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Investigating Sequence Learning in Anthropoid Primates Using Observational and Experimental Methods

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Declaration

The work contained in this thesis was carried out by the author between 2021 and 2022 while a postgraduate student in the Department of Psychology at Durham University. The present thesis has not been submitted to another university for the award of an academic degree in this form. Except where it has been stated otherwise by reference or acknowledgment, the work presented is entirely the author's own.

Statement of Copyright

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Abstract

Sequence learning is a crucial aspect of human cognition, being foundational in humans ability to learn language, develop complex tool use and in the development of cumulative culture. A recent review by Ghirlanda et al (2017) highlights that humans potentially have enhancements in these abilities beyond other animals and therefore sequence learning may be a cognitive capacity that sets us apart from other animals. Understanding how these abilities evolved and may differ in our closest living relatives, the primates, can provide novel insights into these abilities. I start by reviewing the existing literature on observational and experimental research in the anthropoid primates, by providing an overview of the observational and experimental research that has been conducted. Particular focus is paid to the areas of communication, foraging and tool use, as well as evaluating the contributions of different experimental approaches to our understanding of sequence learning abilities in primates. An observational study comparing gorillas and François' langurs was then conducted, which used Markov Chain Analysis to identify whether these primate species differed in the sequences of behaviours they used while browse feeding. This study identified that gorillas exhibit hierarchical sequence structures in their feeding behaviours, where the langurs didn't. An experimental study was also conducted, using a novel puzzle box experiment, aiming to provide experimental data on the manual sequence learning abilities of previously understudied species, in this case François' langurs and black headed spider monkeys. As the results obtained from this experiment were minimal in regard to evaluating sequence learning abilities, results are discussed in relation to improving the procedures of these kinds of experiments. Particularly when working with zoo housed primate populations.

Chapter 1: Sequence Learning in Anthropoid Primates: Review of Observational and Experimental Research

1.1 Introduction

The ability to detect, discriminate and comprehend sequences of behaviours is a fundamentally important aspect of human cognition. This is particularly evident in language where learning how to manipulate phonemes into words and words into sentences, that fit grammatical rules, is the foundation of human communication and allows humans to express complex concepts to each other in the form of language (Christiansen et al., 2002). However, language is not the only domain where sequence learning is likely to be essential. Some evidence for this comes from neurocognitive studies in humans, which have identified that the cortico-basal ganglia-thalamocortical circuits implement hierarchical control in both processing musical and linguistic sequences (Blumenthal-Dramé & Malaia, 2019). As well as evidence from studies identifying interference effects when linguistic and musical stimuli are jointly presented and that priming for sequence structure can be achieved across the domains of language, music, mathematics and descriptions of actions (Van de Cavey & Hartsuiker, 2016). Taken together, these findings indicate that shared cognitive resources are involved in sequence learning across multiple human activities, including music, mathematics, language and action, highlighting the key importance of sequence learning in people’s ability to master a range of human activities.

Sequence learning may also be important in the development of human culture, with the cumulative development of skills, passed across generations, being a key aspect of humans’ ability to adapt to a variety of environments (Mesoudi & Thornton, 2018), particularly in the development of material cultures (Buskell, 2022; Derex, 2022). Learning from others by reproducing the behaviours of others, with a high degree of fidelity, allows for complex behaviours to be passed between individuals, meaning complex skills can become a feature in groups of humans. This form of social learning requires enhanced sequence learning abilities to develop complex behaviours that can be ‘ratcheted’ in complexity with the addition of novel techniques to existing behavioural sequences (Dean et al., 2014). Ultimately, allowing for the production of ever more complex behaviours that one individual would be unable to develop independently. The advancement of complex cultural products, such as music, dance and the manufacture and mastery of complex tool use, requires the learning of complex behavioural sequences, which has contributed to the diversity of human cultural outputs observed across the globe (Stout & Hecht, 2017).

As language, complex tool use and cumulative culture are defining features of humans’ success as a species, an enhanced ability to learn and manipulate behavioural sequences could be an important aspect of how human cognition differs from that of other animals. Ghirlanda et al. (2017) provided some empirical support for this in their analysis, that compared datasets from one hundred and eight experiments using fourteen nonhuman animal species across a diversity of taxa including two primate species (*Macaca mulatta* and *Cebus apella*). They identified that, compared to the other animals examined in the study, humans had an enhanced ability to discriminate between sequences. For instance, the animals tested would often struggle to discriminate sequences of lengths smaller than three elements or less, even after hundreds of trials. Humans in similar studies were able to discriminate between sequences of comparable lengths at an accuracy of 90% in only six to eight trials (Ghirlanda et al., 2017). Humans’ enhanced abilities in this domain may suggest that animals process sequential information differently, with human cognitive abilities being specialised to handle the learning of behavioural sequences.

Ghirlanda et al. (2017) is limited however as it lacks evidence from the great apes and only includes two species of primate, therefore neglecting some of humans closest living ancestors. This is particularly important as observations of material cultures have been observed in great apes, with different groups of the same species developing different methods to achieve the same goals independently (Dean et al., 2014; Fragaszy et al., 2011; Hobaiter et al., 2014). Indicating that great apes have rudimentary cultural practices and traditions and therefore have some of the prerequisite cognitive abilities for cumulative cultural evolution observed in humans (Biro et al., 2003). Investigating sequence learning abilities across other primates can therefore provide insights into the evolution of skills necessary for the development of cumulative culture.

The importance of evaluating evidence from a greater variety of primates is further illustrated by comparative brain research which has identified that, compared to other primates, the great apes and humans have shown considerable expansion in the size of the cerebellum relative to neocortical expansion (Barton, 2012; Barton & Venditti, 2014). The cerebellum is a brain region that has previously been identified as generating internal models for motor sequences (Starowicz-Filip et al., 2017), however, there is also evidence that the cerebellum is important in the cognitive aspect of sequence learning. Experiments involving individuals with cerebellar ataxia identified that feedforward cerebellar mechanisms were required for implicit sequence learning, however in instances where explicit strategies could be used individuals with cerebellar ataxia could compensate, suggesting that the cerebellum plays a crucial role in implicit sequence learning more generally (Leggio & Molinari, 2015; Morgan et al., 2021). Links between the cerebellum and frontal brain regions related to language, such as the Broca’s area, suggest that these sequence learning abilities may be involved in some aspects of learning languages (Higuchi et al., 2009). This is further supported by observations that cerebellar damage in human adults is linked to a number of language impairments that impair verbal fluency (Starowicz-Filip et al., 2017). The relative expansion of the cerebellum in great apes and humans could suggest that selective pressures acting on apes and humans have led to specialisations in sequence cognition (Barton, 2012; Barton & Venditti, 2014). Therefore, further examining these abilities across a diversity of primates, including apes will provide insights into how these abilities evolved in humans, while clarifying how different species of primates may differ in their ability to learn sequences.

Primates are a diverse taxon made up of between three and five hundred species (Rylands & Mittermeier, 2014), which vary considerably in their social behaviours and ecology (Kappeler & van Schaik, 2002). Therefore, understanding how primate species' sequence cognition varies could help provide insights into why species differ in these capacities and what factors contribute to the evolution of more sophisticated sequence learning abilities. A key area in this regard is the diverse social systems of primates, which differ in their complexity (Dunbar & Shultz, 2017). Primate social groups often create the need for communication systems that allow individuals in groups to transmit information to each other to coordinate social behaviours (Cheney & Seyfarth, 2010). In humans, spoken language is fundamentally sequential, requiring combinations of discrete elements into more complex structures, which makes it reasonable to infer that primate communicative systems may show similar structures, in a more primitive form (Zuidema & de Boer, 2018). Investigating these different social and communicative systems can help reveal how communicative sequences are used across primate species and therefore provide insight into primates sequence learning abilities.

Primates also differ in their diets and how they forage, with some species relying on food items that require complex extraction processes. With these involving the coordinated use of behaviours, including tool use. Whereas other species rely primarily on browse feeding, which is cognitively simple form of feeding (DeCasien et al., 2017). In these cases, identifying how different primates learn food extraction sequences can provide insight into primates sequence learning abilities in the physical domain. Considering this, analysing sequence learning in a diversity of primate species will help identify socioecological factors that result in differences in primates' sequence learning abilities, which could help piece together the conditions that facilitated the evolution of sequence learning abilities in our species.

Comparative behavioural studies on primate sequence learning abilities can be broadly categorised into observational studies and experimental studies. Observational studies involve watching primates interacting naturally, either in the wild or in captivity, and extract sequences from these interactions to elucidate their functions and identify how they are structured. This approach allows investigators to collect rich descriptions of the kinds of sequential behaviours different primates produce naturally. Providing important ecologically valid information. However, observational studies are limited because the lack of any sort of manipulation means that it is difficult to ascertain what features of behavioural sequences are actually being learned by the primate producing them. Experimental studies address this gap by presenting primates with tasks involving sequences to interrogate how primates process and learn sequential information.

Covering research from both paradigms can therefore provide a richer understanding of how primates use behavioural sequences in natural settings while also providing an understanding of the underlying processes involved in producing and comprehending these sequences. This review will therefore provide an overview of work related to primates sequence learning abilities spanning both approaches, with an aim to evaluate our current understanding of primate sequence learning capacities and how this relates to their natural behaviours. As has been established, communication and foraging are potentially key areas where primates will vary, so this review will focus predominantly on research related to these areas. Providing a basis for evaluating how species may differ in these capacities and how this relates to their sequence learning abilities.

