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Geographic Variation in Tool Use on *Neesia* Fruits in Orangutans

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ABSTRACT Geographic variation in the presence of skilled behavior may reflect geographic variation in genetic predispositions or ecological conditions (accompanied by reliable expression during development), or it may reflect the vagaries of invention and the appropriate social conditions for persistence. In this study, we compare the feeding techniques and tool-using skills used by orangutans to extract the nutritious seeds from *Neesia* fruits between Suaq Balimbing on Sumatra and Gunung Palung on Borneo, and map the distribution of *Neesia* tool use in Sumatran swamps. We show that neither genetics nor ecology is sufficient to explain the distribution of this tool use, confirming earlier findings on chimpanzees. We conclude that the ability to learn to use tools determines the geographic distribution. It is impossible to distinguish between the history of invention and the conditions for social transmission as the causal factors, but the high density and the social tolerance at Suaq Balimbing create propitious conditions for the maintenance of the skill as a tradition once it has been invented. High orangutan densities in the other Sumatran coastal swamps with *Neesia* tool use support the conclusion that suitable transmission conditions are the critical factor to explain the geographic distribution of skills such as feeding tool use. Am J Phys Anthropol 114:331–342, 2001.

Among primates, only great apes share with humans the tendency to make and use tools in wild populations (Beck, 1980; McGrew, 1992; van Schaik et al., 1999) on a customary or habitual basis (sensu McGrew and Marchandt, 1997). Thus, the study of tool use in great apes may help to identify the conditions favoring its subsequent elaboration in humans.

The geographic pattern in presence and variation in the morphology of complex skills such as tool use may reveal the processes of origin and maintenance of these behaviors. Four main hypotheses have been proposed to account for this geographic variation (Boesch et al., 1994; Wrangham et al., 1994; Boesch, 1996). The incidence of tool use may reflect 1) genetic differences; 2) the presence of ecologically appropriate conditions; 3) the vagaries of invention; or 4) the conditions for reliable social transmission. These hypotheses are not exclusive, since they either refer to necessary preconditions (1 and 2) or the process of development (3 and 4). However, the most interesting question is whether ecological conditions or genetic factors, which must obviously be appropriate to call forth the tool-using skills, are sufficient by themselves. Thus, any geographic pattern in a skill that does not coincide with clear ecological conditions or genetic discontinuities requires an explanation invoking limitations brought about by the nature of the acquisition process. Here we briefly review these hypotheses and their predictions.

Although tool-using behavior is not instinctive, one could argue that subtle genetic differences exist in hand morphology or predispositions toward particular motor patterns that could serve as the operants underlying tool use. These kinds of differences could be expected to coincide with major intraspecific discontinuities, such as between subspecies. However, in chimpanzees, variation in tool use across populations is not obviously linked to subspecific divisions (McGrew, 1992), and nearby populations of the same subspecies can show radical differences in tool use (Whiten et al., 1999). Likewise, whereas orangutans at one Sumatran site show customary tool use, those at another Sumatran site do not show any significant tool use even though they are only some 70 km from each other and are not separated by major genetic barriers (van Schaik et al., 1996). Nonetheless, genetic influences not coinciding with subspecific differentiation may exist in some cases. The genetic hypothesis predicts that the presence or absence of tool-using skills coincides

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with major genetic discontinuities, such as subspecies boundaries.

Ecological conditions are not likely to be sufficient in themselves to explain the geographic pattern of presence and absence of a tool-using skill in chimpanzees: animals at sites with seemingly similar ecological conditions sometimes do not show the expected tool use (Boesch et al., 1994; McGrew et al., 1997). However, subtle ecological differences cannot always be excluded; they might cause a plant species to drop out of the optimal diet, and thus the tool-using skills aimed at that plant species would be absent. The ecological hypothesis predicts that the presence of suitable ecological conditions coincides with the presence of the skill.

Aspects of the learning process need to be invoked as limiting factors when the geographic distribution is patchy, despite suitable ecological conditions or similar genetic background. Thus, it is possible that the incidence of the skill at a site may reflect factors that affect the likelihood that an individual actually acquires the skill in the appropriate ecological context, i.e., the probability of invention or the reliability of social transmission. For a skill to be present at a given site, it was either invented there and subsequently maintained, or it was imported from another site (a process we can call diffusion). Diffusion is social transmission, but between immigrant and resident rather than among residents.

Invention is one of the possible causal factors for patchy geographic distribution. It may be quite common, in which case all animals in all populations should acquire the particular skill, and ecological or genetic factors are needed to explain geographic variation. However, invention may also be rare enough to affect the incidence of a skill in a population. The invention hypothesis makes two predictions about the geography of tool use. First, we expect that the cumulative frequency of exposure to a given problem is the best predictor of the presence of a skill (cf. van Schaik et al., 1999). This frequency is best indexed, all things being equal, by population size. We adopt here a slight variation on the ecological definition of population: the set of animals that have social contact, either directly or indirectly, through dispersing individuals. A second prediction is that, if invention takes place but is not followed reliably by population-wide spread and maintenance, more than one technique may be present within a single population, or only some of the individuals within a population show it, i.e., the tool use does not reach customary or habitual levels (sensu McGrew and Marchant, 1997).

There is ample, albeit indirect, evidence from chimpanzees that most individuals actually acquire their tool-using skills or other learned behavior through social learning (Boesch and Tomasello, 1998; Whiten et al., 1999). Reliable social transmission could also explain systematic differences between populations without a functional basis, based on the reliability of copying of techniques (cf. Boesch and Boesch, 1990). We propose that social transmission (including diffusion) is likely mainly to determine the ubiquity of a given tool-using skill within populations and its long-term presence within the population. Poor transmission conditions produce imperfect horizontal spread of a newly invented technique, thus causing variation *within* populations in the presence of a skill. Likewise, when conditions for horizontal transmission are poor, skills are likely to become very rare, concentrated in certain matrilines, or even disappear in the end from a population, when the matrilines with the skill go extinct. Thus, in areas with good conditions for social transmission, tool-using skills are more likely to be customary or habitual (sensu McGrew and Marchant, 1997) and to be present in the long run.

In order to evaluate these various predictions, we studied the geographic pattern in the use of tools to extract seeds from *Neesia* fruits in Sumatran and Bornean orangutans. The orangutans at Suaq Balimbing in Sumatra use tools in two contexts: 1) to extract insects or insect products from tree holes, and 2) to extract seeds from *Neesia* fruits (van Schaik et al., 1996; Fox et al., 1999). Establishing the presence of insect tool use at a site requires intensive observation of habituated individuals. However, the seed extraction tool use can be established by finding the tools in recently dropped fruits.

In this paper, we explore the distribution of *Neesia* tool use in several Sumatran localities, and compare *Neesia* tool use and feeding behavior and insect tool use between Suaq Balimbing on Sumatra and Gunung Palung on Borneo. We also test the assumption that the benefits from possessing the skill are large enough (i.e., *Neesia* is in the optimum diet set) at both sites needed to evaluate the ecological hypothesis. We conclude that variation in the reliability of social transmission is the most likely cause for the observed geographic pattern.

