

Orangutan cultures revisited

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21.1 Introduction

When examined carefully, virtually all animals show geographic variation in their behavior. Explanations for this variation come in three main classes, which are not mutually exclusive and may indeed interact in potentially complex

ways. First, geographic variation may reflect local adaptation. Thus, variation in behavior is associated with meaningful genetic differences between populations (e.g. Foster and Endler 1999), leading to developmentally stable differences. It is reasonable to assume that this holds true for much of the geographic variation in orangutan life history,

including the rates of immature growth and development, the incidence of developmental arrest in males and the proximate regulation of reproduction, and for variation in brain size, and presumably intestinal morphology, amply documented in this volume (see synthesis in Chapter 24). However, among orangutans, local adaptation is unlikely to be the only source of geographic variation. Among animals with extremely low mortality, such as orangutans (Wich *et al.* 2004b), local adaptation through natural selection cannot be as important as among animals with much higher population turnover, because there is little room for selective mortality unless very long periods of time are available. In addition, slowly developing, large-brained animals such as orangutans learn much of their behavior during ontogeny.

For these reasons, we must take seriously a second mechanism that produces geographic variation: reaction norms, or flexible responses of the same genotype to varying environments. Although the many textbook examples of reaction norms usually refer to morphology or physiology (Futuyma 1998; West-Eberhard 2003), much of the variation in orangutan behavior undoubtedly represents responses to varying ecological conditions or population density. Likely examples include variation in diet, range use and male and female mating strategies.

Finally, the geographic variation in behavior could be cultural, reflecting the combination of innovation and social learning. Field workers studying chimpanzees have for decades invoked this source of geographic variation (Goodall 1973; Kummer 1971; Nishida *et al.* 1983; Nishida 1987; Wrangham *et al.* 1994). Because in descriptive field studies it is very difficult to demonstrate unequivocally that the processes of differential invention and social transmission underlie the pattern of geographic variation, these claims failed to convince more experimentally inclined behavioral biologists (e.g. Galef 1992; Tomasello 1994). Given the obvious intelligence and therefore great behavioral flexibility of primates, in particular great apes, this skepticism was warranted, because broad norms of reaction or parallel innovation are a hallmark of the primate order (Reader and Laland 2002), and cultural explanations must only be invoked if these simpler alternatives can be excluded.

Resolving this issue is important not just to establish the nature of geographic variation in behavior of intelligent taxa such as orangutans, but also because of the obvious relevance to the evolution of human culture and even of human-like intelligence (Whiten and van Schaik 2007). During the past few years, much evidence has accumulated that makes it increasingly parsimonious to believe that, at least among the great apes, we often deal with locally originated innovations that spread and were subsequently maintained by social learning. First, there is the geographic variation in dozens of behavioral variants that look like innovations (novel behavioral variants that arise rather rarely due to some process of exploration and invention: Reader and Laland [2003a]; Ramsey *et al.* [2007]), where the variation is such that at the sites where the variant occurs it is common or universal whereas it is absent at other, ecologically similar sites. This kind of variation has been described for chimpanzees (Whiten *et al.* 1999; 2001) and orangutans (van Schaik *et al.* 2003a), and also, albeit with smaller repertoires, for capuchin monkeys (Perry *et al.* 2003) and for non-subsistence techniques, among Japanese macaques (Leca *et al.* 2007b). Second, the experimental evidence for the more sophisticated, observational forms of social learning (essential for acquiring rare innovations) becomes stronger all the time, especially for chimpanzees (Whiten *et al.* 2005), but also for orangutans (Russon and Galdikas 1995; Stoinski and Whiten 2003). Third, we now have increasingly good descriptive evidence that infant orangutans are loath to explore independently, and instead rely on social learning from their mothers to acquire many of their skills (Jaeggi *et al.* 2008; in preparation). The same thing is suggested by more experimental data. Ecologically naive, reintroduced individuals are known to acquire novel techniques under the influence of peers released earlier (Russon 2003b; Russon *et al.* 2007a). Similarly, unusual variants, such as clothes lifting and cardboard chewing, were maintained across three generations of a matriline founded by an ex-rehabilitant (Binjai) released at Ketambe (Merrill 2004).