1.2 Distinguishing Sequence Learning from other forms of cognition

1.2.1 Behavioural units

Before reviewing the existing sequence learning literature on primates, it is worth discussing in more detail what factors are involved in sequence cognition, that distinguishes it from other cognitive processes. The first aspect of sequence cognition is what is meant by a sequence of behaviours. This may seem trivial but differentiating discrete behavioural elements in non-humans can be difficult. When discussing sequences of behaviours, a sequence element is defined as a discrete and distinct behaviour that can be differentiated from other behaviours in a sequence (Reddy et al., 2022). An important first step then is identifying these behaviours, where there are a number of different methods employed across a variety of modalities. When analysing vocal communicative sequences, regularities in the sound waves are isolated to identify similar vocal elements, exemplified in Suzuki et al. (2016)'s investigation into the composition of Japanese great tits (*Parus major*) calls (Suzuki et al., 2016). In action sequences similar techniques can be used to extract regularities in sequences (Bowling & Fitch, 2015; Reddy et al., 2022). The resolution of analysis is also important in determining what is considered a behavioural unit, for example when understanding sequential structure in language the unit of analysis can be how letters are structured to form words, how words are structured to form sentences or how sentences are structured to form paragraphs. Any of these levels would be reasonable to analyse but the context will determine which is most appropriate. Similarly in determining the resolution of analysis in relation to animal behaviour suitable resolution must be chosen. The identification of and deciding on suitable behavioural repertoires, that make up the units of behavioural sequences to be investigated, is therefore fundamentally important when investigating sequence cognition, as these units act as the building blocks of the sequences of behaviours being observed and analysed.

1.2.2 Describing the Rules Governing Behavioural Sequences

The next important aspect when considering behavioural sequences is identifying how to describe their structure in relation to how the constituent units that make up the sequences connect to each other. The simplest relation between sequence elements is an adjacent dependency, where the relationship between elements exists between adjacent elements in a sequence. For example, in the sequence ABC the relationship could be described as adjacent dependencies if the relationship of elements is described linearly where B is dependent on A and C is dependent on B (figure 1). Animals will often use calls to communicate and one can imagine a very simple call structure with a repertoire of three call units D, E and F, where two call units are combined to create separate calls with distinct meanings e.g ED, FE, DF. In this case these calls can be described by the simple relation between the adjacent elements. In relation to action sequences an adjacency dependency could be viewed in a hypothetical extractive foraging task where a primate must overcome certain obstacles to extract a food item. If the fruit had two layers of protection, a layer of spikes and then a layer of skin the primate must first remove the spikes before removing the skin covering the edible pulp. A simple relation where one action directly follows the next in the sequence.

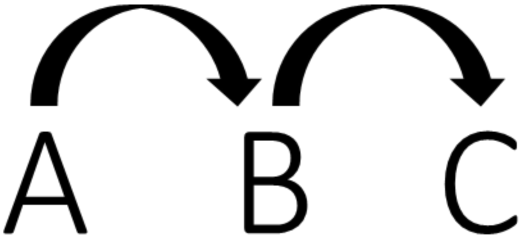


Figure 1: Adjacent dependency relationships between three elements A, B and C

Elements in sequences do not need to exclusively be related to one another based on their adjacent elements. When this is the case it is called a non-adjacent dependency (van der Kant et al., 2020), where the structure of the sequence is such that one element in a sequence is related to a different element in the sequence but is separated by elements situated between the two dependent elements (figure 2). In sentences and grammar, non-adjacent dependency rules dictate correct sentence structure and form the basis of many grammatical rules, thus it plays a crucial role in language learning (Watson et al., 2020). Again, it is easy to imagine how this may be relevant in relation to communicative sequences in animals, where calls may have an underlying structure that includes dependencies interspersed between multiple call elements. Observations of non-adjacent dependencies in animal communications seem to be rare, although there is some evidence in the songs of some bird species such as canaries (Markowitz et al., 2013). To illustrate how non-adjacent dependencies may relate to action sequences it will be useful to return to the hypothetical extractive foraging task. In this case imagine that once the fruits pulp has been exposed it needs to be scraped out with a stick which must be collected before the fruit is processed. The sequence of steps would become, collect the stick, remove the spikes, remove the skin and then use the stick to scrape out the pulp. Collecting the stick is related to the removing of the pulp but the steps of removing the spikes and skin must be completed before the step where the tool is necessary, making the completion of the full sequence reliant on a relationship between elements at separate locations in the sequence.

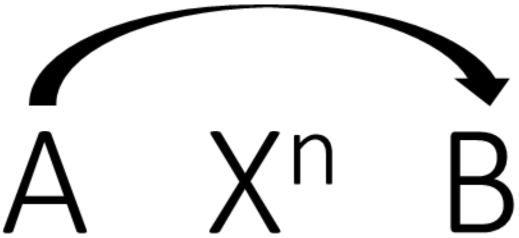


Figure 2: Non-adjacent dependency relationship between A and B, where X^n can be a mutable sequence of elements with varying numbers of units. Although illustrated as such, the non-adjacent elements do not need to be situated at the start and end of a sequence.

The next form of structures in sequences are ‘trees’ and ‘networks’, where behaviours are nested in a set of relationships with other elements that determine which of the behaviours should be performed next (figure 3). These structures afford flexibility and different paths in the tree or network can be chosen for distinct purposes (Weiss et al., 2014). At each step in the sequence, there are multiple potential elements which can be chosen based on the specific needs of the situation. The rules that govern how a sequences should be arranged is sometimes called a grammar or syntax and identifying analogous structures in animal behavioural sequences is important in understanding the evolution of language (Zuberbühler, 2020). It is easy to imagine these kinds of structures in language, with the choice of words used being dictated by the previous elements and the specific message trying to be communicated, while still abiding by the overarching grammar of the specific language being spoken. To understand how this may be relevant when considering action sequences, returning to the hypothetical extractive foraging example, one can imagine a situation where the fruits show a large amount of variability such that the specific elements of the sequence might need to be adapted to the specific circumstance. A different tool may need to be selected and used in a different way depending on the consistency of the pulp, the spikes may need to be removed in a different way depending on their length and the skin may be tougher or softer in certain plants and require a different technique to remove. This may require different elements to be chosen at different points in the task, with a network of potential actions best describing the potential sequences that can be produced by the primate. Like in the example of grammar in language, there exists an overriding structure and rules that dictate success in extracting the pulp but the specific sequences generated and the relations between the elements exist in a network of possible behavioural sequences. Another important aspect of these kinds of sequences is that they can sometimes be described as being structured hierarchically. With evidence of hierarchical structure being the existence of subroutines within larger sequence structures and alternative pathways that can be navigated flexibly, within a higher level sequential structure (Russon, 1998).

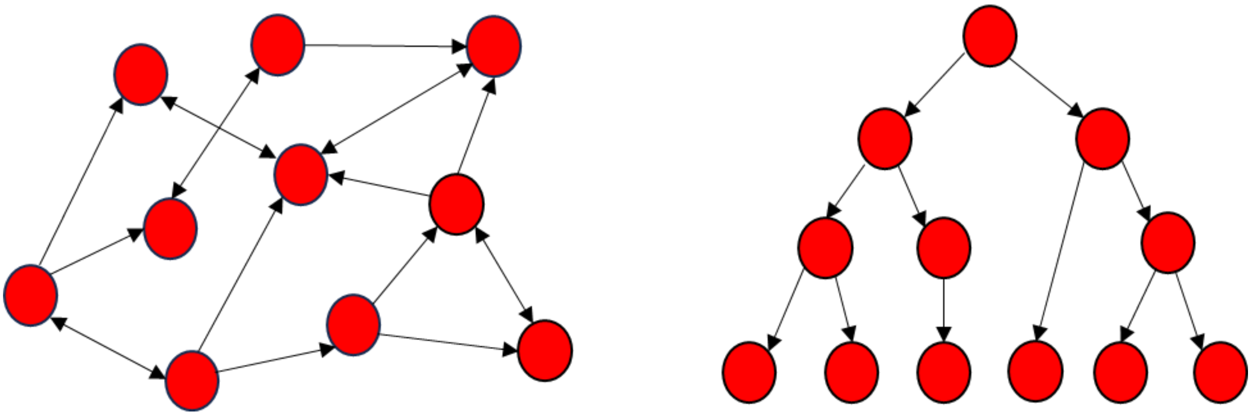


Figure 3 A network (left) and tree diagram (right) depicting relations between different elements (represented as red circles) in a sequence

1.2.3 Evaluating sequence content and context

Besides identifying what makes up a sequence, being able to compare the content of sequences between contexts and species is important in evaluating the sequence learning abilities of primates in relation to each other. When comparing the sequence learning abilities of different species, an important point of comparison is to identify sequence complexity. The complexity of a sequence can be differentiated by a number of factors. One way is increasing the number of possible elements in the sequence. Another is the complexity of the sequences structure and the rules that govern these relations, which can vary in complexity (Smith, 2014). This was illustrated in the last section, with adjacent dependencies being the simplest type of relationship between elements in a sequence and non-adjacent dependencies, networks and trees being more elaborate. A different layer of complexity is related to whether the sequence exists in a network of other elements, the number of connections between the different elements and the stringency of the rules that govern the correct usage of these elements in the network (Guimerà et al., 2002). The production and learning of sequences with more elements and more elaborate rules governing their use are more likely to require more sophisticated cognitive processes, which is an important consideration when comparing the sequence learning abilities of primates.

A related consideration is the context in which sequences are used and the flexibility of these sequences use. If their use is rigid and lacks flexibility or a sequence is repeated in inappropriate contexts this would suggest a lack of comprehension of the sequence. The context where sequences are used is also an important consideration when considering the evolution of sequence learning. Differences in sequence use across diverse situations can help measure how flexible these cognitive faculties are (Carroll et al., 2016). Taking note of the contexts under which sequences are being used also identifies whether processes are shared across different contexts and whether sequence strategies are used across domains or restricted to only one domain. It also enables inferences about what the information being learned from the sequence is in communicative contexts. It is also worth identifying whether, when performing sequence-based actions on a novel task, individuals persevere with a single previously learned sequence rather than adapting to a new required sequence. These aspects of learning do not directly address the learning of behavioural sequences themselves but give a richer understanding of how these skills are utilised in the ecological contexts of the species of interest.

