

Orangutan leaf-carrying for nest-building: Toward unraveling cultural processes

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Abstract We report an empirical study on leaf-carrying, a newly discovered nest-building technique that involves collecting nest materials before reaching the nest site. We assessed whether leaf-carrying by rehabilitant orangutans on Kaja Island, Central Kalimantan, owes to cultural influences. Findings derive from ca 600 h observational data on nesting skills and nesting associations in Kaja's 42 resident rehabilitants, which yielded 355 nests and 125 leaf-carrying cases by 34 rehabilitants. Regional contrasts with 14 other communities (7 rehabilitant, 7 wild) indicated cultural influences on leaf-carrying on Kaja. Association data showed exceptional social learning opportunities for leaf-carrying on Kaja, with residents taking differential advantage of these opportunities as a function of development, experience, and social position. Juvenile males with basic nesting skills were most influenced by social input. Most (27) leaf-carriers had probably learned leaf-carrying when caged and 7 probably learned it on Kaja. Social priming was probably the main impetus to leaf-carrying on Kaja, by simply prompting observers to copy *when* leaf-carrying associates collected nesting materials, *what* they collected, and *where* they used their collected materials. Implications concern acquisition processes and ontogenetic schedules that orchestrate sets of features—needs or interests, cognitive abilities, social preferences—which enable cultural transmission.

Keywords Orangutans · Cultures · Nesting

Introduction

Orangutans and chimpanzees are the only two great apes widely accepted as sustaining rudimentary cultures in the wild (Whiten et al. 1999; van Schaik et al. 2003). Orangutans generate cultures of similar complexity but under strikingly different conditions of highly dispersed social life. An important question is how they do so, especially how they achieve group-wide spread under semisolitary conditions. Nesting offers a good context for exploring this question. Nests support considerable social activity, e.g., resting together, play, sex, and grooming, and nesting practices represent 5/19 probable cultural variants (van Schaik et al. 2003). Leaf-carrying, defined by the collection of nest materials *before* reaching the nest site instead of *afterward*, is a newly identified variant of orangutan nest-building that resembles cultural variants in being widespread at some sites but unknown or rare at others. We conducted an observational study to assess if leaf-carrying is a cultural product in a community where it is especially widespread and to reconstruct how this community achieved its group-wide spread.

Theoretical background

Orangutans, like other great apes, normally use a standard sequence of operations to build nests: Select a site (location, tree species, position in tree), build a foundation (bend, break, and interweave side branches crosswise), make a rim (bend the smaller twigs in a circular pattern), then make a lining (pick and add leafy branches, usually within reach of the nest) (Fruth and Hohmann 1996; Ancrenaz et al. 2004).

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Orangutans also re-use old nests, typically after rebuilding them by refreshing the lining with new leaves (MacKinnon 1974; Fruth and Hohmann 1996). In both cases, orangutans may collect lining materials up to 30 m away from their nest, but they leave the nest to do so *after* building or checking the foundation (MacKinnon 1974; Rijksen 1978). Collecting nest materials in *advance*, i.e., leaf-carrying, has not been reported.

To explore cultural facets of leaf-carrying, we adopted the definition of cultures as systems of collectively shared learned practices, or traditions, that are relatively enduring and depend in part on sharing group-wide (e.g., Fragaszy and Perry 2003a). We accepted practices shared for several months, following some recent trends, although interest has often been limited to practices shared across generations (Fragaszy and Perry 2003b and references therein).

The basis for group-level spread is socially biased learning (hereafter, social learning) plus networks that enable sharing through the group. For convenience, we refer to their effective combination as cultural processes. Social learning alone requires the right mix of learning needs, abilities, and socially tolerant experts (Coussi-Korbel and Fragaszy 1995; Russon 2003b; van Schaik, Preuschoft, and Watts 2004). Group-level sharing requires tolerance networks that allow broad-reaching horizontal or oblique information flow in addition to inter-generational vertical flow (van Schaik and Knott 2001). To support traditions, all these processes must mesh. Infant great apes, e.g., master only basic elements of much adult expertise despite excellent social learning oppor-

tunities with their mothers because they do not yet need it and their abilities are not yet adequate (e.g., Inoue-Nakamura and Matsuzawa 1997).

Ontogeny is probably a key organizing force in cultural processes because it sets the pace for developmental changes that alter learners' needs, abilities, and social learning opportunities (Russon 2003b and references therein). Learning needs and social learning opportunities change from infant to juvenile to adolescent, e.g., with weaning, waning maternal tolerance, then puberty. Abilities also change; cognitive abilities, e.g., continue to develop through juvenility in great apes (Parker and McKinney 1999). Orangutans, sociable as immatures and even gregarious as adolescents, turn more solitary as adults (Russon 2003b; Wich et al. 2004; van Noordwijk and van Schaik 2005). Changing combinations of these features generated by species-specific ontogenetic changes are probably what enable and disable orangutan cultural processes.

Ontogenetic patterns in orangutan nesting suggest when nesting practices may spread widely (Table 1). Functional nest-building skills are normally mastered by late infancy, when association is almost exclusively with the mother. Size, cognition, and safety needs continue to change beyond infancy so nesting skills probably continue to be refined into adulthood (MacKinnon 1974; Horr 1977; Rijksen 1978; Sugardjito 1983). It is mostly juveniles and adolescents that share nests with nonkin, join parties, and interact; as adults, associations become infrequent and transient. These patterns suggest that orangutans are best geared to acquire nesting skills as infants and juveniles (Bernstein 1962,

Table 1 Development of orangutan nest-building

Stage	Wild orangutans			Rehabilitant orangutans		
	Age	Nesting skills	Associates	Age	Nesting skills	Associates
Infant	< 1	Share mother's nest	M(O) ^{3,6} ; S(R) ¹	?	No nest use ^{12,13}	P(O)
	1–1.5	Add to lining of mother's nest ³		?	Re-use old nests ^{12,13}	
	1–2	Build small roundish platform ⁴		?	Add to lining of others'/old nest ^{11,12,13}	
	2.5–3	Build complete nest ⁴		?	Build simple "ground nest", cage	
	3–4	Build functional nest (assisted) ^{3,5,6}		1.5 +	Build small roundish platform ^{4,11}	
Juv.	5–8	Build and use own nest (assisted) ^{3,9}	M, P(S) ^{3,7,8,9,10}	2 +	Build and use complete nest ¹¹	P, NK(O)
Adol. Subad.	8–15 +	Nest independently (refined) ^{8,9}	P(O); C, NK(S) ^{1,2,7,10}	?	Nest independently (refined) ¹⁴	P(O); C(S)
Adult	15 +	Nest independently (refined) ^{8,9}	C(R), O(O) ²			C(R); O(O)

Note. Associates (nesting): M, mother; S, sibling; P, peer; O, offspring; C, consort; NK, other non-kin. *frequency*: O, often (daily); S, sometimes, R, rare. *Skills*: complete (foundation-rim, lining), functional (foundation, rim, lining; used overnight), assisted (functional, built near associate minutes later, i.e., time-assisted and site-assisted); refined (avoid windy sites, locate/build for heavier body/dependent offspring). *Age*: in rehabilitants, opportunity-dependent (shown: youngest age reported, ?? if not specified). *Sources*: *Wild orangutans*: 1, Russon 2003b; 2, van Schaik and van Hooft 1996; 3, van Noordwijk and van Schaik 2005; 4, Rijksen 1978; 5, Fruth and Hohmann 1996; 6, Tuttle 1986; 7, Anderson 2000; 8, Horr 1977; 9, MacKinnon 1974; 10, Sugardjito, te Boekhorst and van Hooft 1987, *Rehabilitants*: 11, Harrison 1960; 12, Peters 1995; 13, Sitaparasti personal communication; 14, Russon personal observation.