The controversy has not died yet (Laland and Hoppitt 2003; Laland and Janik 2006), but regardless of the outcome of the debate, progress will

depend in part on the availability of reliable field data on geographic variation in orangutan behaviors that are likely to qualify as cultural variants. The aim of this chapter is to improve the documentation of this variation among wild populations of orangutans.

21.2 The geographic method

The cultural status of particular behavioral variants can be examined in some detail (e.g. *Neesia* seed extraction: van Schaik and Knott 2001; van Schaik in press), but to get an overview of a species' total cultural repertoire in nature, the procedure most commonly employed is that of geographic comparison of populations, also sometimes called the ethnographic method. It is a method of exclusion (van Schaik 2003), because one must exclude the first two causes of geographic variation mentioned above: local adaptation (and hence genetic differences between populations) and reaction norms (and hence ecological or demographic differences between populations). The logic is based on holding these two factors constant: 'the behavior of two groups with the same gene pool and with the same type of habitat can differ only by culture' (Kummer 1971). Thus, a difference in behavior between two populations may perfectly well be caused only by social learning, provided we can exclude developmentally stable differences due to local adaptation or reaction norms.

This procedure has several biases, and here we document how we tried to deal with them. The biases come in the form of false positives and false negatives (see van Schaik [in press] for more extensive discussion). First, false negatives arise when behavioral patterns are mistakenly considered universal because meaningfully different variants are not recognized. We cannot do much else than accept that all estimates are preliminary, and that future rounds will reveal more variants.

A second source of false negatives is when variants are excluded from the list because their absence in particular populations is correlated with clear-cut genetic or ecological differences, suggesting that many individuals acquire them independently from each other in the absence of any social learning. Here, we merely note that the presence

of ecological and genetic correlates of inter-population variation does not necessarily mean that the behaviors involved are not socially transmitted innovations. van Schaik (in press) discusses the variants with possible ecological correlates in great detail, and with the exception of variant c24 (slow-loris eating; see Table 21.1), concluded that reaction norm explanations based on differences in ecological conditions are less parsimonious than cultural ones. Instead, he suggests that ecological influences are expressed as differential probabilities of innovation due to differential exposure to particular problems. Here, we will therefore consider all these cases to be likely cultural variants. In theory, we can solve this particular problem by establishing for each variant concerned whether it is acquired through social learning (through careful observation in the wild) or whether it is an innovation (through experiments in captivity or the field), each of which should suffice to establish its cultural status.

False positives are perhaps more dangerous for the documentation of cultural variation because they lead to an inflated estimate of the cultural repertoire. They arise when we decide a behavior is cultural because it is absent at one or more sites (without clear ecological correlates), but the absence is artificial, due to an inability to recognize the variants or to insufficient observation time (discussed in detail by van Schaik in press). First, descriptions are often inadvertently incomplete because details may vary between sites in unexpected ways, and misunderstandings commonly arise because for most workers, English is not their first language. A few incorrect entries have been identified and removed from the list; hence, the disappearance of some putatively cultural variants (see below) relative to van Schaik *et al.* (2003a). Second, due to insufficient observation time, rarely performed behavioral variants may not be recorded. If some behavioral variants are quite rare in terms of frequency in some populations but shown more commonly in others, thus producing high prevalence there, we may falsely conclude that we are dealing with the chequerboard pattern brought about by the cultural process. The suspected possible hidden universals have been flagged in Table 21.1, and entered separately at the end.

Table 21.1 Geographic variation in likely cultural behaviors among orangutan sites. Customary and habitual variants are in bold

