Do orangutan innovations reflect traditions?

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PSY 433 Primate Cognition

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LITERATURE REVIEW

Introduction

Orangutans are a part of the primate order separated into two species, *Pongo pygmaeus* and *Pongo abelii*. The great ape is a closely related ancestor of *Homo sapiens* who had a last common ancestor around 13 million years ago (Horai, Hayasaka, Kondo, Tsugane & Takahata, 1995). Primates have large implications on human evolution because of behavioral, cognitive, and physical similarities. Orangutans, in particular are interesting because they may possess innovative behaviors that reflect tradition. Furthermore, they produce innovations but are highly unsocial and therefore unlikely to interact socially with other orangutans in the near vicinity. Studying creative behaviors in orangutans has important implications for the future existence of the species. As deforestation rapidly increases in Indonesia, specifically on the islands of Borneo and Sumatra where the orangutans are located, the extinction rate of this great ape rapidly increases. However, the ability to adapt to constantly changing environments allows the orangutans to somewhat exist in a world where their natural resources are drastically depleted. Investigating how orangutans adapt to these changes can lead to applying findings to natural populations which could decrease the rapid rate of extinction for one of human's closest ancestor. In addition, studying possible traditional behavior in orangutans can give us insight into the origins of human tradition and culture. In the following paper, I will discuss whether or not innovations created by orangutans reflect traditions, focusing on how the methodologies of the experiments affect the results.

Laboratory Experiments

Laboratory experiments conducted with captive animals are common when investigating innovative behaviors in orangutans because they allow for the manipulation of many variables,

yet there are many limitations and results are often contradictory. Dindo and colleagues (2011) conducted a study in Zoo Atlanta with 11 orangutans which evaluated an experimental paradigm known as a diffusion chain in order to explore the ways in which traditions spread through orangutans. A diffusion chain is a form of observational learning where new behaviors are observed by other individuals, allowing them to learn the information and then pass it on. It is unique to study orangutans in this way because they are extremely solitary primates. Therefore, social learning is not necessary. During the experiment, two orangutans were trained to operate a foraging box with an opaque door. One was trained to lift the door, while the other was trained to slide the door which resulted in a food reward in the box. After these two apes were trained, a demonstration session took place with individuals from two separate groups. Each individual was to observe the orangutan either lift or slide the door. When the observation time period ended, the observers were presented with the same task. Two observations were completed via video demonstration because all the individuals were not in the same social group. After solving the task, they would become the demonstrator and thus teach the next orangutan. The lift group completed 20/20 successes, whereas the slide group completed 19/20. These results support the diffusion chain hypothesis suggesting that orangutans learn social behaviors and then transmit them through the group, despite their lack of sociality.

Behavioral flexibility, defined as an "individual's continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already have mastered a previous solution" is important when investigating cumulative cultural evolution in orangutans (Lehner, Burkart & van Schaik, 2011, p. 447) .Traditions or objects manipulated in simple or complex ways often result in a wider range of functions, or better efficiency and productivity. This is extremely relevant to human populations and technology because these modifications

often lead to new developments in society. Previously, the build-up of cumulative cultural evolution has been seen as uniquely human. However, this is still largely debated. Some studies have suggested that chimpanzees show cumulative culture when they crack nuts and use a separate rock for stability. On the contrary, studies have shown that chimpanzees and orangutans tend to conform to techniques and do not sway from the original (Lehner et al., 2011).

Lehner and colleagues (2011) conducted a study in order to determine orangutan's behavioral flexibility and their ability of cumulative techniques under varying situations using a laboratory experiment consisting of seven orangutans. The set-up was reflective of how wild orangutans collect water from deep holes in trees, using two methods called the "branch scoop" and "sponging". There were two transparent tubes with syrup in them, but only one was wide enough to allow them to reach in with their hand. The other tube was too small for their hands, which allowed them to create new techniques to retrieve the syrup. In the first condition, the wide tube was used and participants were provided with sticks, leafy twigs, wood wool, and paper. The task was to obtain the syrup by dipping in the tube with a stick, but this method was not very efficient and the orangutans were found to switch to more efficient techniques utilizing material such as twigs, paper, and wood wool. The second condition used narrow tubes, while keeping the original tools constant. The orangutans were no longer able to use previous methods and created new efficient techniques that would work for the changing condition. The last condition used the narrow tube as well, but the leafy twigs were taken away which resulted in the orangutans once again abandoning their preferred techniques and using new methods such as "squash-and-fish" and "drop-and-fish". In this study, orangutans showed a large amount of behavioral flexibility, but that is not completely representative of a cumulative culture.

