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Literature Review 3
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Zoology 567

My research topic is related to the hunting behaviours of chimpanzees. The order of my papers is determined by most broad to most specific behaviours of chimpanzee hunting. At first the papers discuss background information, basic influences on behaviour and preexisting hypotheses, then move into cultural differences between communities, finally touching base on very specific behaviours seen in special cases through observation.

Mitani, J. C., & Watts, D. P. (1999). Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, *109*(4), 439–454. https://doi.org/10.1002/(SICI)1096-8644(199908)109:4<439::AID-AJPA2>3.0.CO;2-3

Article Summary:

Prior to this article there had been many studies focused on ecological factors, like group structure, to explain the differences seen in hunting behaviours of chimpanzees. It was also well known that hunting group size correlates to hunting success, as well as, seasonal variation. This article explores the demographic influences on the Ngogo chimpanzee community through a 23-month observational study. The paper covers two topics that were highly debated when this paper was published, regarding hunting party size and the effect on the red colobus monkey population. The observations support the hypothesis that the decision to hunt is based mainly off of the number of available hunters, more importantly males than females. The more chimpanzees that are available to participate in a hunt the more likely a hunt will take place. Additionally the paper suggests that the Ngogo red colobus monkey is not under threat from predation of chimpanzees, only having 3% of the population loss per year. Another interesting finding of this paper, that had not been mentioned in the other papers I read is that the amount of meat received by an individual in a hunt depend on three factors, the hunting skill of the individual, meat sharing and theft of meat. All three of these factors have a positive correlation to rank within the chimpanzee community. All of the findings were significant to the scientific community studying hunting behaviours in chimpanzees because they were able to add a considerable amount of information on Ngogo chimpanzees; Which had not been studied properly because the chimpanzees were not yet habituated to the humans, therefore, hunts were rarely observed. This paper also suggest multiple direction of future research in the field of demographic influences on behaviour, more specifically determining which underlying factors determine the inside variation of hunt durations.

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Article Contribution:

This article is included in my review because it provides information on the known differences of hunting behaviour between chimpanzee communities, as well as, direct comparisons of these communities. The article also provides an abundant amount of information on the Ngogo community hunting style and why so most research is done at this particular site. This article provides a new perspective from the prey and describes how red colobus monkeys have been observed to avoid predation. The paper also sets up many different areas of future research, which has been followed up by the same authors in later years.

Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, *61*(5), 915–924. https://doi.org/10.1006/anbe.2000.1681

Article summary:

There are three main hypotheses that had already been proposed prior to this article that predict why chimpanzees hunt and share meat. The nutritional shortfall hypothesis, which predicts chimps hunt during times in which other food sources are not available. The second hypothesis states that male chimps hunt to obtain meat which they use to gain mates (hunting has a relationship to reproductive success). The third hypothesis is that males use meat from hunting as a social tool to form coalitionary bonds. The study investigated which hypothesis was correct for chimps found at Ngogo, which frequently hunt. The study lasted sixteen months, they measured tree density and tree size of the trees that were apart of the chimps diet, as well as, the monthly rainfall. They also studied the amount of encounters and hunts on red colobus monkeys, the number of females and males present, number of oestrous females present, male coalitionary bonds, and male meat sharing. The main findings of the study were that males being present is a good indicator of a hunt happening, males shared meat non-randomly and the sharing of meat between males in fact have a social aid. These findings mean that the third hypothesis best fits the chimpanzees reasoning to hunt, which is that hunting is used as a social tool to form coalitionary bonds. With the other information that was gathered, they found that the first and second hypothesis did not correlate to the behaviours observed in chimpanzees at Ngogo. However, different groups of chimpanzees have been found to follow the other hypotheses. The questions that this paper leaves are why do different groups of chimps provide evidence of different hypotheses of hunting, are there any other factors that may influence hunting behaviour?

Article contribution:

This article was perfect as my first article I read for my literature review because it explained the three existing hypotheses that regard the reason why chimpanzees hunt. This article provided evidence that hunting is done to reinforce social relationships between males. The study provided myself with

important background information that has already been collected in the field, as well as, the ways these hypotheses can be tested through observations. The paper leaves you wanting to know more about what other factors may influence hunting, and why different groups of chimpanzees seem to have different reasons to hunt.

