CHAPTER 20

Innovation and intelligence in orangutans

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20.1 Introduction

Innovation, in the general sense of newly invented behaviors and the processes that create them, is now recognized as an important natural phenomenon in many non-human species. It has significant links with intelligence, it is the engine of cultural revitalization, it can affect ecology by increasing a population's niche breadth, and it may affect the likelihood of speciation (Byrne 2003; Russon 2003b; Reader and Laland 2003a; van Schaik *et al*. 2006a). The current wave of research interest in innovation arose only recently, so concepts and methods are still in flux (Reader and Laland 2003a). Available findings also show limitations typical of early stage research in an area: many of the innovations currently recognized represent post hoc efforts to identify innovations from databases collected for other purposes, and many appear in human-influenced populations so they may have been induced by altered living conditions (van Schaik *et al*. 2006a). Efforts are now under way to systematize study, including developing workable definitions and methods for studying innovation systematically.

This chapter aims to identify provisional innovations in orangutans and to infer the mental processes involved based on two systematic studies of orangutan innovation in the field—one on wild orangutans and the other on free-ranging rehabilitants returned to forest life—and research findings on great ape cognition. We use rehabilitant findings as a means of validating provisional wild innovations, as a source of additional provisional innovations, and as a comparative basis for exploring how, cognitively, orangutans innovate.

20.2 Background

Current standards for conceptualizing innovation were set by Reader and Laland (2003a). They distinguished two faces of innovation, its products and the processes that produce them. As a product, innovation was construed as new or modified learned behavior in an individual that was not previously found in a population; as a process, it concerns the mechanisms that allow an individual to create such new or modified learned behavior and that introduce novel behavioral variants into a population's repertoire (Reader and Laland 2003b).

Van Schaik and colleagues (van Schaik *et al.* 2006a, unpublished data) used definitions developed by Ramsey *et al*. (2007), from Reader and Laland's (2003a) conceptual work, to identify provisional innovations in wild orangutans. They construed innovations as novel learned behaviors in an individual that are not simply a product of social learning or environmental induction. Their aims were to develop criteria that enable identification of provisional innovations from their current products, without having witnessed the innovation process, in particular, methods for establishing the innovation status of a behavior pattern seen in the field based on its current prevalence and properties. Van Schaik *et al*. (2006a) also proposed using captives and rehabilitants to validate provisional wild orangutan innovations, on the view that if a provisional wild innovation is common in captives or rehabilitants who are living in appropriate contexts and free of relevant social influences then it is unlikely to be an innovation, but if it is absent or rare, it is more certainly an innovation.

Here, we introduce data from rehabilitant orangutan populations, first, to help validate provisional wild innovations. Rehabilitants are subject to unusual influences (e.g., orphaning early in infancy, deprivation, human rearing). Provisional wild innovations concern forest expertise, however, so the impact of human rearing and deprivation may primarily concern delay. Virtually all rehabilitants lived normal wild lives before capture so learning guided by biological mothers cannot be entirely ruled out, but most were captured long before the end of 'apprenticeship' with their mothers so maternal guidance was typically brief (see Chapter 23). Almost all are reintroduced to forests different from their natal forest, so they are naive to local ecological conditions at release. Most are released into forests without a resident wild population so they have little access to knowledgeable conspecifics, although those released later sometimes rely on those released earlier (Russon 2006).

Second, we use rehabilitant data to explore what rehabilitants might add to the list of provisional orangutan innovations. We use findings from a study of innovations for dealing with water in forest-living rehabilitants on Kaja Island, Central Kalimantan. We chose water because wild orangutans rarely engage with it, especially ground water. Compared to staying in the trees, it puts orangutans at risk from predators (snakes, crocodiles, felids) and drowning (they cannot swim) and it typically offers little of interest (e.g., no normal foods). Water skills are then most likely learned, because innate predispositions are improbable, so they are potentially innovative. In wild orangutans, only five provisional innovations involving water have been identified—play, washing, and three drinking techniques (van Schaik *et al.* 2006a).

We further take a cognitive perspective on innovation because cognition affects how actors construct behaviors, including how they acquire, organize, and modify them. Great apes typically create new behaviors by building upon existing ones (Gibson 1993; Parker and McKinney 1999). Very few of their behaviors are then entirely new, including those that may derive from insight, so identifying great ape innovations requires establishing what is novel in a variant, i.e., what, precisely, was invented (Byrne 2003). The nature of this novelty depends on the steps that actors take in acquiring behavior and the level of detail at which they distinguish and organize behavior: elsewhere, this has been termed behavioral grain (Byrne 1999; Fox *et al*. 1999; Byrne *et al*. 2001a, b; Russon 2003a). Resolving grain has been described as 'carving behavior at the joints', where actors define the joints, or identifying the mental units that actors use to generate performances (Case 1985; Byrne 1999; Byrne *et al*. 2001a). Grain is thus crucial to identifying innovations because it defines the pace and level at which an actor handles novelty.

Grain may be particularly difficult to identify in great apes because their cognitively governed behaviors are often multi-stage, multilevel mixtures of many components. Great ape components include action elements (single motor actions that cause observable change to a target), procedures (combinations of elements organized to handle narrow tasks), and programs (procedures and action elements organized alone or in relatively simple combinations to solve complex problems) (Russon 1998; Byrne *et al*. 2001a, b; Parker 2004). Their procedures often manipulate simple relations between objects and their programs are often organized hierarchically (Gibson 1993; McGrew 1992b; Matsuzawa 1996; Byrne and Russon 1998; Parker and McKinney 1999; Russon 1998, 2004; Yamakoshi 2004). An example in orangutans is a multi-step, hierarchical program for extracting meristem (heart) from tree palms (Russon 1998). Basic steps are: enter palm crown, extract new shoot and bite meristem from its base section by section, exit palm; optional steps are: check new shoot, prepare work area, store sections. Several steps are procedures (e.g., prepare work area, extract new shoot in sections), each coordinating multiple action elements. Prepare work area, for instance, includes action elements of picking up and discarding debris from the center of the palm's crown, pushing obstructing leaf petioles (away from the crown's center) and pushing one central petiole (to a horizontal position, for use as a work-seat). Importantly, components may vary in origin and flexibility. Origins can include innovation, insight, ecological induction (i.e., shaping by physical affordances and constraints), and social learning (Byrne and Byrne 1993; Byrne *et al*. 2001a, b). Flexibility depends partly on physical constraints (e.g., leaves aren't good hammers nor rocks good probes, probes must suit the physical task) and partly on experience (e.g., availability of learning opportunities).

From a cognitive/grain perspective, then, orangutans could innovate at several levels: entire programs, procedures, or action elements. Evidence suggests that great apes rarely invent programs—they probably acquire them socially; their program level components tend to be stable and lower level components to be modifiable, a combination that allows maintaining standardized routines and adjusting them to local contingencies; and they typically acquire action elements by trial and error, i.e., ecological induction (Byrne and Byrne 1993; Byrne and Russon 1998; Parker and McKinney 1999; Russon 1998, 1999; Boesch and Boesch-Achermann 2000; Byrne *et al*. 2001a, b; Stokes and Byrne 2001; Morimura 2006). Orangutan innovation then probably focuses on lower level components in general, because these are relatively flexible, and procedures in particular, because action elements are typically environmentally induced. Apparently novel programs are probably products of gradually building more complex structures upon pre-existing simpler ones; if they qualify as innovative, they probably represent multiple innovations rather than a single one.

20.3 Findings

20.3.1 Provisional wild orangutan innovations

Van Schaik *et al*. (2006a) applied their geographic and local prevalence approach across seven wild orangutan sites (see Box 20.1) and identified 43 provisional innovations, arranged in three broad categories (comfort, sociosexual, subsistence). A subsequent round of cross-site comparisons for the orangutan culture project (see Chapter 21) led to removing some and adding several more provisional innovations. This approach now identifies 54 provisional innovations in wild orangutans

Box 20.1 Wild orangutan data

Van Schaik *et al.* (2006a) distinguished innovations in stable wild orangutan populations from their geographical prevalence, local prevalence, and properties. They identified a behavior as a provisional innovation if (1) it is not universal in a given population, i.e., where ecologically possible, its geographic and local prevalence is low (i.e., absent in some populations or low prevalence in all populations) and (2) its absence in individuals owes to lack of knowledge, not observational artifacts.