Not only are laboratory experiments needed, but also additional comparative experiments are integral to primate studies in order to evaluate evolutionary theories. However, the actual set-up of comparative studies in separate primate species often results in bias or unfair advantages to one group or the other. Using a comparative method in order to investigate the innovativeness of all great apes, Manrique and colleagues (2013) presented five chimpanzees, five bonobos, three gorillas, and seven orangutans with a foraging box in a captive setting. The apes encountered three apparatuses individually which only differed in how to retrieve the grape. The first apparatus had a hole in the middle of the box which allowed the apes to use their fingers to get the grape, known as the fingering technique. The second apparatus had a higher hole which enabled the subjects to come up with the lifting technique where they used their handle on the bottom and their hands. The third apparatus had no hole, which meant the apes had to use the shooting technique and use the lever to fling the grape through the top. All the great apes except for the orangutans were successful in all the tasks while being quick and efficient. This study suggests that orangutans do not show behavioral flexibility.

Innovations between captive and wild populations are bound to be different as a result of their different lifestyles. Lehner and colleagues (2010) used a comparative method to build on previous studies and to contribute a new data point to previous lists of innovations in wild orangutans. Using an ethogram, various behaviors of orangutans were observed and then compared to a previous list created about wild populations in new research. Many various experiments were conducted in order to allow the captive orangutans to build innovations with objects that may reflect their natural environment. Some of the tests include "bag-use", "foot-in-mouth", and "tree-hole tool-use". Four out of ten of the behaviors on the list were seen as innovations. The study confirmed that the innovation list created in past research is significantly

valid when determining innovations in orangutan populations. However, there were an additional 13 innovations recorded in captive orangutans than wild ones which implies that captive orangutans are more innovative.

There is extremely low ecological validity in the aforementioned experiments. Ecological validity is integral to studying primates because results in laboratory experiments could be explained in terms of many other variables. For example, orangutans would not participate in a diffusion chain in their natural setting because they are solitary animals and do not go out of their way to interact with other orangutans as it is not necessary for their fitness (Dindo et al., 2011). Lehner and colleagues (2011) attempted to mimic an orangutan's natural setting by providing them with items they would receive in their natural environment. However, is it truly possible to represent an orangutan's natural setting when you present them with tubes filled with syrup and continuously manipulate the objects in their presence? The orangutans in Lehner and colleagues (2010) study provided the fact that most of the behavior was observed indoors because the orangutans rarely went outside. There is a big different for behavioral opportunities indoors versus outdoors. In addition, captivity may predispose orangutans for experiments such as these because the orangutans are used to change and familiar with manipulating novel items in their environment. Captive orangutans most likely associate novel objects with positive reinforcement and reward. The orangutans in Lehner and colleagues (2010) study may have been conditioned to be more likely to approach new objects because they are curious about them, which could attribute to the fact that captive orangutans were seen as more innovative. Food extraction methods in laboratory experiments seem to be a very common technique when evaluating innovative behaviors in primates (Dindo et al., 2011; Lehner et al., 2011; Manrique et al., 2013).

This has been the most reliable method in the past, but tradition calls for other behaviors that do not involve food. Therefore, there should be more laboratory experiments without food.

This is not to say that laboratory experiments are unnecessary to primate research because they do provide understanding. Particularly in the case of orangutans, this may be one of the only ways to study them as their population becomes increasingly small in the wild. Some laboratory experiments provide compelling evidence of innovative behaviors, but some show strong evidence that orangutans are not innovative. This leads to many discrepancies in the area of primate research, but other methods may lead to more valid results.

Armchair Analyses

It is often hard to compare cultural evolution in humans and nonhuman primates because their culture is not well preserved in the archaeological record. In addition, it is difficult to compare different species since they each have unique functions and abilities. Kamilar and Atkinson (2014) conducted statistical analyses using a comparative method of humans, chimpanzees, and orangutans by examining cross-cultural variation relative to nestedness. The researchers define cultural assemblages as being nested if "cultures with a small repertoire of traits tend to comprise a proper subset of those traits present in more complex cultures" (p. 111). A total of six datasets that quantified geographic variation in cultural traits were collected for the purpose of this study. Statistical methods were then conducted to determine if cultural traits showed a random distribution or a nested structure. Cultural traits for humans included material culture, basketry, and technological traits. For chimpanzees and orangutans, cultural traits were behavioral traits that were "material and gestural in nature". Results indicate that humans and chimpanzees show a strong amount of nestedness, but orangutans do not. In other words, cultural

diversity was shown to be significantly nonrandom in humans and chimpanzees and displayed high amount of hierarchical structures.