1967; Rijksen 1978; Galdikas 1982) and best positioned for horizontal/oblique social transmission as juveniles and adolescents.

Rehabilitant orangutans, ex-captives under rehabilitation to forest life, may offer useful insights into developmental influences on horizontal and oblique social transmission. Virtually all were wild-born and orphaned at capture, although captive experiences vary widely (e.g., age, duration, conditions). Their acquisition of forest skills is thus delayed, deprived of full maternal support, and affected by what was learned before capture, during captivity, and in rehabilitation. Nesting skills are no exception: some ex-captives arrive as competent nest builders; others do not even try (Rijksen 1978; Peters 1995). Nonetheless, given appropriate opportunities, infant and juvenile rehabilitants acquire typical nest-building skills much as wild orangutans do: they master making linings first and more difficult skills later (see Table 1). Prolonged delays can interfere; adolescent and subadult male rehabilitants have shown more difficulty learning nesting skills socially than infants and juveniles, despite their sociability and mature abilities (Rijksen 1978; Galdikas 1982). Important for horizontal and oblique social transmission is that most ex-captives reach rehabilitation as older infants or young juveniles, where they are cared for in conspecific groups (Smits et al. 1994; Swan and Warren 2000; Russon 2002), so immature peers and other non-kin are their main companions.

Current study

Aims of this study were to assess cultural influences on leaf-carrying in the rehabilitant community on Kaja Island, Central Kalimantan, where it is exceptionally

widespread, and to analyze how it spread throughout the community. We expected to find leaf-carrying acquired more readily by juveniles than by older rehabilitants and to find evidence of social influences in leaf-carrying.

Methods

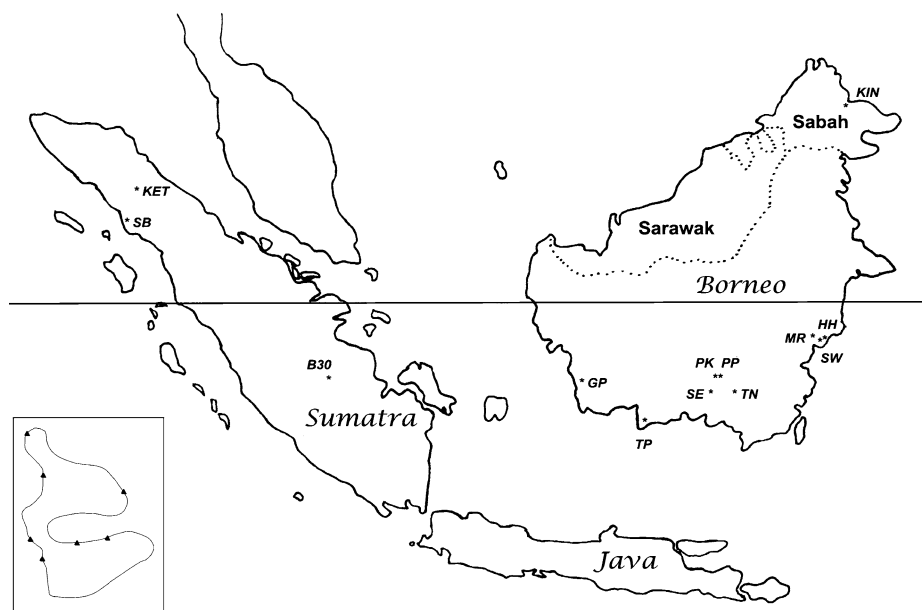
We collected observational data of leaf-carrying by rehabilitants on Kaja island, background information on their acquisition of leaf-carrying and other nesting skills, and information on leaf-carrying at other sites.

Observations

Subjects

Subjects were 42 ex-captive orangutans being rehabilitated by the Orangutan Reintroduction Project at Nyaru Menteng (NM) and living semifree forest lives on Kaja island in 2004 and 2005 (see Appendix). NM had placed rehabilitants on Kaja during the 2.5 years preceding the start of our study (i.e., since November 2001), as their final phase of rehabilitation before permanent release to a protected forest (Fig. 1). Residents were mainly juveniles and adolescents; three females were near-adult (primiparous). Individual backgrounds varied on age on arrival, time at NM, and primary housing at NM (Socialization cages—large cages for peer groups, or Midway House—a training forest for older infant and juvenile groups). Their lives before NM (e.g., provenance, captive ex-

Fig. 1 Orangutan forest sites surveyed for leaf-carrying. *Wild.* Sumatra: KET, Ketambe; SB, Suaq Balimbing. Borneo: GP, Gunung Palung; TP, Tanjung Puting; SE, Sebangau; TN, Tuanan; KIN, Kinabatangan. *Rehabilitant.* Sumatra: B30, Bukit Tigapuluh. Borneo: TP, Tanjung Puting; PK, Pulau Kaja; PP, Pulau Palas; MR, Meratus; SW, Sungai Wain; HH, Halfway House. *Insert (lower left):* Pulau Kaja with feeding sites (outline shows shoreline; feeding sites were in the forest set back 10–20 m from the river's edge)



periences) cannot be determined accurately, mainly because holding orangutans captive is illegal in Indonesia.

Setting

Kaja island lies in the Rungan River ca 35 km north of Palangkaraya, Central Kalimantan, Indonesia (S 2°1', E 113°47'). Habitat is ca 108.5 ha of decent forest mixed with a few old gardens, much of it inundated during wet seasons; it produces a good range of orangutan foods (Sidiyasa 2001; Sidiyasa et al. 2001) and demands relatively complex navigational and other forest skills. NM delivered supplementary food to five to seven sites on the island twice daily, ca 9:00 and 14:00, and monitored residents' progress ca 4 h/day (Fig. 1).

Sampling

We observed nesting on Kaja within a focal individual sampling framework. To maximize nest-building data, we recorded every nesting, in any orangutan, observed during follows and shifted to scan sampling at late afternoon to better detect night nests. Orangutans often congregated and nested overnight near feeding platforms so scans yielded up to 6 night nests daily. All four authors participated in data collection. NM staff monitoring rehabilitants concurrently also contributed reports of nesting and corroborated observational assessments of leaf-carrying and nesting skills.

Measures

For each nesting, we recorded standard nest parameters (Morrogh-Bernard, Husson, and McLardy 2002), nest construction behavior, and social learning opportunities.

For nest construction, we recorded type (i.e., build anew, rebuild, re-use as is) and behavior sequence (e.g., travel to/from nest, leaf-carry, building techniques, nest usage). Criteria for leaf-carrying were collecting nest materials before reaching the nest site, transporting them to the nest site without using them (i.e., excluding items used as hats or umbrellas during travel), then using them in nest construction. We recorded materials collected (species, where possible), how obtained, and how used (lining, cover, foundation). From June 2004, we rated whether leaf-carrying was unnecessary: criteria were that fresh leaves were abundant at the nest site and the orangutan added more leaves once in the nest, or the nest was already usable (i.e., new or newly rebuilt). Unnecessary leaf-carrying is more consistent with social than ecological influences.