Number	Site	Sua		Ket		GP		TP		Sab		Tua		Ku		LK		Possibly hidden universal?
		S	P.a.	S	P.a.	B	P.p.w.	B	P.p.w.	B	P.p.w.	B	P.p.w.	B	P.p.m.	B	P.p.m.	
Island		psw		dry		dry		psw		psw _v		psw		dry		psw		
(Sub)species		P.a.		P.p.w.		P.p.w.		P.p.w.		P.p.w.		P.p.w.		P.p.m.		P.p.m.		
Habitat		psw		dry		dry		psw		psw _v		psw		dry		psw		
c1	Snag riding: Ride on pushed-over snag as it falls, then grab on to vegetation before it crashes	A	A	A	A	C	C	R	R	H	H	A	A	A	A	A	No	
c2	Kiss squeak with leaves: Using leaves on mouth to amplify sound, then drop leaf	A	R	C	A	A	C	A	R	H	H	A	A	A	A	A	No	
c4	Leaf wipe: wiping face with fistful of squashed leaves, then drop (in kiss squeak context)	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	No	
c9	Scratch with stick: using detached stick to scratch body parts	A	A	A	A	R	R	R	R	R	R	H	H	A	A	A	No	
c10	Auto-erotic tool: using tool for sexual stimulation (female and male)	A	C	A	A	A	A	A	A	A	A	P	A	A	A	A	No	
c11	Raspberry: spluttering sounds associated with nest building	C	A	A	A	C	A	C	A	A	A	A	A	H	A	H	No	
c12	Symmetric scratch: exaggerated, long, slow, symmetric scratching movements with both arms at same time	C	R	A	A	A	A	A	A	A	A	A	A	A	A	A	No	
c13	Twig biting: systematically passing ends of twigs used for lining of nest past the mouth (sometimes including actual bite) during last phase of nest building	C	A	P	A	A	A	H	H	H	H	A	A	A	A	A	No	
c14	Leaf napkin: using handful of leaves to wipe latex of chin	A	R	A	A	A	A	A	A	A	A	C	A	A	A	A	No	
c15	Branch as swatter: using detached leafy branches to ward off bees/wasps attacking subject (who is raiding their nest)	H	H	R	R	R	R	R	R	A	A	H	H	A	H	A	No	
c16	Leaf gloves/cushions: using leaf gloves to handle spiny fruits or spiny branch, or as seat cushions in trees with spines	E	C	E	E	R	R	E	E	E	E	A	A	R	R	A	No	
c17	Tree-hole tool-use: using tool to poke into tree holes to obtain social insects or their products	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	No	
c18	Seed-extraction tool use: using tool to extract seeds from the protected fruits of <i>Neesia</i> sp.	C	E	A	A	A	A	E	E	E	E	E	A	A	A	A	No	
c19	Branch scoop: drinking water from deep tree hole using leafy branch (water dripping from leaves)	H	A	A	A	A	A	H	A	A	A	A	A	A	A	A	No	
c24	Slow loris eating: capture and eat slow loris hiding in dense vegetation	H	H	A	A	A	A	A	A	A	A	A	A	A	A	A	No	
c25	Nest smack: smacking sounds associated with nest building	A	A	A	A	A	A	R	C	C	C	?	A	A	A	A	No	
c26	Carry leafy branch to different tree in which subject starts to build nest using carried leaves as lining, pillow or cover (Tuanan: <i>Camposperma</i>)	A	A	A	A	R	R	R	H	H	H	?	A	A	A	A	No	

c27	Branch cushion: covering (non-spiny) big branch(es) with few leaves or leafy branches, then sit or lie on it	A	H	R	H	H	C	?	A	No
c28	Throat scrape: deep throat sound made by female toward offspring	A	A	A	R	A	H	?	A	No
c29	Moss cleaning: cleaning hands with moss	A	A	A	A	H	A	?	A	No
c30	Chewing leaves into pulp then smearing foam over body (selected parts chosen) until fur all wet	A	A	A	A	A	A	?	A	No
c31	Male and female use the same nest to spend the entire night (during consortship)	A	A?	R	A	A	A	?	C	No
c32	Tooth cleaning: chewing and spitting out leaves after eating (sticky?) fruit	A	A	H (?)	A	A	H	?	C	No
c34	Using <i>Asplenium</i> fern to rest or sleep in	A	R	A	A	A	A	?	C	No
c38(ex-114)	Coercive hand-holding: male firmly holds female's hand/wrist for long period of time during consort	A	A	A	R	R	H	?	R	No
c39 (ex-117)	Water play (wild splashing) on ground	E	E	A	P	R	H	?	A	No
c6	Bunk nests: build a nest a short distance above the nest used for resting (during rain)	A	A	A	P	R	R	A	H	Yes
c7	Sun cover: building cover on nest during bright sunshine (rather than rain)	A	H	A	A	A	R	C	C	Yes
c8	Hide under nest: seek shelter under nest for rain	A	R	A	R	A	R	C	P	Yes
c21	Bouquet feeding: using lips to pick ants from fistful of dry, or fresh, or rotting leaves (nests)	C	C	C	C	A	H	A	H	Yes
c23	Dead twig sucking: breaking hollow (dead) twigs to suck ants from inside	C	C	A?	C	H	H?	A?	A	Yes
c33	Copulation on female's nest	A	H	C	R	A	R	?	R	Yes
c35	Nest as social refuge: female on nest left alone by otherwise coercive male	P	P	P	P	H	A	?	A	Yes
c36(ex-17)	Biting through vine to swing Tarzan-style across gap	R	R	R?	R	R	H	A	A	Yes
c37(ex-113)	Biting through vine to release tree for swaying to reach adjacent tree	R	A	R	A	R	H	?	A	Yes