METHODS

Neesia feeding at Suaq Balimbing

We studied feeding behavior and tool use on *Neesia cf. malayana* fruit in a wild population of Sumatran orangutans at Suaq Balimbing (3°04′ N, 97°26′ E), Leuser Ecosystem, Sumatra, Indonesia, part of the world's largest contiguous orangutan population (Rijksen and Meijaard, 1999). The orangutans occur at a very high density (7 individuals/km^2) in coastal swamp forest. In this study, some 50 independent individuals have been followed since August 1993, using focal animal samples, if possible from nest to nest, for a total of over 17,000 hr. Activities were scored instantaneously every 2 min; feeding refers to behaviors directly involved with food gathering, processing, and ingestion (thus if an animal has dropped its food but continues to process it in its mouth, while sitting back, it still feeds). Reports of feeding time and use of tools during feeding refer to 1995. More detailed descriptions of techniques were collected over the years, especially in 1998 and 1999. Feeding rates were estimated during focal follows by recording the handling time between picking up one *Neesia* fruit until picking up a subsequent *Neesia* fruit. It was usually impossible to retrieve the fallen fruits to count directly the number of seeds actually ingested; estimates were therefore derived from other fallen fruits. In the last phase of the fruiting season, an unknown number of seeds have already disappeared from the fruits, and this number was estimated by checking fallen fruits not used by the orangutans. The latter estimates are therefore particularly likely to contain a wide margin of error.

Neesia feeding at Gunung Palung

Orangutans at the Cabang Panti research site (1°15′ S, 110°10′ E) in Gunung Palung National Park, Indonesian Borneo (West Kalimantan) have been followed as part of this study since August 1994, for a total to date of over 25,000 hr of observation on over 50 individually recognized individuals. Time of initiation and termination of all primary activities, including feeding, was recorded on a continuous basis. Feeding involved all behaviors consistent with the definition used at Suaq (above). The *Neesia* eaten at Gunung Palung is *Neesia altissima*, a similar species to that eaten at Suaq. Feeding rates were estimated as at Suaq. Fruits were dropped by the orangutans after eating them and were then picked up by the researchers. We counted number of seeds that had been eaten through examination of the distinct impressions left where seeds had been present.

Plant processing and nutritional biochemistry methods

Processing of *Neesia* seeds for nutritional analysis took place at Gunung Palung. Typically, the orangutans at Gunung Palung would only open up one or two sections of each fruit. The other sections were then opened and the seeds counted and weighed while wet and while dry. Arils on the apex of *Neesia* seeds were weighed separately. Samples were dried in a kerosene drying oven at 40°C for approximately 2 weeks. Dried samples were weighed and sealed in plastic bags for transport back to Harvard University.

All nutritional analyses were conducted in the Nutritional Chemistry Laboratory in the Anthropology Department at Harvard University. Crude protein (CP) was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Pierce and Haenisch, 1947). The digestion mix contained Na_2SO_4 and $CuSO_4$. The distillate was collected in 4% boric acid and titrated with 0.1 N HCL. The detergent system of fiber analysis (Goering and van Soest, 1970), as modified by Robertson and van Soest (1980), was used to determine the neutral-detergent fiber (NDF), or total cell wall fraction. Lipid content was measured using petroleum ether extraction for 4 days at room temperature, a modification of the method of the Association of Official Analytical Chemists (1984). Dry matter (DM) was determined by drying a subsample at 100°C for 8 hr and hot-weighing. Total ash was measured by ashing the above subsample at 520°C for 8 hr and then hot-weighing at 100°C. Organic matter (OM) was calculated as 1 minus ash multiplied by DM. The remaining total nonstructural carbohydrates (TNC) were estimated by subtraction (100 − (NDF + CP + lipid + ash)).

Caloric content was calculated based on the energetic value of the above nutrient fractions, assuming the values of 9 Kcal/g lipid, 4 Kcal/g CP, and 4 Kcal/g TNC, taken from values used for humans (National Research Council, 1980). Total calories consumed per day were calculated as in Knott (1998, 1999). A fiber digestion coefficient of 0.543 (Milton and Demment, 1988) was used and multiplied by 3.3 Kcal/g (Conklin and Wrangham, 1994). The Kcals of metabolizable energy per gram of food item were multiplied by the grams of each food item ingested per bout to obtain a measure of Kcals consumed during each feeding bout.

Geography of tool use

The presence of certain sticks inside fallen fruits is a telltale sign of tool use. Tools can be distinguished from sticks or branches that got stuck in the fruits as they fell because tools are straight, almost invariably peeled, and usually thoroughly wedged in the cracks. Hence, we looked for tools among fruits on the ground under *Neesia* trees in northwestern Sumatran swamps with orangutans during or soon after the fruiting season.

To assess the presence or absence of tool use on *Neesia*, three requirements must be met. First, there must be *Neesia*. This implied that we limited our search to suitable swamp areas, especially areas close to rivers or hillsides, where running water is found. All remaining separate swamp areas within the range were identified and most were visited. Swamps are being converted to agricultural plantations or selectively logged, largely by illegal loggers (Robertson and van Schaik, 2001) at unprecedented rates. Since *Neesia* is a major timber tree, probably the most important species sought by timber poachers, it is increasingly difficult to find mature adult trees, even in areas where they used to be abundant just a few years ago.

Second, there must be orangutans. Even inside the range, orangutans need not be present at the time of the survey. Once loggers have been active inside a swamp, orangutan densities plummet, at least in part because among the four most commonly taken tree species in the swamp, two (*Neesia* and *Sandoricum beccarianum*) are key orangutan food species. Thus, even if some *Neesia* were left, there were not always orangutans there. In addition, in some areas east of the Alas River that we visited,