Their procedures rule out all explanations for the absence of a non-universal behavior in an individual or at a site *except* failure to innovate. Only sites with enough observation time to control against observational artifacts are eligible, and behaviors are disqualified as innovations if their presence/absence correlates tightly with ecological conditions. A non-universal behavior that is entirely absent in at least one population is a provisional innovation if ecological conditions are suitable, enough observations are available where it is absent, and it has high prevalence in some other populations. A non-universal behavior that is present but rare in several populations is probably an innovation if ecological or observational reasons for its absence in most individuals can be ruled out (e.g., rare need, special performer class, inappropriate ecological conditions).

Procedures also evaluate whether minor differences between behaviors, or 'modifications', are distinct variants. Minor differences detectable by observers may not be significant to actors, e.g., alternatives that are interchangeable or have no functional value, variation along a gradient (Fox *et al.* 1999). Multiple modifications at a site were treated as distinct variants if different individuals consistently used different modifications or the same individual used modifications in functionally distinct ways. If an individual used multiple modifications interchangeably within one bout or on different occasions in what can reasonably be called the same context, they were not treated as distinct variants.

Provisional wild orangutan innovations were identified from extensive focal observations at Tuanan, Central Kalimantan, findings from six other sites that contributed to the orangutan cultures project (van Schaik *et al.* 2003a), incidental comparisons with two sites in Sabah (Lokan, Ulu Segama), and unpublished data on suspected universal behaviors compiled in preparation for van Schaik *et al.* (2003a) (see Fig. 1—site map, in Preface).

(see Table 20.1; see also Tables 21.1 and 21.2). For this chapter, we ordered entries by broad function (comfort, sociosexual, subsistence) and functional form (wiper, probe, rake).

20.3.2 Comparing wild orangutan innovations with rehabilitant controls: validation

Van Schaik *et al.* (2006a) suggested that if naive rehabilitants acquire a provisional wild innovation readily given relevant ecological conditions, the likelihood increases that this variant is instead a product of environmental induction. This proposal is based on the assumption that rehabilitants and wild orangutans are the same except that rehabilitants have not been exposed to the local innovation repertoire because virtually all were captured from the wild as youngsters and from forests different from those into which they are released.

Rehabilitants may differ from wild orangutans in several important ways, however. First, they may simply have more time to experiment than wild orangutans, given that most are provisioned. Second, they may have more opportunities for social learning once released, typically being more gregarious and more socially tolerant than wild orangutans because of rehabilitation practices (peer-dominated social housing) and age (most are released and studied as immatures). Competencies already present in individual ex-captives, innovations included, could then spread more easily among rehabilitants. This could affect their forest behavior if they apply competencies acquired in the wild before capture (especially in those captured at older ages), in captivity, or in rehabilitation (van Schaik *et al.* 1999). How much this affects rehabilitants' forest behavior post-release is unclear. In some cases it may (Russon *et al.* 2007a) but most rehabilitants were captured as young infants before they could have mastered important forest competencies: many, for instance, cannot build nests, travel arboreally, or recognize forest foods (Peters 1995; Russon unpublished data). As captives, most experienced impoverished, even abusive conditions that deprived them of important learning experiences, both social and physical (Peters 1995; Kuncoro 2004; Grundmann 2006; Ian Singleton personal communication). Even during rehabilitation, many were kept in cages, and basic forest training is rarely provided in the release forest. For these reasons, most are unlikely to enter forest life with enriched knowledge or skills acquired elsewhere.

Third, some differences between wild and rehabilitant behavior reflect ecological or methodological differences. In rehabilitants, for instance, leaf carry for nesting is probably not an innovation because it is likely induced by captive cage conditions (Russon *et al*. 2007a). Differences in skilled nesting and feeding entries may reflect sampling differences (rehabilitants were not always observed until nesting) or the fact that rehabilitants are often studied as immatures and so have immature competencies (e.g., reuse old nests, use simple feeding techniques; Peters 1995). Rehabilitants may more often acquire water and invertebrate foraging skills because they are often more terrestrial (Peters 1995; Kuncoro 2004; Grundmann 2006). Sociosexual differences may reflect rehabilitants' immaturity, which could result in fewer sexual and competitive variants, or their orphan peer-reared backgrounds, which could lead to stronger affiliative bonds between unrelated individuals.

Our first approach was therefore simply to compare the behavior of released forest-living rehabilitants with the list of provisional innovations in wild orangutan communities to test the suggestion that rehabilitants may help validate entries (see Box 20.2 and Table 20.1). Naive rehabilitants could have acquired a provisional wild innovation readily, by ecological induction, if that variant occurs in most relevant rehabilitant populations. A provisional wild innovation could also be considered as possibly ecologically induced if it was reported in forest-living rehabilitants under *c*. 4 years old, because orangutans this young may learn primarily through experiential contingencies (Parker and McKinney 1999) and rehabilitants this young had little if any access to knowledgeable social input. We also considered whether entries reflect rare need, which could give the incorrect impression that a behavior is innovative (Byrne *et al*. 2001 a, b; Stokes and Byrne 2001; van Schaik *et al*. 2006a). Rehabilitants showed several provisional wild innovations in the appropriate (rare) circumstances, which suggests that these variants reflect rare need and may not qualify as innovations. Using these criteria, rehabilitant data suggest reconsidering whether the following variants qualify as provisional innovations.

Leaf wiper: clean body (M2). Rehabilitants in four of the five forest communities considered use leaf wipers to clean their bodies. All rehabilitant forests are mutually isolated so social transmission between communities is impossible. Rehabilitants' greater terrestriality may increase needs for wiping although many of the cases reported are not ground-related (e.g., wipe mucus from nose/eye, wipe off ants). If terrestriality is a factor, low prevalence in the wild may reflect rare need of a standard behavior instead of innovation.

Leaf wadge poultice for wound (M4). Evidence in favor of accepting poultice use as a provisional innovation is that it has been observed only at Sabangau and one rehabilitant site whereas wounded orangutans have been observed at multiple sites but did not use poultices, i.e., many individuals have been observed under apparently 'right' circumstances. However, if only certain types of injury are amenable to poultice treatment, only certain types of leaves are suitable for making poultices, or either is hard to come by, then rare occurrence of this behavior could reflect rare need rather than lack of knowledge. This variant may well still be innovative, although more information on the types of wounds treated this way and the types of leaves used would be helpful in resolving the rare opportunity concerns.

Symmetric scratch (M11). Rehabilitants in four of the five forest communities have been reported symmetric scratching, as young as 3–4 years old. The variant described for the wild is highly exaggerated and frequently repeated. This variant has reached cultural status in one population, however, so the exaggerated form could represent ritualization via social learning post innovation. More careful observations and comparisons are needed to reach a final decision.

Table 20.1 Provisional innovations in wild orangutans with rehabilitant comparisons

Item code	Provisional innovation[A]	Original code[B]	Age of youngest actor	Rare need	Wild								Rehabilitant				
					Sumatra		Borneo						Borneo				
					SU	KE	GP	TPw	SA	TU	KU	KI	ME	SW	SL	PK	TPr
	Comfort																
M1	Leaf napkin: wipe latex off chin	C14	3–4								C		Rs	Hs	Hs	Hs	Hs
M2	Leaf wiper: clean body	I2					R		R				Rs	H+	H+	H+	H+
M3	Moss wiper: clean hands	C29							H		?		Rs	Hs	Hs	Hs	Hs
M4	Leaf wadge poultice for wound	I19	5–6	Y					R		?				R		
M5	Leaf pulp foam, smear on body	C30							H		?						
M6	Leaf chew: clean teeth	C32		Y?			P		?	R	?	C	Rs				Rs
M7	Stick tool: pick to clean teeth	I22				P							Rs		R+	R+	?
M8	Stick tool: clean nails	I23				P							Rs		Rs	Rs	
M9	Stick tool: scratch body	C9	5–6					R	R	R	H		R	Rs	Rs	H+	Hs
M10	Wash face/arms in tree-hole water	I24						R		R			Rs	Rs	Hs	R+	R+
M11	Symmetric scratch	C12	3–4		C	R							R		R	R	R
M12	Shelter from rain under nest	C8	?			R		R		R	C	P					?
M13	Bunk nests	C6	(6–7)					P	R	R		H	?	?	R	Rs	?
M14	Sun nest cover	C7	?			H				R	C	C					?
M15	Leaf branch cushion	C27	4–5			H	R	H	H	C	?		Rs	H+	R+	H+	Rs
M16	Rest in *Asplenium* fern	C34				R					?	C	Hs	Rs	Rs	E?	?
M17	Leaf 'bundle' (doll)	I4		N/A			R	R		R						Rs	
M18	Carry leaves to nest in advance	C26	(6–7)					R	R	H	?		C	R		C	C
M19	Nest twig bite	C13		N/A	C		P		H	H			?	?		?	?
M20	Water (splash) play on ground	C39	3–4	N/A	E	E		P	R	H	?	A	H	H	C	C	C
	Sociosexual																
X1	Branch drag display	I9	(4–5)		E	E					?	R		Rs	Hs		
X2	Snag ride	C1	8–9					C	R	H			Rs	Rs	Hs	H	
X3	Kiss squeak with leaves	C2	6–7			R	C		R	H	H					R+	
X4	Kiss squeak plus leaf-wipe	C4						C									
X5	Long call *vibrato* with finger pulse	I20	M adult					Rs	R		?		E	E	E	E	?
X6	Hide behind detached branch	I12		Y		R		R	?	?	P	R	Rs	Rs	Ps	R	Rs
X7	Sneaky nest approach to conspecific	I3	(5–6)			R	R						Rs	Rs	Rs	Rs	Rs
X8	Throat scrape	C28	F adult					R		H	?		?	?	E	?	R
X9	Nest build + smacks	C25		N/A					R	C	?					R	
X10	Nest build + raspberry	C11		N/A	C				C			H					