Sites are ordered from west to east. Sites are Sua, Suaq Balingbing; Ket, Ketambe; GP, Gunung Palung; TP, Tanjung Puting; Sab, Sabangau; Tua, Tuanan; Ku, Kutai, Mentoko area; LK, Lower Kinabatangan.

Islands: S, Sumatra; B, Borneo.

Habitat: dry, dry-land forest, usually mixed riverine and lowland dipterocarp; psw, peat-swamp forest.

P.a., *Pongo abelii*; P.p.w, *Pongo pygmaeus wurmbii*; P.p.m, *P. p. morio*.

Numbers in the first column refer to numbers in van Schaik et al. (2003a) and van Schaik et al. (2006a); new variants numbered from c24 on. The numbers follow van Schaik et al. (2003a) (see also Chapter 20).

Cell entries: A, absent; C, customary, shown by all or most relevant individuals at a site; E, absent for clear ecological reason; H, habitual, shown by multiple individuals; P, present with unknown prevalence, usually meaning rare; R, rare, i.e. low prevalence.

21.3 The orangutan 'culture table'

21.3.1 The new sample

We have generated a new and up-to-date overview of geographic variation in orangutan behaviors, with a special emphasis on possible cultural variants. The table of possible and likely cultural variants produced by van Schaik *et al.* (2003a) was based on a 3-day meeting in 2002, in which representatives of all sites with long-term data on wild orangutans convened to discuss a preliminary list of candidate cultural variants and to identify new ones through plenary discussion of site descriptions and video footage from multiple sites. This meeting employed the same criteria as employed in the chimpanzee comparisons (Whiten *et al.* 1999, 2001), including those for prevalence at a given site. Note, however, that none of the studies represented in this first round had focused specifically on collecting data on geographically variable behavioral variants.

In 2006, a second round of comparisons between sites was conducted by email, during various small-scale meetings, and during a 1-day meeting, where most sites were again represented. In this second round, we engaged in several iterations of comparisons of new variants. The most important difference with the first round are the inclusion of two new, intensively studied sites, Sabangau and Tuanan (both in Central Kalimantan, Borneo; see the Preface), systematic updates for some others (Ketambe, Gunung Palung, Lower Kinabatangan) and many opportunistic updates for others (Tanjung Puting). However, new records continue to accumulate, so some questions remain for some sites (considered absences in this chapter). No new observations were available for Kutai (Mentoko) and Suaq. As in the first round, we decided to include in Table 21.1 only those sites with at least 4 years of intensive observations of at least 25 individual orangutans and 10,000 contact hours. However, observations at some additional sites are mentioned where relevant. In particular, interesting records emerged from the study at Sibual-Buali in north Sumatra, where Renie Djoasmoro and Nahot Simanjuntak studied a small and isolated orangutan population. It was premature to include the results of ongoing field studies elsewhere.