Klein, H., Bocksberger, G., Baas, P., Bunel, S., Théleste, E., Pika, S., & Deschner, T. (2021). Hunting of mammals by central chimpanzees (*Pan troglodytes troglodytes*) in the Loango National Park, Gabon. *Primates*, *62*(2), 267–278. https://doi.org/10.1007/s10329-020-00885-4

Article Summary:

This article was the first observational study conducted on the newly habituated group of Rekambo community of chimpanzees located Loango National Park. The goal of this study was to observe hunting patterns of the Rekambo chimpanzees such as frequency, strategies and hunting success. Prior to this study there have been two hypotheses proposed relating to food availability having an influence on hunting frequency. The nutrient shortfall hypothesis states that chimpanzees hunting increases during times of low fruit availability. The nutrient surplus hypothesis states that chimpanzees hunt in times of high fruit availability because chimpanzees have high energy reserves. The Rekambo chimpanzees were observed from May 2017 to March 2019 on an ad libitum basis, in addition fruit availability per month was calculated with a specific equation. The findings showed that the community hunted two species of monkey most frequently that had never been documented before in other chimpanzee communities, as well as a duiker species. It was also found that the hunting frequency was higher in the Rekambo chimpanzees than other communities, consisting of hunts lasting usually seven minutes; hunts were more successful when more individuals participated. Rank does not fully determine the participation in hunt, however more research should be done in this area to determine other influencing factors. Most importantly, the study found that Rekambo chimpanzees hunt most frequently during times of higher fruit availability which supports the nutrient surplus hypothesis. More research should be done to determine whether other factors like prey availability or other ecological factors effect annual hunting frequencies. These findings significantly improve the knowledge surrounding chimpanzee hunting behaviours by adding basic understanding of newly habituated communities.

Article Contribution:

This article was chosen to be a part of my literature review because it added a significant amount of new information to the topic of hunting behaviours in chimpanzees. The article adds addition support to the preexisting nutrient surplus hypothesis stating that chimpanzee hunt more frequently when fruit availability is higher. The article touches on a lot of important background theory and information about preexisting hypothesis, in addition to a lot of comparison to other chimpanzee communities. The article

provides many different directions of future research and investigations in not only the Rekambo chimpanzees but other communities as well.

Watts, D. P., & Mitani, J. C. (2002). Hunting behaviour of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *23*(1), 1–28. https://doi.org/10.1023/A:1013270606320

Article Summary:

This article explains why chimpanzees hunt and the ecological factors that may influence hunting behaviours between communities. Prior to this paper, it was known that hunting frequencies change throughout the year, but it was unclear why there is such a large amount of variation in hunting frequencies. The authors of the article gathered observations and data during an 11 month period in 1998 to 1999 at the Ngogo chimpanzee site in Uganda. The major findings were that the Ngogo community had an overwhelming preference for red colobus monkeys as prey during hunts. As well as, rates of red colobus hunts were much higher in this community when compared to others, this could be because of large portion of males and large hunting party sizes within the community. In the same fashion, the number of kills, amount of meat, and probability of capturing the red colobus monkey all increased as the number of males increase within the hunting party. The two most important findings was that the Ngogo chimpanzees follow the nutrient surplus hypothesis which states that behaviours like hunting and hunting patrols (chimpanzee actively looking for prey to hunt) are more frequent when there is high fruit availability, and that hunting is in fact easier to complete when the canopy structure is broken. These findings about the canopy structure are significant to the topic of hunting in chimpanzees because this paper was the first paper to provide quantitative evidence that broken canopies are better to hunt in because the prey can be easily cornered and caught. Future research was suggested throughout the paper including research on cheating and the effect on meat sharing and meat intake, additionally research could be done on the ecology of red colobus monkeys and the effects of hunting on the population in Kibale National Park.

Article Contribution:

This article was chosen to be a part of my literature review because it provides a lot of background information, explains certain hypotheses and theories, and of course provides the first quantitative evidence that canopy structure can influence hunting behaviours. The paper supports previous findings on the Ngogo chimpanzees while adding new evidence which supports multiple different theories. The article also suggests area which need further research in both regarding chimpanzee and red colobus monkey populations. Many graphs and visuals are provided in this article which makes it easier to visualize and summarize the data that was collected.