This study provides evidence that the skills involved in sequential cultural evolution may have come about with the last common ancestor of humans and chimpanzees. Past research involving human and chimpanzee culture has resulted in incongruity and includes examining geography, genetics and local ecology as an explanation for cultural behaviors. This study is unique in the sense that it has a wide dataset to analyze the hierarchical structure of various populations. It contributes to ecologist's understanding of the evolution of the ecosystem and how individuals comprise diversity in the ecosystem. In addition, it provides us with a very important gap between orangutans and chimpanzees or humans. This type of analysis is important because it brings together various disciplines in order to investigate culture as whole, a more anthropological approach. Often, this vast amount of data is important because it leads to new understandings and the ability to fill in gaps within research. It also provides evidence against the theory that orangutans have traditions.

Observation of Free-Range Orangutans

Jaeggi and colleagues (2010) conducted an observational study which aimed to evaluate if young orangutans learned food behaviors via social learning or independently. The researchers used a focal sampling method by observing individuals from night to day and included many variables such as amount of time spent co-foraging, amount of independent exploration, diet composition, overlap of diet composition within group, selective observation of particular food items, and amount of teaching. For the most part, young orangutans co-foraged with their mother. They also had very similar diets and rarely ate novel food items. Before trying new food, the young would look up to the mother, suggesting that they are extremely reliant on their

mother for foraging. One individual was an immigrant who was placed into the group and showed significant differences in diet. These preferences reflected her past diet in her previous habitat. Her offspring then exhibited the same type of preferences as her mother for food. These results are indicative of social learning through transmission by orangutans. Tasks that were more cognitively demanding including the extraction of embedded food, show an increase in observation and practice by the young. However, there were no observations of teaching at any point in the study. This observational study provides strong evidence that orangutans are extremely reliant on social transmission for their diet, especially when observing and practicing extractive foraging skills, therefore reflecting a culture of food traditions. This may be because of the long life history of orangutans, a lot of which is spent directly associated with the mother.

Observational studies sometimes serve to enhance previous data, such as the study conducted by van Schaik and colleagues (2006). This observational and comparative study contributed to the data on innovations in orangutan populations. Focal sampling and detailed narratives were used to examine the wild population of orangutans, and six other datasets were obtained for comparison. The results indicated that some behaviors should be added, whereas some should be taken away because they seemed to have a "hidden universal".

Observational studies are often difficult when studying a particular topic because there is so much to observe. However, there is a high amount of ecological validity which allows for comparison between captive populations and wild populations. There is a trade-off of not being able to control for certain variables, but it is realistic and shows orangutans in their natural habitat. One extremely important factor to this study is that it investigated young orangutans. Young orangutans are important to study because they provide evidence for social learning,

suggesting that there may be a sensitive period for social learning. Because of the solitary nature of primates, adult orangutans may not be the most useful to study.

Observation of Rehabilitated Orangutans

In order to better understand how culture is dispersed through various groups, Russon and colleagues (2007) conducted an observational study of rehabilitant orangutans investing leaf-carrying. Prior to the study, the participants had been on the island for two and half years. A focal sampling method was used in which data collected included all aspects of nest-building. Data from previous databases was also collected for comparison on 14 other orangutan populations in the area. Leaf-carrying was not consistent across populations. Rehabilitant orangutans tended to show this behavior more often than wild orangutans. In addition, the participants showed preferences towards the type of material used, including the species of plant. There was a strong indicator of cultural influences on leaf-carrying and nest building.

Another study which observed rehabilitant orangutan populations investigated water-related behaviors in order to recreate the steps that were taken to get to the new innovation and obtain the main influences (Russon et al., 2010). The data was collected through continuous event recording within four individual focal samples. The amount of water-related behaviors strongly correlated with an orangutan being an innovator. In order to reconstruct the pathways to innovations, precursors were identified post hoc. They were based on the similarity of function and form, with the highest amount being three which reflects a low cognitive complexity.

Observation of rehabilitated orangutans is similar to study captive orangutans, but also similar to studying captive populations. The primates may be somewhat conditioned for certain behaviors, but they are able to observe them in a natural setting. The study on leaf-carrying is important to studying culture in orangutans because it focused on the developmental conditions

that may affect learning (Russon et al., 2007). Normally, the skills needed to build a nest are acquired during infancy and juvenility, but this process is interrupted in rehabilitant orangutan populations. They do not have the tight mother-infant bond needed to adapt and to learn how to survive. It was found that juveniles are still able to acquire these behaviors, but it is more difficult in adults. The study conducted by Russon and colleagues (2010) is similar because it focuses on the process behind innovativeness, not simply the outcome. Observational studies in rehabilitant populations are limited in the fact that the orangutans were captive before. Previous to being released, they could have acquired innovative behaviors, but there is no way to know. There is already evidence that ex-captive orangutans possess more innovative behaviors than wild orangutans. It is also impossible to know the background of rehabilitated primates because more often than not they were a result of the pet trade or illegal poaching. However, as the population of orangutans continues to decline, this may be the only type possible to study.