X11	Auto-erotic tool	C10		N/A		C					P		R		H	H	R?
X12	GG rub	I1		N/A	R		R	R		R			Rs		R+		
X13	Coercive hand-hold	C38	M adol					R	R	H	?	R	R	R		H	?
X14	Female refuge in nest from coercive male	C35	Adol		P	P	P	P	H		?						
X15	Copulation on female's nest	C33	Adol			H	C	R		R	?	R	R+	?	E	H+	?
X16	Share night nest with consort	C31	Adol			?	R				?	C	R	?	E	H	?
	Subsistence																
S1	Branch scoop: drink tree hole water	C19	(4–5)		H				H				?	?	Hs	Rs	Rs
S2	Leaf scoop: drink water	I5	5–6				R							R		Hs	R
S3	Leaf sponge: drink water	I11	3–4			R			R						H+	Hs	H+
S4	Pitcher plant drink, bite off bottom then drink liquid via bottom	I18				E			?	R	?		E	?	E	E	?
S5	Bouquet ant feed	C21	4–5		C	C	C	C		H		H	R	C	R	H	R
S6	Leaf glove to get into biting ants nest (to avoid bites)	I21							R		?	?			Rs		
S7	Break dead twigs, suck ants out	C23	4–5		C	C	?	C	H	H?	?		H+	Cs	H+	H+	?
S8	Stick tool: extract tree-hole insects	C17	5–6		C								R	Rs	R	?	Hs
S9	Stick tool: extract *Neesia* sp. seeds	C18			C	E			E	E	E		E	Rs	E	E	
S10	Stick chisel: open termite/ant nest in log/on ground	I13	3–4			R		R					H	Rs	H	Hs	?
S11	Stick chisel: open durian fruit	I25				R				E	?			Rs	Rs		
S12	Leaf glove/cushion: spiny item	C16			E	C	E	R	E	E		R					
S13	Slow loris capture and eat	C24			H	H									Rs	Hs	
S14	Branch swatter: against attacking bees/wasps (actor raids the nest)	C15	(6–7)		H	H	R	R	R		H	H	Hs	Rs		Rs	?
S15	Branch protector: against bees	I26	6–7							R	?	P	H+		?	?	?
S16	Branch hook to pull adjacent tree	I15	3–4	Y	?	?			R	R	?				R	R	?
S17	Bite vine: release vehicle tree	C37		Y	R		R		R	H	?				Rs		Rs
S18	Bite vine: for Tarzan swing	C36		Y	R		R		R	H	?					Rs	

[A]Variant identifiers; for full definitions see van Schaik *et al.* 2006a, Chapter 20.

[B]Entry code, per van Schaik *et al.* (2006a).

[C]Cell entries show age (in years) or age class of the youngest orangutans reported performing this variant; ages bracketed if they represent a similar variant; blank = no information available.

KE, Ketambe; SU, Suaq Balimbing; GP, Gunung Palung; TPw, Tanjung Puting—wild; SA, Sabangau; TU, Tuanan; KU, Kutai; KI, Kinabatangan; ME, Meratus; SW, Sungai Wain; SL, Samboja Lestari Forest School; TPr, Tanjung Puting—rehabilitants.

Site cell entries: blank, variant absent or probably absent; P, variant present, unknown prevalence; R, rare; H, habitual; C, customary; ?, unknown; E, ecologically precluded; Ps/Rs/Hs/Cs, similar variant present/rare/habitual/customary; P+/R+/H+/C+, recorded variant present/rare/ habitual/customary and similar variant also present.

Box 20.2 Rehabilitant orangutans

Data on free-ranging rehabilitant orangutans, i.e., ex-captives readjusting to free forest life, were used as a basis for validating provisional wild orangutan innovations, suggesting extensions to the repertoire, and insights into orangutan innovative processes.

For the validation exercise, existing databases from systematic behavioral studies by AER at five rehabilitant sites in Borneo were reviewed: Camp Leakey/Tanjung Puting (1989–9191), Sungai Wain (1995–2001), Meratus (1999–2003), Kaja Island (2004–2005), and Samboja Lestari (2006) (see Fig. 23.1—site map, Chapter 23).

For extending the list and exploring innovative processes, systematic data were collected on water-related behavior in one rehabilitant community. Subjects were 43 juvenile to near-adult rehabilitants living semi-free forest lives on Kaja Island, as the final stage of their rehabilitation to forest life at the BOS Foundation Orangutan Reintroduction Project, Nyaru Menteng. Kaja lies in the Rungan River in Central Kalimantan (S 2°1′, E 113° 47′). Habitat is 108.5 ha of decent forest, much of it inundated during wet seasons (Sidiyasa *et al.* 2001). Water behavior on Kaja was observed for 1397 hours, within a focal individual sampling framework, from May 2004 to December 2005. All instances of water-related activity were recorded as detailed narratives, describing location, context, behavior sequence, variations, aims, and companions. Observations yielded 1551 events of 47 functionally distinguished water variants in 41 rehabilitants.

In the Kaja study, a behavior's innovation status was based on local prevalence. We identified provisional innovations, conservatively, as water variants that were uncommon on Kaja island (i.e., seen in <8 members) or common on Kaja but unknown elsewhere (i.e., probably innovations that had spread). Life on Kaja was intensely social, so even rare variants could spread easily and in most cases it was impossible to judge credibly whether common variants owed to ecological induction or social influences.

Innovation studies on Kaja and in the wild took different approaches to identifying provisional innovations, but both were based on innovative products as currently performed, both used prevalence criteria, and both have been used to study innovation elsewhere so they should converge. The criteria used to identify provisional innovations in Kaja data almost certainly underestimate the range of innovations.

Leaf branch cushion (M15). Rehabilitants in three of the five forest communities have been reported using leaf branch cushions, as young as 4–5 years old. One possibility is that this may reflect their region of origin. However, leaf branch cushions are reported in East Kalimantan for rehabilitant but not wild orangutans and since rehabilitants are typically reintroduced to their area of origin, it is unlikely that East Kalimantan rehabilitants acquired branch cushion skills in their region of origin. Other possibilities are that leaf branch cushions may originate in cage life for rehabilitants or their absence in many wild populations may reflect rare need or inadequate reporting.

Water (splash) play on the ground (M20). Water play is rare in wild orangutans and altogether absent in Sumatra, but universal and common at rehabilitant sites; it is also known in captives. 'Need' is not an appropriate descriptor for play but a similar condition, rare opportunity, may pertain to wild orangutans. Ground water can be dangerous to forest-living orangutans, so individual knowledge or social influences (e.g., maternal guidance) could constrain opportunities for using it. Naive rehabilitants acquire water play rapidly given access to ground water, so water play could be a simple product of ecological induction because such constraints are absent. Rehabilitants lack maternal guidance, tend to be more terrestrial than wild orangutans (Peters 1995; Kuncoro 2004; Grundmann 2006), and are typically rehabilitated in areas selected for their safety—all of which could increase their likelihood of engaging with the terrestrial environment in general. No particular skill is indicated so water play seems mainly to entail knowledge that water is fair game for play. Rehabilitants typically live in peer-dominated social milieux and at some sites they may be exposed to use of water by familiar humans, so social influences cannot be entirely ruled out.