1.2.4 Learning of Behavioural Sequences

The previous sections have covered important features related to aspects of the sequences themselves that help classify behavioural sequences when they are discussed in relation to sequence learning. However, the actual learning of sequences has been neglected up to this point. To appreciate species differences in sequence learning abilities it is important to consider the underlying cognition involved in sequence learning and what aspects of behaviour are likely to facilitate this learning.

The previous sections have highlighted that sequences can be structured in specific ways that describe the relations between specific elements. Therefore, an important consideration when understanding sequence learning is uncovering distinct aspects of cognition that facilitate the learning of these structured sequences. Ghirlanda et. al (2017) identified that there was substantial difference in the abilities of animals compared to humans in relation to the learning of sequences. In modelling why this may be the case they present an account that suggests that humans have an enhanced memory for sequences and that non-human animals may differ by relying on discriminating sequences based on a simple memory trace in working memory, which can facilitate the learning of very short sequences, but fails when larger sequences need to be learned (Ghirlanda et al., 2017). It may also be the case that differences in the ability to comprehend specific structural regularities in sequences such as non-adjacent dependencies or grammar rules may facilitate learning in some species and therefore produce variation in species abilities to learn sequences that rely on these kinds of relations (B. Wilson et al., 2020). A process that may be similarly important and is known to be important in human sequence learning is chunking. A cognitive strategy which aids the learning of a sequence by decreasing the required processing space by grouping sequence elements into larger meaningful wholes, allowing for better retention of longer sequences (Gobet et al., 2016). Potential cognitive differences between species sequence learning abilities are likely to be linked to observed differences in specific brain regions specialising in the learning of sequences, highlighted by research already conducted that showcases expansions in the cerebellum in humans and great apes compared to other primates (Barton & Venditti, 2014) and expansions in areas in Broca's region compared to great apes in humans (Gallardo et al., 2023). Evaluating whether differences in the cognitive strategies used by different primates influence species differences in sequence learning, as well as investigating the differences in brain organisation likely to explain some of these differences, is therefore an important consideration when understanding sequence learning in primates.

An important aspect of the human literature on sequence learning relies on making a distinction between whether sequence learning is explicit or implicit. With explicit learning describing learning where the individual is consciously aware of the learning of the associated relationships between elements and implicit learning describing learning that takes place independently of conscious awareness (Song et al., 2007). A more in depth discussion of this aspect of sequence learning is beyond the scope of this review and, as explicit learning references conscious awareness, experimental approaches used in humans to differentiate the two learning styles are difficult if not impossible to implement in non-human subjects (Church et al., 2021). Instead, a more appropriate consideration is to consider how flexibly sequences, or the learned structures related to sequences, can be used by primates and whether they show evidence of adaptability and comprehension in the form of iterative problem solving and the development of novel sequences of behaviour. Differences in primates ability to iterate and combine sequence elements in constructive ways is an important consideration when comparing primates sequence learning abilities particularly as it relates to the evolution of cumulative culture and language (Vandervert, 2018).

Another consideration is to recognise how sequence learning develops across ontogeny. As primates develop, they are likely to need to learn behavioural sequences to effectively interact with conspecifics and their environment, as it is unlikely that the full range of behavioural sequences expressed during the lifespan are entirely innately preprogrammed. Tracking how certain capacities develop can help clarify at what stage certain sequential processing is possible and what processes are necessary for developing primates to learn the range of skills necessary to survive. Relating back to the specific learning processes occurring at the level of cognition and the brain, cognitive capacities and relevant brain regions may mature across development, providing insight into the important stages related to the development of these skills. Why primates differ in certain sequence learning abilities may therefore be discovered by focussing on the developmental trajectories of these traits.

It is not enough to focus on individual primates though, as most Primates live in social groups, which contribute in important ways to learning (Whiten, 2000). It is necessary to consider how and whether primates facilitate the learning of behavioural sequences by learning from each other. Therefore, understanding how social learning relates to the learning of sequences is an important additional focus. Primates are able to imitate the behaviours of others (Catmur et al., 2009) so imitation is likely an important social learning pathway when developing sequences of behaviour. In the case of communicative sequences, such as calls, how the usage of certain signals is learnt and learning to appropriately react to the signals of others, is likely to be facilitated by attending to the reactions and responses of group members. With this facilitating the associations between signals and appropriate responses (Janik & Slater, 2000). As primates differ in their social organisations recognising the role of the social environment is an important point of comparison when considering between species differences in primates sequence learning abilities.

Constraints of the environment and the specific physiology of the primate, beyond its cognitive abilities, also need to be considered when trying to piece together the relevant factors related to sequence learning across the primate order. Understanding how an actor relates to the environment while performing a sequence of behaviours and how this may constrain the task may affect how we interpret the production of a sequence of behaviours. One way this may present itself is that some of the aspects of cognition assumed to be represented as cognitive capacities of the primate may in fact be offloaded to the environment in a task specific manner. Returning to the hypothetical extractive foraging task presented in section 1.2.2, removing the spikes must be performed before removing the skin, which must be performed before accessing the pulp due to the physical constraints of the task imposed by the structure of the task itself. In this case it may not be the case that a primate performing this sequence of behaviours represents the task as a coherent sequence, instead approaching the task one step at a time, with no specific appreciation that the task is sequentially structured. Relatedly, if an experimenter were to provide this fruit to a diverse range of primates with distinct body organisations, some may fail to access the pulp due to physically not being able to remove either of the two barriers, and it would be wrong to ascribe these differences to specific cognitive deficits in the failing species. Considering sequence learning in this frame represents an embodied approach to understanding sequence learning, which highlights the importance of both body and environment in the production of consistent sequences of behaviour (A. Wilson & Golonka, 2013). With these considerations being particularly important when comparing across a group as diverse in their ecologies as primates.

1.3 Observational Research on Sequential behaviours in primates

1.3.1 Communicative sequences

Observational research can help identify how and in what contexts sequences are used, and how this varies across species. Communication is a key area in which behavioural sequences are manipulated across a variety of contexts and there is evidence that great apes perform vocal exchanges in relation to a variety of situations (Leroux & Townsend, 2020). One of the more well-studied example of these vocalisations is in relation to encountering and interacting with food. Chimpanzees (*Pan troglodytes*) have been shown to perform pant-hoots, which identify an individual, and food calls that are used in the context of gathering food. An analysis of chimpanzees, at the Budongo Forest site in Uganda, aimed to identify whether these calls are combined and under which contexts combinations are used (Leroux et al., 2021). A collocation analysis identified that the pant hoot-food call combination was not due to randomly stringing two elements together. The pant hoot-food call combination was found to be elicited when feeding on larger food patches and when individuals would join a feeding party. These calls would also be elicited more frequently when high ranking individuals would join a food patch, suggesting that this call combination may have the effect of coordinating feeding (Leroux et al., 2021). The non-random combinatorial nature of this call suggests that chimpanzees can combine distinct elements to create new structures that can be used in different contexts to convey different meanings.

Bonobos (*Pan paniscus*) also produce call sequences on encountering food (Clay & Zuberbühler, 2009). Compared to chimpanzees though, bonobos produce longer calls built from sequences of five different call elements. The composition of these calls were not random strings, with the frequency of different elements varying depending on the individuals preference for the food item they encountered (Clay & Zuberbühler, 2009). Gorillas also produce calls related to food and have a repertoire of vocalisations that they use across different contexts to coordinate social feeding behaviours. However, whether these are used sequentially is unknown (Miglietta et al., 2021).

Vocal behaviours are also used by great apes to communicate socially relevant information. Orangutan (*Pongo pygmaeus*) males produce sequences of Long Calls to communicate across large distances. When the acoustic characteristics of long call sequences were analysed, they differed when produced spontaneously, in response to a disturbance or when the male calling has displayed by pushing over a dead tree. In response to these calls, females would modulate their ranging behaviour, moving away from spontaneously produced calls but not changing their ranging to the other two, high arousal contexts (Spillmann et al., 2010). A separate study identified that information about the caller is encoded in these calls, as females would preferentially approach the Long Calls of dominant males (Mitra Setia & van Schaik, 2007). These results provide evidence that females are able to extract information from these call sequences that allow them to modulate their behaviour appropriately. In populations with high densities of orangutans, individuals would produce more original sequences that were less predictable, whereas individuals in low density locations would produce more consistent calls containing a more complex repertoire (Lameira et al., 2022). This suggests that social environment is an important factor when understanding the development of great ape vocal sequences.

Chimpanzees produce combinations of pant-grunts and pant-hoots, which acts as a greeting, when approaching an individual not seen in a few hours or days (Kojima et al., 2003). When documenting different populations of chimpanzees, Girard-Buttoz et al (2022) found that the combinations of these greetings differed. In the Taï community, the greeting hoot started with pant hoots and ended with pant-grunts, whereas in the Budongo community this order was reversed. This difference may be due to long term differences in intragroup aggression, with the Budongo groups having historically higher rates of aggression meaning signalling submission immediately with the pant-grunt first may be beneficial in this group context (Girard-Buttoz et al., 2022). Immediate proximate differences between groups and their habitats were inadequate in explaining these order differences, which could indicate a role for usage learning for this vocal sequence during ontogeny.

When bonobos move between separate subgroups, they will also use calls to communicate with other groups, these calls are made up of high hoots and whistles (Clay et al., 2011). Analysis of call usage indicates that these combinations are used in different contexts. Individuals were more likely to move to a new group when they produced a Whistle-High hoot combination than after producing just high hoots. The structure of this combined Whistle-High hoot call would also differ if a call were being given in response or spontaneously, with a modified whistle element being used when the call was a response, which may help the listener interpret whether the call is a response to their call (Schamberg et al., 2016).