For social influences on leaf-carrying, we recorded social learning opportunities at nesting (e.g., nesting associates,

proximity) and nest-related interactions linked with social learning (e.g., peer, share, joint nest building, steal). Nesting associates were other orangutans within 50 m at nesting; they are good indicators of social tolerance because more familiar companions nest closer together (Fruth and Hohmann 1996). Proximity of nesting associates was coded as close (0–5 m) or distant (5–50 m). Interactions around nesting were recorded in terms of participants' actions and their consequences.

Background information

We reviewed NM archives and interviewed staff that had worked extensively with these rehabilitants about rearing and nesting backgrounds. Archival data included date and estimated age at NM intake, location of confiscation/surrender, NM housing (type, duration), date of transfer to Kaja, and earlier nest-building data. Knowledgeable staff were questioned on each rehabilitant's nest-building and leaf-carrying skills before and immediately after transfer to Kaja.

Other sites

Table 2 shows all sites assessed for leaf-carrying. We followed common practices of consulting published literature, knowledgeable researchers and staff, and databases collected for other purposes (e.g., Lefebvre and Bouchard 2003).

Following other cultural assessments of orangutan nesting practices, we considered leaf-carrying to be shared group-wide if it was *customary* or *habitual* (i.e., shown by most/all or by several relevant group members) and assessed all sites despite substantial ecological variation (van Schaik et al. 2003). Orangutans probably select nest trees, sites, and materials for features like location, tree morphology, and presence/absence of irritants. Good sites and good materials are not guaranteed to cooccur, so leaf-carrying could owe to ecological conditions virtually anywhere.

Results

Kaja findings represent ca 600 h of observation from May through December 2004, which yielded 355 nesting incidents including 125 cases of leaf-carrying in 34/42 orangutans (Table 2). Leaf-carriers collected nesting materials as far as 50 m from the nest site, both leaves ($n = 109$) and other items (e.g., sacks, boxes; $n = 16$). We recorded more old than new and more night than day nests; leaf-carrying (leaves only) targeted old-night nests disproportionately (see Table 3).

Table 2 Distribution of leaf-carrying in forest-living orangutans

Sites	Region (project)	Habitat	Study (years/h)	LC Rate (OUs)	LC Rate (nests)	Dataset available
Wild orangutans						
Ketambe ¹	N Sumatra	Alluvial lowland, montane	32/50,000	A	0	Singleton, van Noordwijk, van Schaik (1994–1999)
Suaq Balimbing ²	N Sumatra	Coastal peat/transitional/back swamps, riverine, hill	5.5/17,000	A (0/50)	0	
Gunung Palung ³	W Kalimantan (GPOP)	Montane, granite, lowland alluvial, peat and freshwater swamp	10/25,000	A	0	van Schaik, Wich (2003–2004)
Tanjung Puting ⁴ (Camp Leakey)	C Kalimantan (ORCP)	Lowland, heath, swamp	33/6,800	A	0	
Tuanan ⁵	C Kalimantan	Peat swamp	1.25/5,000	R (3/15)	R	
Sebangau ⁶	C Kalimantan (OUTROP)	Peat swamp	1.5/3,500	A (0/16)	0	
Kinabatangan ⁷	Sabah (KOCP)	Secondary mixed lowland dipterocarp, seasonal freshwater swamp	7/10,000	A (0/25)	0	
Rehabilitant orangutans						
Bukit Tigapuluh ⁸	C. Sumatra (SOCP)	Lowland	2/10,000	A (0/36)	0	Praje (2002–2004) Russon (1990–2001)
Tanjung Puting ⁹ (Camp Leakey)	C Kalimantan (ORCP)	Lowland, heath, freshwater swamp	2/720	C (6/10)	29% (14/48)	
Tanjung Puting ¹⁰ (Tanjung Harapan)	C Kalimantan (PHKA)	Lowland, heath, freshwater swamp	None	A	0	
Kaja Island ¹¹	C Kalimantan (BOS-NM)	Island training forest, seasonally inundated, ca 108 ha	0.7/600	C (34/42)	35% (125/355)	Current study (2004) NM monitor (1999–2004)
Palas Island ¹¹	C Kalimantan (BOS-NM)	Island training forest, seasonally inundated, ca 20 ha	None	H (9/27)	??	
Sungai Wain ¹²	E Kalimantan (BOS-W)	Lowland dipterocarp, swamp	6/2,100	R (1/26)	1% (2/196)	Russon (1995–2000)
Halfway House ¹³	E Kalimantan (BOS-W)	Coastal training forest, fruit-enriched, ca 10 ha	None	C (most)	??	
Meratus ¹⁴	E Kalimantan (BOS-W)	Montane	4/2,270	H (7/14)	11% (18/170)	Kuncoro (2002) Russon (1999–2003)

Note. LC Rates: cells show leaf-carrying rates: C, customary (> 50%); H, habitual (21–50%); R, Rare ($\leq 20\%$); A, Absent (0%); ??, unknown. Bracketed values are sample sizes: # leaf-carriers/# orangutans, # LC cases/# nestings. *Region/Project*: Projects operating sites: GPOP; Gunung Palung orangutan project; ORCP; Orangan research and conservation project; OUTROP; Orangan tropical peatland project; KOCP; Kinabatangan orangutan conservation project; SOCP; Sumatran orangutan conservation programme; PHKA, Indonesian forest and nature conservation agency; BOS-NM and BOS-W, BOS Foundation reintroduction projects at Nyaru Menteng and Wanariset. *Sources* (personal communication unless otherwise noted): 1, Rijksen (1978); Utami, Wich, Wich et al. (2004); 2, van Schaik, Singleton, Wich et al. (2004); 3, Knott; 4, Galdikas (1978); 5, van Schaik, Wich; 6, Morrogh-Bernard, Husson, Morrogh-Bernard et al. (2003); 7, Ancrenaz, Lackman-Ancrenaz, Ancrenaz et al. (2004); 8, Praje; 9, Russon; 10, Tanjung Puting National Park staff; 11, Russon, Handayani, Kuncoro, Ferrisa, Nyaru Menteng staff; 12, Peters (1995); Russon; 13, Sitaparasi, Utami; 14, Kuncoro, Russon.

Table 3 Distribution of nests and leaf-carrying on Kaja Island

	New	Old	$\chi_{(1)}^2$ test ^{a,b}	<i>P</i>
Total nests				
Day	60	54	21.77	< 0.0001
Night	60	163		
Leaf-carrying				
Day	6	6	7.48	0.006
Night	15	77		

Note: Cells show number of nests/leaf-carrying events per category. Five nests were dropped because a key nest value (old/new, day/night) was not recorded during data collection.

^a χ^2 tests whether nests in our sample were distributed evenly over the four categories.

^b χ^2 tests whether leaf-carrying was directed to these four categories in proportion to their distribution in the nest sample.