Hide behind detached branch (X6). Rehabilitant orangutans and various haplorhine primates are known to hide behind many types of visual barriers, and great apes are known for their ability to understand and act on the basis of another's visual perspective (e.g., Byrne and Whiten 1990; Hare *et al.* 2000; Shillito *et al.* 2005). Thus hiding per se may not be innovative in orangutans and hiding behind a detached branch may reflect rare need—a rare conjunction of events wherein a threat prohibits use of more common ways of hiding such as moving behind dense vegetation or out of visual range. Combining these two components could nonetheless still be innovative.

Bouquet ant feed (S5). This has been reported in all five rehabilitant communities considered here, in rehabilitants as young as 4–5 years old. The absence in a few wild populations may thus reflect inadequate reporting.

Break dead twigs, suck ants out (S7). This has been reported in at least three of the five rehabilitant communities considered here, in rehabilitants as young as 4–5 years old, and may therefore reflect a foraging pattern that is not very innovative.

Stick chisel: open ant or termite nest (S10). Chiselling an invertebrate's nest open with a stick chisel has been reported in four of the five rehabilitant communities considered here, in rehabilitants as young as 3–4 years old. However, its absence in most wild populations, despite its being easily recorded, suggests that this is not a behavior that is easily induced ecologically, but rather requires some innovation. Greater terrestriality could be one factor facilitating chiseling in rehabilitants.

Branch hook adjacent tree (S16). In rehabilitants and wild orangutans, branch hook occurred in situations that suggest rare need: in traveling, the target tree was unreachable from the actor's current position and standard means of reaching it had failed or were unavailable (Fox and bin'Muhammad 2002; Russon personal observation). *Branch hook* could then represent a technique used only when typical ways of reaching a target location are restricted. It has also been observed in rehabilitants as young as 3–4 years old.

Bite vine to release vehicle tree (S17), *bite vine to Tarzan swing (S18).* Van Schaik *et al*. (2006a) suggested that crossing a gap when the choice of trajectory is restricted by some threat could be a rare situation that favors biting. This situation is also rare in rehabilitants, but they often bite vegetation to break it, typically when manual techniques are awkward or insufficient (Kuncoro, personal communication; Russon unpublished data). If their manipulators are occupied with other tasks, like suspensory positioning or supporting an infant (Cant 1987a; Russon 2002), rehabilitants may tear vegetation apart with one hand and teeth. If vegetation is more easily broken using three than two manipulators, they may use both hands to hold it taut and teeth to bite it apart. Similar manual–biting mixes are reported in chimpanzees (Morimura 2006; Ohashi 2006). Biting may also be relatively common in rehabilitants because most are studied as immatures, who lack adult strength. Similarly aged wild immatures may have less need to bite through vegetation because their mothers help them cross gaps that are difficult to bridge (chapter 12). Together, this suggests that both entries may represent rare need although the rare component may be the difficult trajectory alone; rare use of biting may reflect preference for manual methods rather than lack of knowledge.

20.3.3 Comparing wild orangutan innovations with rehabilitant controls: modifications

Rehabilitant data often included modifications of provisional wild innovations. Examples include using attached versus detached leaves, making a cushion on the ground or a platform versus on a branch, using different leaf species, using grass, coconut fibre, or corn husks as well as leaves for wipers, using branch swatters against bees when not raiding their nests, using fern leaves versus detached leafy branches as bee swatters, using other items for erotic stimulation (partner's hand, floor) as well as genito-genital rubbing, and sucking dead twigs for termites versus or as well as ants. Many of these modifications differ only in the items used (e.g., grass versus leaf wiper, wipe eye versus chin) or functional detail (e.g. swat bees when not versus when raiding their nest, branch drag to invite play versus threaten). It may then be useful to validate provisional wild innovations with rehabilitant modifications included.

First, including rehabilitant modifications revives the question of how to distinguish variants, and the issue of what grain is appropriate for defining variants. Rehabilitants used some modifications interchangeably in one bout or in the same context on different occasions. Using van Schaik *et al.*'s (2006a) criteria for distinguishing variants, the relevant entries may thus not qualify as different. Accordingly, differentiating the following entries is worth reconsidering.

Leaf napkin: wipe latex off chin (M1), leaf wiper: clean body (M2), moss wiper: clean hands (M3).

Within one bout, individual rehabilitants have used one leaf wiper to clean multiple body parts (face, hands, other parts). Rehabilitants also use leaf wipers to clean multiple substances (e.g., faeces, biting ants). The items orangutans use as wipers also suggest some interchangeability. Rehabilitants use leaves, grass, coconut fibre, corn husks, cloth, and plastic as wipers. One wild Kutai infant *c*. 4 years old used three items as wipers to clean *Diospyros borneensis* latex and fruit debris from around its mouth during one 30 minute feeding bout—attached leaves, detached leaves (twice), and a fruit itself (Russon, Kuncoro and Ferisa personal obesrvation). Each time it used items from the *D. borneensis* tree within easy reach, appearing to observers to pick whatever was available and suitable as a wiper and treating the three items as functionally interchangeable. In Sabangau, multiple items can serve as wiper agents (leaf, moss) and targets (latex and feces; face and other body parts). With rehabilitants included, application of van Schaik *et al*. (2006a) criteria suggests that wiper entries distinguished by specific wiper tool items (leaf, moss) and targets (body parts, substances) may not qualify as distinct variants. Tentatively, it may be worth combining them into a single entry, 'wiper'.

Leaf branch cushion for resting (M15), leaf glove/ cushion for spiny items (S12).

Some individual rehabilitants arrange leaves as cushions on branches, the ground, and logs so cushion site can be interchangeable and therefore may not qualify as a defining distinction. Cushions do not serve obviously different functions in resting versus foraging contexts, so context may not constitute a functional distinction. The procedures described are also the same, the equivalent of making a nest lining: break one or two branches, place them on the chosen site, and sit/lie on them. Accordingly, it may be useful to redefine *branch cushion* as *seat cushion,* and delete the 'rest' component from the description in van Schaik *et al*. (2006a). The cushions used in spiny trees may be more elaborately constructed than some branch cushions so further observation may be needed to clarify the nature and importance of differences.

Bouquet ant feed (S5), leaf glove to get into biting ants' nest (S6), leaf glove/cushion for spiny item (S12).

For both gloves, function could be construed as protecting hands against items that inflict prick types of pain. At Ketambe the two uses appear to be differentiated (gloves are used for spiny items but not biting ants), but *leaf gloves for spiny items* have become cultural at Ketambe so usage could have altered with social transmission. In rehabilitants, *leaf glove for biting ants* may be linked to, or even derived from, *bouquet ant feed*. Most ants for which rehabilitant bouquet feed is reported inflict bites. The way rehabilitants bouquet-feed on biting ants suggests that this is a dual purpose technique that both manages the rate at which ants exit the nest and protects against their bites (Russon personal observation). Bouquet feed has not been reported for biting ants in wild orangutans, however, so the function here is limited to managing foraging. Further observations focused on variations in usage, acquisition, and form may help clarify the relations and distinctions among them.