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Boesch, C. (2002). Cooperative hunting roles among Taï chimpanzees. *Human Nature*, *13*(1), 27–46. https://doi.org/10.1007/s12110-002-1013-6

Article Summary:

This article is a summary of the findings and observations of Taï chimpanzees in regard to cooperative hunting and the learning process. The article describes the challenge of hunting red colobus monkeys due to the fact that they live in an arboreal environment. Taï chimpanzees, in particular, hunt in continuous forests which require extreme coordination between hunters because the red colobus monkeys cannot be cornered easily. Compared to other chimpanzee groups, the Taï chimpanzees use group hunts and collaboration more than solitary hunts. The article summarizes the four main hunting roles among the Taï chimpanzees; the ambusher, the blocker, the chaser and the driver. Any hunter can perform any of the four roles, even during a hunt the roles may switch multiple times. Specific roles and participation improved meat access, this indicates that the roles were monitored by the group in order to be strict regarding meat sharing.

Learning hunting roles was also discussed, it has been found that Taï chimpanzees started to approach colobus monkeys, but it was only once they reached about 10 years old that they were not afraid of the monkeys when they fought back. At 10 years old the chimps had started to hunting more efficiently, however, learning the complex roles of hunting takes upwards of 20 years of practice. It was also found that older chimps showed an increase in frequency of ambushes and anticipations while huntings compared to younger chimps. It is believed that one of the reasons as to why the learning process is so slow is because the chimps need to understanding the other species as well as its own group; further research is needed especially on different groups of chimps where the learning could be different.

Article Contribution:

This article was chosen for my literature review because it explains the extreme cooperation that is needed between chimps to efficiently hunt as a group, as well as, the expensive learning process that is associated with hunting. It provided a lot of background information and synthesis on the topic of hunting in chimpanzees, including comparisons of multiple chimpanzee groups. The article emphasizes work done on Taï chimpanzees but still leaves you wondering why there are such drastic differences in hunting and learning strategies between groups of chimpanzees throughout Africa.

Hobaiter, C., Samuni, L., Mullins, C., Akankwasa, W. J., & Zuberbühler, K. (2017). Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo forest, Uganda. *PLOS ONE*, *12*(6), e0178065. https://doi.org/10.1371/journal.pone.0178065

Article Summary:

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In this article the authors observed two neighbouring groups of chimpanzees to compare hunting and prey preferences in respect the differing levels of habituation in both groups. Studying the extent of social and cultural factors which effect hunting and meat sharing had never been studied before this paper, studies had only ever looked at tool use in chimpanzees in regard to cultural learning. Cultural has not been studied in the context of hunting behaviours; Instead studies have focused on social structure or canopy structure, similar to the majority of papers listed in this review. The authors use preexisting data, as well as new observations of Sonso and Waibira chimpanzees. The groups were observed through group timed sampling every 15 minutes on a daily basis, throughout a 12 year study time. Waibira chimpanzees are a newly habituated group, and it was found that the group had no basis in prey type, while Sonso chimpanzees had a basis towards Guereza colobus monkeys and group hunting. It was also found that hunting rates tends to increase throughout the years that a group is present. In the Sonso chimpanzees access to meat is mostly determined by dominance rankings, whereas the Waibira chimpanzees determined meat access by whomever was a part of the hunt. A clear difference was found between the two neighbouring chimpanzee communities in both hunting and prey preference, and also meat sharing protocols. These behavioural differences were found to be in result of human observers and level of habituation in addition to socially learned traditions. Future research should be done of the effects of habituation on chimpanzee hunting and prey preference. Similarly, early data of the Sonso chimpanzees should be examined to see if there was a shift from the majority of hunts being solitary to group hunts.

Article Contribution:

This article was chosen to be a part of my literature review because it describes that differences in hunting between chimpanzees groups can due to cultural differences and socially learned traditions. This was the first paper to hypothesize that hunting differences may be in response to socially learned traditions and habituation of a chimpanzee group. The paper also provided background information on meat sharing and harassment in chimpanzees. It provides many directions of further research in understanding habituation of groups and what this does to the prey preference and styling of hunting performed by different chimpanzee communities.