21.3.2 General patterns

Table 21.1 gives an overview of all the geographically variable behavior patterns that are likely to be cultural. It lists six sites from Borneo, the first four from the geographic range of the subspecies *Pongo pygmaeus wurmbii*, the last two from that of *P. p. morio*. It then lists the two Sumatran sites (*P. abelii*) for which there are long-term data. The entries are listed according to the number system provided in van Schaik *et al.* (2003a) and the additions given in van Schaik *et al.* (2006a). Because most of the variants have been described in detail by van Schaik *et al.* (2006a), we do not repeat these descriptions here.

The likely cultural variants are divided into two groups: The first 26 are those that are very likely to be cultural, i.e. represent innovations that spread through social learning and are maintained in the population by social learning. The next groups of nine variants are presumably cultural as well, but for them we cannot exclude the possibility that they are hidden universals (discussed below). The classification is slightly different from that reached by van Schaik (in press), due to the availability of new information.

Compiling a list like this inevitably involves several editorial decisions, which may or may not be correct, but we tended to err on the safe side. To give one example, at one of the sites, Lower Kinabatangan, orangutans regularly play with the local gibbons. Should we consider this an orangutan innovation? First, playing with gibbons may spontaneously occur everywhere if the proper conditions arise. Lack of records may reflect lack of opportunities, or lack of habituation of the gibbons. Second, if it is an innovation, it is also possible that the innovator was the gibbon, not entirely unreasonable given that gibbons are known to play with other primates as well, and their much faster locomotion makes it harder for orangutans than for gibbons to initiate a play bout. This case was therefore left out.

Also left out are a variety of feeding techniques. Examples include rubbing spiny fruits, such as *Durio*, on branches in order to remove the spines and allowing the animal to bite into the fruit's rind to open it; or removing the bark from the terminal

twigs of the *Dyera* tree to eat the soft pithy wood inside it; or using branches in various ways to crack the hard seeds of *Mezzettia*; or spitting into the fur of the forearms a foamy mass of spit and fruit pulp of a variety of species of which the seeds are eaten but the pulp is removed first; or taking a large amount of stem of the fern liana *Stenochlaena palustris* into the mouth, chewing it into a pulpy wadge, and expectorating the wadge (after extracting the juice), etc. The reason for this is not that these are definitely not innovations—many of them may well be—but that it is nearly impossible to get reliable comparisons across sites given the difficulties of identifying the species involved.

21.3.3 Hidden or true universals

Some behaviors that were in the first round considered possible cultural variants are now regarded as universals, because subsequent observation at the site or sites where they were thought to be absent has shown that they were in fact present. These behavior patterns are thus universals: *Kiss squeak with hands* (c3: using closed fists, open fists [like trumpet], or flat hands on mouth [or fingers in mouth] to amplify sound, *building play nests* (c5: by immatures), *snag crashing* (c20: pushing over dead standing trees or snags; is rare at several sites in Sabah [N. Kuzo, personal communication]), and *nest destruction* (c22: rummaging through old orangutan nests for insects). In addition, we conservatively consider the following variants universal, although they have not been recorded for each site and may be truly absent somewhere: *nest blanket* (adding loose leaves on top of body in nest [not a roof, because that is braided or woven together]), and *nest roof* (adding a woven lid to nest, separate from rest of nest).

Several other behavioral variants in Table 21.1 are suspected to be universals, despite their being reported as absent at some sites. They tend to occur rarely and are often inconspicuous, but they are recorded for most sites, so their lack of universal prevalence may be due to biased sampling. Even if recorded at very few sites, this could still be true if the context in which the behavior is shown is very rare and may easily be missed, even in long-term studies.

Note that the true criterion must be that a hidden universal is not recorded because the proper context for it arises only rarely or it is overlooked by observers. It is quite possible that all the possible hidden universals are real innovations, but ones that are invented rather easily and thus arise frequently, even though the animals find themselves only rarely in the appropriate context. The entries in Table 21.1 are therefore conservative. For instance, under the anecdote compilation approach used by ornithologists studying innovation (Lefebvre *et al.* 1997), most of them would have been recorded as innovations.

21.3.4 Rare innovations

Some behavioral variants are almost certainly innovations, but are of too low a prevalence at any site to reach cultural status, i.e. they may not spread very well through social learning because they are too rare, inconspicuous, or uninteresting (non-salient) to observers (cf. van Schaik *et al.* 2006a). The 19 known cases are compiled in Table 21.2, which otherwise uses the same conventions as Table 21.1. We list them here because they may turn out to be cultural, i.e. acquired through social learning by most actors, when more data come in.