Second, including rehabilitant modifications alters geographic prevalence patterns. We compared geographic prevalence of provisional wild innovations at wild vs rehabilitant sites, including rehabilitant variants that are (1) exact matches to and (2) modifications of wild entries. We included entries from the original list of provisional wild innovations for which at least four rehabilitant and four wild sites had at least two good absence/ presence estimates (n = 43). We rated prevalence as different for entries where geographic prevalence differed between wild and rehabilitant sites by >25 %. Table 20.2 shows the results of these

Table 20.2 Geographic prevalence of provisional wild innovations in wild vs rehabilitant orangutans

Category	Item code	Provisional innovation	Geographic prevalence: wild vs rehabilitant orangutans	
			Exact match	Modifications
Comfort	M12	Shelter from rain under nest	W	W
	M14	Sun nest cover	W	W
	M6	Leaf tooth cleaner	W	E
	M7	Leaf bundle ('doll')	W	E
	M5	Leaf pulp foam, smear on body	E	E
	M4	Leaf wadge poultice for wound	E	E
	M3	Moss wiper: clean hands	E	R
	M8	Stick tool: clean nails	E	R
	M1	Leaf napkin: wipe latex off chin	E	R
	M15	Leaf branch cushion	E	R
	M9	Stick tool: scratch body	E	R
	M10	Wash face/arms in tree-hole water	E	R
	M18	Carry leaves to nest in advance	R	R
	M7	Stick tool: pick to clean teeth	R	R
	M20	Water (splash) play on ground	R	R
	M11	Symmetric scratch	R	R
	M20	Leaf wiper: clean body	R	R
Sociosexual	X14	Female nest refuge from coercive male	W	W
	X3	Kiss squeak with leaves	W	W
	X10	Nest build + raspberry	W	W
	X12	GG rub	W	E
	X6	Hide behind detached branch	W	R
	X7	Sneaky nest approach to conspecific	W	R
	X1	Branch drag display	E	E
	X4	Kiss squeak plus leaf-wipe	E	E
	X9	Nest build + smacks	E	E
	X13	Coercive hand-hold	E	E
	X2	Snag ride	E	R
	X11	Auto-erotic tool	R	R
Subsistence	S12	Leaf glove/cushion: spiny items	W	W
	S18	Bite vine: for Tarzan swing	W	W
	S14	Branch swatter	W	E
	S17	Bite vine: release vehicle tree	W	E
	S13	Slow loris capture and eat	W	E
	S6	Use glove to get into biting ants' nest	E	E
	S11	Stick chisel: open durian fruit	E	E
	S7	Break dead twigs suck ants out	E	E
	S16	Branch hook to pull adjacent tree	E	E
	S5	Bouquet ant feed	R	R
	S10	Stick chisel: open termite/ant in log/on ground	R	R
	S3	Leaf sponge: drink water	R	R
	S2	Leaf scoop: drink water	R	R
	S8	Stick tool: extract tree-hole insects	R	R

Geographic prevalence: entries compare geographic prevalence of provisional innovations in wild vs rehabilitant orangutans, based on rehabilitant variants that are (1) *exact matches* and (2) *modifications*.

W, wider prevalence in wild orangutans; E, roughly equal prevalence in wild and rehabilitant orangutans; R, wider prevalence in rehabilitant orangutans.

two comparisons. Considering rehabilitant variants that appear to match provisional wild innovations exactly, geographic prevalence is wider in wild orangutans for 15 entries, roughly equal for 17 entries, and wider in rehabilitants for 11 entries. Considering rehabilitant variants that are modifications of provisional wild innovations, geographic prevalence was wider in wild orangutans for 7 entries, roughly equal for 16 entries, and wider in rehabilitants for 20 entries. Broadly interpreted, geographic prevalence of provisional wild innovations was wider in rehabilitants for most stick tools, all wiper tools, drink tools, water play, washing, simple nesting techniques, sneaky behaviors, and riding vegetation.

The broad points raised are that (1) rehabilitant data validate provisional wild innovations differently depending on what behaviors are included, largely because of the grain problems they suggest, and (2) from some perspectives, rehabilitants may be more innovative than their wild counterparts.

20.3.4 Extending the list of orangutan innovations: rehabilitant innovations for water

Using rehabilitant data for validation purposes considers only provisional innovations identified in the wild. The rehabilitant communities we considered are forest-living, so they may generate different local innovations that can extend understanding of innovation in orangutans living in species-typical conditions. Russon *et al*. (in preparation) explored what rehabilitants may add to the repertoire of provisional innovations via a systematic study of behavior with water (see Box 20.2). Water variants were identified as potential innovations if they were rare on Kaja island (i.e., reported in <8 members) or common on Kaja but unknown elsewhere. These criteria identified 19 provisional water innovations on Kaja (see Table 20.3). Kaja water variants include all five water-related provisional innovations identified in wild orangutans—*wash in tree-hole water (M10)*, *water play (M20)*, *branch scoop drink (S1)*, *leaf scoop drink (S2)*, *leaf sponge drink (S3)*—plus *branch hook (S16)* (included because its use on Kaja was crossing water); all but *M20* also qualified as possible innovations on Kaja by within-population criteria. Kaja rehabilitants also used scoops and sponges for water purposes beyond drinking (e.g., bathe, play), to access water in locations beyond tree holes (e.g., on the ground), and made from items other than leaves (e.g., scoop—cup, bottle, coconut shell; sponge—moss, coconut fibre, corn leaves, leaf bouquet).

At least concerning water, Kaja rehabilitants showed a much wider repertoire of provisional innovations than wild orangutans, even though the criteria used probably still underestimate Kaja rehabilitants' repertoire of water innovations. All but three of the provisional water innovations on Kaja (wash face/arms in tree-hole water, splash water, copulate in water) represent skills, some of them sophisticated, so their acquisition probably involved considerable involvement with water. There was no indication that these skills were obvious or inevitable products of experience with water, however. All except tree bridges were rare on Kaja and highly individualized solutions to difficult versions of the relevant task (Russon *et al.* in preparation).

20.3.5 Innovation and cognition

As a step toward inferring what was innovated, we assessed what is novel in provisional innovations following Byrne (2003). We estimated novelty as the difference between provisionally innovative variants and (1) standard wild variants and then (2) rehabilitant modifications. We used standard wild variants to approximate prior knowledge because we did not know which behaviors an actor knew when it created a provisional innovation. We used rehabilitant modifications to suggest the kinds of changes that orangutans tend to generate beyond known behavior. The features that these methods identified as probably novel, their distribution, and examples are shown in Table 20.4.

We compared each provisional wild orangutan innovation with more standard wild variants in order to isolate the novel features. Differences between these two suggested five types of novelty:

1. using new combinations of known components,
2. using known behavioral components for new purposes,
3. adding tool use to a known technique,

Table 20.3 Additional provisional water-related innovations in rehabilitants

Kaja variant	Kaja (number OU)	Wild (number sites)	Rehabilitant (number sites)	Comments
Pull water to retrieve floating item. Dip hand in water between self and item floating out of reach, repeatedly *pull* water (create current) to draw item closer, grab item	3			
Intercept. Travel to intercept then grab an item floating away with current	2			P: C S: 7
Dredge with tool. Dredge pond bottom for sunken items using a stick tool	1			
Sponge drink. Use item to absorb water, then squeeze, wring, or suck water from sponge into mouth	2	4 (I11)	4H TP, PK, SL, SP	P: C, h, c S: 1, 2, 3, 5, 6
Dig sand hole, drink water. Dig sand hole, wait until it fills with water, drink from hole	5			P: C, B, m S: 4, 6
Branch scoop. Dip leafy branch into hole with water in it, drip water into mouth.	1	2 (C19)	3H TP, PK, SL	S: 1, 4, 5
Wash face/arms. Wash face or arms with water from tree hole	1	2 (I24)	1R PK	
Submerge. Deliberately submerge body, head included, under the surface of the water (no functional goal clear, possibly practice for obtaining items sunk in deep water)	1			
Swim. Travel a short distance through water free-floating: glide or rudimentary paddle	2			
Tool test depth. Test water depth with stick	2		2R PK, TP	P: G S: 2, 4, 8
Use floating log 'boat'. Travel over water on floating vegetation.	3		2R TP, PK	P: C S: 3, 4
Branch hook (to cross water). Find/make branch with hook at end, hook outer branch of overhanging tree and pull it within reach	1	2 (I15)	2R PK, NM	P: C S: 1, 2, 5, 15
Tree bridges. Bend tree until crown lies in water, walk across water on bent tree	22			
Splash water. Splash water at companion to attract attention	4			P: C, G S: 6, 13, 14
Copulate in water. Male pulls female into water then copulates with her there	1			
Hide in water. Travel in deep water, ducked down so that only the top of the head is visible, to avoid opponents	4			
Eat fish. Take and eat fish from water (most floating, dead but some alive)	1	1		P: b?, m S: 9, 10, 16
Eat water-logged rengas fruit. Grope river/pond floor to retrieve sunk rengas fruit, eat it	6			
Soak food. Soak food in water, eat food plus absorbed water (sugar cane, soap)	3		1C PK	P: C, ca S: 2, 11, 12

Kaja variant, entries name and define provisional water innovations on Kaja, i.e., variants used by $<$20% of community members or common variants not reported elsewhere

Orangutans: Kaja (number OU), cells show number of Kaja rehabilitants who performed a variant; Wild (number of sites), cells show number of wild sites where each variant has been reported (if variant is provisionally innovative, identification code is in parenthesis) and the relevant sites (KU-Kutai); Rehabilitant (number of sites), cells show number of rehabilitant sites where each variant is known, the highest reported local prevalence level.

