared to level off with approaching adulthood. At 14 y old, males were using, on average, 3 sections per palm.

Qualitative Changes—Further acquisition beyond early juvenility was also predicted in the form of refinements to functional skills, with juveniles and adolescents emphasizing elaborations and efficiencies, respectively. From the skill components identified, several were chosen as exemplifying three categories: (1) essentials, (2) elaborations, and (3) efficiencies (Table 3). Essentials were components necessary to an effective mature technique. Elaborations were components that extended the mature technique by adding options, exploring alternatives, or increasing the amount of heart consumed. Efficiencies were components that increased the speed of processing or reduced energy expenditures.

Age effects on these categories were tested by generalized linear mixed logistic models with multivariate normal random effects. Individual curves were fit for each category. Sex and age by sex effects were significant for each category, so individual curves were also fit for males vs
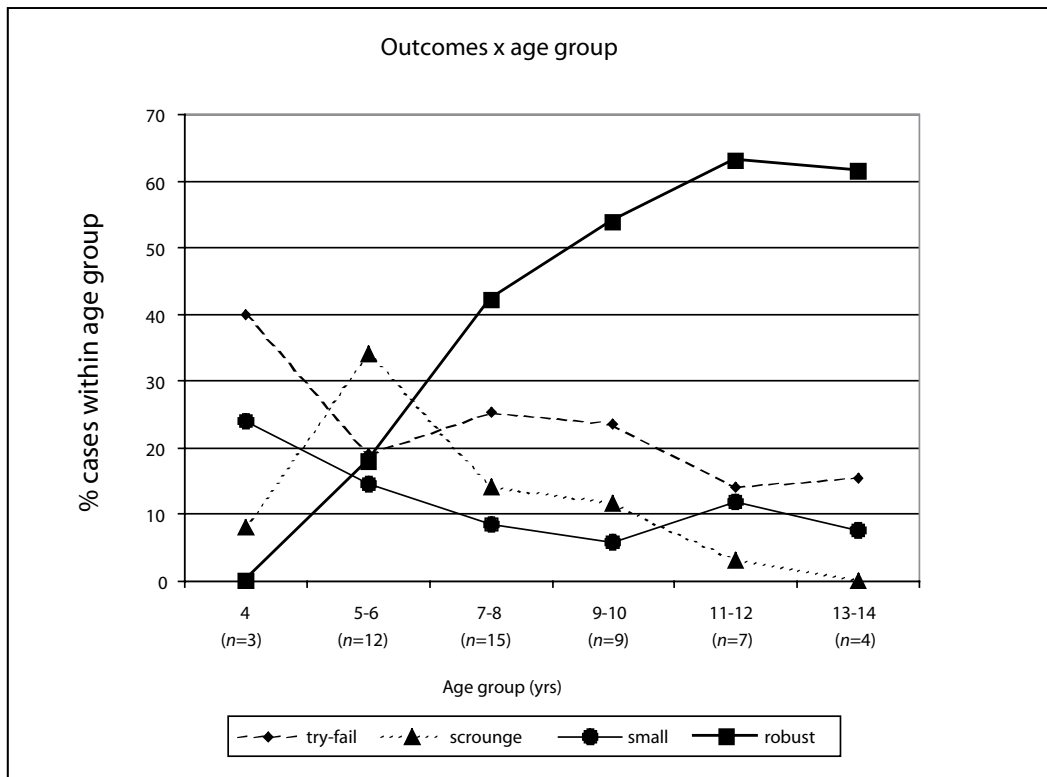
Figure 1. Change in outcome pattern with age; values plotted are the percentage of bouts with each outcome, calculated within each age group. Scrounge: actor successfully obtained heart by scrounging (all palms); try-fail: actor tried to obtain heart but did not succeed; small/large: actor successfully obtained heart from small/ large palms by independent efforts; no try: not shown, as it was not relevant to older immatures.

Table 3. Bandang heart skill components classified as essentials (functional), elaborations, and efficiencies

Class	Description	Components included
Essentials	Components essential to successful execution of the mature technique (i.e., applicable to all palms)	Subsection spear Bend section tip Self-correct errors
Elaborations	Components that expand the range, flexibility, or effectiveness of techniques	Move obstructions Make workseat Store section remains Collect sections
Efficiencies	Components that improve net food intake (e.g., increase extraction speed, reduce unnecessary features)	Extract whole spear in fewer sections Consecutive pulls

females. All curves were overlaid (Figure 2) to assess their relationship.