Assessing leaf-carrying for cultural influences

Regional contrasts

The regional contrasts approach accepts learned practices as cultural if variation across sites cannot be explained ecologically (Whiten et al. 1999; van Schaik et al. 2003). Figure 1 and Table 2 show the distribution of leaf-carrying over contributing sites.

Leaf-carrying is known at only one of seven wild orangutan sites surveyed, Tuanan. One year's data yielded 20 cases in two adult females and one unflanged male (van Schaik and Wich unpublished). Tuanan orangutans always carried tarantang leaves (*Camptosperma coriaceum*) picked up to 50 m from the nest site; they traveled carrying the leaves, sometimes parked them to feed, then continued to a nest site and used them to make nest covers or linings (12 new, 8 old). Sebangau orangutans also prefer tarantang for nesting; they sometimes carry tarantang leaves around, but never for nesting (Husson and Morrogh Bernard unpublished). At Suaq Balimbing, an adult male once carried leaves into an old nest but used them as an umbrella or food, not for the nest (Singleton unpublished).

In rehabilitants, leaf-carrying was customary at three sites (Kaja island, Halfway House, Camp Leakey), habitual at two (Meratus, Palas island), rare at one (Sungai Wain), and absent at two (Bukit Tigapuluh, Tanjung Harapan). Almost all Halfway House residents leaf-carried in December 2004 but the practice was unknown from 2000 to 2002, when many residents neither built nor even used nests. Leaf-carrying was more common on Kaja than Palas although the two islands lie at most 10 km apart in the same river. In Sungai Wain, a juvenile male twice carried leaves onto a feeding platform and worked them into a nest.

The major pattern is that leaf-carrying is common at rehabilitant sites but rare at wild sites. Rehabilitants leaf-carry at sites as ecologically different as Meratus, Camp Leakey, and Kaja; wild orangutans do not across sites as similar as Tuanan and Sebangau. We also assessed several ecological factors hypothesized to explain leaf-carrying across all sites: physical necessity, preference, efficiency, and (for rehabilitants) earlier learning.

Physical necessity Leaf-carrying could be necessary if nest materials are only available *far* from nest sites. If materials are available even 15–30 m away, orangutans normally leave their nest midconstruction to collect them. Poor availability may apply to Tuanan (van Schaik personal communication) but Sebangau habitat is similar and its orangutans do not leaf-carry. Rehabilitants' overuse of nest areas, e.g., near feeding sites, could create poor availability. Denuded nesting areas characterize two rehabilitant sites where leaf-carrying is common, Camp Leakey and Halfway House, but not the other three, Meratus, Palas, and Kaja. Poor availability may favor leaf-carrying but is not enough to induce it. On Kaja, leaf-carrying was often unnecessary (35% of cases, by 19/34 leaf-carriers), which is inconsistent with ecological necessity. One juvenile male carried one spindly twig to an old nest, nowhere near enough to rebuild it. Others carried 15–20 leafy branches to their nest but once in it, picked and added more leaves within easy reach.

Efficiency Collecting materials in advance could be more efficient than backtracking, time-wise and energy-wise. If so, leaf-carrying should be more common in wild orangutans, who face serious energetic constraints (Knott 1998), than in rehabilitants, who are typically provided additional food. Evidence shows the reverse. Efficiency is also improbable on Kaja. Its rehabilitants often leaf-carried unnecessarily and leaf-carriers often left their nests after partial construction to collect even more leaves—immediately eroding any efficiency gains.

Preference Orangutans may prefer particular materials for each nest structure. Lining or cover preferences probably concern comfort (Husson personal communication). Preferences could induce leaf-carrying if preferred materials are only available far from the nest site.

Leaf-carrying suggests preferences at Tuanan, Kaja, and Meratus. Tuanan leaf-carriers chose *C. coriaceum* exclusively, a species that may have parasiticidal properties (Mabberley 1997). Kaja leaf-carriers showed several preferences, e.g., *Dillenia excelsa* (kaja), *Cratoxylum* sp. Preference is not enough to generate leaf-carrying, however. If it was, wild orangutans at Sebangau and Kinabatangan should leaf-carry. In Sebangau, *C. coriaceum* is the most popular choice for single tree nests (Gibson and Morrogh-Bernard unpublished).

In Kinabatangan, orangutans show high levels of nest reuse and shorter than normal active periods (Ancrenaz et al. 2004, Wich personal communication) so nest comfort may be particularly important. Leaf-carrying is unknown at either site. Neither can preference explain all leaf-carrying on Kaja: some rehabilitants carried kaja leaves into old nests in kaja trees then picked and added more kaja leaves once in the nest.

Preference might play a determining role under luxury living conditions that allow playful exploration and preference-guided behavior (Reader and Laland 2003; van Schaik et al. 2003). Orangutans may be so well nourished and free from stress at some sites that they can afford to build ideal nests every night. Conditions may qualify as luxurious on Kaja; conditions are similar on Palas, however, where at most 9/27 rehabilitants leaf-carried.

Previous learning Rehabilitants may have learned leaf-carrying while caged and then transferred the practice to forest life. Caged orangutans are often given bedding materials (e.g., leaves, sacks) on the cage floor near nesting time, so they have to carry materials to a site before they can build a nest. Virtually all rehabilitants were caged, some for years. Information on caging during captivity is not reliable, so we assessed rehabilitation caging only. Even programs that emphasize rehabilitation in forests, like Camp Leakey and Nyaru Menteng, cage ex-captives for safety, health, or re-socialization (e.g., those who cannot build nests). If cage-based learning causes leaf-carrying, leaf-carriers should be common at all rehabilitant forest sites. They are not. Leaf-carrying levels should be higher at sites used by projects that emphasize rehabilitation in cages (e.g., Sungai Wain) than those associated with minimal caging (e.g., Camp Leakey), and higher in rehabilitants caged for longer periods. Evidence shows the reverse: leaf-carrying was rare in Sungai Wain and common at Camp Leakey, and rehabilitants that learned leaf-carrying on Kaja were caged for shorter periods than those that did not learn it (5.5 ± 8.4 months vs. 21.5 ± 11.9 months, $F_{1,13} = 6.96$, $p = 0.02$). The implication is that cage-based learning does not entirely explain leaf-carrying in forest life, at Kaja or elsewhere.

Rehabilitants may have learned leaf-carrying in the wild, prior to capture, and introduced it to NM groups. The likelihood seems low because leaf-carrying is known in only one wild community, Tuanan, and it is uncommon there. NM obtained most Kaja rehabilitants in Central Kalimantan (34 vs. 5/3 West Kalimantan/Java) but natal communities cannot be established with confidence. Ex-captives' provenance is genetically assessed to the species level (Sumatran–Bornean) but additional information is limited to the point of confiscation/surrender, which can be far from the birthplace (e.g., Bali, Japan), and illegal owners' claims, which are unreliable.

Summary No single ecological factor explains leaf-carrying but several acting together might. Too few sites are represented to assess this possibility systematically but some sites suggest several interacting ecological factors. Prerelease caging plus nest site overuse might explain leaf-carrying at the Halfway House, for instance. No such interactions were evident at Kaja or Meratus, so regional contrasts point to cultural influences on leaf-carrying at both sites.