Stern, M., & Goldstone, R. (2005). Red colobus as prey: The leaping habits of five sympatric old world monkeys. *Folia Primatologica*, *76*(2), 100–112. https://doi.org/10.1159/000083616

Article Summary:

This article was the first to question and test the preexisting hypotheses of why red colobus monkeys are the preferred prey choice of chimpanzees. There are three preexisting hypotheses regarding red colobus monkeys as prey which include factors of fixed search images due to higher encounter rate, higher frequency of living in isolated trees and discontinuous canopies, and poor or lack of choices while

try to escape chimpanzee predation. The authors examined the slow flight hypothesis and narrowed the prey preference down to two influencing factors, leaping habits and evacuation time due to canopy type. Observations were made over a three month period on 5 different species including red colobus species, as well as measurements regarding tree characteristics and canopy structure. The authors found that red colobus monkeys have a longer leap preparation time than all other species that were observed, leap preparation lasting an average of one-second longer. It was also determined that the hypothesis of being preferred as prey because of being in a discontinuous canopy was not supported by the evidence that was gathered. The likely reason why chimpanzees prefer red colobus monkey is that both male and female red colobus monkeys take a significantly longer time to leap out of a tree. This information is significant to the study of chimpanzee hunting behaviour because it allows insight into the reasoning behind the disproportional prey choice of chimpanzees. The articles suggest further research into alternate reasons of this prey choice, for example the red colobus monkey may be preferred because of taste. This is very interesting because I had never even thought to think about the taste of the monkey as part of chimpanzee preference.

Article Contribution:

This article was chosen to be a part of my literary review because it provides a new perspective of the prey as to why chimpanzees have such a disproportional preference towards red colobus monkeys. This paper is significant because it narrowed the preexisting hypotheses to one influential factors of leap preparation times. What stood out for me was the line of future research that this paper suggested, which was that the preference may be related to preferred taste of red colobus monkeys. This pushes the research in a new direction, that was never considered before.

Watts, D. P., & Mitani, J. C. (2015). Hunting and prey switching by chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo. *International Journal of Primatology*, *36*(4), 728–748. https://doi.org/10.1007/s10764-015-9851-3

Article Summary:

This article explores the relationship between chimpanzees and their prey choices from an ecological perspective. The authors main objective was to determine whether the chimpanzees at Ngogo made an effort to switch their prey of choice due to the decline of population of the red colobus monkeys in the area, if so would this allow the population of red colobus monkeys to recover. This article is significant to this topic because it was the first time that scientist examined ecological aspects of hunting behaviours which effect both the chimpanzees and the red colobus monkey populations. The article provides lots of background information on prey switching, which is seen in many different predator-prey relationships outside of primates. The authors used their own data which was collected throughout 2005

to 2006, as well as previous data collected between 1995 and 2014 on the chimpanzees located at Ngogo. Data included hunting rates, prey choice, prey body mass, as well as calculations for the likelihood of encounter of red colobus monkeys and other prey species. It was found that the hunting rate stayed constant, however the rate of hunting of the red colobus monkeys had decreased over the 20 year study. With this being said, it's important to note that the likelihood of hunt being pursued when encountering a red colobus monkey had not changed. The likely explanation of the decrease of red colobus hunts is because the chimpanzees do not see them as regularly due to their decrease population size. These findings are significant to understanding the relationship between chimpanzees and their prey of choice; since chimpanzees are not obligate carnivores the frequency of hunting and prey choice can lead to large impacts of prey populations and the ecology of the forest.

Article Contribution:

This article was chosen to be a part of my literature review because it provides information on prey switching, as well as new perspectives of the prey ecology in addition to the ecology of chimpanzees in regard to hunting behaviours. The paper supports many of the previous findings on the chimpanzees of Ngogo while adding new information. This article advances the knowledge of the field by providing evidence that chimpanzees do not prey switch in an effort to provide relief to the red colobus monkey populations in Kibale National Park, like obligate carnivores would do.