Gorillas also produce sequences of calls during social interactions. Although the specific function of call sequences remain unknown, a syntactic analysis found that five distinct elements would be combined into sequences, and these differed between mountain gorillas and western lowland gorillas, who differ in environment and social behaviour (Hedwig et al., 2014). Overall, these examples from great apes highlight that vocal sequences are used across a variety of contexts and that call combinations can modulate the meaning of these calls.

Great apes also use gestures to communicate and compared to vocalisations and facial expressions, gestures appear to show greater flexibility in usage within and between populations (Fröhlich & Hobaiter, 2018). Comparing gesture use across great apes has indicated that gesture use correlates more weakly between contexts and different groups compared to vocal and facial communications, which could indicate an enhanced role of learning and cultural transmission, with their meaning being more open to modification and adaptability than vocal sequences (Pollick & de Waal, 2007). The relative flexibility of gestures compared to the fixed vocal repertoires of great apes and other primates is some of the evidence used to propose that gestural communication is a crucial prerequisite to language (Prieur et al., 2020). Identifying whether there is evidence of sequential gesture use in the great apes may therefore also be important, due to the importance of sequence production in language, to identify whether these sequences show evidence of structure and whether gesture sequences communicate novel meaning.

The existing work on primate gestural sequences identifies that great apes produce sequences of gestures, with both chimpanzees and gorillas having been documented producing sequences of gestures (Genty & Byrne, 2010; Hobaiter & Byrne, 2011). Looking at these sequences in gorillas identified that sequences of gestures were used mostly in play and that many are repeats of the same gestures or gestures of similar meaning. There was also little evidence that increasing the number of signals was more likely to increase the likelihood of a response from the recipient. Markov transitions between the behaviours identified that gestures formed two clusters associated with regulating play, either during close contact or at a greater distance (Genty & Byrne, 2010). Taken together these findings suggest that gestural sequences are not used to communicate semantically different signals or emphasise the meaning of the signal used, but as a way of tuning the behaviour of the recipient continually during social behaviour. With gestural sequences not conveying specific semantic information and not conforming to a specific syntactic structure.

In a study of the wild chimpanzees of the Sonso community at Budongo, it was identified that sequences of gestures weren't uncommon. Looking at the use of sequences by age identified that older chimpanzees were more likely to use single gestures and were also more likely to be successful at eliciting a response then younger chimpanzees. Sequences were found to generally be less likely to elicit an accepted response from the recipient, although sequences that included one of the more successful gestures (if the gesture was used in isolation) were more likely to get a response than sequences that did not use these gestures. This suggests that young primates use sequences of gestures as a strategy to increase the likelihood they get the correct response and learn through experience the most effective single gestures to use, decreasing their reliance on sequences as they become more adept at selecting the single most effective gestures to use. A process referred to by the authors as repertoire Tuning (Hobaiter & Byrne, 2011). Overall although there are observations of gestural sequences in great apes, unlike call sequences, there is little evidence that specific sequences of gestures are associated with novel meaning and there is no strong evidence of specific sequential structure in these gesture sequences.

However, the discussion of great ape communication so far has focussed largely on studies that focus on one modality, which may risk missing an important layer of complexity when communication occurs in multiple modalities. Combining gestures with vocalisations to modulate the meaning of vocalisations has been observed in bonobos, where contest hoots can be used in both agonistic and playful contexts between subadult males (Genty et al., 2014). It was identified that contest hoots were paired with softer gestures during play compared to being compared with rougher gestures when the interaction was antagonistic. The use of gestures therefore can act to modulate the meaning of vocal sequences or act as distinct communicative signals themselves (Fröhlich et al., 2016; Genty et al., 2014). A study of 28 chimpanzees at the Chimfunshi Wildlife Orphanage Trust in Zambia, where focal observations of 28 semiwild chimpanzees ranging from infants to adolescents was conducted, aimed to look at multimodal signal production across a range of contexts. The study identified that multimodal communication was evident even in infancy but multimodal signal production frequency increased with age. Suggesting that multimodal communication, although developing early, develops across ontogeny. They also identified that multimodal signals were most often used during aggression and playful contexts, where multimodal signals may disambiguate the meaning of the signals used, reducing the risk of being misunderstood (Doherty et al., 2023). This may be particularly important in play and aggression contexts where clear messages of intention are essential. Although these studies do not specifically address sequential communicative signal use (with multimodal signals being simultaneous production of signals from different modalities and therefore not specifically sequential) They do illustrate that multimodal signals likely enhance the existing communicative repertoires of great apes in important ways. Understanding whether sequences of multimodal combinations occur and understanding their role in great ape communication would enhance our understanding of the potential role of behavioural sequences in great ape communication.

The study of communicative sequences in primates is not restricted to the great apes, with a lot of work on gibbons and monkeys. Gibbons are extremely vocal primates and will produce songs with a repertoire of call notes. These songs serve multiple functions including deterring conspecifics from their territory, attracting mates, advertising pair bonds and protecting themselves against predators (Raemaekers et al., 1984). Analysis of the great call of agile gibbons (*Hylobates agilis*) identified that components of the start and climax of the song had distinguishing features that may be used to distinguish individuals across large distances (Oyakawa et al., 2007). Investigations into male Mueller's gibbon (*Hylobates muelleri*) calls identified that these songs are sequentially structured. In this species male songs were found to have a phrase inserting structure with a starting element A and an end element B with a phrase between them N. eleven types of A-B sequences were identified with a variety of N elements being inserted between these elements (Inoue et al., 2020). A different analysis using agile gibbon calls also identified that the sequences of calls in these songs followed rules and were not strung together randomly (Marler & Mitani, 1989).

To identify if differences in call structure is relevant to behavioural contexts experimenters recorded the vocalisations produced by lar gibbons (*Hylobates lar*) in response to predators and songs produced during routine morning calls. To elicit predator calls from the gibbons model leopards, pythons and eagle models where presented to the gibbons (Clarke et al., 2006). Gibbons reliably called when exposed to the terrestrial predator models but not the eagle model. Investigating structure of these calls in different contexts found that these calls differed in composition when elicited by predators compared to when performed in the duetting situation. There was evidence that other individuals can interpret these differences, as members of neighbouring groups would call in response, with calls differing in structure compared to the calls they would respond with during duets, male group members who had strayed away from the group would return to the group in response to these calls while performing a predator call themselves. These findings show that gibbon songs are structured and that differences in call structure are flexible to uses in various contexts.

A lot of work on monkey vocal sequence usage is in the context of alarm calls to warn conspecifics about predators (Zuberbühler et al., 1999). Titi monkeys (*Callicebus* *nigrifrons*) produce calls when confronted with a predatory animal (Cäsar et al., 2012). Similar to the previously mentioned study, model predators were used to elicit these calls, which in this species were made up of distinct A and B calls. When a raptor was present in the trees when observed the alarm call would be pure A calls, if the raptors were observed on the ground the A call would be interspersed with B calls. If the cat were found on the ground sequences of B's would be produced however if the cat were observed in the trees a B call sequence preceded by a single A call would be produced. The length of these calls would be longer in response to the cat compared to the raptor threat (Berthet et al., 2017; Cäsar et al., 2013). These differences in call sequences therefore suggest that Titi monkeys are able to encode both position and type of predator in their alarm calls. Similar findings have been found across a diverse set of species. Male putty nosed monkeys have been found to use distinct combinations of 'hacks' and 'pyows' between terrestrial and aerial predators, with these calls also conveying the identity of the caller and whether the male intends to travel to avoid the threat (Arnold et al., 2008). Male blue monkeys (*Cercopithecus nictitans*) would also use 'hacks' and 'pyows' in distinct combinations in predator specific ways and call rates were related to distance and location of predators (Murphy et al., 2013). Guereza colobus monkeys (*Colobus guereza)* and king colobus monkeys' (*Colobus polykomos*) alarm calls containing snorts and roars with the composition of these calls depending on whether alerting for a leopard or crowned eagle (Schel et al., 2009).

Campbell monkeys (*Cercopithecus campbelli*) have a particularly complex combinatorial call system composing of six distinct call elements, the size of this repertoire is doubled from three elements (boom, 'krak' and 'hok') using an affixation rule which adds an 'oo' suffix creating three more distinct elements 'Krak-oo', 'wak-oo' and 'hok-oo' (Ouattara et al., 2009a). Analysis of these calls identified nine distinct combinations used in different contexts. Six of these were distinct and were elicited in response to leopards and crowned eagles, with one being a general predator call given when a predator is only heard and not seen. Three call types were unrelated to predation indicating group movement, a branch falling or indicating an interaction with a neighbouring group. These call sequences and their variants usage indicate that sequences produced by these monkeys convey information about the event they are communicating about, the level of threat and group movements (Ouattara et al., 2009b).

As illustrated by the Campbell monkeys, monkeys do not only use vocal communication to signal danger to conspecifics and vocal communication can be used in social contexts. Studying vocalisations in social contexts in female Diana monkeys (*Cercopithecus diana*) identified four call elements, H, L, R, A that could be uttered alone or in combination with other elements (Candiotti et al., 2012). Different call combinations would be uttered in different social contexts with LA combinations being elicited more often during positive social interactions and RA combinations were associated with negative social situations. The LA and RA elements show similarities between the affixation seen in the Campbell monkeys ‘oo’ suffix. However, in the Diana Monkey case the addition of the A element appeared to function as an identifier with the L or R element adding contextual information as to whether the situation carries positive or negative valence (Candiotti et al., 2012). Adult Campbell monkeys will exchange vocalisations during friendly social interactions. Females contact calls were shown to be combinations of discrete vocal units, a short harmonic, a combined harmonic with a broken arch and a combined harmonic with a full arch. Short harmonic calls were associated with foraging behaviours, combined harmonics were both preferentially used during vocal exchanges and during vigilance behaviours, the combined harmonic with a full arch was also significantly used in contexts where individual identity would be worth signalling such as when the group was at the edge of their territory, when the caller was on the ground and when the density of other primate species nearby was high (Coye et al., 2018).