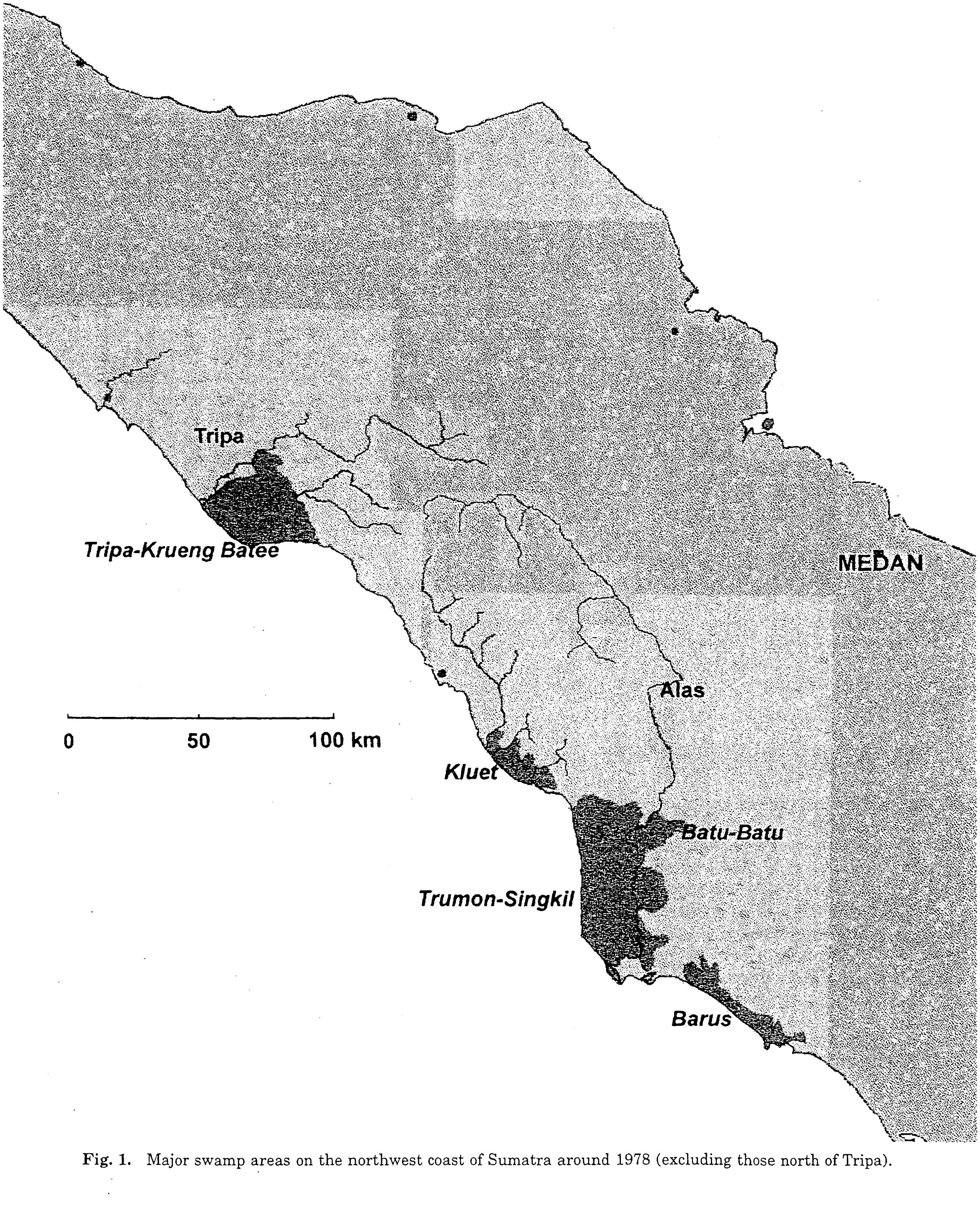

Fig. 1. Major swamp areas on the northwest coast of Sumatra around 1978 (excluding those north of Tripa).

orangutans were hunted by new settlers and ecologically extinct.

Third, there must be recent fruits. At Suaq Balimbing, *Neesia* fruits on average once a year, but is rather irregular, sometimes skipping a year, sometimes having two crops in a year. Also, fruiting at Suaq was found not to reliably predict fruiting in swamps to the north, where we had to wait several years for a fruiting season to coincide with our visits to the area.

TABLE 1. Kcal/100 g of Neesia *seeds and arils*[1]

	% ash	% dry matter	% organic matter	% TNC	% lipid	% crude protein	% NDF	Total Kcal/100 g
Neesia seed	1.1	91.4	86.5	31.7	46.0	12.4	9.9	590
Neesia aril	5.3	91.4	90.3	5.8	77.7	9.1	7.4	759

[1] Values are percentage weight of organic matter ((1 − % ash/100) × % dry matter); dry matter is caldulated at 100°C; TNC, total nonstructural carbohydrates; NDF, neutral detergent fiber; total Kcal/g were calculated assuming the values of 9 Kcal/g lipid, 4 Kcal/g crude protein, and 4 Kcal/g TNC.

The geographic range of the Sumatran orangutan is known in some detail (Rijksen and Meijaard, 1999). Figure 1 shows the distribution around 1978 of major coastal swamp areas inside this range, taken from official topographic maps. Small stands of *Neesia* may also be found occasionally in isolated swampy places farther inland. Since the mapping, most areas have undergone dramatic declines, especially during the 1990s (van Schaik et al., 2001). In the end, only the following swamp areas provided reliable samples to establish the presence or absence of tool use (Fig. 1): 1) Suaq Balimbing, in the Kluet swamp complex; 2) Ie Ndamai, in the Trumon-Singkil swamp complex; 3) Krueng Seumayan, in the Krueng Batee-Tripa swamp complex; and 4) Muara Singgersing in the Batu-Batu swamp. Sites farther south no longer yielded swamps with both orangutans and *Neesia*; possible fragments farther north could not be visited due to civil unrest. Several small sites inland said to contain *Neesia* have not yet been examined. Given the large home ranges of individual orangutans (Singleton and van Schaik, in press), we assume that the presence or absence of the skill at a site reflects presence or absence for the swamp as a whole.

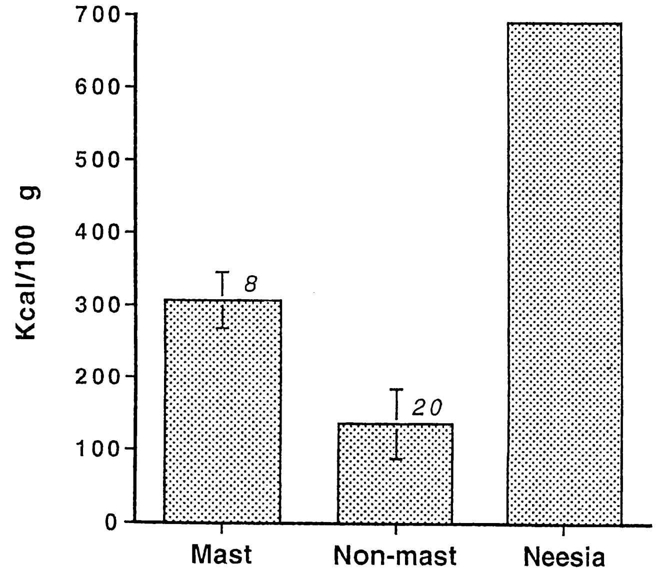

Fig. 2. Energy values of *Neesia* seeds as compared to other orangutan foods in Gunung Palung, during the period of food superabundance ("mast") and at other times. Error bars are standard deviations; number of species is indicated above column.

Establishing absence of tool use

Once a single unequivocal tool is found at a site that is otherwise suitable, its presence is established. To estimate the likelihood of its absence, we estimated the parameter of the Poisson distribution in areas with known tool use by counting the number of tools found in a large sample of potentially suitable fruits. Fruits were considered potentially to contain tools if they had dehisced, but had not dried out to the point that the "valves" were curled back and the cracks between them so wide that no tool would remain stuck in them. Also, the outside should not be discolored and the stinging hairs had to be recognizable to ensure that the fruits were fresh enough to have undecomposed tools in them. Finally, we only searched under trees in which orangutans had been eating, as shown by the presence of nests in or near the trees and of long, torn stalks on the fruits (if fruits are shed by a tree, the stalks are very short). These samples were taken during June 1998 and July 1999.