The main pattern evident in Figure 2 is that these three categories were introduced in the order of essentials, elaborations, and efficiencies. Figure 2 shows the youngest orangutans (young juveniles < 6 y old), male and female, as using essential skills almost exclusively. Older juveniles (6 to 8 y old), both male and female, added elaborations, and a few males were beginning to add efficiencies. Adolescents (> 8 y), both male and female, were the main users of efficiencies. Females and males showed different age trends. In females, the probability of using all three skill categories increased continually with age; for males, it first increased, then it peaked on all three categories ca 10 y of age, and then dropped. The drop in skill refinement in males may reflect a sampling artifact, however; few males were observed at 14 y of age, and they were observed infrequently.
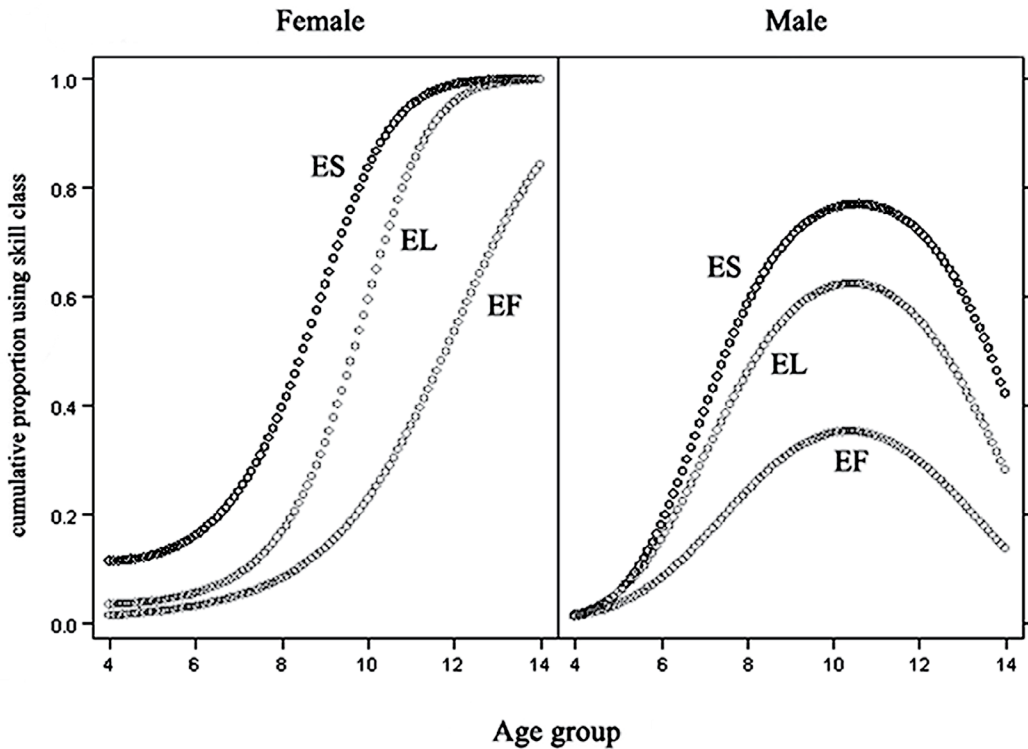
Figure 2. Relationship between skill component classes (essentials, elaborations, and efficiencies), age, and sex; ES = essentials, EL = elaborations, and EF = efficiencies.

These analyses are consistent with expectations that the acquisition of bandang heart skills would continue beyond early juvenility and that the kinds of refinements made to already functional skills by older immatures would suggest a developmental progression shaped by the kinds of changes they undergo.

Discussion and Conclusions

These findings support views that the acquisition of some difficult foraging skills may be paced by development in great apes in the sense of a variously constraining and enabling progress. As in wild great apes, these rehabilitant orangutans mastered these foraging skills to functional levels by early juvenility. Other studies of rehabilitants have reported similar findings (Peters, 1995). Advancing from basic to mature techniques was also consistent with cognitive development, which enables the necessary cognitive abilities around this point.

In these rehabilitants, mastering bandang heart skills to functional levels also involved working through a graded problem space, from easier to more difficult instances of the task. Novices started by scrounging; then tackled small, easy palms; and finally advanced to larger, more difficult palms.

Grundmann (2006) described an adolescent female progressing through the same sequence. Both expert orangutan assistance and variation in the food itself helped novices find easy places to start their learning and then to increment their progress. In this context, findings concerning scrounging are noteworthy. Scrounging has been shown to give young novices access to foods beyond their own foraging abilities, and it is correspondingly common in young learners; it subsequently drops off, however, as independent skills are mastered (Boesch & Boesch-Achermann, 2000; Grundmann, 2006). Changes over time found here in the rates of scrounging and mature technique success (i.e., scrounging rates peaked early then fell off as mature technique success improved) are very similar to those reported. Far from undermining learning, scrounging seems to strongly support it.