R, rare; H, habitual; C, customary; and the relevant sites, PK, Kaja island; TP, Tanjung Puting; SL, Samboja Lestari forest school; NM, Nyaru Menteng forest school; SP, Sepilok.

Comments: P (other primates): other non-human primates reported performing variant. C, chimpanzee (*Pan troglodytes*); B, bonobo (*Pan paniscus*); G, gorilla (*Gorilla gorilla*); h, gibbon (*Hylobates* sp.); s, siamang (*Symphalangus syndactylus*); c, cebus (*Cebus* sp.); b, baboon (*Papio* sp.); ca, *Chlorocebus aethiops*; m, *Macaca* sp. S (sources): Sources of Supporting evidence.

1, van Schaik *et al.* (2006a); 2, Russon unpublished data; 3, Galdikas (1982b); 4, Russon and Galdikas (1993); 5, Russon; Handayani; Kuncoro; Ferisa in preparation; 6, Yamakoshi (2004); 7, Iversen and Matsuzawa (2003); 8, Breuer (2005); 9, Hamilton *et al.* (1975); 10, Kalimantan Prima Coal personal communication; 11, Boesch (1991); 12, Hauser (1988); 13, Parnell and Buchanan-Smith (2001); 14, Nishida (1993); 15, Whiten *et al.* (1999); 16, Watanabe (1989); Leca *et al.* (2007a).

Table 20.4 Probable novelty in provisional wild orangutan innovations

Probable novelty	Frequency (% variants)	Examples
Provisional wild innovations vs standard wild variants		
New combination: perform several standard variants in new combinations	31 (57)	M13 *Bunk nests*: build two standard nests in a novel combination, one above the other X3 *Kiss squeak with leaves*: newly combine leaf with standard kiss squeak to amplify sound X9/10 *Nest build with smacks/raspberry*: newly combine standard nest building with smack/raspberry sounds[1]
Novel tool: newly use tool for task typically handled manually	22 (41)	M9 *Stick body scratcher*: scratch with stick vs manually X11 *Auto-erotic tool*: stimulate with tool vs socially/manually S9 *Stick tool extract Neesia sp. seeds*: extract *Neesia* seeds with tool vs manually
Novel items: use novel items (agent, target) to perform standard variant	18 (33)	M1/2/3 *Leaf napkin wipe latex off chin, leaf wiper clean body, moss wiper clean hands:* wipe selected body parts with leaf/moss tool vs manually M16 *Rest in Asplenium fern*: rest in *Asplenium sp.* epiphytic fern vs other vegetation
Novel operation: add new operation to standard variant	7 (13)	S9 *Stick tool extract Neesia sp. seeds*: add new tool operation, scrape out stinging hairs—an operation not used (or needed) when fruits are opened manually
Novel function: use standard variant or item for new purpose	22 (41)	M6 *Leaf chew to clean teeth*: chew leaves for cleaning vs consumption M12 *Shelter from rain under nest*: use nest for cover vs resting surface M14 *Sun nest cover*: Cover nest to protect against bright sunlight vs rain
Provisional wild innovations vs rehabilitant modifications		
Tool use difference: use manual method or different tool vs novel tool	10 (19)	M4 *Leaf wadge poultice for wound*: treat wound by applying poultice vs manually/orally X3 *Kiss squeak with leaves*: kiss squeak against leaf vs. twig/tree surface S1 *Branch scoop drink tree hole water*: dip branch vs rock into water then drink S2 *Leaf scoop drink water*: make scoop from one leaf vs two leaves
Item difference: perform same variant with different agent/target items	36 (67)	M18 *Carry leaves to nest in advance:* select *C. campnosperma* vs other leaf species X6 *Hide behind detached branch*: hide behind branch vs tree, building, floating log X12 *GG rub*: stimulate genitals on partner's genitals vs fingers, toes, ear, belly button S3 *Leaf sponge drink:* sponge with leaf vs grass, coconut/corn husk, rubber sponge
Behavior topography difference: enact functionally equivalent variants with different behavior	18 (32)	M4 *Leaf wadge poultice for wound*: treat wound with poultice (select, collect, and chew leaves, place chewed leaf wadge on wound) vs orally (suck, lick) or manually (pick, poke) X7 *Sneaky nest approach in fruit tree*: sneaky approach by building successive nests vs doing other distracting activities, e.g., fake eat, examine vegetation, groom
Different purposes: same variant used for different or wider purposes	27 (48)	M18 *Carry leaves to nest in advance*: carry leaves to nest in advance to repel insects or parasites vs or comfort or social gesture X1 *Branch drag display*: branch drag display to provoke withdrawal vs. invite play

[1]Whether nest-related raspberry and smacking sounds are identical to those used in non-nesting situations remains uncertain.

4. incorporating new agents or target items into a known technique, and
5. using new operations to achieve common goals.

From most to least common, probable novel features in provisional wild innovations were: new combinations (57% of entries), newly use tool (41%), new purposes for known components (41%), new agent or target items (33%), and new operations (13%) (see Table 20.4). Percentages total more than 100% because one innovative variant could differ from standard variants on several features. Probable novelty involved a single feature for 41% of provisional innovations and two, three or four features for 39%; 17%, and 4% respectively.

In addition to matching 28 provisional wild innovations, rehabilitants performed modifications of provisional wild innovations. Comparisons between provisional wild innovations and rehabilitant modifications indicated these differences: rehabilitants used the same technique but with different agent/target items (63%), with different or no tools (18%), with altered behavioral topography (32%), for different purposes (12%), or for a wider range of purposes (36%).

Both comparisons suggest that provisional wild innovations differ in relatively small ways from standard wild variants and similar rehabilitant behaviors. The greatest novelty suggested in provisional wild innovations was four features, for *leaf wadge wound poultice (M4)* and *leaf chew–tooth clean (M6)*. These variants have been confirmed at only one (M4) or three (M6) wild sites each so their purposes and origins are not well understood.

These comparisons also raise grain issues in defining provisional innovations. Tool entries illustrate the complexities. 'Tool' is a general category that subsumes at least four features, each of which can vary within functional limits: *tool type* (e.g., probe, wiper, hammer, sponge), *agent* (e.g., stick or rock as hammer, twig or grass shoot as probe), *target(s)* (e.g., insects, seeds, face and latex), and *operation,* the particular object-object relation manipulated between tool item and target (e.g., wiper—leaf *rubs* substance off body; sponge—leaf *absorbs* liquid). Type and operation are not isomorphic because some tool types can be used for several operations (e.g., hammer—pound/knap; chisel—carve/stab). In this light, some provisional innovations are defined at different grains. *Leaf napkin* (M1) and *stick chisels (S10, S11)*, for instance, specify tool *type* (wiper, chisel), *agent* (leaf, stick), *operation* (rub, stab/tear open), and *targets* (chin and latex, termite nest, durian fruit). In contrast, *autoerotic tool (X11)* leaves three features unspecified and all can vary. In rehabilitants, erotic tools vary in *type* (probe—female, sheath—male, massager—both), *agent* (e.g., stick or finger as probe, fruit pulp or partner's belly button as sheath, leaf or partner's genitals as massager), and *operations* (e.g., insert, encase, rub). Some current entries should then perhaps be redefined. We offer two examples below. For both, what components are different for actors needs to be established before grain can be determined correctly.