Durability and expansion on Kaja

Shared practices must be relatively long lasting to qualify as cultural. We adopted a 6-month durability criterion (see Perry et al. 2003). We also assessed increase in the number of performers over time, i.e., expansion, as another feature taken to be diagnostic of cultural phenomena (Perry et al. 2003).

Leaf-carrying on Kaja suggests both. Concerning durability, leaf-carrying was common in all 8 months of the study and 17 residents leaf-carried for 6 months or more. Figure 2 shows findings suggesting expansion. Seven rehabilitants identified as non-leaf-carriers during our study were first seen leaf-carrying at or past the end of the study. Their first leaf-carrying was mainly to old nests (6/7) and unnecessary (6/7), suggesting early stages of acquiring nesting skills and socially guided learning. Three rehabilitants first seen leaf-carrying at the end of the study all leaf-carried in the first nesting we observed, suggesting a shift from no nest building to nest building guided by social input. In the four rehabilitants first seen leaf-carrying later, we recorded several normal nestings (2, 3, 4, 14) before seeing leaf-carrying. The two higher values suggest socially guided change from nesting normally to nesting with leaf-carrying.

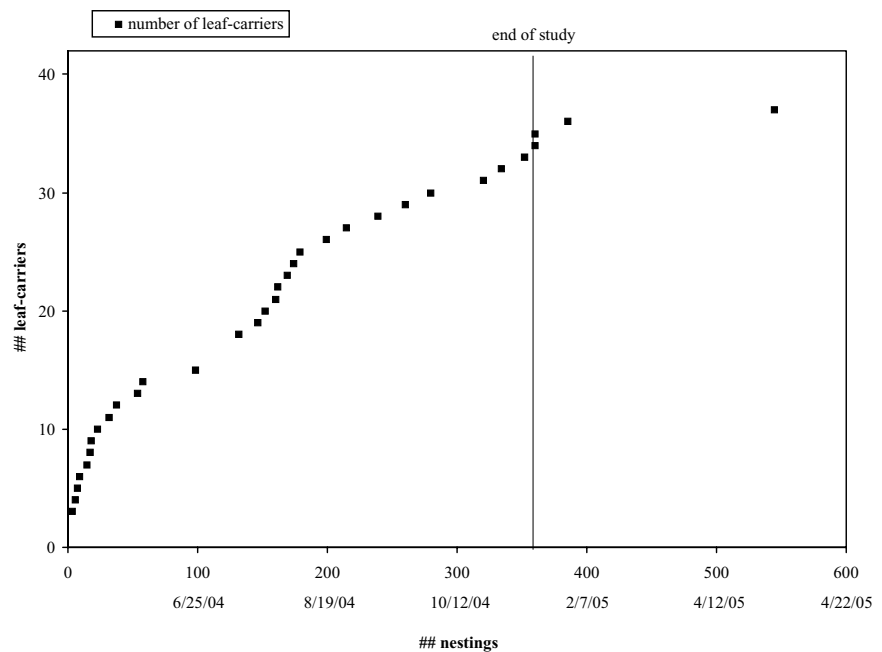
Direct social influences

Regional contrasts provide relatively weak evidence for cultural practices (e.g., Fragaszy and Perry 2003a), so we assessed direct social influences on leaf-carrying. Data permitted analyses for Kaja and Meratus.

Kaja We restricted quantitative analyses to systematically collected data (337 nestings, 116 leaf-carrying cases; archival and incidental reports dropped) using SAS 9.1 and SPSS 12.

The island's small size, elevated orangutan densities, and provisioning regime all probably induced high association rates (Sugardjito et al. 1987; van Schaik, Deaner, and Merrill 1999; Singleton and van Schaik 2001; van Schaik and Knott 2001; Singleton et al. 2004). Most residents had preferred feeding sites but preferences were multiple and shifting, so associations often formed and split over a few hours. Most rehabilitants feeding at a feeding site tended to nest

Fig. 2 Increase in number of leaf-carriers on Pulau Kaja, during and beyond the study



nearby, so nesting was highly social: associates were present in > 88% nestings. A single orangutan had up to 16 associates at one nesting and 29 different associates over the study. In comparison, Meratus rehabilitants had maxima of 6 and 11 associates, respectively, and wild orangutans have rare and smaller nest groups (ca 5–9) (Rijksen 1978; Fruth and Hohmann 1996). Leaf-carrying and leaf-carrier rates on Kaja were 35% and 81%, respectively, so a nesting orangutan should have an opportunity to observe leaf-carrying if 4 or more nesting associates nested concurrently. This situation occurred in 60% of night nestings. Interaction accompanied 32% of nestings by 31 orangutans, and at least one partner leaf-carried in 37% of these interactions.

We found no significant differences in social influences between those who did versus did not leaf-carry, based on nesting associations and nesting interactions (see Table 4). Failure to detect differential social influences could owe to high nesting association levels, the great majority of leaf-carriers, the heavy influence of external pressures on association, and/or social changes since learning. Associations on Kaja were very labile, given changes in development, forest skills, seasonality, and periodic introductions of new individuals.

We therefore compared rehabilitants who almost certainly learned leaf-carrying on Kaja (“learners”) with those who did not (“nonlearners”) (see Appendix). Where our data were unclear, we relied on NM archives and staff judgments. By our most conservative estimate, 27/34 leaf-carriers acquired leaf-carrying before moving to Kaja: 8 leaf-carried at the Midway House and 19 presumably leaf-carried because they were primarily cage-housed. We classified the other 7 leaf-

carriers as learners: all came from the Midway House, built nests but did not leaf-carry there, and did not leaf-carry on arriving on Kaja. We classified the final 8 orangutans, never seen leaf-carrying on Kaja or beforehand despite opportunities, as nonlearners.

Learners and nonlearners are compared in Table 5. The two groups did not differ reliably in social learning opportunities as indexed by nesting associations or interactions. We therefore assessed factors that may have led to taking differential advantage of social learning opportunities: development (age: at release, relative to the founder of leaf-carrying on Kaja, relative to puberty at first exposure to leaf-carrying on Kaja), experience (nesting competence at release, time on Kaja), and dominance. Staff identified the founder as Yuni, who arrived on Kaja in April 2003. Multivariate analyses showed significant differences: compared to nonlearners, learners were comparatively younger at release, had spent less time caged at NM, and had lived longer on Kaja. More learners were juveniles (prepubertal) when first exposed to leaf-carrying on Kaja and younger than Yuni. More learners than nonlearners were competent nest builders at release and subordinate, although the latter difference did not reach significance.

