

**REHABILITANT ORANGUTANS AND THEIR DESCENDANTS AT
KETAMBE: THE ROLE OF SOCIAL LEARNING IN INTRA-
POPULATION DIFFERENCES**

Introduction

Ex-captive orangutans introduced into natural populations provide a unique opportunity to explore issues related to social learning of variable behaviors. In this chapter, I will examine the unusual behaviors exhibited by a rehabilitant orangutan and descendants of rehabilitants at Ketambe, and evidence for opportunities for social learning by other resident orangutans.

To address the possibility of culture in non-human species, Imanishi (1952; reviewed in Nishida, 1987; and Wrangham et al., 1994) defined culture as “socially transmitted adjustable behavior.” To investigate the distribution of cultural behaviors in chimpanzees and orangutans, researchers have looked for evidence of behaviors that vary between populations without any clear, relevant ecological differences (van Schaik et al., 2003a; Whiten et al., 1999, Chapter 2; Whiten et al., 2001).

However, “socially transmitted adjustable behavior” can also vary within

populations. Sometimes, it is simply a matter of degree: tree-hole tool use by orangutans (*Pongo pygmaeus abelii*) at Suaq Balimbing is far more commonly performed by females in the southern/central social cluster than the northern social cluster (van Schaik et al., 2003b). At other times, behaviors can be absent in certain age or sex classes: in chimpanzees (*Pan troglodytes*) at Mahale, grooming-hand-clasp is performed only by adults, although younger individuals appear to know how to perform it (Nakamura, 2002). Similarly, the leaf-clip display is used by certain age/sex classes in chimpanzees in different contexts at different sites. In Mahale, it is performed by young adult males and estrus adult females (Nishida, 1980), but in Tai, adult males leaf-clip as part of their drumming display sequence (Boesch, 1995).

In some cases, variation in behavior can more clearly be attributed to different opportunities for social learning. Among Japanese macaques (*Macaca fuscata*), novel behaviors spread most rapidly to the innovators' most frequent social partners, such that more than four years after the innovation of sweet-potato washing, those outside the innovator's social circle still did not display the behavior (Kawamura, 1959; reviewed in Nishida, 1987). Other innovations in this species involving special louse-

egg-handling techniques during grooming spread first through one matriline (Tanaka, 1998). It also appears that the unusual behaviors exhibited by rehabilitant orangutans can be attributed to observational learning differences, in that the orangutans performing these behaviors are more often in close proximity to humans who (usually inadvertently) model behaviors that rehabilitant orangutans later reproduce (e.g. Russon and Galdikas, 1993).

In this chapter, I will provide evidence for the perpetuation of unusual behaviors in rehabilitant orangutans and their descendants, and highlight what it reveals about social learning. One rehabilitant female, her wild-born daughter and her grand-daughter continued to perform unusual and possibly maladaptive behaviors, 27 years after her initial introduction to the site. Wild residents and their descendants at Ketambe do not perform these behaviors, despite evidence for opportunities to learn the behaviors from the rehabilitants and their descendants. The persistence of these behaviors in the rehabilitant descendants is a clear example of vertical social transmission of a limited, matrilineal tradition among orangutans. The absence of such behaviors in wild orangutans, despite evidence of opportunities for social learning, indicates selectivity in either the types of behaviors or the models

chosen for observational learning in orangutans.

Selectivity in social learning

Social transmission of adjustable behaviors refers to some form of learning that is influenced by social interaction. Generally, we assume that observation of a model performing a behavior has influenced the learner to understand something new about the environment and its affordances, or to observe and replicate specific aspects of the model's behavior (cf. social learning or imitation, Heyes, 1993). While debate has raged over the exact definitions and processes involved in such learning, there is little doubt that the ability to learn socially is widespread in anthropoid primates and many other vertebrate taxa (see Chapter 1 for review). Observational learning between conspecifics can lead to “vertical” social transmission (offspring learning from a parent), “horizontal” social transmission (individuals of the same generation learning from one another) or “oblique” social transmission (unrelated individuals of different generations learning from one another, Cavalli-Sforza and Feldman, 1981).