Marmosets (*Callitrichidae spp.*), a family of small social platyrrhine monkey, use vocal communication to keep in contact with conspecifics in the thick leafage of the forests they inhabit. The makeup of these calls in pygmy marmosets (*Cebuella pygmaea*) was found to vary depending on the distance they were from conspecifics. The elements of these calls changed based on their acoustic properties with long calls being used at long distances and Trills and J calls being used at short distances or short and medium distances, respectively. The calls used at short distances were more easily degraded by the environment than the long call suggesting that the different call types are used adaptively to communicate across different distances in their habitat (de la Torre & Snowdon, 2002). Analysing the structure of Common Marmoset (*Callithrix jacchus*) calls identified that these calls are structured and follow multiple rules, with calls being modified during turn taking. It is unclear what the function of these call sequences is, which requires further study (J. Huang et al., 2022).

Interestingly longitudinal studies, observing common marmosets across development, have identified that marmosets show high plasticity in their vocal development (Gultekin et al., 2021). All calls are present in the first postnatal month, suggesting that the basic repertoire of call elements is present from birth. Across development, three stereotyped stages are described, in the first stage after two postnatal weeks marmosets produce highly repetitive vocal behaviours that are stereotypical across individuals with call types being unsegmented, this is followed by an intermediate stage from six to thirty eight weeks where postnatal call types became more segmented and across individuals an increased individuality in their call sequences is seen but a diversity in transitions between elements in call sequences is still shown, in the final stage call type use and transitions between call segments becomes stable and call transitions differ across individuals (Gultekin et al., 2021). Similarly in pygmy marmosets, analogous juvenile behaviour has been observed, with long strings of mixed call types named pygmy marmoset babbling, across development this babbling decreased until being absent in adulthood (Snowdon & Elowson, 2001). When young marmosets were hand reared, and therefore had less contact with adults during development, long term effects on call sequence development was observed, with their vocalisations being characterised as subadult in their structure (Gultekin & Hage, 2018). These findings provide some insights into the development of mature vocal behaviours potentially indicating that social learning mechanisms are involved in their refinement.

Outside of the great apes gestural communication is less commonly observed in primates, but a few documented examples exist. These include observations of gestural communication in olive baboons (*Papio anubis*) (Molesti et al., 2020), bonnet macaques (*Macaca radiata*) (Gupta & Sinha, 2019) and red-capped mangabeys (*Cercocebus torquatus)* (Schel et al., 2022) and similar to the great apes, the use of gestures in monkeys shows evidence of flexibility and intentionality (Aychet et al., 2020; Schel et al., 2022). Therefore, gestures are an important consideration when investigating the potential sequential aspects of communication in monkeys, potentially increasing the repertoire of available signals beyond the auditory domain. One study aimed to investigate the sequential aspects of the red-capped mangabeys communication repertoire and used an approach that incorporated signals across modalities, including the incorporation of gestures (Aychet et al., 2021). To do this, network analysis was performed on sequences of multimodal communicative behaviours extracted from focal videos of 25 captive red-capped mangabeys. This identified that red-capped mangabeys would produce multimodal communicative sequences that coupled different signal types and different sensory modalities flexibly. Some sequences were specifically used in aggressive or affiliative interactions, potentially indicating that certain signal sequences are associated with specific meanings that elicit specific responses from the receiver, although identifying whether differences in meaning are associated with specific syntactic rules would need further investigation. Complexity of sequences also differed among contexts with play and aggression eliciting the most complex sequences, indicating that context is important in deciding the types of sequences produced (Aychet et al., 2021). Although further investigation is needed, these results suggest that red-capped mangabeys multimodal signal sequences, including gestures, as part of their communicative repertoire. While also highlighting the importance of considering multiple modalities when documenting the range of communicative sequences primates produce.

1.3.2 Foraging and Tool Use Sequences

Extracting food from the environment potentially requires primates to learn complex sequences of behaviours to effectively sustain themselves. An area of particular interest in this regard is the use of tools, with great apes being renowned for their use of tools in extractive foraging contexts (Musgrave & Sanz, 2018). However, it is worth noting that tool use is not restricted to foraging in primates. Gorillas (*Gorilla gorilla*) have been observed using branches to test the depth of water while wading (Breuer et al., 2005). Orangutans (*Pongo abelii*) will use leaves and hold them in their mouth to increase the lowering the frequency of the call, which could function to exaggerate the size of the caller (Hardus et al., 2009). Bonobos, who do not readily use tools in the wild during extractive foraging, have been documented using tools in social contexts such as play, self-cleaning, creating cover during heavy rain, soliciting mating, swatting insects or throwing objects at others (Samuni et al., 2022). An example of tool use unrelated to foraging in monkeys comes from observations taken from black handed spider monkeys where females would use sticks to scratch themselves (Lindshield & Rodrigues, 2009). These examples highlight that primate tool use is not restricted to the domain of extractive foraging, but the majority of work related to tool use in primates is related to its use in extractive foraging which will be the focus henceforth.

Chimpanzees, in particular, have been shown to use a variety of tools to forage (McGrew, 2013). One example is that chimpanzees chew leaves to form a sponge that they then use to collect drinking water by placing the sponge in the water source, allowing it to saturate and then placing the sponge back into the mouth to be sucked on (Hobaiter et al., 2014). This behaviour is universal among chimpanzees (Whiten et al., 2001) but variations of the behaviour exist such as moss sponging, where instead of leaves moss is used, and leaf sponge reusing, where individuals will use the discarded moss sponges of others. An analysis on these two variations of this behaviour aimed to identify how variations in tool use sequences may develop. A network diffusion analysis identified that the more likely mechanism of transmission of the moss sponging variant, was social transmission, whereas leaf sponge reuse was more likely to be individually acquired. Indicating that social and individual learning mechanisms were important for the spread of variants in tool use behaviours. The potential importance of social learning is also illustrated by comparing chimpanzees nut cracking behaviours between groups. Chimpanzees can use stones or wood to crack open nuts by placing the nut on a tree root or rock to act as an anvil and then hitting the nut with the rock (Inoue-Nakamura & Matsuzawa, 1997). Studies have identified that the selection of the type of tool used differed between groups and that these differences are likely cultural, with different groups of chimpanzees using different strategies to extract nuts using these methods, requiring different numbers of hits to open the nuts even when controlling for tool choice (Biro et al., 2003). Although these studies don't specifically address the sequential aspects of tool use tasks, they do highlight the potential role of social learning in developing variations in tool use behaviours and maintaining cultural variation between groups.

One example is the use of sticks to fish out termites from their mounds (C. Sanz et al., 2009). Chimpanzees will select a herb stem to use and would often modify this stem by fraying the end using their teeth. They would then straighten the frayed end using their fist and insert the tool into the mound. While repeating the fishing action chimpanzees maintained the stem by repairing the brush tip. Chimpanzees also used the other blunt end of the stick to brush away debris from the entrance of the hole, then returning to use the brush side to collect more termites. In some cases different tools will be used sequentially, with a thicker stick being used to perforate the termite mound and the frayed fishing tool then being used to collect the termites (Musgrave et al., 2021). This tool use behaviour requires multiple distinct steps and therefore may require specific sequential processes to learn. This is made evident in a study on the chimpanzees living in the Goualougo Triangle in the

Republic of Congo, which aimed to identify the ontogeny of termite gathering techniques (Musgrave et al., 2021). Using longitudinal recordings of 25 immature chimpanzees at termite nests identified that the manipulation of tools and the development of individual behaviours related to the task developed early in ontogeny before the age of two years old. However critical sequential aspects of the task, including the manufacture of brush tipped probes as well as using tool sets sequentially occurred later in development after three years of age. Suggesting that the ability to develop hierarchical sequence organisation occurs later than the ability to learn elements of the tasks potentially requiring higher order processes such as program level imitation (Musgrave et al., 2021).

Interestingly, differences between the trajectory of skill development in the order and time of acquisition of aspects of the task was observed between chimpanzees located in Gombe or Goualougo, potentially due to numerous ecological factors related to the task. One of these factors is that in Goualougo termite fishing occurred year round, whereas it was restricted to only a few months in Gombe, limiting the opportunities to learn and practice the necessary skills at Gombe (Musgrave et al., 2021). Socially relevant factors related to the task also varied between sites, such as the observation that in Goualougo mothers are more likely to respond positively to sharing tools and tool transfer occurred more readily (Musgrave et al., 2020). Resulting in social learning opportunities differing between the sites. These findings highlight the importance of the specific ecological and social contexts surrounding the developing primates in dictating the specific trajectories the learning of behavioural sequences can take.

Chimpanzees will also use tools to extract honey from beehives and, what is interesting about this behaviour, is that it is an example of using an elaborate set of tools with varying functions during the foraging process (C. M. Sanz & Morgan, 2009). Sticks and branches with different characteristics are modified and used in different ways at different points in the extraction process. A pounder is a thick stick used to remove protection from the entrance of the hive, an enlarger is a stick that is used to stab and enlarge compartments within the hive, collectors are used to scoop the honey out of the beehive and swabbers are used to spoon and dip the honey from the open beehive. Tools that are specifically equipped for each of these tasks must be selected and made from available branches with a sequence of steps being involved in making each of these different tool types. Once tools have been made and an adequate set of tools is available, they will be used on hives in predictable sequences of movements. The hive will be accessed using the pounder and cavities in the hive will be enlarged using the enlarger tool, collectors, swabbers or hands will then be used to extract honey. However sequences show elements of flexibility and are adaptable to the specific features of the hive being tackled, with enlargers and collectors being switched between and behaviours repeated depending on the specific architecture of the hive (Boesch et al., 2009). The elaborate organisation of this task potentially highlights numerous features potentially indicative of more complex cognition. The manufacture of the tools for different aspects of honey extraction requires specific sequences and the selection of specific tool sets for honey extraction suggests a sophisticated comprehension of the task. The sequence of manipulations needed for honey extraction is organised hierarchically into specific steps, with different tools being associated with these different steps making the process more complex than other examples of tool use in chimpanzees, such as nut cracking (Inoue-Nakamura & Matsuzawa, 1997). The behavioural sequence is even flexible with certain steps being repeated or revisited depending on what is required when extracting the honey (Boesch et al., 2009).