RESULTS

Neesia description and nutrient composition

Neesia cf. malayana fruits are large, five-angled woody capsules (up to 22 by 10 cm). The fruits contain highly edible seeds with a brown testa, consisting of 46% lipid (percent organic matter; *Neesia altissima*) (Knott, 1998, 1999). The tree protects these seeds against seed predators by growing a very tough woody husk. Before they are ripe, the fruits are closed and woody, and almost impossible to open, even with a machete. However, the seeds are already edible, and there are no irritant hairs yet. As the fruits ripen, they dehisce and a mass of irritant hairs surrounding the rows of seeds becomes exposed. Toward the end of the season, the seed develops a small red lipid-rich aril. These arils are composed of 78% lipid (percent organic matter; *Neesia altissima*) (Table 1). Late in the season, the orangutans eat only this lipid-rich attachment. In Sumatra, no other animals were seen to eat *Neesia*, but in Borneo, hornbills appear to be important dispersers. Using their bills, they pluck out and swallow the seeds with the fatty aril attached, and later regurgitate the seed (T. Laman, personal communication).

Neesia seeds and arils contained the highest percent lipid and highest Kcals per gram of any of the 101 orangutan foods tested at Gunung Palung by Knott (1998, 1999, and unpublished observations). Thus, their potential contribution to maintaining adequate orangutan diets is substantial. Figure 2 compares the Kcal/100 g of *Neesia* to foods eaten during the "mast" period of high fruit availability and the nonmast period of low fruit availability. *Neesia* was higher in calories than any of these other foods. These differences imply that the fitness payoff to efficiently extracting *Neesia* seeds and arils, i.e., inventing tool use, could be dramatic.

Neesia feeding behavior in Suaq Balimbing

For the study of tool use, it is important to distinguish between before and after dehiscence. When the fruits are large and contain large seeds, but are still closed with hairs that are not yet fully developed, they can be eaten without tools. However, they are so difficult to open that only adult males or occasionally large subadult males or large adult females can open them. The animals manage to open the fruit by tearing off a valve. To achieve this, they keep the fruit in their mouth and pull it away from the face with one hand and both feet, while hanging by one arm.

After the fruits open, the orangutans at Suaq Balimbing most commonly use tools, i.e., short straight branches with the bark stripped off, to overcome the fruit's defense of stinging hairs. They hold the tool in their mouth, insert it into the cracks between two valves, and then strongly move it up and down inside the crack and thus detach the seeds from their stalk. In the process, they also dislodge numerous hairs, and they often wipe off the accumulated hairs with the back of a finger. After this, the seeds can be pushed toward the open top of the fruit and scooped out with one finger, with the (hand-held) tool, or most commonly, dropped straight into the mouth. Then, seed coats are removed and spat out. In the final phases of the fruiting season, the whole seeds are spat out and only the oily attachments are eaten.

All independent animals in the population observed in *Neesia* trees with ripe fruit used tools. Tools were often made before entering the tree, were used on multiple fruits, and were sometimes carried to the next tree. At other times, however, several tools were discarded in quick succession. Individuals usually moved to a comfortable sitting spot after picking the fruit. Commonly they would pick several fruits and carry them in hand or foot or mouth. At the end of a day feeding on *Neesia*, the animals would be thirsty, more so than on other days, and drink water from treeholes or directly from the flowing parts of the swamp.

Fruits were sometimes put aside after having been worked on for a short while, and carefully lodged to prevent them from falling. The function of this was not directly obvious, but in several cases we saw animals return to these fruits after an hour or more. A plausible explanation for this behavior is that the tool that was in use was not of the right thickness and the animal parked the fruit until it had a tool of the right dimensions.

Figure 3 shows the progression of visits with and without tool use by the three major age-sex classes for one season at Suaq in 1995. During the first 2 months, most visits were mainly by adult males, who broke open the closed fruits without using tools. Approximately after 2 months, fruits started to open and more age-sex classes came to the trees and used tools. In Figure 4a, the season is broken down into these two periods (corresponding approximately to before and after the opening of the fruits). Before opening, most visits are by adult males; after opening, all age classes visit and males make up only about a quarter of the visitors χ^2 [2] = 17.78, $P < 0.0001$). After opening, most animals used tools, especially females (Fig. 4b; χ^2 [2] = 6.15, $P < 0.05$), and *Neesia* became the predominant fruit in the diet until the very end of the season.

Feeding behavior on *Neesia* followed basically the same pattern in two other documented fruiting seasons. In 1999, however, the fruiting season was quite drawn out, and it was noted that toward the very end, some individuals could get access to the seeds without tools because the cracks had become wide enough and the seeds were apparently easily dislodged. However, by then these fruits tended to contain fewer seeds.

Comparison with Gunung Palung

The above feeding pattern can be contrasted with that found in Gunung Palung on Borneo. At Gunung Palung, orangutans most commonly ate *Neesia* seeds by tearing off one or more of the valves. Generally, the fruits were already beginning to dehisce when they were ripped open. Seeds were then picked out with the fingers. Drinking was observed on 4.5% of days in which *Neesia* was eaten.

During 2,808 follow days conducted between August 1994 and August 1999, *Neesia* was eaten on 77 days by 14 orangutans, including both males and females. No tools were ever observed to be used. At Suaq, during 1995, *Neesia* was eaten on 91 days and tool use was observed in 65% of these follows (this is a conservative estimate because tool use was not always easy to see). Thus, it is highly unlikely that tools were used to eat *Neesia* at Gunung Palung but were simply not observed.

Neesia feeding at Gunung Palung did not reach the prominence that it did at Suaq (Fig. 5). In 1997, only 35% of 123 focal follows involved animals spending at least 5% of their fruit-eating time on *Neesia* during the *Neesia* season (and 30% of 46 follows in 1995), whereas at Suaq Balimbing in 1995 the number for the comparable period was 93% (of 67 follows after fruit dehiscence; or 65% of all focals during the time that at least some animals were eating *Neesia*; see Fig. 3). Clearly, tool use makes for greater concentration on *Neesia*. However, the data also indicate that *Neesia* is part of the optimal diet set at both sites.

In 1995, during a period of severe food shortage (Knott, 1998, 1999), males at Gunung Palung who ate *Neesia* were able to significantly increase their daily caloric consumption over males who did not eat