We also detected several sex differences (Table 6). Males leaf-carried unnecessarily to old-night nests more often than females and more males than females did this, but males did not differ from females in rates of using or leaf-carrying to old-night nests. Related sex differences may have originated at the Midway House. Among Kaja residents from the Midway House, those that leaf-carried at the Midway House were disproportionately female and younger than those that did

Table 4 Social and developmental factors in leaf carrying: Kaja and Meratus

	Leaf-carriers	Non-leaf-carriers	Test	<i>P</i>
<i>Kaja</i>				
Social influences			$F_{6,35} = 0.15^a$	0.411
Average associates/nesting	4.77 (1.58)	4.31 (2.99)	$F_{1,40} = 0.46$	0.503
Maximum associates/nesting	9.18 (4.00)	7.00 (3.96)	$F_{1,40} = 1.92$	0.174
Close associates/nesting	0.72 (0.53)	1.08 (1.11)	$F_{1,40} = 1.89$	0.177
Interactions/nesting ^b	0.37 (0.30)	0.42 (0.50)	$F_{1,40} = 0.16$	0.691
Nest sharing/nests	0.59 (1.02)	0.38 (0.52)	$F_{1,40} = 0.33$	0.571
Leaf-carriers among nesting associates	0.88 (0.20)	0.95 (0.09)	$F_{1,40} = 1.14$	0.291
Background at Midway				
Age at leaving Midway (mean, SD)	4.44 (0.56)	5.22 (0.87)	$F_{1,15} = 4.73$	0.046
<i>Meratus</i>				
Social Influences			$F_{6,6} = 9.88^a$	0.007
Average associates/nesting	1.62 (0.59)	1.00 (0.57)	$F_{1,11} = 3.77$	0.078
Maximum associates/nesting	5.14 (1.46)	2.83 (1.69)	$F_{1,11} = 9.63$	0.010
Close associates/nesting	0.71 (0.29)	0.11 (0.10)	$F_{1,11} = 24.10$	0.001
Interactions/nesting ^b	0.48 (0.28)	0.26 (0.38)	$F_{1,11} = 1.51$	0.245
Nest sharing/nests	0.36 (0.22)	0.03 (0.08)	$F_{1,11} = 11.05$	0.007
Leaf-carriers among nesting associates	0.85 (0.20)	0.29 (0.29)	$F_{1,11} = 17.03$	0.002
Proportion sharing nests	1.00 (7/7)	0.29 (2/7)	$\chi_1^2 = 7.78$	0.006

Cells show mean (standard deviation) unless otherwise specified.

^aMultivariate *F*-test (Pillai's trace).

^bNesting interactions: share nest, steal nest, take abandoned nest, cooperative nest build, observe nest building, play in nest, copy nest-building activities.

Table 5 Learners and nonlearners on Kaja: social, developmental, and experiential factors

Factor	Learner	Non-learner	Test	<i>P</i>
Social influences			$F_{4,9} = 0.32^a$	0.860
Average associates/nesting	4.10 (2.06)	4.17 (1.69)	$F_{1,12} = 0.01$	0.941
Maximum associates/nesting	8.00 (5.20)	6.29 (2.93)	$F_{1,12} = 0.58$	0.462
Close associates/nesting	0.72 (0.72)	0.57 (0.60)	$F_{1,12} = 0.18$	0.679
Interactions/nesting	0.5 (0.42)	0.48 (0.50)	$F_{1,12} = 0.04$	0.849
Age and experience			$F_{6,8} = 4.64^a$	0.025
Age at release	5.29 (0.95)	6.81 (1.44)	$F_{1,13} = 5.69$	0.033
Age at first LC exposure ^b	-0.71 (0.76)	0.25 (0.71)	$F_{1,13} = 6.51$	0.024
Age relative to LC founder	-0.71 (0.76)	0.75 (0.71)	$F_{1,13} = 15.02$	0.002
Time on Kaja (months)	32.57 (2.23)	23.75 (9.65)	$F_{1,13} = 5.54$	0.035
Time caged at NM (months)	5.57 (8.36)	21.50 (13.89)	$F_{1,13} = 6.96$	0.021
Nesting competence at release ^c	0.89 (0.28)	0.38 (0.52)	$F_{1,13} = 5.52$	0.035
Social dominance (1/7 vs. 4/8)	0.14	0.50	$\chi_1^2 = 2.14$	0.14

Cells show mean (standard deviation) unless otherwise indicated.

^aMultivariate *F*-test (Pillai's trace).

^bAge at first LC exposure is measured relative to puberty.

^cNesting competence at release: 0 = no nest building skills, 0.25 = use old nest, 0.5 = use old nest and refresh lining, 1.0 = build and use complete nest.

Table 6 Sex differences in leaf-carriers and leaf-carrying on Kaja

	Male	Female	Test	<i>P</i>
Leaf-carrying to old-night nest				
Rate, unnecessary overall (mean, SD)	0.67 (0.38)	0.15 (0.30)	$F_{1,23} = 14.17$	0.001
Rate, proportion of leaf-carriers	12/14	7/19	$\chi_1^2 = 7.90$	0.005
Rate, use old-night nest	58/130	105/217	$\chi_1^2 = 0.46$	0.50
Rate, leaf-carry to old-night nest	37/51	40/54	$\chi_1^2 = 0.03$	0.86
Midway background				
Rate, competent nesters	4/7	10/10	$\chi_1^2 = 6.28$	0.04
Rate, leaf-carriers	0/7	8/10	$\chi_1^2 = 13.50$	0.0002

not. Males from the Midway House tended to acquire nesting skills, leaf-carrying included, later than females from the Midway House: most of the females acquired both skills as infants but most of the males did not until juvenile. In May 2005, staff reported leaf-carrying in four current Midway House residents—all, again, females.

All nonlearners had traits likely to inhibit social learning. Four were dominant in the Kaja community and adolescent when first exposed to leaf-carrying on Kaja; two of them had reputations as nest stealers, one was recently released and had been home-reared. Of the four lower ranking nonlearners, three were adolescent when first exposed to leaf-carrying on Kaja and three tended to nest alone. Loners and the home-reared adolescent had limited social learning opportunities. The other traits have been found to hamper social learning in rehabilitant orangutans. Dominants learn poorly from subordinates (Russon and Galdikas 1995), dedicated nest thieves are delayed in learning nesting skills (Rijksen 1978), and adolescents have more difficulty learning nest building socially than infants or juveniles (Galdikas 1982).

Meratus Meratus showed similar patterns. Among 14 rehabilitants we observed nesting, seven leaf-carried: six juveniles, one young adult female. All six juveniles were members of stable friendship dyads (Joshua-Victor, Ayumi-Itang, Baron-Luna), released from Wanariset's Halfway House training forest in 2001–2002. Three of them (Itang, Joshua, Victor) occasionally traveled, foraged, and nested with the adult female (Maya). Maya had always been caged, but had ca 4.5 years more forest experience than the juveniles and was the first seen leaf-carrying in Meratus (July 2002).

We compared nesting associations between leaf-carriers and non-leaf-carriers (Table 4). Meratus nesting associations and interactions mapped directly onto leaf-carrying: more leaf-carriers shared nests, leaf-carriers shared nests more often, and leaf-carriers shared nests only with other leaf-carriers (non-leaf-carriers shared only with non-leaf-carriers). Leaf-carriers more often had associates at nesting (maximum, average, close) and a higher proportion of their nesting associations included leaf-carriers. Juveniles mainly generated these patterns; Maya's nesting associations rates were much lower.

In the six juveniles, all but two leaf-carrying cases involved copying between members of a friendship dyad. Two dyads (Ayumi-Itang, Baron-Luna) leaf-carried cooperatively: Baron then Luna, e.g., carried leaves to a nesting site, jointly built one nest there using the leaves, and then shared the nest. Four of the six juvenile leaf-carriers were among the youngest rehabilitants followed (three were < 5 years old at release) and had weak nesting skills (Russon, Kuncoro, Handayani personal observation) They may have acquired leaf-carrying via Maya, the only adult female available and the first known leaf-carrier in Meratus. Itang, e.g.,

once watched Maya rebuild an old nest and then climbed in with her. Luna depended heavily on Baron and probably acquired leaf-carrying via him; how he learned is not obvious from our data.