Chimpanzees may be the more ubiquitous tool users in the great apes but orangutans (*Pongo abelii*) also extract food using tools. One example of this is using sticks to extract seeds from the *Neesia* fruits, which have stinging hairs, that must be avoided (Van Schaik & Knott, 2001). When the fruit is ripe and opens the seeds can be accessed by the orangutans and to do this they use short straight branches, stripped of their bark and placed in the mouth, that are directed down a crevice in the fruit containing the seeds. These seeds can then be retrieved and dropped into the mouth directly or retrieved with a finger or tool.

Similar to in the chimpanzees, these abilities were distributed differently across the species range. *Neesia* tool use was associated with high concentrations of orangutans suggesting that increased chance of social contact in this usually solitary ape may affect the spread of this behavioural adaptions (Van Schaik & Knott, 2001).

Although wild gorillas have not been observed using tools, they do use distinct manual strategies in processing certain food types. Neufuss et al. (2019) identified 19 manual actions, which shows a reasonably high degree of manipulative flexibility during the extractive foraging of three plant types, two of which were difficult to process, being protected by stinging hairs. A different process was used for each plant type incorporating at least twelve of each hand grips. These methods had discrete hierarchically organised stages suggesting a high degree of cognitive control (Neufuss et al., 2019). Indicating that these tasks require specialised cognitive mechanisms to learn and accomplish. A study comparing the approaches taken by both a captive and wild population of gorillas (*Gorilla gorilla*) while processing nettles also identified that the two populations differed in their approach to the task but used similar repertoires of motions, suggesting that gorillas naturally develop a repertoire of hand movements which they employ to learn complex multi process skills. With the specific approach taken to these tasks being learnt from other individuals through social transmission, giving rise to distinct local traditions (Byrne et al., 2011).

Evidence of tool use is sparser in monkeys but it has been documented. Capuchin monkeys for example (*Cebus spp.*) will use rocks to crack nuts, similarly to chimpanzees (Falótico, 2022; Fragaszy et al., 2011). Capuchins tool use appears to be flexible as they will vary the tool used depending on the hardness of nuts and adjust how they strike the nuts and how they grip the stone. Tool use learners also become more efficient across time as they learn to properly manipulate the components (Falótico, 2022). Tool use in capuchins is not restricted to nut cracking as capuchins also use rocks for digging, dislodging dead wood to find insects, breaking off a different larger rock with another rock, use sticks as probes to find arthropods and reach water and in rare occasions use multiple tools sequentially (Mannu & Ottoni, 2009).

Long-tailed macaques (*Macaca fascicularis*) have also been observed using stones to open oysters (Gumert et al., 2011). A study investigating the tool use of the long-tailed macaques in Khao Sam Roi Yot National Park, Thailand found that hammering using the stones could be classified into three classes based on the surface of the tool used to hit the oysters with the three hammering classes being made up of 17 action patterns, whose differential use distinguished the hammering classes (Tan et al., 2015). To document the development of these hammering behaviours, longitudinal observational data on the object manipulation and tool use bouts of juveniles was analysed to identify how tool use changed across time. This analysis found that tool use developed across several years and that macaques first began in infants at the age of one to three months with very simple manipulations such as picking up objects, carrying objects from one place to another and manipulating them in the hand or mouth. Between one and a half years and two and a half years a wide variety of combinations of manipulations are explored, with many of these combinatorial manipulations not being goal oriented or non-functional. Towards the end of this period though these behaviours more resemble tool use but are still often erroneous and attempts unsuccessful. This development would eventually be channelled into developing the correct sequences of behaviour necessary for effective tool use between the ages of two and a half years and three and a half years, with this competence in tool use, manipulations become restricted to successful tool use bouts and the variety of manipulative actions is therefore reduced (Tan, 2017). These findings suggest that the development of tool use sequences are learned is through experiential feedback based on exploratory manipulations of tools across a protracted period of time.

Another study on this population aimed to identify which group members unskilled juveniles would focus on when observing other group members performing tool use tasks. Interactions with tool users was motivated in all age groups predominantly with scrounging or stealing food but young macaques would also watch tool users and explore tool use objects, therefore exhibiting some interest in the act of tool use itself. In fact, all Juveniles and infants were observed interacting with tool users, with this figure only being forty nine percent in adults. Juveniles were found to preferentially interact with tool users who were kin, older and individuals with higher rates of tool use who required fewer strikes to crack the oysters. The motivation for this bias may be enhancing opportunities to scrounge food, but this would still provide an opportunity to learn from more effective tool users (Tan et al., 2018). Biasing which tool users juveniles observe may therefore provide higher quality learning opportunities modulating social learning during critical developmental periods. This may be a common strategy that facilitates the learning of new skills in primates and could be relevant to the learning of new behavioural sequences during developmental, which could be facilitated by biasing observations towards more effective individuals.

Long-tailed macaques feed on prickly pear cactuses (*Optunia sp*.) that must be processed before they can be effectively fed on (Tan et al., 2016). Long-tailed macaques were observed processing prickly pear cactuses on Nom Sao Island, in Khao Sam Roi Yot National Park, Thailand, where videos were taken. The processing steps were characterized as being acquire fruit, transport fruit, process the fruit on a substrate, expose pulp and eat the fruit, with seventeen behavioural elements being found to be used across the process. Each of these stages involved multiple potential elements, with the acquire fruit stage also including subroutines depending on the placement of the fruit. Processing the fruit on a substrate involved either washing the fruit in water or sweeping, rolling and pushing the fruit on sands or rocks, with this seeming to remove short fine hairs named glochidia, which can become embedded in the skin and cause injury to the macaque. This multistage sequential process shows evidence of hierarchical organisation, having optional and alternative pathways in the process, with evidence that the macaques omit unnecessary steps. After being interrupted by a dominant group member one individual was found to pick up from where he left off rather than retreading already completed steps, providing evidence that individuals following these steps may be able to distinguish between different steps in the overall sequence of behaviours (Tan et al., 2016).

1.3.3 Summary of Observational Research

The use of sequences in vocal communication is widespread across anthropoid primates, with species using call combinations to communicate to conspecifics in a range of contexts, including social interactions and predator avoidance. Although primate vocal repertoires are usually small, acoustic analysis, as well as behavioural measures analysing context of use, has identified that different combinations of vocal elements augment the meaning of calls, expanding the range of messages that can be produced (Zuberbühler, 2018). Longitudinal studies, watching the development of these calls across the lifespan, point to the vocal repertoires of primates being relatively fixed at birth (Fedurek & Slocombe, 2011). Experience and social learning however appears to play a role in the learning and refinement of call sequences into discrete call types and that the learning of these skills requires practice across ontogeny (Gultekin et al., 2021).

With gestural communication, like vocal repertoires, the selection of gestures used by apes seems to be fixed and shared across species, but the use of gestures appears much more flexible and varies considerably between species and between different groups of individuals within the same species (Fröhlich et al., 2019). Although initial reports suggested that great apes may use gestural sequences the evidence suggests that gestural sequences don’t confer new meanings and serve a different purpose than sequences of calls. In gorillas the use of sequences of gestures in quick succession appears to be a way of tuning the behavioural sequences of a partner during a social behaviour. With the sequence itself not being structured to convey a new or specific meaning above those conveyed by single gestures (Genty & Byrne, 2010). In chimpanzees however the use of gesture sequences appears to be a strategy used by developing primates that helps them learn the most effective single gestures to use in a process known as repertoire tuning (Hobaiter & Byrne, 2011). Interestingly in one of the few monkey species where gesture use has been investigated, preliminary evidence suggests that red-capped mangabeys use sequences of multimodal gestures, which appear to be used in specific contexts (Aychet et al., 2021). Which may highlight the need for more multimodal studies across a diversity of primate species as this may identify another layer of communicative sequences which are missed when work is restricted to a single modality.

Extracting food and learning to use tools to solve novel problems is also an area where learning behavioural sequences is likely to be important. Across the great apes there is considerable evidence that tools are used in a variety of contexts and variation in this tool use across populations of the same species suggests a role of social and cultural learning in the acquisition of these skills. Tool use behaviours in chimpanzees appear to show evidence of structure, with honey extraction even appearing to show evidence of sophisticated hierarchical organisation (Boesch et al., 2009). Across development the acquisition of the sequential aspects of tool use also appear to take years suggesting a protracted developmental process (Musgrave et al., 2021). In gorillas, who do not use tools as readily during foraging than chimpanzees, the manipulations they use when approaching different food items is sequentially structured and variable across groups suggesting that combining manual skill elements to solve problems requires social learning more generally in apes (Byrne et al., 2011).

Like gestural communication tool use has predominantly been observed in the great apes but exceptions do exist. Capuchins show evidence of tool use involving rocks similar to chimpanzees (Falótico, 2022). Long tailed Macaques also use stone tools to break apart oysters, with this behaviour taking years to mature and having a distinct developmental trajectory (Tan, 2017). Aspects of social learning of these abilities are also likely to be important and juveniles will preferentially observe more effective tool users which may enhance their learning of the tool use sequence (Tan et al., 2018). Long tailed macaques also show evidence of more sophisticated sequential food processing use in their processing of prickly pears, which requires multiple stages, with some evidence pointing to hierarchical processing abilities, which were previously presumed to be exclusive to the great apes and humans (Tan et al., 2016).