Socially learned behaviors can include different types of skills and signals (see Chapter 2). While mockingbirds may replicate sounds somewhat indiscriminately (e.g. car alarms in cities), most primates studied appear

more selective about which behaviors they will reproduce. A laboratory study of chimpanzees found that they were most likely to imitate behaviors that were clearly useful in solving a problem; the chimpanzees follow strategies they see working to achieve a goal, and ignore other unsuccessful strategies that are demonstrated (Myowa-Yamakoshi and Matsuzawa, 2000). Another such study revealed that chimpanzees are more likely to reproduce behaviors that are just beyond their current level of competence than behaviors that are too simple or too advanced (Myowa-Yamakoshi and Matsuzawa, 1999).

Primate social learning may also depend on the learner's relationship with the model or the perceived value of the model. Field experiments with chimpanzees showed that they were much more likely to attend to the behavior of models who were older or in the same age-group as themselves, and unlikely to attend to models younger than themselves (Biro et al., 2003). A similar process may explain the spread of sweet-potato washing in Japanese macaques (described above). This preference for attending to the actions of older demonstrators implies that learners seek models likely to know something useful. This interpretation is bolstered by another laboratory tool-use experiment with chimpanzees showing that they observe

experienced tool-users only if they have not successfully completed the task themselves (Hirata and Morimura, 2000).

Finally, research has revealed the importance of affiliative social bonds in observational learning. Laboratory studies with capuchin monkeys (*Cebus apella*) show that innovation and learning are inhibited when social vigilance is required (Fragaszy and Visalberghi, 1990). Differences in the expression of tool-use between and within primate species are related to social tolerance (van Schaik et al., 1999). Rehabilitant orangutans are more likely to copy behavior of either humans or other orangutans with whom they share an affiliative bond (Russon and Galdikas, 1995).

Rehabilitant orangutans

There are several past and present projects focused on reintroducing captive orangutans into wild orangutan habitat. Early projects attempted to do this at locations where wild orangutans were found, with researchers simultaneously studying the wild population and their ex-captive charges (Rijksen, 1978). Researchers have noted the propensity of these young rehabilitant orangutans to copy the behaviors they observe while in the care of humans, even if such behaviors are not rewarded, occasionally dangerous, and frequently discouraged by human caretakers (Russon and Galdikas,

1993).

At Ketambe, an orangutan rehabilitation project was started in 1971 (Rijksen, 1978). Thirty-one ex-captive orangutans were brought to the Ketambe field station between July 1971 and August 1974. Little or nothing was known about the capture and experience of the (generally juvenile) orangutans prior to their confiscation and delivery to the field station. The typical track for a healthy rehabilitant upon arrival was (1) to be kept in a cage at the site for a few weeks or months under quarantine, (2) to be released around camp, receiving daily provisions of food but allowed to roam freely, then (3) have provisioning withdrawn (and often be transported to the far end of the site from camp) as they became competent at surviving in the wild. The young rehabilitants generally formed a cohort that socialized frequently during the period of provisioning. After release at Ketambe, several rehabilitant orangutans died through predation (clouded leopard attacks) or disease, and several others disappeared (Rijksen, 1978) or were transferred to other areas for release (C. van Schaik, pers. com.).

Based on Rijksen's recommendations, the rehabilitation project at Ketambe was halted in 1978, and all of the remaining orangutans not successfully reintroduced to the wild were sent to Bukit Lawang, in the town of Bohorok

at the eastern edge of Gunung Leuser National Park, approximately 100km east of Ketambe (C. van Schaik, pers. com.). A rehabilitant male, Usman, left the Ketambe area in 1972, and was seen by a reliable witness about 15km away in association with two wild orangutans in 1974 (Rijksen, 1978). Two ex-captive orangutans remained in the wild at Ketambe, successfully bred with wild orangutans, and were regularly seen in the following years: the females Binjei and Getty. Getty was found dead near the Ketambe River on 16 December 1997. The young infant she was nursing at that time died shortly after Getty's body was found (S. Utami Atmoko, pers. com.). Getty is survived by her adolescent son, Herman, who was often seen in the company of other young orangutans in the Ketambe population in 1999-2000.

History of the Binjei matriline

A female orangutan was brought to Ketambe in 1972, after being confiscated in the town of Binjei near the regional capital, Medan (Rijksen, 1978). She was estimated to be about 7 years old at that time. This orangutan, named Binjei, has since had four offspring and three grand-offspring (Figure 5.1). Elen and Erwin were not seen often in the mid-to-late 1990's, and they may have died (S. Utami Atmoko, pers. com., S. Wich, pers. com.). Tati was

occasionally seen at the edge of the study area near the Alas River in 1999 (this study, S. Utami Atmoko, pers. com.) Harto was still nursing and dependent on Binjei at the time of this study. Ans was nursing Kelly, and Chris was an independent (nulliparous) adolescent female at the time of this study.