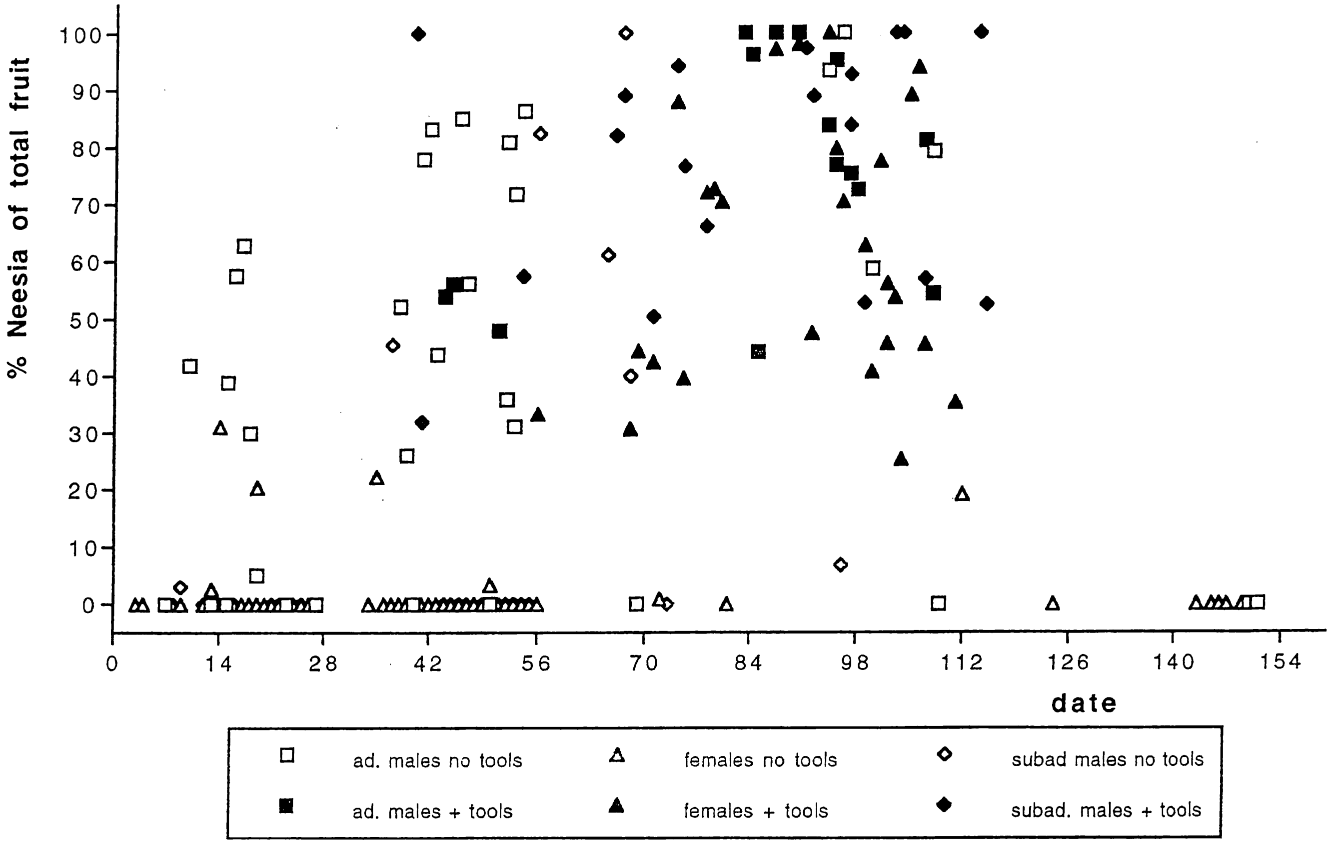

Fig. 3. Patterning of visits to *Neesia* fruit trees during focal follows at Suaq Balimbing during the 1995 fruiting season. ad., adult; subad., subadult. "Date" refers to Julian date.

Neesia (Fig. 6). Comparisons of intake rates between Gunung Palung and Suaq Balimbing are hampered by the enormous variance between samples, but mean values for adult males and females are similar (Fig. 7). However, as noted above, total feeding time is much higher in Sumatra, perhaps because no valves need to be broken off and because there is no injury to fingers. Consequently, the use of feeding tools produces an energetically significant improvement in overall caloric intake.

Geography of *Neesia* tool use in Sumatra

Presence of tool use in swamps. Suaq Balimbing is not the only site in Sumatra where *Neesia* seeds are extracted using tools. Tool use was established in a coastal swamp near Ie Mdamai, ca. 10 km south of Trumon (Fig. 1). At this site, animals were directly observed using the tools in August 1996, using the same techniques as at Suaq Balimbing (which is at 40 km linear distance). A 3-km nest survey indicated a very similar orangutan density to that of Suaq Balimbing. A total of 19 tools was found, both on the ground under trees in which focal animals fed and stuck in fallen fruits. The site was logged in 1997.

Along the Krueng Seumayam (3°45′51″ N, 96°36′53″ E), tools were found stuck in fruits under the last few remaining large *Neesia* trees in the area in July 1999, for a total of only 7 intact ones (along with 5 broken ones). All other trees had been logged. Earlier surveys had not yielded unambiguous data. No estimate of orangutan density could be made any more, but in general, in this swamp, orangutan densities had previously been found to be lower than in the Kluet swamp (which contains Suaq).

Absence of tool use in Muara Singgersing. At sites with tool use, we could determine the rate at which tools were present in fruits found on the forest floor (at the end of the fruiting season). Unfortunately, we could not separately estimate the rate for fruits dropped by orangutans because they could not reliably be distinguished from fruits that had fallen for other reasons (however, at Krueng Seumayam we noted that some trees had probably never been visited by orangutans, biasing the rate down). In any case, the rate of tool presence was 0.030 at Suaq Balimbing (3 likely tools out of 99 suitable fruits inspected; one of the samples at Suaq was well after the end of the season, making unambiguous recognition difficult), and 0.034 at Krueng Seumayam (8 out of 237 suitable fruits inspected), or an overall mean rate of 0.033.

At Muara Singgersing in the Batu-Batu swamp, we were able to examine 127 suitable fruits in three locations during three separate visits (2°44′39″ N,

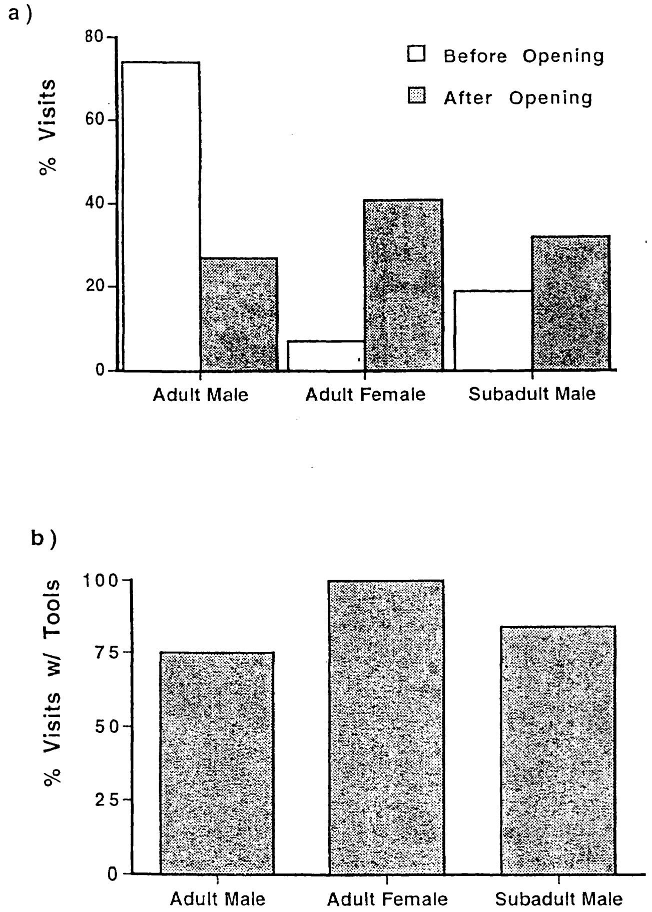

Fig. 4. **a:** Distribution of feeding sessions over the three main age-sex classes during first 2 months (when almost all fruits were undehisced) and the rest of the 1995 *Neesia* fruiting season (when almost all were dehisced) at Suaq Balimbing. **b:** Proportion of feeding sessions in *Neesia* involving tool use for the three main age-sex classes at Suaq Balimbing after the first 2 months of the 1995 season (mostly open fruits).