Stick tool: extract insects (S8) and *stick tool: extract seeds (S9)* are known only in wild orangutans at Suaq Balimbing. Both involve using stick tools to extract embedded foods—basically, probe tools. Some evidence suggests these two uses represent distinct variants. First, all individuals in Suaq Balimbing differentiated the probe tools they made to extract seeds and insects: seed tools were reliably shorter, wider, and less often stripped of bark (Fox *et al*. 1999). Second, tool manipulations used in the two tasks are clearly distinct: careful dipping versus scooping and forceful wiggling. Third, one cluster of females at Suaq hardly ever used insect tools but were as adept as others at using seed tools (van Schaik *et al*. 2003b). Other evidence, however, suggests orangutans may construe the two uses as unified. First, probing is one of the great apes' two most dominant tool operations, it is typically used to obtain hidden foods (nesting insects, bone marrow in monkey skulls), within the primates tool probing is unique to great apes, and hidden foods are consumed primarily by great apes (Yamakoshi 2004). Notably, both seed and insect tools are used to poke and scrape (Fox *et al.* 1999). Second, several individuals used both seed and insect tools. Thus one principle, probing, might govern both seed and insect tool extraction. The two techniques could have fundamental similarities for orangutans and observable differences could represent the motor action level flexibility typical of great ape tool use. One female for which data were plentiful modified all her probe tools case by case, so she may have worked from the understanding that a probe tool was needed for all these foods and adjusted her chosen stick to local conditions (Fox *et al*. 1999). Some evidence then suggests lumping these two entries as one variant that is expressed with context-related functional modifications, while some suggests maintaining the current distinction.

Carrying leaves to nest in advance (M18). At Tuanan, several orangutans collect *Campnosperma coriaceum* leaves, carry them to their nesting site, park them while making a nest foundation, and then use them to make a nest lining, cover, or pillow. *C. coriaceum* is the only species used this way, possibly because *C. coriaceum* leaves may have parasiticidal qualities (Mabberley 1997). This is consistent with *C. coriaceum* being the most popular choice for tree nests in Sabangau (see Chapter 19) although it is not at Tuanan. In contrast, at all rehabilitant sites, advance leaf carrying for nesting is common but several leaf species are used. Rehabilitant data suggest leaf species is not a functional distinction. This suggests that orangutans may distinguish the items serving a variant at some sites but not others, depending on the local functions served.

20.4 Discussion

The prevalence method has already generated an extensive list of provisional wild orangutan innovations. The varied ways in which these variants have been identified and defined expose a rich array of complexities to be unraveled. We compared rehabilitants' behavior with these provisional innovations as one means of exploring these complexities. Because rehabilitants have different experiences than their wild counterparts, this attempt at validation has its limitations, but it nonetheless raises important issues for studies of spontaneous innovation in free-ranging orangutans and other great apes. It suggests reconsidering some entries, redefining others, and raises methodological issues including difficulties in identifying the proper grain of analysis.

We also treated sites with released rehabilitants as additional populations of forest-living orangutans to explore extensions to the list of provisional innovations. While the extensions we considered concern water-related behavior only, the exercise suggests that rehabilitants generate innovations similar in quality to those produced by wild orangutans but are more exploratory and creative than their wild counterparts (Table 20.2). One implication is that rehabilitants may not provide a good basis for validating the prevalence approach to identify innovations, at least not in orangutans and perhaps other great apes. The same may be true for conspecifics held in zoos (Lehner in preparation).

Isolating the probable novelty in provisional innovations suggests that orangutan innovation typically involves relatively minor changes to existing behaviors in the form of component-level changes to stable programs. Even the two entries that suggest innovative programs, catching and eating vertebrates (slow loris, fish) and swimming, are probably rooted in standard behavior. Capturing vertebrates could build on existing skills for capturing fleeing conspecifics or invertebrates. Swimming looks strikingly novel but traveling through buoyant media characterizes orangutan arboreal locomotion, which involves manipulating canopy compliance (Povinelli and Cant 1995; Thorpe *et al*. 2007b). Rehabilitants' lunge and glide technique for swimming short distances closely resembles the standard orangutan technique for swaying vehicle trees to cross canopy gaps. Their capacity to repeatedly extend their existing capabilities in new directions and to appreciate similarities between situations that seem very different on the surface is nonetheless impressive.

20.4.1 Why are released rehabilitants more innovative?

If rehabilitants are more innovative than wild orangutans, the question is why. We consider three possibilities. First, their tendency to innovate may be affected by the lack of maternal guidance. Almost all were deprived of mother and community when captured as infants. Social learning and culture contribute substantially to orangutans' acquisition of expertise in the wild (Russon 2002, 2003b; van Schaik *et al*. 2003a). Social input channels immatures toward some and away from other features of their environment, effectively altering ecological influences (Huffman and Hirata 2003; Ohashi 2006). Rehabilitants, deprived of normal social constraints, may engage with facets of their environment that their wild counterparts normally ignore or avoid; ground water is one example. Rehabilitants' lack of expert social guidance, especially maternal, also leaves them with little choice but to invent their own solutions. This could lead to developing cognitive styles geared to independent problem-solving more than to social learning.

Second, humans may have replaced mothers as parental figures. Captive life before release may have enhanced the salience of humans and their artifacts, which could bias rehabilitants to atypical behaviors by providing them with experiences not available in the wild. The extent of human influence on individual ex-captives varies, however, and how much human influences affect forest behavior is unclear.

Third, rehabilitants may appear more innovative than wild orangutans because most were studied as immatures, mainly juveniles and adolescents. Immature great apes may vary their behavior more than adults, probably because they continue to modify their skills until nearly adult (Corp and Byrne 2002a; Biro *et al.* 2006; Humle 2006; Ohashi 2006). Mastering adult foraging skills, for instance, can involve learning through juvenility in many primate species, including chimpanzees and orangutans, often to improve efficiency (Matsuzawa 1994; Corp and Byrne 2002b, Lonsdorf *et al*. 2004; Humle 2006; Russon 2006). However, special attention has been paid to immature wild orangutans at several sites (Suaq, Ketambe, Tuanan; see also Chapter 12) and they still seem less innovative than rehabilitants. Multiple factors then probably contribute to the difference, but the lack of the mother as a reliable behavioral guide is probably the most important in forcing rehabilitants toward independent exploration, and thus innovation.

20.4.2 Cognitive foundations of great ape innovation

The types and levels of novelty suggested by provisional innovations are consistent with what is known about great ape cognition (Byrne and Byrne 1993; Gibson 1993; Matsuzawa 1996; Byrne and Russon 1998; Russon 1998, 2004). All provisional innovations identified are consistent with the characteristics of great ape cognition identified below.

1. Behavioral competencies are constructed piecemeal, over time, by combining several behavioral components into larger programs. Variations are often generated by recombining components in different patterns.

2. Beyond infancy, behavioral programs and procedures are typically organized hierarchically. This allows individuals, on a facultative basis, to: vary the components they use across performances, vary the sequential organization of a routine to suit current conditions, incorporate alternative or optional components or procedures/subroutines in a particular performance of a given routine, fix errors as they occur, and iterate specific components or procedures until predefined criteria are met.

3. Great apes' capacity for understanding and manipulating physical cause–effect relations supports generalized tool and proto-tool making and use (McGrew 1992b; van Schaik *et al*. 1999; Byrne 2004; Yamakoshi 2004). Coupled with their dexterity, this may allow them to invent certain types of tools easily under diverse living conditions, like probes, hammers, sponges, or gloves (Huffman and Hirata 2003). Their causal understanding appears to extend to a limited range of physical object–object relations, which probably constrains the types of tools they can invent. This may explain why virtually all the tools in provisional wild orangutan innovations—scratcher, scraper, wiper, sponge, poultice, swatter/fan, hook, probe, scoop, lever/pry tool, missile, chisel/hammer, cover, stimulator, glove/cushion, amplifier, and container—are also known in wild chimpanzees (McGrew 1992b; Whiten *et al*. 1999; Yamakoshi 2004).

4. Great apes can classify items by function, i.e., identify a group of functionally equivalent items. This allows them to vary the items used to make a given kind of tool or achieve a given function (e.g., leaf wadge, coconut fibre, or grass can function as a sponge) and to substitute unusual items for more common ones within standard functional skills (Boesch and Boesch-Achermann 2000; Russon 2004; Humle 2006; Ohashi 2006;).

5. Great apes can entertain multiple representations of a given item, so one item can be used for multiple purposes. In chimpanzees, e.g., a leaf can be a drinking vessel, wiper, probe, material for making a sponge, grooming stimulator, courtship signaller, or medication (Huffman 1997). Accordingly, items or actions already in their behavioral repertoire can be co-opted for or applied to new uses. In orangutans, nests offer a good example.