In sum, observational studies provide rich insights into the behavioural sequences used by a wide range of species across various contexts. However, observation alone provides limited information about the learning involved in acquiring these skills and gives no indication of what is actually being learnt about the sequence. Controlled experiments are therefore required to fill in these gaps.

1.4 Sequence Learning in Experimental Tasks

1.4.1 Playback and False Grammar Experiments

Playbacks of conspecific calls have been used to identify how primates respond to them to understand what information is extracted from them. An early experiment of this kind presented wild agile gibbons with recordings of normal calls or calls that had been rearranged (Marler & Mitani, 1989). The gibbons responded differently to rearranged calls compared to recordings of standard gibbon calls suggesting that the structure of these calls is significant to what they communicate. Similar playback experiments have been conducted in Diana monkeys where they were exposed to calls produced by Campbell monkeys, which they live in mixed groups with (Zuberbühler, 2000). Playing back Campbell monkey calls specifically used for either leopards or eagles to Diana Monkeys showed that they acted similarly to when they heard the predator’s call itself, suggesting that they are able to act appropriately to the information encoded in these calls. The call Campbell monkeys’ use to signal the presence of a leopards is a ‘krak’, which they will suffix with an ‘oo’ sound when the call is for an unspecified threats (Coye et al., 2015). When the unsuffixed form used to signal the presence of a leopard was played to Diana monkeys they remained vigilante for longer and produced more of their own alarm calls compared to when the unspecified threat ‘krak-oo’ call was used. Providing evidence that Diana monkeys can discriminate the difference between the two call types and comprehend the concatenation of elements from another species calls.

Putty nosed monkey alarm calls are sequences of ‘Hacks’ and ‘Pyows’ with the composition of sequences of these calls signifying different things, with sequences starting with ‘hacks’ signifying an aerial predator and sequences beginning with ‘pyows’ signifying the presence of a leopard. However, a different type of sequence will also be produced, a short sequence with a ‘pyow-hack’ included within a mixture of hacks and pyows, with observations indicating that these calls signify group movement (Arnold & Zuberbühler, 2006). Playback studies of these calls identified that the proportion of ‘pyows’ and ‘hacks’ in these call sequences did not change the response of the monkeys suggesting that the composition of the short ‘pyow-hack’ did not modify the calls meaning (Arnold & Zuberbühler, 2012). This has led to a disagreement in how to interpret what these calls convey, with one suggesting that calls containing ‘pyow-hacks’ are interpreted idiomatically, with the sequence as a whole being interpreted as a signal to move. Suggesting that the elements of these sequences are not considered individual, rather the combination acts to increases their vocal repertoire (Arnold & Zuberbühler, 2012). Assigning more abstract meanings to the calls, with ‘pyow’ ‘being a general alert call and the hack being a more serious non-ground movement related alert (signifying group or predator movement), combined with pragmatic principles, may retain the ‘pyow-hack’ sequences linguistic combinatoriality while still explaining the data consistently (Schlenker et al., 2016). Both explanations make distinct predictions that need to be elaborated on by further studies.

To further investigate the ability of bonobos to discriminate conspecifics feeding call sequences, researchers used playback studies to identify what, if any information bonobos could infer from these calls (Clay & Zuberbühler, 2011). In an initial experiment, kiwi fruits (a high preference food) and apples (a lower preference food) were placed at different ends of the outside area of two groups of captive bonobos outside enclosure. The two bonobo groups used in this experiment share the outside feeding area, which they would be released into separately at different feeding times. Directly before being released a food call associated with apples or kiwi fruits from one of the other groups members would be played directly prior to releasing a group. Outside of the baseline preference to search the kiwi location, bonobos were found to modulate their feeding behaviours based on the call sequence they were exposed to, increasing their time spent searching at the kiwi location when the high preference food call was played and increasing their time spent searching at the apple site after being exposed to the low preference food call.

A different experiment trained two captive bonobos to prefer blue or pink primate chow, with a control where the individual had no preference (Shorland et al., 2022). These preferences were shown to other group members by allowing them to watch the trained individuals eat while being given both chow types. Playbacks of the food related calls made by the trained bonobos were played to bonobos before individuals were let into a room where they had been previously trained that two different trays held one of the coloured chows. If the playback was sourced from the blue-preferring individual, the listener would preferentially search the blue containing tray, whereas when they were exposed to the control calls no preference was shown. These results suggest that bonobos use others call sequences to augment their foraging by extracting information from these food calls based on the caller’s food preferences.

A modification to the playback experiments described are artificial grammar experiments, which rely on generating a set of stimuli that follow grammatical rules to identify whether the subjects are able to identify disruptions to these rules after continuous exposure to the artificial grammar. The artificial grammars used in these experiments do not need to be in the auditory domain and studies have used generated sets of visual objects that conform to a specific grammar rule.

An example of one of these experiments performed on common marmosets familiarised subjects with a sound set made up of recordings of the species natural call repertoire with low and high calls edited to exhibit an LH^nL grammar (Reber et al., 2019).

The first discrimination phase of the experiment introduced new numbers of H elements while also introducing sequences missing the first or last L. The second discrimination phase introduced elements where the inverse rule was used (i.e. HL^nH). To determine whether the subjects were able to identify sequences that broke the rules of the grammar playback of the sequences was done behind the seated position of the marmoset and frequency of head turns when a sound was played was recorded. With this set up they identified that marmosets were able to identify discriminate rule violating sequences, showing that marmosets were significantly more likely to turn towards the playback apparatus when sequences that were consistent to the rule played (which is different than other primates that are more likely to turn for rule violating sequences). However, in the HL^nH there was no difference suggesting that the rule learnt in the familiarisation stage was not transferred to this similar stimuli set with the same rule (Reber et al., 2019).

Similar experiments on cotton-top tamarins (saguinus Oedipus) (Newport et al., 2004) and squirrel monkeys (*Saimiri sciureus*) (Ravignani et al., 2013) using artificial grammars showed that they were also able to identify violations to both adjacent and non-adjacent dependencies. An experiment comparing these abilities between humans, marmosets and chimpanzees identified that all three species were able to differentiate non-adjacent dependencies in the artificial grammars presented (Watson et al., 2020). These experiments have not only been conducted in the auditory domain with experiments using visual stimuli and tracking rule violations in visual sequences providing consistent results as the auditory sequences (Milne et al., 2018). However, in this particular experiment non-adjacent dependencies were not identified by the monkeys, which may be due to adjacency relationships present in the grammar interfering with non-adjacency dependency learning, as seen in human infants (Watson et al., 2020). These experiments use long habituation periods to ensure that maximal time is given to learn the relations between the stimuli, however a modified version of this kind of experiment exposed chimpanzees and humans to stimuli for a much shorter period. These results identified that dishabituation occurred when the positional regularity of the sequences was broken but not when adjacency rules were broken (Endress et al., 2010). This may suggest that chimpanzees are able to extract positional information about element placement in sequences spontaneously, whereas more protracted exposure may allow for learning of relationships between elements.

Controlled experiments also allow for neurophysiological tests to be conducted. A study using EEG on macaques habituated to an artificial grammar containing adjacent dependencies identified event related potentials to rule violations (Attaheri et al., 2015). A similar study identified event related potentials related to non-adjacent dependency rules in macaques, with the event related potentials being very similar to those observed in human infants when exposed to the same kind of stimuli (Milne et al., 2016). Indicating that non-adjacent dependencies are detected at the neuronal level in primates. A review of functional MRI studies comparing humans and primates identified that areas in the ventrolateral prefrontal cortex may act to identify simple adjacent dependencies in sequences whereas when processing hierarchical or non-adjacent dependencies incorporates dorsolateral areas of the prefrontal cortex and that these functions are conserved in humans and primates (B. Wilson et al., 2017).

1.4.2 Active sequence learning tasks

Along with artificial grammar experiments, researchers also train experimental subjects to discriminate between sequences as a means of identifying how readily sequences can be learnt (Ghirlanda et al., 2017). A key difference between artificial grammar experiments and sequence training is that the way in which learning is assessed is often based on active learning of sequences or grammar rules across multiple trials, rather than habituating the subjects to a set of stimuli involving implicit learning then watching how they react when the rules of this set are broken.

To measure sequence discrimination, often serial response times are measured across a training regime, to evaluate the speed at which a subject can recognise or reproduce a sequence. In experiments using Guinea baboons (*Papio papio*) (Minier et al., 2016; Rey et al., 2019), a touch screen automated learning device presented a sequence of dots in one of nine quadrants of the screen, which would be pressed by the baboons in exchange for a reward. Subjects in these tasks would be presented with random sequences of dots initially but would then be presented with dots that would conform to a specific pattern. In these experiments, the decrease in reaction time during the pattern phase suggested that the baboons were able to identify and perform more quickly based on these sequences, exhibiting their abilities to distinguish statistical dependencies in sequences. However, baboons did differ in that they were unable to distinguish more global non-adjacent dependencies across the whole sequence, which humans were able to (Minier et al., 2016; Rey et al., 2019).

A similar study, involving rhesus macaques and tufted capuchin monkeys, specifically aimed to identify whether non-adjacent dependencies could be identified (Bowden et al., 2021). In this task, monkeys used a joystick that controlled a cursor, which they would need to place in the correct place on a target to receive a reward. A sequence of stimuli would appear before the target, with an adjacent predictor stimuli appearing directly before the target and a non-adjacent predictor stimuli being placed somewhere else in the sequence. Both species showed decreased reaction times when an adjacent predictor was presented and this decrease in reaction time was magnified by how high the transition probability between the adjacent element and the target was. No decrease in reaction time was found with the non-adjacent dependencies, suggesting that non-human primates may struggle with learning these kinds of dependencies.