97°57′25″ E; 2°45′06″ N; 97°55′37″ E; 2°43′43″ N; 97°54′33″ E), all in areas with orangutan nests, but no tools were found. The probability of finding no tools with a Poisson parameter of $P = 0.033$ in $n = 127$ trials is $P = 0.014$. Hence, we conclude that tool use on *Neesia* is probably absent in Muara Singgersing.

However, we did find many dehisced fruits that had complete valves broken or bitten off after the fruits had dehisced, in three different locations. Orangutans at Gunung Palung normally break off *Neesia* valves after they have begun to dehisce. However, at Suaq Balimbing, orangutans bite off whole valves only before the fruits dehisce, and we only find undehisced fruits with missing valves on the forest floor. Moreover, the incidence of fruits with valves bitten off at Suaq or Krueng Seumayam is very low, less than 1%, and obviously these fruits are only found at the beginning of the season. At Muara Singgersing, they were common among the dehisced fruits on the forest floor (at least 22 out of 132 = 16.7%). We therefore conclude that these modifications to the fruits at Muara Singgersing were made by orangutans, where they eat them in ways similar to those at Gunung Palung.

At one location, we also found dehisced fruits that had holes gnawed through their husks. In that location, 9/14 fruits that had been modified had holes in them, and only one had both holes and valves bitten off. Although we never saw animals eat the fruits, it is possible that orangutans caused these changes to the fruits. The damaged fruits were clearly associated with trees that had orangutan nests in or near them. In the degraded forests at Muara Singgersing, many of the smaller trees that were found to have fruit did not have orangutan nests nearby; these fruits were always intact. It is of course possible that other animals, e.g., porcupines, were eating *Neesia* elsewhere, and not at Suaq, because the fruits at Suaq would tend to be empty once they reach the forest floor. However, if orangutans made these holes, it suggests that multiple techniques exist in this population, perhaps because smaller animals can only use the gnawing and not the breaking technique.

Geography of tree hole tool use (insects)

As noted in the Introduction, the orangutans at Suaq Balimbing also use tools to extract insects or honey from treeholes. None of the long-term field studies at other sites on Sumatra (Ketambe, Renun) or on Borneo (Gunung Palung, Camp Leakey in Tanjung Puting, Mentoko in Kutai, Danum Valley, Lokan, Sengatta River) have yielded evidence of tool use from treeholes (Fox et al., 1999). Nonetheless, at all these sites, orangutans do forage for insects, and do, with varying frequency, examine treeholes. At Gunung Palung, orangutans spent approximately 2.7% of feeding time eating insects overall, although during certain months it ranged as high as 12% of feeding time. Given the high number of observation hours, it is very unlikely that tool use to extract insects or their products has simply been missed.

DISCUSSION

The results of this study are inconsistent with the genetic hypothesis. It is true that *Neesia* tool use is not known for the Bornean subspecies: it is absent in Gunung Palung and also not reported for Tanjung Puting, where *Neesia* is also found (Galdikas, 1988). However, the absence in Muara Singgersing in Sumatra shows that the distribution does not simply follow subspecies boundaries. Likewise, treehole tool use is not found on Borneo, but also not in other well-studied Sumatran populations with habituated animals. Cultural independence is achieved across dispersal barriers, but at such distances genetic similarity may still be quite high through indirect contact that is well beyond the dispersal distance of individual animals. For instance, although the Alas River separating this area from the Trumon-Singkil swamp

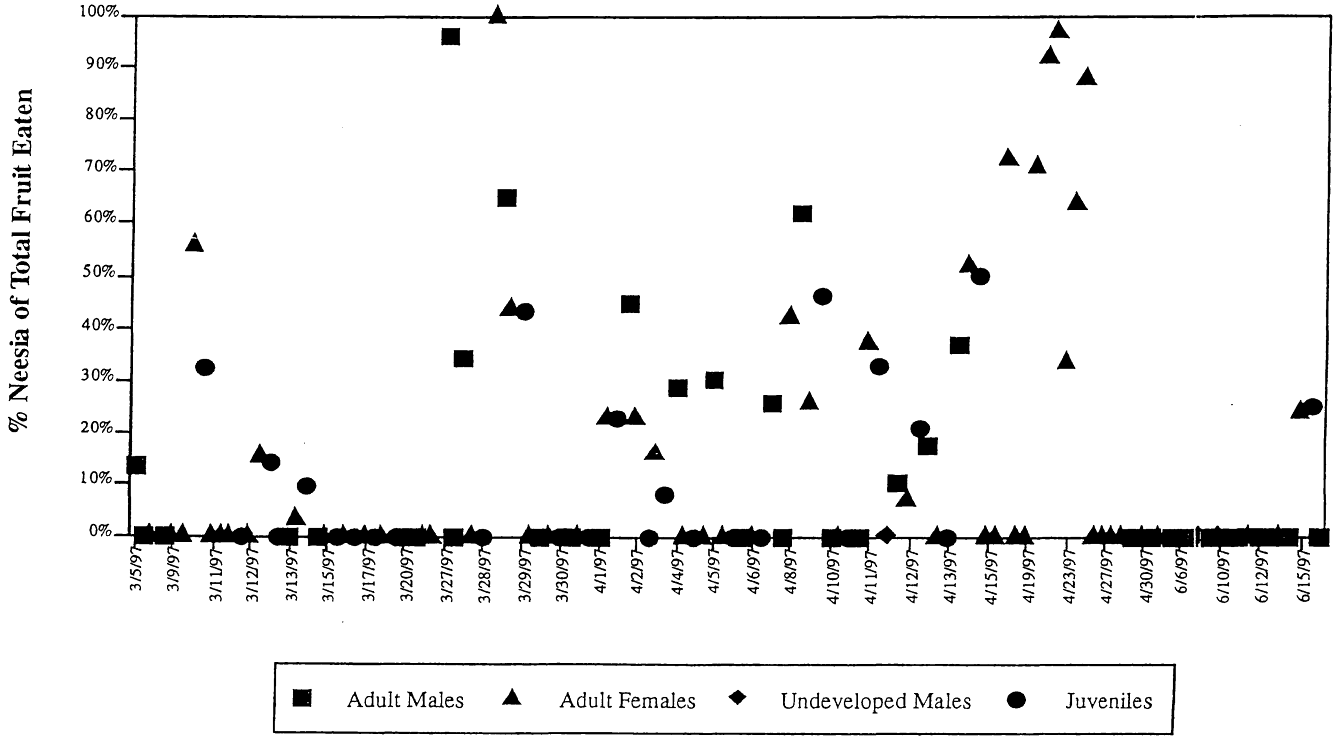

Fig. 5. Patterning of visits to *Neesia* fruit trees during focal follows at Gunung Palung during the 1997 fruiting season (conventions as in Fig. 3).