21.4 Discussion

21.4.1 Genetic correlates?

One of the main criticisms against the geographic method is that some of the variation documented is simply variation between species or other taxonomic units, which raises the possibility that the behavioral differences reflect genetic differences. Because the Sumatran and Bornean orangutans have recently been elevated to represent distinct species (see Chapter 1), this criticism is potentially powerful. Indeed, 17 of the 26 entries in Table 21.1, or 65%, are limited to one of the islands. However, van Schaik (in press) calculated that the expectation, given that there are two Sumatran and six Bornean sites, and given that the incidence across sites varies, is somewhere between 54% and 88%, so the observed value is even toward the lower end of the range expected if innovations were

Table 21.2 Likely innovations that do not reach high enough prevalence in any population and are therefore not (yet) considered cultural

Number	Site	Sua		Ket		GP		TP		Sab		Tua		Ku		LK		Possibly hidden universal?
		S		S		B		B		B		B		B		B		
		<i>P.a.</i>	<i>P.a.</i>	<i>P.a.</i>	<i>P.a.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.m.</i>	<i>P.p.m.</i>	<i>P.p.m.</i>	<i>P.p.m.</i>	
	Habitat	psw	dry	dry	dry	dry	dry	psw	psw	psw	psw	psw	psw	dry	dry	psw	psw	
i1	GG rub: females rubbing their genitals together	R	A	R	R	R	R	R	R	A	R	R	R	A	A	A	A	No
i2	Use leaf to clean body surface	A	A	R	A	R	A	A	A	R	A	A	A	A	A	A	A	No
i3	Sneaky nest approach: building a series of nests, while approaching conspecific in fruit tree	A	R	R	R	R	A	A	A	A	A	A	A	A	A	A	A	No
i4	Leaf bundle ("doll"): carried around and taken to nest	A	R	R	R	R	R	R	R	A	R	R	A	A	A	A	A	No
i5	Leaf scoop: drinking water from ground or stream using leaf as vessel (drinking directly from vessel)	A	A	R	A	R	A	A	A	A	A	A	A	A	A	A	A	No
i9	Branch dragging display on the ground	E	E	A	A	A	A	A	A	A	A	A	A	?	?	R	R	No
i11	Sponging: drinking water using crumpled leaves	A	R	A	A	A	A	A	A	R	A	A	A	A	A	A	A	No
i12	Hiding behind detached branch from predators or humans	A	R	A	A	R	A	R	?	?	A?	A?	A?	P	P	R	R	Yes (habituation)
i13	Stick as chisel (1) to open termite nest in log or ant nest on ground	A	R	A	A	R	A	R	A	A	A	A	A	A	A	A	A	No
i15	Branch hook: using detached branch to pull branch of adjacent tree to within reach	?	?	A	A	A	A	A	A	R	R	R	R	?	?	A	A	Yes (habituation)
i18	Drink from bottom of pitcher plant after biting through bottom (not drink like cup!)	A	E	A	A	A	A	A	A	A	R	R	R	?	?	A	A	No
i19	Poultice use: chewing leaves and applying resulting poultice to wound	A	A	A	A	A	A	A	A	R	A	A	A	?	?	A	A	No
i20	Long-call vibrato: using fingers to make pulses at end of long call (fingers come over head onto lips)	A	A	A	A	A	A	A	A	R	A	A	A	?	?	A	A	No
i21	Use gloves to get into ants' nest (and avoid being bitten)	A	A	A	A	A	A	A	A	R	A	A	A	?	?	?	?	No
i22	Tooth pick: use a small stick to clean teeth	A	P	?	A	A	A	A	A	A	A	A	A	?	?	?	?	No
i23	Nail cleaning: use small stick to clean under finger nail	A	P	?	A	A	A	A	A	A	A	A	A	?	?	?	?	No
i24	Washing face and arms with water from tree hole	A	A	A	A	R	A	R	A	R	R	R	R	?	?	A	A	No
i25	Stick as chisel (2) to open durian fruit	A	R	A	A	A	A	A	A	A	E	A	A	?	?	A	A	No
i26	Cover head with leafy branch or leaves against stinging bees (not swatting)	A	A	A	A	A	A	A	A	A	R	R	R	?	?	P	P	No

distributed randomly across the sites, regardless of on which island they are. More importantly, none of the 14 variants limited to Borneo is found at all 6 sites—a pattern inconsistent with a simple genetic determination model.