As a sub-adult, Binjei became the dominant female among the rehabilitant orangutans. When the dominant male among the rehabilitants was removed from the population, Binjei performed behaviors similar to those the male had performed when new rehabilitants were introduced. Where the male had inspected the genitals of newly introduced ex-captive females, and on at least two occasions mounted them (though failing to achieve intromission), Binjei would restrain new females and insert a finger or thumb into their vagina (while stimulating her own genitals with her hallux). Such behavior has not been reported for other female orangutans (Rijksen, 1978).

Rijksen (1978) further reports that Binjei formed close social bonds with several rehabilitant females. As an adolescent, Binjei also formed a close, long-term bond with the adolescent female Yet, a wild resident orangutan. After reaching sexual maturity, Binjei (like most maturing female orangutans) became less socially tolerant with her peers. Rijksen reports that

Binjei became “aggressively intolerant towards other females..., including her former bond partner [Yet]” (1978, pg. 292).

Unusual behaviors seen in rehabilitant orangutans

Rehabilitant orangutans, even once fully reintroduced to the rainforest habitat, frequently exhibit behaviors not seen in wild orangutans, which are likely to be a result of their captivity and subsequent close contact with humans (Rijksen, 1978; Russon and Galdikas, 1993; Russon and Galdikas, 1995). For instance, recent rehabilitants were far more likely to travel on the ground and approach humans than wild orangutans at Ketambe (Rijksen, 1978; see Russon and Galdikas, 1993 for similar behaviors in Bornean orangutans).

Rehabilitants seem to engage in more affiliative behaviors than wild orangutans, often in ways similar to interactions most often seen between mothers and their young in wild orangutans. One behavior reported for Binjei and the other rehabilitant orangutans at Ketambe was the tendency to “bridge” for one another (reach from one tree to the next while traveling, then hold branches from both trees while the other crosses on or next to the bridging orangutan). Rijksen (1978) reports that he observed Binjei helping a new juvenile rehabilitant, who was trapped in a tree, across a gap, noting

that this was the first social interaction observed between the two orangutans. Bridging is most often performed by mothers for their juvenile offspring (though females have sometimes been seen to assist their heavier male consorts in this way). Binjei also “fostered” some of the younger rehabilitants, even suckling the ex-captive male Bumi concurrently with her own daughter Ans. Allo-grooming was more common among rehabilitants than wild resident orangutans (though still rare), most often occurring between orangutans who were in frequent close association (what Rijksen describes as “bond-partners”, 1978). Of the few allo-grooming incidents seen with wild orangutans, two were between an adolescent wild orangutan female (Yet) and a rehabilitant juvenile female (Barby). Most other allo-grooming observations were of wild mothers grooming their offspring.

Rijksen (1978) further reports that rehabilitant orangutans were commonly seen chewing cloth or cardboard taken from the field station. He notes that wild orangutans sometimes chewed cloth or cardboard they took from the rehabilitant orangutans, but he does not report wild orangutans coming into camp to take these materials themselves.

Unusual behaviors in rehabilitant orangutans represent clear evidence of behavioral variability within populations. The perpetuation of these

behaviors, their distributions within the population at Ketambe, and the social relationships of rehabilitants and their descendants over time illuminate aspects of the role of social learning in behavioral variation within a population. I will present evidence of the persistence of unusual behaviors in the descendants of rehabilitant females over decades and generations. I will show that other, wild resident orangutans probably had opportunities to learn these behaviors, but do not exhibit the behaviors, and I will discuss some possible interpretations for this evidence.

Methods

Both wild-born and rehabilitant orangutans were observed at the Ketambe research site in Gunung Leuser National Park (see Table 3.2 and Figure 2.1).

Only independent adult and adolescent orangutans (both wild resident and rehabilitant matriline) were chosen for focal follows for this study. Daily activities of focal animals, including social encounters and nest building bouts, were recorded from May 1999 to May 2000 by M. Isa, Nuzuar S. Hut and me. Table 5.1 shows focal observation time for Binjei, Ans, Chris (see figure 5.1) and Herman (adolescent son of the rehabilitant female Getty). Including these four, 14 identified orangutans were followed for a total of

1625 hours.