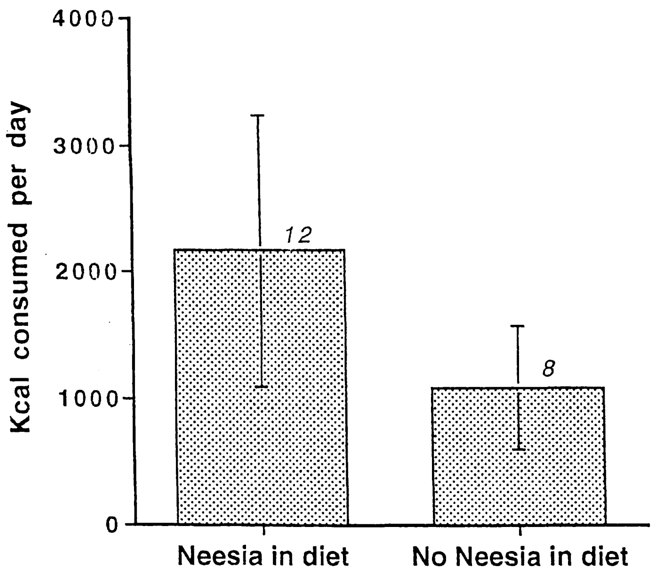

Fig. 6. Estimated caloric intake of one adult male orangutan at Gunung Palung on days with and without feeding on *Neesia*, during the 1995 *Neesia* season in Gunung Palung. Vertical bars refer to one standard deviation; numbers above the bars are sample sizes (complete follow days). The difference is significant (t-test, $P < 0.02$): males could double their caloric intake by eating *Neesia*.

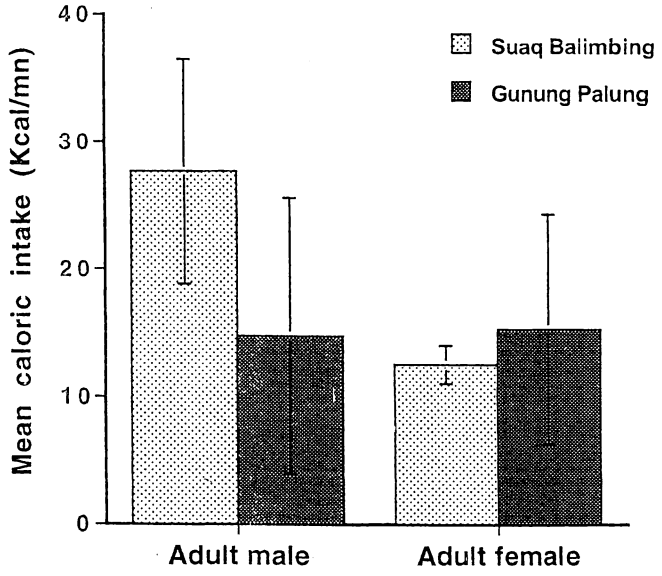

Fig. 7. Estimates of caloric intake on *Neesia* seeds and arils for adult males and females at Suaq Balimbing and Gunung Palung. Vertical bars refer to one standard deviation. The samples for Suaq females are almost certainly underestimates because they refer to the very beginning and very end of the period with open *Neesia* fruits; the male samples for Suaq are for before dehiscence (without tools).

(where *Neesia* tool use does occur) is impassable, occasional crossing is expected higher up the river (Fig. 1), and until recently the forest stretched down to the two swamps. Thus, it is likely that the genetic distance between Muara Singgersing and Trumon-Singkil is less than that between Suaq Balimbing and Krueng Seumayam, in both of which this tool use is found.

The results are also incompatible with the ecological hypothesis. The extraction of social insects or their products from treeholes through tool use is only found in Suaq Balimbing among the habituated populations, even though treeholes occur everywhere. In both Gunung Palung and Muara Singgersing, *Neesia* seeds are eaten, obtained with considerable effort on the part of the orangutans, and yet no tools are used. At Gunung Palung, less time is spent each day eating *Neesia* than at Suaq Balimbing. While this could theoretically indicate that more profitable species are found, and *Neesia* thus is no longer part of the optimum set of species (MacArthur and Pianka, 1966), this possibility is refuted by the enormous energetic returns on *Neesia* feeding (Fig. 4). It is therefore the difficulty of feeding on the well-protected fruits that is likely to limit its time in Gunung Palung.

Hence, this study shows that both the genetic and ecological hypotheses cannot explain the geographic distribution of orangutan tool use. The genetic hypothesis can be rejected because the tool use pattern does not match the subspecies pattern. The ecological hypothesis is rejected because *Neesia* is present and an important dietary component in the areas where it has been compared. These findings parallel those on chimpanzees, especially for the well-studied case of nut cracking with stone tools (Boesch et al., 1994; McGrew et al., 1997). Obviously, if clear ecological or genetic contrasts had been found, the individuals in the various populations must still have invented these skilled behaviors or learned them socially, but the elimination of genetic or ecological factors allows us to identify the tool acquisition process as the critical factor to determine the incidence pattern of these skills. We must therefore examine the history of invention and the process of acquisition during an individual's ontogeny.

The absence of a skill at a site could be due to lack of invention or due to a low rate of invention accompanied by inadequate social transmission. On the other hand, what the presence of a skill at a site reveals about these processes largely depends on the pattern of distribution among individuals at sites in which the skill is found. A patchy distribution at sites, with some animals showing the skill but others not, is consistent with frequent invention and poor horizontal transmission (and hence also poor diffusion). When a skill is found among all individuals of the population, and it is also uniform, this indicates highly reliable social transmission (and diffusion). When this happens, the rate of invention becomes almost irrelevant. At this stage, it is difficult to disentangle the relative roles of invention and social transmission conditions as causal factors for the variation among populations.

The first question is whether invention is rare enough to account for the incidence pattern. If so, the probability of presence would be correlated with population size in independent populations. In order to evaluate this prediction, we must first determine the number of independent cases. There are three in Sumatra. First, the Kluet and Trumon-Singkil swamp were until recently separated by some 12 km of dryland forest. It is conceivable, in light of known home range sizes and the presence of transients (Singleton and van Schaik, in press), that an animal born in one area can occasionally end up being a resident of the other. Second, the Krueng Batee-Tripa swamp is over 100 km from the Kluet swamp, without a major swamp area in between (Fig. 1). Third, the Batu-Batu swamp is separated from the other areas by the impassable Alas River. The likelihood of successful transfer when the river breaks through a meander is also fairly low (because orangutans cannot swim, the resulting oxbow and marsh will be a barrier for years, and the meander loops have been heavily used by people for centuries).

The two independent swamp areas with tool use both originally had sizable populations: the Tripa-Krueng Batee swamp had an estimated 1,350 individual, and the Kluet swamp with the Trumon-Singkil swamp combined had an estimated 4,000. Although the narrow Batu-Batu swamp was demographically connected to other swamp areas farther south, it probably had the smallest population size of the Sumatran swamps, given its smaller overall area and our impression of lower densities even before disturbance. No estimates of Bornean swamp populations are available, but the presence at multiple sites on Sumatra and the absence at multiple sites on Borneo are consistent with the systematic higher densities observed in Sumatra (Rijksen and Meijaard, 1999). Thus, it is possible that tool-using skills were only invented in the largest populations.