Taken together, evidence is consistent with the expectation that orangutans typically innovate at the intermediate level of procedures. Examples here are leaf carrying for nests, using a poultice, bunk nests, leaf bundles, coercive hand-hold, sponging, leaf gloves, and branch hook. Normally, component detail (simple actions, specific targets) may not define distinct variants; this is especially important for functional variants, where detail must be flexible for instrumental reasons. Nonetheless, leaf-carrying at Tuanan shows that what looks like behavioral detail may represent a significant functional distinction. Difficulties lie in identifying which detail represents meaningful distinctions and obtaining sufficiently large samples to confirm them. Clearly important for future work are studies of acquisition, as one basis for better understanding the grain of variants that may be innovative and how orangutans construct behavioral techniques. At this point, it may be appropriate to combine provisional wild innovations that are currently distinguished only by action elements and to reconsider those defined by cultural status.

20.4.3 Methodological implications

Finally, these findings have several important implications for methods that attempt to identify innovations from current variants, the prevalence method included.

1. A current variant may well differ from its founding innovation. Social transmission may be inexact and biased in great apes. Especially for functional behavior, great apes typically copy the modeled program or goal and generate behavioral details independently (Byrne and Byrne 1993; Byrne and Russon 1998; Call and Tomasello 1998; Myowa-Yamakoshi and Matsuzawa 2000; Stokes and Byrne 2001; Humle 2006). Given how social and individual learning operate in great apes, cultural variants in particular are liable to differ from the original innovation. Models' preferential use of some of the components they know would also favor learners' acquiring preferred components only because of differential social learning opportunities. Furthermore, current variants may represent passing phases in the lengthy process of building and honing behavior, and the grain of changes can vary with age and experiential factors (Inoue-Nakamura and Matsuzawa 1997; Parker and McKinney 1999; Stokes and Byrne 2001; Huffman and Hirata 2003; Russon 2004, 2006). When actions are first combined, for instance, they are probably handled as separate elements but after frequent use in combination they may be chunked or integrated into a larger, unified component (Case 1985; Byrne *et al*. 2001a; Biro *et al.* 2006). Both imprecise social transmission and individual change could generate the change over time reported for some great ape and monkey traditions; most evidence suggests that it is variant details that are primarily affected (Watanabe 1994; McGrew 1998; Huffman and Hirata 2003; Perry 2003; Perry *et al*. 2003). The extent to which this kind of change over time matters probably depends on research questions.

2. Current variants that are very similar can originate from different processes, so it is risky to impute origins from current performance. Advance collection of leafy nest materials is a prime example. At Tuanan, it may represent an innovation to repel insects or parasites but in rehabilitants, it probably originated from ecological influences (cage conditions) and was revived in forest life by social priming (Russon *et al*. 2007a). This problem may be less acute if only wild populations are compared, although this remains to be proven.

3. Until innovation has been studied systematically at more sites, identifying innovations relies heavily on post-hoc review of data collected for other purposes. This always limits the accuracy and completeness of reports. For innovation, it may exacerbate grain problems. Especially for behaviors that were beyond the scope of the originating study, data are unlikely to have been recorded at a uniform level of detail. Thus the study of innovation, just like that of culture (see Chapter 21), requires a new round of observations following each round of comparisons.

4. Work by Byrne's group shows how large samples must be to define great ape variants. Programs are easily recognized because they tend to be stable but their organization and components are flexible, so defining variants fully requires enough data to identify all components at all levels. Actors who know multiple techniques for handling a given task may use some more often than others, and low-level components in particular are often used flexibly in response to local conditions or preferences (Stokes and Byrne 2001; Corp and Byrne 2002a; Morimura 2006). Byrne's group (Byrne *et al*. 2001 a, b; Stokes and Byrne 2001) identified 70–190 different action elements for one feeding technique and even 9–22 event samples per actor underestimated the number of action elements known for some actors. The variability shown by available data can easily underestimate true flexibility, which creates a risk of defining a variant at too fine a grain.

5. Rare need is recognized as problematic. Innovations often show low prevalence but low prevalence may have other causes, including rare need, rare opportunity, or low preference. Rare need or opportunity may account for low prevalence in some of the current provisional innovation entries. Low preference is also a probable cause of low prevalence because great ape actors hone their techniques for efficiency (Byrne *et al*. 2001b; Corp and Byrne 2002a; Stokes and Byrne 2001; Russon 2006). The problem is especially acute for the anecdote compilation technique used in most previous comparative work on innovation (Ramsey *et al.* 2007).

6. Current criteria for distinguishing variants could suggest that modifications are interchangeable when they are not. A rehabilitant event involving *Branch scoop drink (S1)* and *Leaf sponge drink (S3)* illustrates the problem. A juvenile male *c*. 6–7 years old drank water from a stream four times within one drinking bout (*c*. 2 min). He (1) sipped directly, (2) dipped one hand into the stream then held it over his head to drip water into his mouth, (3) picked a leafy twig, dipped it into the stream, then held it over his head to drip the water from the leaves into his mouth (branch dip), and (4) immediately after branch dipping, put the same leaves in his mouth, chewed them into a wadge, dipped the wadge into the stream, then sucked water from the wadge (Russon personal observation). Using all four modifications in one bout might suggest functional equivalence but observers' impression was that he varied them deliberately to increase the amount of water obtained. Similar sequential variation occurs in wild orangutans (Fox and bin'Muhammad 2002) and chimpanzees (Biro *et al*. 2006; Humle 2006; Morimura 2006). The implication is that using multiple modifications within a single bout for ostensibly similar purposes may not imply functional equivalence.

7. Ecological influences on behavioral differences can be very subtle. The classic example is chimpanzees' differential use of long vs short wands for dipping driver ants (*Dorylus* spp.): this difference was originally attributed to social transmission but later found to owe to 'microecological' factors (Humle and Matsuzawa 2004; Humle 2006). Collecting leaves for nesting in Tuanan is a probable orangutan example: leaves of a single species are probably collected for their chemical properties (Russon 2006). While such subtle differences may still be innovations, even if linked to ecological factors, this is another reason for reconsidering entries defined at very fine levels of detail. A further concern this raises, however, is how much ecological influence constitutes ecological induction and thereby disqualifies a variant as innovative.

20.5 Conclusion

In the study of innovations as species-normal in wild orangutans, prevalence data have brought to light a rich range of behaviors that are potentially innovative. Challenges to current prevalence-based findings were shown up by comparing them with the behavior of forest-living rehabilitants, typical wild orangutan behaviors, and cognitively governed skills in great apes. These comparisons, as validation exercises, each raised questions about some provisional wild innovations. Prominent issues include valid empirical bases for inferring behavioral novelty, identifying the nature of the novelty involved, and determining the grain at which to define it. These comparisons also contribute to understanding innovative processes: empirical comparisons help isolate the probable nature of the innovation in a given variant; comparisons with immature rehabilitants suggest the importance of maternal channeling in encouraging or constraining innovation; and cognitive findings offer suggestions on how to conceptualize the creative processes involved.

Questions raised for some provisional wild innovations probably owe to reliance on post-hoc analyses of existing databases, so there may be no other option now than to define them at the level of detail given in observers' reports. Systematic data collection designed specifically for the study of innovation should resolve many of these problems. Important considerations raised here include sampling and data collection systems that include the flexibility in components (e.g., sequential information on changes in form across repetitions within a bout). Other questions can be addressed by combining prevalence indicators with additional evidence. The problem of rare need is recognized, for instance, so estimation of rare need at a site would alleviate some of the confounds associated with rare prevalence.

The grain issue currently looms large. Not only is it a concern in determining the level of detail at which to define innovations (Russon *et al*. 2007b), it is also now a concern in defining cultural variants. Redefining chimpanzee traditions in fine detail (e.g., soaking water with green vs dry leaves, obtaining water from the ground vs tree holes) has expanded the list from a few dozen entries to several hundred (Whiten 2007). How much of this expansion is warranted likewise depends on resolving grain. This is likely to be an especially difficult task, given the difficulties in determining the proper grain at which to analyse great ape behavior in general, but it is nonetheless critical to understanding both their traditions and their innovations.

Beyond methodological issues, a very provocative outcome of these comparisons is evidence showing rehabilitants to be more innovative than wild orangutans. We identified a variety of factors that could potentially contribute to this difference. Regardless of the causes for this difference, however, these findings suggest that rehabilitants may be especially useful in studying the kinds of innovations that great ape minds are capable of generating, more so than working wild orangutans. Following up both suggestions could yield important insights in orangutans' innovative potential.

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