For social interactions, observers recorded the start and end of any time when another independent individual was within 50, 10 and 2 meters of the focal individual. The age/sex class and name of the other was recorded whenever it could be determined. Social contacts with juveniles and adolescents were noted only when their mothers were not within the same distance class (e.g. if the mother was less than 50m but more than 10m away, and her dependent juvenile offspring were within 10m, it would be recorded as 50m for the mother, but the juvenile would only be entered as a unique social partner in the 10m or less distance class). For 10 meters and 2 meters, observers also recorded which individual actively approached and which actively left proximity, and often made notes regarding the behavioral context.

Videotapes of orangutan behaviors were captured by Nuzuar S. Hut and me on an *ad libitum* basis, using a Canon ES4000 Hi-8 analog camcorder. For each incident videotaped, we noted the identity of the orangutan(s) being videotaped, the identity of any food species (or tree species used for nest-building), and the time (for comparison to the time-code recorded by the camera). In all, about 34 hours of orangutan behavior were videotaped at Ketambe. Some of the videotapes were of animals being followed for focal

data, while some was not.

During the months of August and September 1999, M. Isa kept records of which orangutans entered camp, noting the identity of the orangutan, the time they entered and left camp, and the major behaviors performed in camp.

I discussed the unusual behaviors of rehabilitant orangutans and their descendants with several researchers and field assistants while I was at Ketambe in 1999 and 2000. For further clarification and confirmation, I corresponded with Chris Schürmann, who studied orangutans at Ketambe from 1975-1979, Carel van Schaik, who observed orangutans at Ketambe from 1977-1992, Sri Suci Utami Atmoko, who has studied orangutans at Ketambe from 1993 to the present, and Serge Wich, who observed orangutans at Ketambe from 1997 to the present.

Results

Table 5.2 provides a summary of which orangutans were observed or reported in camp, taking cloth or cardboard, drinking near the camp water pump (this study only) or coming to the ground (this study only). In all cases, it is only rehabilitant orangutans or their descendants who perform these behaviors at Ketambe, though wild residents have been reported

entering camp.

Other's reports of unusual behaviors in rehabilitants and their descendants, and wild residents' opportunities to observe them

Chris Schürmann confirmed that rehabilitant orangutans took cloth and cardboard from camp from 1975-1979. He is certain that wild orangutans never took clothes or cardboard in that time. He noted that the wild adult male Jon, the wild female Yet, and several wild subadult males were frequent social partners of Binjei.

Carel van Schaik reported Binjei and other rehabilitants chewing cardboard taken from camp and taking clothes. He had seen rehabilitants playing with the water pump in camp. He recalled the wild resident males Doba and Jon, and the wild resident females Yet and Pluis coming into camp, but never saw wild resident orangutans taking clothes or cardboard.

Sri Suci Utami Atmoko reported that Getty and Herman, as well as Binjei, Ans and Chris, were known to take clothes and other items from camp. She had never observed or heard of the wild (non-rehabilitant-descended) orangutans taking artifacts or materials from camp, though the wild orangutans Yet, Nur, Boris and Dedi did sometimes enter camp.

Serge Wich confirmed that Binjei, Ans and Chris were the only orangutans coming into camp and taking things in recent years. He noted that few other wild orangutans have entered camp recently, but that Yet probably got the closest to camp the most often.

Several researchers and assistants at Ketambe in 1999 and 2000 indicated that Binjei, Chris and Ans sometimes came into camp and took things, and they advised caution with leaving blankets, shoes and clothes out and unattended where orangutans might take them. They were also very careful to immediately burn cardboard and other refuse to prevent the local wildlife (primarily the orangutans and some long-tailed macaques, *Macaca fascicularis*) from taking things. While I was there in 1999, one researcher lost a shoe that was later found torn and with gnaw-marks, and another discovered a blanket lodged up in a tree at the edge of the clearing around camp (there were no human witnesses to what transpired, but the consensus was that orangutans were to blame).