Pruetz, J. D., Bertolani, P., Ontl, K. B., Lindshield, S., Shelley, M., & Wessling, E. G. (2015). New evidence on the tool-assisted hunting exhibited by chimpanzees (P*an troglodytes verus*) in a Savannah habitat at Fongoli, Sénégal. *Royal Society Open Science*, *2*(4), 140507. https://doi.org/10.1098/rsos.140507

Article Summary:

This article describes the hunting that is observed at the Fongoli site which contains a group of Savannah chimpanzees. This group is particularly unique because they are the only group of chimpanzees that are known to use tools while hunting prey. With the addition of tools it was found through observation that females and younger chimpanzees had an easier time hunting and successfully catching prey. The group was observed between 2005 and 2014, study began in 2005 because the group was newly habituated. The most common prey of the Fongoli chimpanzees is the Galago, which is a smaller primate; Galago prey makes up most of the tool assisted successful hunts by females. It was found that 30% of all successful hunts were carried out by females, which is quite high compared to other chimpanzee sites. Even more so, 47.6% of successful tool assisted hunts at Fongoli were carried out by females. There was a higher than expected amount of tool assisted hunts carried out by juveniles males and females, almost all chimpanzees over the age of 2 years old had been recorded hunting with tools. A significant impact on

hunting success was determined by the sex and age of the chimpanzee, being that older males had the most success. The findings of this article are extremely important not only for anthropology purposes but also understanding the behaviours of chimpanzee hunting through comparison of other communities. The authors present question throughout the paper that need future research. An example would be the emphasis on the study female hunting behaviours to determine the nature of sex differences in chimpanzees foraging patterns. Similarly, further investigation on why chimpanzees, other than adult males, do not hunt as often at other sites is needed to understand how the social structure is founded and maintained.

Article Contribution:

The article was a good addition to my literature review because it had an anthropology perspective of tool assisted hunting, which is definitely different from all of the other papers I have read on hunting behaviour of chimpanzees. This was the first time tool assisted hunting was studying, which is a big jump of knowledge in this field of science and anthropology presenting many new ideas and new information. The article presents many new questions about why only males hunt in most communities, and pushes for the a more vigorous study of female chimpanzee foraging and hunting behaviours.

Videan, E. N., Fritz, J., & Murphy, J. (2007). Hunting and occasional consumption of prey items by chimpanzees at the primate foundation of Arizona. *International Journal of Primatology*, *28*(2), 477–481. https://doi.org/10.1007/s10764-007-9126-8

Article Summary:

This article was the first to document and report on the hunting behaviours or predatory behaviours of chimpanzees in captive environments. The study was conducted from observed from security footage of the chimpanzees in the outdoor enclosure at the Primate Foundation of Arizona during a period of two and a half years. Hunting occurred when a species of prey entered the outdoor closure, the foundation tried to keep this from happening at the risk of spreading diseases. Prey species included mice, doves, squirrels, small birds and lizards which are not the typical prey of wild chimpanzees. There was a total of 18 hunts that were observed, the majority of them were done by a single individual who would chase and grab the prey by their hands. Most commonly the prey would be grabbed and would die from the head being bit or the breaking of their necks which indicate that the killing was intentional. Some of the hunts would end by consuming the meat, in contrast some chimpanzees would leave the prey behind in the enclosure. Board comparisons were made between captive and wild chimpanzees, for example wild chimpanzees typically hunt as group, while this is rarer to see in captive chimpanzees. This research provides significant importance to the study of hunting behaviours because it provides a new perspective of hunting in a captive environment. The article suggests that further studies should be done comparing

captive and wild chimpanzee hunting behaviours more throughly to hopefully explain these big differences that can be seen in the two groups. In addition research should be done on the development of hunting behaviours in captive chimpanzees, as well as the challenges of maintaining the health of captive chimpanzees during hunting of prey.

Article Contribution:

This article is important to add to my review because it was the first paper to observe hunting behaviours in captive chimpanzees. This paper just introduces the basic information found about the predatory behaviours that were observed at the Primate Foundation of Arizona, which provides a huge advance in the topic of hunting in direction that wasn't consider prior to this paper. The paper questions whether captive chimpanzees have similar behaviour as seen in wild chimpanzee hunting, even though many factors are in fact different. The paper also purposes further research regarding how hunting behaviours in captive chimpanzees are developed.