Experiments

Haun and colleagues (2012) investigated the ability for individuals to acquire behaviors demonstrated by the majority of the group, known as majority biased transmission, in a comparative study of chimpanzees, humans, and orangutans. In the first part of the experiment, the participants were provided with three different colored boxes and holes on the top of each one. Prior to the true experiment, there was one minority demonstrator trained to prefer one color and three majority demonstrators who were trained to prefer a different color. To begin the experiment, the minority dropped the ball down the same colored hole three times and received an automatically triggered food reward. Next, the three majority dropped the balls simultaneously down a different colored hole. The observers watched and were allowed to enter after five minutes. They were permitted to drop three balls down the holes, receiving a food

reward for all the balls dropped. Orangutan's answers were random, whereas 7/9 chimpanzees and 9/16 children responded to the majority. In the second part of the experiment, behavioral information was addressed as frequent or rare, while the number of demonstrators was kept stable. The only variation to this part of the experiment was it consisted of two demonstrators, rather than four. One was demonstrator was to drop three balls in a colored box and the second was to drop a single ball. The observers then completed the same task in the first part of the experiment. Chimpanzees and orangutans exhibited random behavior, whereas the children provided more frequent behaviors. Altogether, the amount of individuals completing a task mattered more than the amount of times a task was completed in chimpanzees. Both of these factors contributed to children's behavioral repetitive behavioral nature and neither made a significant different to the orangutans.

Field experiments are often the most difficult method because they involve a lot of work. A comparative field experiment is even more difficult because of the various locations of participants. In addition, it is hard to find an experiment that is not biased towards one group. For example, this method of dropping balls in holes may be biased toward young children because they have encountered such tasks before. On the other hand, an orangutan is unlikely to have an opportunity in their natural setting that allows them to drop balls in holes. Although this setting is more representative of a natural setting, it does not take into account the sociality of orangutans. Orangutans may have not attained majority-biased behaviors because they are solitary individuals with social learning opportunities typically coming from mother-infant relations. As a result, the orangutans will most likely copy only one individual and not worry about the rest of the group, simply because that is not in their nature.

Proposed Study

If I were to further research in this area, I would conduct a field experiment with a free-range population following in the footsteps of Lehner and colleagues (2011). I would follow an approach similar to theirs by investigating whether or not wild orangutans can obtain behavioral flexibility under varying conditions, which suggests a cumulative culture. I propose that orangutans would show a high amount of behavioral flexibility in the wild, showing that wild orangutans have tradition.

My field-study would consist of multiple wild juvenile orangutans. The juveniles have the largest implication on social learning because they are at the only age where most social interactions occur and there might be a sensitive development period for orangutans. Instead of using plastic tubes and putting water in them to represent a tree in the wild, I will locate an actual tree and manipulate it so I am able to watch what happens. There would be two different trees, with a large hole and with a small hole. Using an opportunistic method, I will set-up a video camera that would run constantly in order to observe the orangutan's behavior.

In the first condition, I plan to observe the orangutans manipulating the tree with the wide hole while providing them with sticks, leafy twigs, and wood wool that will all come from the surrounding environment. Next, I wish to observe behaviors of the orangutans dealing with a small hole in a tree while providing them with the same materials.

After understanding how orangutans react to various sized holes in the trees, I will study them under varying conditions. Therefore, I will repeat the previous two conditions except I will remove various items that I had provided them with. This will allow me to understand how orangutans react when their environment changes, a very important implication for the future as orangutan populations continue to decrease. If we can understand how orangutans adapt to man-made changes, then we can enact conservation policies that may better help the low population.

Future research such as this work needs to focus on the realism of experimental procedures. Otherwise, it is difficult to generalize the data to other populations. Ecological validity is extremely important when studying primates because it leads to new understandings about human behavior. My study is important because it has strong ecological validity and it allows to observe the behavioral changes made by orangutans. Studying traditions in animals is often very difficult because "tradition" is hard to define. By determining the behavioral flexibility of orangutans, we can start the process of understanding how a tradition by orangutans is made. If the orangutans only practice certain techniques under certain conditions or because of ecology, then it may not be seen as a tradition. However, more research needs to be focused on predispositions for traditions. In addition, the focus of the research must be on juveniles because they have the highest ability for social transmission.

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