Video records of rehabilitant descendants in camp

On 31 May 1999, Nuzuar and I followed Chris (I took notes while Nuzuar videotaped). We met her in the forest not far from camp at 08:00. At 11:28 she began moving directly toward camp. By 11:45 she had reached camp

and was carrying some dark blue cloth, apparently the tattered remnants of a T-shirt. We did not see her enter camp to take it, so we suspected she had cached it in a tree at the edge of camp (she had probably stolen it off a clothesline at camp at least several days earlier -- I never discovered who had lost a dark blue T-shirt, or when it might have been taken). She kept the cloth with her, focusing her activities on it (sucking, tugging, or twisting it) for stretches of up to 46 minutes, or merely carrying it in a hand (in her mouth or draped over a shoulder), until 16:22. Chris remained in camp, foraging on unripe *Aglaia* sp. fruits, *Ficus racemosa* fruits and the leaves of *Erythina subumbrans*, some epiphyte stems and the cambium of a liana (all items included in wild resident orangutan diets). Ans and Kelly came into camp at 17:18, and remained there with Chris until 19:02 when they built their night nests (see Appendix II for details).

Chris was also videotaped chewing and playing with cloth on 28 April 2000 (by Nuzuar). She spent at least 1 hour and 45 minutes handling cloth on that day.

Herman was videotaped in camp on 29 April 2000 (by Nuzuar). He came to the ground behind the water pump to drink water from a puddle.

Recorded camp visits

Orangutans entered camp on six days while notes were kept (Table 5.3). Herman, Chris, Ans (and her dependent daughter Kelly), and Yossa (the adolescent son of the wild resident female Yet) came into camp during these observations. They primarily entered camp to eat the fruits (figs) of *Ficus racemosa*, though Ans also drank from a puddle of water behind the pump one day. They stayed as few as 2 hours and 20 minutes, but more often remained and built night nests adjacent to camp.

Social partners of rehabilitants and their descendants

Figures 6.2a-d show the percent of observation time that each focal had nearest neighbors at $\leq 50\text{m}$, $\leq 10\text{m}$, and $\leq 2\text{m}$. Binjei, who was nursing a small infant, spent very little time in parties during this study. Herman, an adolescent male, spent over half of his time in parties. The percent of each focal's time spent in parties that was spent with each social partner for $\leq 50\text{m}$, $\leq 10\text{m}$, and $\leq 2\text{m}$ distance classes are shown in Figure 5.3. While Chris and Ans spent the majority of their social time in parties with other members of their matriline, this was not the case for Binjei. Herman spent more time with wild orangutans than with rehabilitants or their descendants.

Table 5.4 indicates other focal orangutans that were recorded with

rehabilitants or their descendants as social partners in these distance classes, and which social partners the rehabilitants were seen with during their focal follows. Seven wild orangutans were seen with members of the Binjei matriline during their focal observations, including three not seen during focal follows of members of the Binjei matriline. Four wild orangutans were seen with Herman, including two not seen during Herman's focal follows. Records of where these social interactions occurred were not kept, so it is unclear how much of this time was in camp where clothes or other items could be taken and where cloth handling usually occurred

Discussion

Rehabilitant orangutans introduced in habitats with resident wild orangutan populations constitute a sort of unintentional field experiment on the acquisition and persistence of unusual or novel behaviors within a given habitat. The fact that Ketambe's successful rehabilitants and their descendants continue to perform behaviors not seen in wild orangutans is relevant to the issue of social learning in two important ways. First, the fact that these unusual behaviors have been passed down to at least two

descendant generations from Binjei, an ex-captive, is clear evidence for vertical social transmission of learned behaviors. Second, the fact that this behavior has not spread from the innovators to other members of the population, despite evidence of opportunities for social learning, indicates that orangutans are selective about what behaviors they adopt after observing them in others.

During the 1970s, when several rehabilitant orangutans were at Ketambe, many of them showed handling of clothes, and Binjei (and perhaps others) were known to eat cardboard taken from the garbage pit. In our terminology (Chapter 2), the handling of clothing would be a weal skill or unknown, whereas the cardboard chewing could be a subsistence skill (since the contents are actually ingested). However, the practice of taking clothes or other items from camp and chewing or handling them has not spread to the rest of the Ketambe population. It is limited to two surviving matriline: Binjei and her descendants; and Herman (son of the rehabilitant female Getty).