These findings also support the view that major developmental changes continue to affect foraging beyond weaning, so acquisition of foraging skills should continue as well, and advances may be constrained or guided by the changes linked with each developmental period. This study tracked orangutans until near adulthood and found evidence of acquisition continuing throughout. Some trends suggested the leveling off of age-related

change by late adolescence, but others did not. As one example, the oldest males studied here, near adults, extracted robust bandang spears in three or more sections; wild adult males can do so in one (Rodman, pers. comm.), so these near adults were likely to continue increasing efficiency as they entered adulthood. Further, qualities predicted to characterize juveniles' vs adolescents' skill refinements, based on physical and social changes linked with these developmental phases, were found in these rehabilitants (i.e., efficiencies vs elaborations). Note that these analyses focused only on refinements expected in juveniles and adolescents; further refinements could be introduced later, but were not explored in this study.

The finding that males and females differed in their developmental progression is consistent with male-female differences in strength and behavioral orientation. Male orangutans tend to be stronger than females because they are larger—even as immatures and especially after puberty, which generates a growth spurt in males (see Russon, 2003, and references therein). Greater strength gives males an advantage with bandang heart because it allows greater success and speed in extracting spears. Males may focus on socio-sexual more than ecological concerns, especially post-puberty, so they may be less invested in refining foraging skills (Boesch & Boesch-Achermann, 2000). The drop in male skill refinement later in adolescence that was suggested by these rehabilitant data may reflect a sampling artifact, but it is also consistent with different approaches to foraging by males and females.

Findings also suggest skill acquisition at two levels: (1) skill components (basic skills, e.g., subsection, move obstructions, make workseat) and (2) techniques (organized sets of skill components, e.g., subsection then pull sections, iteratively). This recalls characteristic patterns of chimpanzee tool use. Chimpanzees are said to use both a tool kit, the complete repertoire of tools that an individual can use, and tool sets, subsets of tools assembled to handle different tasks. The notion of a tool set implies programs that organize a set of skill components into a technique. The orangutan skills studied here concerned manual rather than tool skills, but they likewise suggest a skill kit, the complete repertoire of skill components, and skill sets, subsets of skill components combined into a technique. Acquisition at both skill and technique levels showed developmental influences. Several authors have shown that great apes' manual and tool techniques reach similar levels of cognitive complexity (Byrne & Russon, 1998; Russon, 1998; Stokes & Byrne, 2001). This suggests that it is not tools per se that are associated with sophisticated foraging techniques. Non-tool-assisted techniques can be equally sophisticated and suggest similar acquisition trajectories.

These findings on orangutans' acquisition of foraging skills, while they concern only one food posing one particular configuration of challenges and atypical orangutans, show patterns that closely resemble those reviewed earlier in wild great apes. Rehabilitants similarly mastered functional level foraging skills early in the juvenile period, followed similar trends through adolescence, and took similar approaches to advancing their skills. Interesting is that some developmental influences appear to be robust enough to withstand and recover from the sorts of disruptions to social and physical rearing that rehabilitants represent. To that extent, these findings may contribute to understanding the acquisition of complex skills in orangutans and other species with similar life histories. The value of the notion of a problem space may lie in what it suggests about acquisition patterns in long-lived, large-brained species that face difficult survival problems. It suggests an approach to identifying where to penetrate a difficult problem space, building skills to tackle discrete task features, organizing sets of skills into techniques, working from easier to harder on both skill and technique levels, and handling difficult tasks in the problem space relative to current skills and task demands (i.e., assessing whether a particular instance can be tackled and, if so, assembling and organizing the set of skills to address it).

Cetacean and great ape habitats and foraging are worlds apart, and the two taxonomic groups are genealogically distant. Cetacean species are known for their intelligence (e.g., bottlenose dolphins and killer whales) and share important features with great apes that were linked with the patterns discussed here. These include high intelligence, large brains, high encephalization, long life histories, lengthy development (physical, cognitive, social), difficult foraging problems, sophisticated foraging skills, tool use, and complex social lives (Connor et al., 1992; Mann et al., 2000; Reiss & Marino, 2001; Rendell & Whitehead, 2001; Marino, 2002; Krutzen et al., 2005). Some of the broader patterns discussed here may then be relevant to understanding their cognition—for example, cognitive capabilities change substantially as a function of development, some difficult problems constitute rich problem spaces rather than unified tasks, behavioral expertise is acquired by progressively building from basic to sophisticated skills, behavioral expertise may be organized in terms of skill kits and sets, learners (and perhaps teachers) may select tasks within a problem space according to learners' current abilities and limitations, acquisition of behavioral expertise may combine social with individual learning, and acquisition of

difficult skills may extend beyond early juvenility. In foraging, for instance, chimpanzees' cooperative hunting for large vertebrate prey may have parallels in cetaceans. It entails sophisticated knowledge of other species, complementary roles, and coordinating actions with hunting team members (Boesch & Boesch-Achermann, 2000). Given the similarities already reported in cetacean and great ape cognition, other avenues of potential similarity may be worth exploring.

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