Spreading leaf-carrying on Kaja

To tease apart the processes supporting group-wide sharing, we reconstructed the spread of leaf-carrying through the Kaja community.

All Kaja leaf-carriers arrived on the island with leaf-carrying or very closely related skills. Those from socialization cages had probably been shaped to collect nest materials in advance, through the common cage routine of providing bedding materials near nesting time. They probably mastered little else while caged because the only basis for learning is bedding materials, which are preselected, prepared, and changed daily. Some may have mastered other nesting skills in the wild, depending on age at capture; the most probable is making linings, including selecting, picking, and transporting leafy materials, because it is the earliest acquired. Leaf-carriers who probably learned on Kaja all had functional nesting skills on arrival, so they could select, pick, and transport leafy materials for linings. Those who leaf-carried at the Midway House already had all requisite skills.

Prior skills do not explain leaf-carrying on Kaja, however, because none of these rehabilitants leaf-carried immediately on arrival. The probable reason is that additional learning is required, either additional skills that could not be learned in cages (e.g., selecting and picking nest materials, sleeping in tree nests) or changing the timing of collecting nest materials. Even those who leaf-carried at the Midway House did not immediately leaf-carry on Kaja, so habitat change may create new hurdles (e.g., new tree species).

Given the option of reusing old nests, the additions needed to generate leaf-carrying on Kaja are minor refinements to existing skills that could be generated by simply establishing new associations and cues. Priming could achieve this, in the sense of enhancing the likelihood of enacting known practices (Byrne 1994). Fortuitous accidents could induce some priming, but social priming was probably more important. In particular, associating with leaf-carriers at nesting could prime collection of leaf materials earlier in the nesting sequence. Beyond priming, associating with leaf-carriers at nesting could prompt use of tree nests and nest material selection by mechanisms like stimulus enhancement. Nest-related interactions also involved considerable observation and in ca 15% of these observations, learners watched a partner leaf-carry and then copied adding leaves to the nest. Consistent with this social view, 24/34 Kaja leaf-carriers were seen leaf-carrying within 16 months *after* the probable founder's (Yuni's) arrival. In contrast, of 23 rehabilitants who were leaf-carriers before moving to Kaja and who arrived on

Kaja before Yuni, none were seen leaf-carrying *before* Yuni arrived—even 14 that had already lived on the island for 12–18 years. This does not imply that associative learning alone generated leaf-carrying on Kaja. All Kaja leaf-carriers scheduled leaf collection flexibly in nest building, suggesting mental reorganization of the nesting sequence. This is more consistent with hierarchical cognition, which is within the reach of juvenile great apes (e.g., Byrne and Russon 1998; Russon 1998; Parker and McKinney 1999).

Given the exceptionally rich social learning opportunities on Kaja, that leaf-carrying appeared in some rehabilitants but not others is important in suggesting additional factors that affect spread: age, sex, social position, and prior skills. In learners, these factors were expressed as an interrelated set of traits linked with development: functional nesting skills (7/7), male (5/7), juvenile when the founder arrived (6/7), younger than the founder (6/7), and preference for older close associates at nesting (6/7). Functional nesting skills may boost interest in and abilities for adopting leaf-carrying. The juvenile male pattern may reflect male tendencies to master forest skills later than females, perhaps because males focus more on social skills (Peters 1995; Lonsdorf et al. 2004). Preferences for older associates have also been seen in juvenile males elsewhere: they played mostly with older males and shared nests with same-age or older females (Peters 1995). In orangutans, juvenile status facilitates learning nesting skills socially: juveniles are semidependent, tolerated as such, and follow and copy their mothers as faithfully as pull toys or shadows (Horr 1977; Russon and Galdikas 1995). Adolescents were slower to leaf-carry on Kaja despite their gregariousness and advanced cognition. These patterns jibe with other studies showing that development fosters and constrains great apes' acquisition of nesting skills (Bernstein 1967; Galdikas 1978; Rijksen 1978) and that orangutans are selective of whom they learn from and what they learn (Russon and Galdikas 1995). This interrelated set of traits found in Kaja learners boosted chances that learners would follow and nest near older associates and when they did, they could and would copy their practices—leaf-carrying included.

Conclusion

Findings point to cultural influences on spreading leaf-carrying on Kaja. Leaf-carrying was learned, customary, relatively enduring, possibly expanding, incompletely explained by ecological factors, and aligned with social influences. Its spread on Kaja, as reconstructed, is consistent with the view that development is critical in enabling widespread sharing and that juveniles are best positioned to spread nesting skills widely in orangutans. Leaf-carrying is an easy operation that does not become more difficult with age. Juveniles need nesting skills, have the abilities to learn them,

and enjoy tolerance that enables social learning within networks of same-aged or older nonkin.

Broader implications depend largely on how closely these rehabilitants resemble wild orangutans or other great apes in acquiring and spreading skills. Given appropriate opportunities, they show striking similarities to wild orangutans and other great apes in learning ecological skills: basic skills are mastered by later infancy, refinements continue through juvenility then level off, interest in social learning with non-kin is prominent in juveniles (e.g., sharing nests, observing others' foraging), juvenile learners direct attention to experts of similar age or older but not younger, and sensitive periods for learning are evident (Bernstein 1967; Galdikas 1978; Inoue-Nakamura and Matsuzawa 1997; Anderson 2000; Biro et al. 2003). Rehabilitant leaf-carrying also resembles wild orangutan nesting traditions (van Schaik et al. 2003): all are stylistic refinements of standard nest-building techniques. Finally, Kaja rehabilitants' nesting showed sex differences that are paralleled in wild chimpanzees' termite-fishing: infant-juvenile males acquired skills later than females despite no obvious differences in social learning opportunities (Lonsdorf et al. 2004). Overall, rehabilitants' needs, abilities, and social preferences conform to species-typical developmental expectations. Relative to culture, their leaf-carrying conformed to predictions based on wild patterns, that juveniles and adolescents would readily share skills. These findings then support the view that developmental scheduling is important in enabling cultural processes in great apes by synchronizing sharing opportunities with learners' willingness and abilities to use them (e.g., Biro et al. 2003).

Rehabilitation programs stand to benefit from recognizing the importance of respecting normal developmental patterns. Reintroduction has better chances of success if ex-captives are released to forest life as juveniles, because of their optimal potential for learning ecological skills, and if rehabilitant communities are managed to develop strong adolescent networks and to provide juvenile learners with access to older, more experienced members. Implications for wild orangutan conservation are also worth considering. Orangutan cultures are probably adaptive, so the integrity of orangutan communities should be fundamental to conservation programs. If juveniles and adolescents play key roles in cultural transmission, then promoting robust juvenile and adolescent cohorts should be a central consideration. Threats to reproductive rates, infant survival, or dispersal, e.g., can impair cultural processes because they result in weakening juvenile and adolescent networks.