The observations at Sibual-buali, Sumatra, while insufficient to be included in Table 21.1, can be used to further assess island differences. Thus, while kiss squeaks on leaves seemed to be limited to Borneo, they have now been observed at Sibual-buali. Similarly, nest smacking sounds are common at Tuanan on Borneo, but similar sounds were also heard at Sibual-buali. On the other hand, nest raspberries are customary at Suaq on Sumatra, but similar sounds are customary at Sabangau on Borneo.

Due to the addition of Sabangau and Tuanan, we now have four sites within the range of *P. p. wurmbii*, along with Gunung Palung and Tanjung Puting. As the entries in Table 21.1 show, only a single one of the 26 likely cultural variants (branch cushion) was found at all 4 of them. Van Schaik (in press) provides a more detailed analysis of possible genetic influences by comparing nearby sites, and finds little evidence for a genetic influence. Overall, therefore, although the island forms of orangutans, and even the subspecies, are distinct in several respects, suggesting meaningful genetic differences between them (see Chapter 24), the behavioral variants compiled in Table 21.1 above do not follow these genetic discontinuities. Since we have already shown elsewhere that ecological differences between sites are not likely to account for the behavioral differences between them, the results strongly suggest that the entries in Table 21.1 reflect cultural variants.

21.4.2 Variation across sites

It is clear that variation in observation intensity, in both total observation time and in keenness of observers, has affected the number of variants recorded per site. Table 21.3 shows that the total number of recorded variants is low for Kutai and likewise fairly low for Suaq, which were only included in the first round. This implies that during the second round, observers have become primed toward recording innovations. The sites

with dedicated observers keen on recording innovations (Ketambe, Sabangau, Tuanan, and to some extent Tanjung Puting, through the memory of a long-term observer) have the highest numbers. We cannot therefore directly compare the numbers across sites because the heterogeneity in observation effort has increased.

Nonetheless, sites differ in both the total number of cultural variants and the proportion of variants that are cultural. Suaq still has a rather high absolute number and the highest relative proportion of cultural variants, suggesting that at this site variants are most likely to be spread by social learning, as suggested by the strong correlation with sociability (van Schaik *et al.* 2003a; Whiten and van Schaik 2007). Fruitful island comparisons, however, will rely on the results of the new round of observations at Suaq, currently in progress.

21.4.3 The cultural repertoire of orangutans

At present, we have 26 or 35 cultural variants in the orangutan behavioral repertoire, depending on how conservative one is. As stressed above, however, these numbers should be taken as preliminary, for a variety of reasons.

In section 21.2 we discussed the possible biases of the geographic method. We may overestimate the taxon's cultural repertoire for two reasons. First, it is often difficult to establish with certainty whether a behavior pattern is absent from one of the sites. We dealt with this by labeling nine of the variants as possible hidden universals. The reason for this is that the second round has produced evidence for the presence of several false positives in the first round, despite strenuous attempts to avoid that, in that some behaviors have now been recorded there, making the variants present at all sites. We dealt with the second positive bias, not recording variants at a site due to insufficient observation time, by only including sites with truly long-term studies, often by a team of observers. Note that this bias refers to the total repertoire of orangutans. Paradoxically, scoring an absence at a site due to insufficient observation effort increases the taxon's repertoire.