However, invention alone cannot explain the pattern of variation. Once invented, a new tool-using skill must be spread by social transmission and maintained by social transmission after it has become habitual or customary. It is conceivable that this type of tool use may be invented at a rare but regular frequency in other orangutan populations, but that in most populations opportunities for social learning are too rare to prevent the trait from going extinct again. Incidental tool use has been seen at all long-term study sites, including those without regular feeding tools. At Ketambe, on Sumatra, for instance, some individuals have been seen to use "gloves" of leaves to handle spiny fruits (S. Utami, personal communication). Similarly, at Gunung Palung on Borneo, two individual orangutans have been seen to use leaves as scoops for drinking. One was an adult male who rarely engaged in this behavior and never in the presence of other individuals. The other was an adult female whose offspring have so far not exhibited this behavior. That these behaviors have not become habitual in the population, even though the context is common enough to allow it, suggests that adequate conditions for social transmission must be present for an invention to persist: some level of gregariousness and some level of tolerance during foraging (van Schaik et al., 1999). At Suaq, the two kinds of feeding tool use are customary. The orangutans there are also the most gregarious and socially tolerant among the known study populations (van Schaik, 1999; van Schaik et al., 1999). Likewise, the two other swamps with known *Neesia* tool use have high densities, and therefore probably above-average gregariousness and social tolerance. Hence, suitable transmission conditions are probably the critical factor to explain the geographic distribution of skills such as feeding tool use in orangutans, and probably also in chimpanzees (van Schaik et al., 1999). To test the validity of this conclusion, it would be interesting to establish the universality of tool use among individuals in other populations with *Neesia* tool use, and also whether the presence of *Neesia* tool use predicts that of treehole tool use.

The ability to extract *Neesia* seeds with tools is likely to enhance fitness because it produces significant energy returns. The same argument applies, albeit perhaps less forcefully, to tool use on treeholes. The fitness benefits of tool-using suggest selective benefits for the underlying capacities, and the question arises as to what extent natural selection has honed them in orangutans, and whether the abilities for exploration and invention or for social learning have been selected for most strongly.

Invention of a skill such as tool use on *Neesia* fruits must be very rare, or else at least some individuals or matrilines in all sites would use the skill. The absence of nut cracking with stone tools beyond a dispersal barrier (see above), and the presence of very different techniques with different efficiencies for ant fishing (Boesch and Boesch, 1990), support that this argument also holds for chimpanzees. If social transmission is reliable enough, skills can be maintained in a population even if invention of a novel skill is quite rare. The implication is that great apes are better copiers than inventors, and human cultural history is consistent with this idea as well (Boserup, 1981). One possible interpretation of this difference is that natural selection has been stronger on social learning abilities than on invention abilities, provided that these abilities are cognitively distinct enough to be subject to independent selection. One possible reason is that marginal improvements in copying abilities bring greater fitness returns than similar improvements in invention abilities, because social learning capitalizes on the pooled skills of many others, unlike individual learning or invention.

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LITERATURE CITED

Association of Official Analytical Chemists. 1984. Fat (crude) or ether extract in animal feeds: direct method. In: Williams S, editor. Official methods of analysis of the Association of Official Analytical Chemists. Arlington, VA: Association of Official Analytical Chemists. p 159–160.

Beck BB. 1980. Animal tool behavior: the use and manufacture of tools by animals. New York: Garland STPM Press.

Boesch C. 1996. The emergence of cultures among wild chimpanzees. Proc Br Acad 88:251–268.

Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. Folia Primatol (Basel) 54:86–99.

Boesch C, Tomasello M. 1998. Chimpanzee and human cultures. Curr Anthropol 39:591–614.

Boesch C, Marchesi P, Marchesi N, Fruth B, Joulian F. 1994. Is nut cracking in wild chimpanzees a cultural behaviour? J Hum Evol 26:325–338.

Boserup E. 1981. Population and technological change: a study of long-term trends. Chicago: University of Chicago Press.

Conklin NL, Wrangham RW. 1994. The value of figs to a hind-gut fermenting frugivore: a nutritional analysis. Biochem Syst Ecol 22:137–151.

Fox EA, Sitompul AF, van Schaik CP. 1999. Intelligent tool use in wild Sumatran orangutans. In: Parker ST, Miles L, Mitchell R, editors. The mentality of gorillas and orangutans. Cambridge: Cambridge University Press. p 99–116.

Galdikas BMF. 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. Int J Primatol 9:1–35.

Goering HK, van Soest PJ. 1970. Forage fiber analysis. In: Agricultural Research Service, Agricultural handbook, no. 379. Washington, DC: USDA [booklet].

Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19:1061–1079.

Knott CD. 1999. Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability. Ph.D. thesis, Harvard University. 355 p.

MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. Am Nat 100:603–609.

McGrew WC. 1992. Chimpanzee material culture: implications for human evolution. Cambridge: Cambridge University Press.

McGrew WC, Marchant LF. 1997. Using the tools at hand: manual laterality and elementary technology in *Cebus* spp. and *Pan* spp. Int J Primatol 18:787–810.

McGrew WC, Ham RM, White LTJ, Tutin CEG, Fernandez M. 1997. Why don't chimpanzees in Gabon crack nuts? Int J Primatol 18:353–374.

Milton K, Demment MW. 1988. Digestion and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human diet. J Nutr 118:1082–1088.

National Research Council. 1980. Recommended dietary allowances, 9th ed. Washington, DC: National Academy of Science.

Pierce WC, Haenisch EL. 1947. Quantitative analysis. London: John Wiley & Sons, Inc.

Rijksen HD, Meijaard, E. 1999. Our vanishing relative: the status of wild orang-utans at the close of the twentieth century. Wageningen: Tropenbos Publications.

Robertson JB, van Soest PJ. 1980. The detergent system of analysis and its application to human foods. In: James WPT, Theander O, editors. The analysis of dietary fiber in food. New York: Marcel Dekker, Inc. p 123–158.

Robertson JMY, van Schaik CP. 2001. Preventing the extinction of the Sumatran orang-utan. Oryx 35:26–38.

Russon A, Galdikas B. 1995. Constraints on great apes' imitation: model and action selectivity in rehabilitant orangutan (*Pongo pygmaeus*) imitation. J Comp Psychol 109:5–17.

Singleton IS, van Schaik CP. In press. Orangutan home-range size and its determinants in a Sumatran swamp forest. Int J Primatol.

van Schaik CP. 1999. The socioecology of fission-fusion sociality in orangutans. Primates 40:73–90.

van Schaik CP, Fox EA, Sitompul AF. 1996. Manufacture and use of tools in wild Sumatran orangutans. Naturwissenschaft 83: 186–188.

van Schaik CP, Deaner RO, Merrill MY. 1999. The conditions for tool use in primates: implications for the evolution of material culture. J Hum Evol 36:719–741.

van Schaik CP, Monk KA, Robertson JMY. 2001. Dramatic decline in orang-utan numbers in the Leuser Ecosystem, northern Sumatra. Oryx 35:14–25.

Whiten A. 1998. Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). J Comp Psychol 112:270–281.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. Nature 399:682–685.

Wrangham RW, de Waal FBM, McGrew WC. 1994. The challenge of behavioral diversity. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, Marquardt LA, editors. Chimpanzee cultures. Cambridge: Harvard University Press. p 1–18.