Factors beyond those illustrated by leaf-carrying undoubtedly influence orangutan cultural processes. In the wild, for instance, adolescents may be more central to group-wide sharing than juveniles, being the most gregarious age class. If group-wide sharing requires synchronizing needs, abilities, and social opportunities, however, then gregariousness

alone is not enough. It is therefore significant that great apes master different skills at different points in development (van Noordwijk and van Schaik 2005). Strength-based or sexual skills, e.g., may be mastered during adolescence, not as juveniles. Further, skills that juvenile great apes master to functional levels may not represent full adult mastery because later developmental changes may induce elaborations, efficiencies, or other adjustments. The implication is that some skills may spread best via juveniles, but skills that concern later developing needs and abilities may spread via adolescent networks. Primate practices with different developmental learning trajectories probably spread via different social networks, because they interest different learners and require different abilities (e.g., Huffman and Hirata 2003). Understanding orangutan cultural processes probably lies in sorting out when developmental scheduling brings specific needs together with the requisite abilities and social opportunities in support of sharing.

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Appendix: Orangutans on Kaja Island: background, nesting, and leaf-carrying (LC)

Name	Sex	NM arrival ^a			Kaja arrival	Age 12/04 ^a	Total LC, nests	NM caged ^b	NM housing ^c	NM nesting ^d	NM LC ^e	Kaja LC	Kaja learn LC ^f
		Source	Date	Age									
Alfa	M	CK	12/99	3.5	11/01	8	1, 2	1	M	O	N	Y	Y
Cakra	M	CK	08/00	4	11/01	8	1, 5	1	M	Y	N	Y	Y
Didik	M	CK	12/99	4	01/02	8	3, 6	10	M	Y	N	Y	Y
Kepleh	M	CK	12/99	3	11/01	7	5, 8	1	M	Y	N	Y	Y
Menteng	M	CK	03/01	4	05/02	7.5	10, 12	1	M	Y	N	Y	Y
Markisa	F	CK	11/00	4.5	01/02	8	1, 5	2	M	Y	N	Y ^g	Y
Sif	F	CK	04/00	5.5	11/01	10	3, 15	1	M	Y	N	Y	Y
Emen	F	CK	01/00	4.5	06/03	8.5	0, 4	41	S	N	P	N ^g → Y	N → K
Fitun	M	CK	01/01	6.5	01/04	9.5	0, 2	36	S	N	P	N ^g → Y	N → K
Nopy ^h	F	Java	05/01	7.5	01/03	10.5	0, 10	20	S	Y	P	N ^g → Y	N → K
Omega	M	CK	11/99	4	02/02	8.5	0, 2	27	S	?	P	N ^g → Y	N → K
Dave	M	CK	12/99	3	11/01	7.5	0, 1	1	M	N	N	N ^g	N
Lona	F	Java	05/01	6	03/03	9	0, 8	22	S	Y	P	N	N
Mas	M	CK	02/00	4	11/01	8.5	0, 3	4	M	?	N	N ^g	N
Zidane	M	CK	08/00	4.5	05/02	8.5	0, 2	21	S	Y	P	N ^g	N
Agul	M	CK	01/00	4.5	01/04	9	1, 1	27	S	N	P	Y	K
Awa	F	CK	02/00	1.5	11/01	6.5	24, 42	4	M	Y	Y	Y	K
Bonet	M	WK	05/02	3	04/03	5	1, 2	11	S	Y	P	Y	K
Cindy	F	CK	05/00	6	01/02	10	3, 7	20	S	Y	P	Y	K
Dagoy ^h	F	CK	03/00	12 +	02/02	16 +	2, 5	23	S	Y	P	Y	K
Danur	M	CK	08/00	4.5	05/02	8	10, 21	21	S	Y	P	Y	K
Gadis	F	CK	04/00	3	11/01	7	1, 7	2	M	Y	Y	Y	K
Hema	F	CK	12/99	2.5	01/02	7	1, 4	1	M	Y	Y	Y	K
Inung	F	CK	04/00	3	11/01	7.5	1, 5	2	M	Y	Y	Y	K
Jacky	M	CK	03/00	3.5	02/02	8	8, 29	23	S	Y	P	Y	K
Jamiat	M	WK	04/01	6	05/02	9	7, 13	13	S	Y	P	Y	K
Jane	F	CK	11/99	4	06/02	8.5	1, 7	31	S	Y	P	Y	K
Jon-Jon	M	WK	02/02	7.5	01/04	10	1, 1	23	S	N	P	Y	K
Leonora	F	CK	08/00	4	01/02	8	1, 12	1	M	Y	Y	Y	K
Lesta	F	CK	12/99	4.5	06/02	9	3, 12	30	S	N	P	Y	K
Matilda	F	CK	09/00	4	11/01	8	1, 9	1	M	Y	Y	Y	K
Mawar ^h	F	CK	11/00	7	01/02	10.5	1, 7	14	S	Y	P	Y	K

Appendix: Continued.

Name	Sex	NM arrival ^a			Kaja arrival	Age 12/04 ^a	Total LC, nests	NM caged ^b	NM housing ^c	NM nesting ^d	NM LC ^e	Kaja LC	Kaja learn LC ^f
		Source	Date	Age									
Matilda	F	CK	09/00	4	11/01	8	1, 9	1	M	Y	Y	Y	K
Mawar ^h	F	CK	11/00	7	01/02	10.5	1, 7	14	S	Y	P	Y	K
Mita	F	CK	11/99	4	04/03	8.5	1, 9	41	S	?	P	Y	K
Pedro	M	WK	02/02	9	01/04	11	7, 14	23	S	Y	P	Y	K
Secilia	F	WK	12/99	2	01/02	6.5	2, 6	2	M	Y	Y	Y	K
Sendy	F	CK	04/00	4	02/02	8	14, 20	22	S	Y	P	Y	K
Shelli	F	Java	05/01	7.5	05/03	10.5	2, 2	24	S	?	P	Y	K
Simona	F	CK	03/00	4.5	05/02	8	1, 2	26	S	Y	P	Y	K
Sumeh	F	CK	08/00	4	11/01	8	1, 10	8	M	Y	Y	Y	K
Uban	M	CK	12/99	4	05/02	8.5	2, 3	1	S	Y	P	Y	K
Wildon	M	CK	11/00	4	04/03	7.5	3, 8	29	S	Y	P	Y	K
Yuni ⁱ	F	CK	12/99	4	04/03	8.5	4, 12	40	S	Y	P	Y	K

^aArrival at NM: Age (est.) and source from NM records, CK/WK—Central/West Kalimantan.

^bDuration of caging at NM: (NM records, est. 1 month if unstated).

^cPrimary housing at NM: M—Midway House, S—Socialization Cages.

^dNesting at NM: O—old nests only, ?—unknown.

^eLC at NM (per two independent reports by reliable staff): Y—observed (Midway), P—probably (Socialization cage housed), N—never observed (Midway).

^fLearn LC on Kaja (see text): K—probably LC before move to Kaja, N → K—no LC during study, LC post study.

^gClassification based on NM archives or reliable staff, because observations were unclear or < 5 nestings were observed (median leaf-carrying rate on Kaja was 30%, so a sample 4 of nestings per orangutan should detect leaf-carrying).

^hCarrying infant born during study.

ⁱDied 11/04.

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