However, a third source of positive bias not discussed above is that some of the variants

Table 21.3 Number of cultural and non-cultural variants per site

Site	Sua	Ket	GP	TP	Sab	Tua	Ku	LK
Island	S	S	B	B	B	B	B	B
(Sub)species	<i>P.a.</i>	<i>P.a.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.w.</i>	<i>P.p.m.</i>	<i>P.p.m.</i>
Habitat	psw	dry	dry	psw	psw	psw	dry	psw
Number of very likely cultural variants (C, H)	8	5	3	3	6	10	4	5
Number of likely cultural variants (possibly hidden universals)	2	4	2	2	2	4	2	3
Innovations that are not cultural at this site	4	15	11	17	17	11	2	7
Total number of recorded innovations	14	24	16	22	25	25	8	15

considered as separate may in fact be the same. Thus, variants c14, c29, and i2 are probably the same, having been described in somewhat different contexts with somewhat different materials. Russon *et al.* (see Chapter 20) and Ramsey *et al.* (2007) discuss this demarcation problem, but it is clear that one would decide they represent the same variant if some individual animals use all three of them whereas others use none of them. Since they tend to be seen at different sites, for now there is no compelling evidence to consider these three identical.

The current list may also underestimate the repertoire, potentially by a large margin. First, some variants might not have been recorded. While the number of such missed variants is hard to estimate, we deliberately did not record some classes of behaviors. Thus, we did not compare most feeding techniques on fruits or vegetable matter. Their inclusion might have produced a much longer list. With the steady improvement of botanical knowledge, we should soon be able to make such comparisons. It is even possible that the mere choice of a food item, even if it does not require special processing techniques, varies culturally (this possibility is currently under active investigation by a team working at three Bornean sites: Sabangau, Tuanan, and Sungai Lading, which is located between these two sites, all of them separated from each other by a major river). Likewise, we did not consider the possibility that universal vocalizations have geographical variants, as in bird dialects. We did include distinct calls, often produced without involvement of the vocal cords, such as throat scrapes (c28) or

different nesting sounds (c11, c25) because they are qualitatively distinct across populations.

We already included most of the behavioral variants that, while having ecological correlates, probably reflect innovations, so this source of negative bias was probably largely eliminated. A third source of negative bias not considered so far is that some of the entries in the second Table (21.2) may in fact be cultural. Admittedly, whether we regard a variant as cultural is a matter of definition: how many individuals must have acquired the variant under the influence of social learning? Assuming the pattern approach can serve to identify such cases, at least some of the rare variants may in fact have spread to at least some others.

Finally, some of the hidden universals and even some of the true universals may in fact be cultural, especially if the origin of these innovations is rather predictable. Obviously, there comes a point where the line between innovation and plastic reaction norms becomes blurred, but the true criterion for cultural status should be whether most individuals acquire the variant during ontogeny through independent learning or through social learning. By that criterion, even some true universals may be cultural variants, because the actions of conspecific role models strongly affect their acquisition, such as in nest building (see Videan [2006] for an elegant example with chimpanzees).

The point of this discussion is not to argue that everything orangutans do is culturally acquired, but that depending on the exact definitions employed, cultural repertoires may be much larger than what we have been able to document so far,

even if the current state of documentation is still open to criticism.

21.4.4 Future work

It should be stressed again that there are still many uncertainties for many of the variants. For instance, is twig biting really absent at Ketambe? When night nests are built high and around dusk, it may be very difficult to record its presence. On the other hand, the orangutans at Ketambe also do not make any nesting sounds, which are associated with twig biting and pillow making. New studies that focus explicitly on parts of the repertoire, such as nest building, are needed to solve these issues. In fact, such studies are now underway (A. Gibson, in progress).

These uncertainties should not be taken to imply that it is still likely that geographic variation in orangutan behavior is not cultural. There are too many examples where ecological or genetic differences are very unlikely to have caused the checkerboard patterns observed, as for the nesting sounds or the kiss-squeak variants (discussed in van Schaik [in press]). Also, for some tool-use techniques, such as the seed extraction from *Neesia* fruits, checkerboard patterns have been documented, even at rather short physical distances but where dispersal barriers prevent diffusion (van Schaik and Knott 2001), and social learning is suggested by selective social attention by immatures (van Schaik 2004; cf. Jaeggi *et al.* in preparation). The challenge for the next generation of field studies is to establish through observation of selective social attention which behavioral variants are culturally transmitted and to estimate for selected behavioral

systems (e.g., nest building, feeding) which aspects are affected by social influence. (E. Meulman, in progress).

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