During this study, Chris was the orangutan most often seen going into camp, taking clothes and other items, carrying them and chewing them for extended periods of time. Chris probably learned this behavior from Ans, who had

learned it from her mother, Binjei. Binjei may have been the first to adopt this behavior at Ketambe, or she may have learned it from the other rehabilitant orangutans that were there in the 1970's. This fits the definition for "tradition" (a behavior pattern persisting from the innovator's generation to future generations), a proposed condition for attributing culture to a species (McGrew, 1992; McGrew and Tutin, 1978). As this behavior does not appear to serve any adaptive purpose (and in fact may be maladaptive, as it is actively discouraged by the researchers and assistants in camp), it may also fit the "non-subsistence" condition for culture (McGrew, 1992; McGrew and Tutin, 1978).

In just one year of focal observations, four orangutans from rehabilitant lineages came into contact with eight independent wild orangutans. Though records do not indicate whether these contacts took place at camp, where cloth and cardboard might be acquired and there would be opportunities to learn the associated behaviors, it is likely that such opportunities occur. The wild orangutans at Ketambe are very well habituated to human activities after three decades of regular contact with human observers, so human presence and activities should not inhibit wild orangutans from approaching camp. In the past, Binjei had regular, affiliative social contact with Yet

(when the two were adolescents), and many wild orangutans (especially males, including Jon, Doba and Boris) followed them and visited camp. Moreover, the wild residents Yet, Nur, Boris and Dedi came into camp during the 1990's, with Yet probably visiting camp most frequently. It is likely that Yet and other wild resident orangutans had many opportunities over the years to observe Binjei, Ans, Chris, Getty or Herman acquire, chew and handle cloth, but the wild residents did not add these behaviors to their repertoires.

Ex-captive orangutans are known to use social learning cues about what items are edible in their new environment. They appear to proceed cautiously, sampling a small quantity of a food item used by a human or another orangutan, then later eating more and adopting the item as part of their dietary repertoire (Rijksen, 1978; Russon, 2002). Rijksen (1978) reported that wild orangutans sometimes chewed cloth or cardboard they took from the rehabilitant orangutans, but he does not report wild orangutans coming into camp to get these materials themselves. Perhaps the wild orangutans were using a similar strategy, but found cloth and cardboard unpalatable upon testing.

The fact that no wild orangutans (original Ketambe residents or descendants

of these original residents) engage in cloth-handling or cardboard-chewing behaviors supports the proposal that orangutans are choosy about which behaviors to emulate and/or which models to observe for social learning. To the wild residents, the behavior of the introduced individuals and their descendants is apparently not worth copying, despite ample opportunities to observe these behaviors.

However, the descendants of introduced individuals persist in these unusual behaviors. The persistence of traditions through vertical social transmission within these lineages attests to either the importance of early experience in setting behavioral preferences in orangutans, or the high regard the mother holds as a model in orangutan social learning. This indicates that, while rehabilitants' peculiar behaviors are unlikely to spread throughout the population, caution must be exercised in orangutan reintroduction if such "unnatural" behaviors are to be minimized in the rehabilitant's descendants.

How can the universality of the apparently functionless nest raspberry at Suaq Balimbing (Chapter 4) be reconciled with the failure of the apparently functionless "cloth handling" tradition to spread to others at Ketambe? It could merely be an issue of time-depth in the behavior: the nest raspberry innovation could have arisen centuries ago at Suaq Balimbing, but we know

with some certainty that cloth handling did not appear at Ketambe until after 1971 (when the first rehabilitant orangutans were brought there, Rijksen 1978). Perhaps the adoption threshold for nest raspberries is lower than for cloth handling – that is, cloth handling may be more demanding for new adopters (more complex in terms of choosing and acquiring cloth, or with a greater fear barrier to overcome because of proximity to the ground and to humans), or nest raspberries may more intrinsically rewarding to new adopters. Perhaps there is a function for the nest raspberries that was not revealed by comparative analysis of the data available. Or perhaps the nest raspberry was innovated or adopted by a very social Suaq Balimbing orangutan who was considered a “good model” by others, whereas Binjei and Getty were clearly “outsiders” at Ketambe with limited connections and low status (“poor models”). The latter scenario is most likely, given the selectivity shown in model choice by primates (Myowa-Yamakoshi & Matsuzawa 1999, 2000, Biro et al, 2003) and the theoretical work supporting choosiness in cultural learning (Henrich & Gil-White, 2001).