A cross-species review of sequence training experiments comparing learning curves across trials, suggested that humans were much better at learning sequences compared to other animals, with a huge number of trials (up to thousands) being needed to teach the study animals sequences with three or greater elements (Ghirlanda et al., 2017). The non-human primates included in this study were no exception with the macaque and capuchin data showing similarly high trial numbers to the other species tested. An illustration of this comes from a study which tested two rhesus macaques on their ability to respond to sequences using a joystick device which they moved into position based on the position of a circle on a screen (Heimbauer et al., 2018). It was identified that the monkeys performed the task more quickly when the circles conformed to grammatical rules, with sequences being varied from four to eight circles. However, this took up to fifty trials, with each trial containing potentially containing over one hundred attempts. So considerable training is required to learn the relations between elements during these tasks compared to humans.

A more freeform sequence learning task was used to investigate the ontogeny of communicative abilities in captive bonobos and chimpanzees (Gillespie-Lynch et al., 2011). Both species had access to a lexigram board and could use it to communicate with the experimenters across three years from the age of one year old to four years old. These communications were documented across the three years to identify how novel symbol combinations were generated and whether they were contextually meaningful. For both species symbol combinations are initially dependent on the experimenters conversational input by processes of deferred imitation, imitation of a sequence after being demonstrated and joint construction where the experimenter and ape would work together to form communicative sequences. As the apes become older they rely less on conversational inputs to construct novel sequences and create relevant symbol combinations independently. Although the system of communication used is not natural this potentially suggests that there are distinct stages of communicative learning in apes with early stages relying heavily on conversational input and later stages involving increased creativity in communicative sequences.

These sequence training tasks are also useful in identifying the roles of brain regions related to sequence learning. An experiment aimed to identify the role of the cerebellum in sequence learning by using cynomolgus monkeys with cerebellum lesions (Nixon & Passingham, 2000). The task involved training these monkeys to use a joystick, with stimuli presented on a screen indicating the movement of the joystick required by the participants. Correct choices resulted in a pellet reward and response time and number of errors was measured. The monkeys were tested on their ability to learn sequences before and after surgery. They found that the sequence learning was impaired in the post operative monkeys, but their findings did not suggest a role in cognition, instead suggesting that its role may be involved in the process becoming automatic.

1.4.3 Tool Use and Puzzle Box Tasks

The previously described paradigms have focussed largely on discriminating auditory or visual stimuli in, for the most part, artificial conditions. Puzzle box and tool use experiments differ, in that they require the experimental subjects to actively engage with the stimuli to receive a reward; for this reason, they may more accurately emulate the skills used by these primates in the wild when facing tasks involving sequence learning.

Canteloup et al. (2020) exposed vervet monkeys to a simple puzzle box where individuals could either open the lid or pull a compartment to receive the food reward. These were exposed to two groups of wild monkeys with one groups most dominant female learning the lift method and the dominant male of the other group learning the pull method first. Which method was observed being used by conspecifics significantly increased the likelihood that they would also use the same technique. Although the manipulation here is not sequential, this provides evidence that social transmission of skills in the physical domain may be an important feature in anthropoid primates (Canteloup et al., 2020). A different task presented macaques (*Macaca mulatta*) with two tools with them needing to be used in the correct order to receive a food reward (Hihara et al., 2003). In this experiment macaques needed to use two tools in sequence in the correct manner to acquire a food item providing evidence that some monkey species, like apes, are able to perform sequential tool use tasks in captive settings. The macaques were able to learn this short tool use sequence quickly suggesting they are capable of creating original manual sequences to achieve novel goals.

Although the above task involved monkeys, Predominantly, these tasks have focussed on the ability of great apes to learn novel tool use sequences. One of these studies presented captive chimpanzees, bonobos and orangutans with an out of reach reward and gave the apes two tools which were too small to reach the food but were long enough to reach four out of reach tools that differed in length (Martin-Ordas et al., 2012). In the first difficulty, apes could use the initially presented tools to reach the food; in the second difficulty any of the four tools placed out of reach is long enough to reach the food but neither of the two provided tools is long enough; in the third difficulty the longest tool is the only tool that will reach the food; in the final difficulty the longest tool is the only tool that will reach the food but is out of reach of the first two tools, so one of the intermediate sized tools must be taken first using one of the first tools and then the newly acquired tool must be used to retrieve the longest too. Twelve of the fifteen apes were able to reach the food in the sequential trials but as the difficulty increased success rates decreased, however apes were able to grasp the second and third difficulty within only a few trials. The apes would also modulate their strategies depending on the distance of the longest tool and the distance of the food. If the longest tool was easy to access, they would use it regardless of food distance however, increasing the difficulty of acquiring the longest tool increased the likelihood that they would choose a different appropriately sized tool. This study shows that the great apes are capable of independently learning complex tool use sequences and can modulate their approach based on task parameters.

A task aiming to identify how social learning impacted tool use gave chimpanzees a selection of tools to use to extract juice from a container. This experiment identified that exposing individuals to novel demonstrations of how a tool can be used for a task allowed new skills to diffuse and build on previously learnt tool use behaviour (Vale et al., 2017). A task comparing chimpanzees to gorillas tool use provided a simulated termite mound where sticks could be used to extract food rewards. In this task chimpanzees were quicker at learning to extract food compared to the gorillas, which may have been facilitated by an increased number of social members at the mound observed in the chimpanzees, which may have increased the ability to imitate other individuals successful techniques (Lonsdorf et al., 2009). A similar study comparing groups of human children, chimpanzees, and capuchins sequence learning abilities, used a puzzle box that could be solved in three stages. Both primate groups performed poorly on this task with only 1 individual reaching the third stage and 4 reaching the second stage out of 33 chimpanzees similarly only 2 of the 22 capuchins were able to reach stage 2. Children on the other hand performed much better with at least two individuals from each five of the eight groups of five children completing the hardest difficulty. The primates would primarily attempt the task as individuals, whereas children saw the task as a social one, with children instructing each other on how to complete the task and increased tolerance for multiple individuals around the apparatus (Dean et al., 2012). Suggesting that a number of distinctly human prosocial techniques augment the children's learning ability that are not present in the primates.

1.4.4 Summary of Experimental Research

Following from the observational work, indicating that call combinations are relatively common across primates and across contexts, playback experiments have attempted to identify what information these calls convey. Experiments in Diana monkeys (Zuberbühler, 2000), putty nosed monkeys (Arnold & Zuberbühler, 2006) and bonobos (Clay & Zuberbühler, 2009) have identified that primates are able to extract meaningful information from these call sequence to modify their behaviour and that monkeys concatenate calls to increase their repertoires. However, as illustrated by the inconsistent results from the putty nosed monkeys (Schlenker et al., 2016), evidence that primate calls are combinatorial in a linguistic sense is much sparser with two conflicting hypothesis explaining the existing data adequately (Schlenker et al., 2016). Therefore, although primates do use call combinations in wild settings it is unclear what sequence features are extracted by primates in these experiments.

Experiments using false grammars and examining non-adjacent dependencies in playback and interactive learning tasks suggests that primates are able to consistently learn the relationship between adjacent dependencies in grammars in learning tasks (Heimbauer et al., 2018). However, the evidence for non-adjacent dependency learning is much less consistent with some experiments suggesting that some species are able to learn these dependencies whereas others are unable to. A difference in task design may explain these inconsistencies however as when mixed grammars were used primates were unable to learn the non-adjacent dependencies but were able to learn the adjacent dependencies (Endress et al., 2010). This potentially indicates that adjacent dependencies overshadow the learning of non-adjacent dependencies in primates. Studies using sequences of varying lengths identified that considerable training is required to teach primates in these tasks the sequences and the rules that dictate them, suggesting that sequences greater than three elements are considerably difficult for primates to learn (Ghirlanda et al., 2017).

Experimental paradigms of this kind have also begun to unravel the neurophysiological basis of sequence cognition. For example, EEG studies have identified event related potentials in the brain related to adjacency dependencies and non-adjacent dependencies in primates across sequence learning tasks, suggesting that discrimination of these dependencies are made and have a neurophysiological basis (Milne et al., 2016). Comparative fMRI scans have identified that an evolutionarily conserved brain pathway between the ventrolateral prefrontal cortex and the dorsolateral prefrontal cortex being identified as important in both human and primate sequence cognition (Bischoff-Grethe et al., 2004). The role of the cerebellum has also been investigated suggesting that one of its roles in sequence learning may be to automatise learned sequences.

These tasks have predominantly dealt with sequences in the visual and auditory domain whereas, as highlighted by the observational studies, sequence cognition likely extends into the domain of manual skills. These experiments have identified that the great apes and some monkey species are able to learn sequential tool use tasks, with great apes being able to learn complex sequences of tool use to extract food rewards (Martin-Ordas et al., 2012). A consistent theme in this research has been identifying the role of social learning in the acquisition of new skills (Vale et al., 2017), social network studies on tool use learning have identified that learning by observation of conspecifics plays an important role in primates learning of new tool sequences, however compared to humans primates do not approach these tasks socially (Dean et al., 2012).

1.5 Discussion

1.5.1 Appraisal of both paradigms

This review has thus far given an overview of the existing observational and experimental research that explores sequence learning in the anthropoid primates. Both approaches provide separate, but related, insights into how primates deal with behavioural sequences. Observational approaches allow researchers to identify sequences of behaviour produced by primates, while interacting in natural settings. This is useful, as it provides information on the contexts in which species use different sequences of behaviours, which can be used to infer the kinds of selective pressures that moulded these behaviours. Identifying discrete behavioural elements can provide insight into the natural repertoires of species and identify structure in the sequences themselves. Observations across the lifespan can also provide insights into how these capacities change across development and comparisons between different groups of primates can allow one to infer the role of social learning. Using this approach has provided a wide array of examples of sequential behaviours used across a diversity of contexts and species. However observational research is limited in that it is difficult to identify what features of sequences are being learnt by the primates, beyond their behavioural responses to the calls as a whole.

Experimental approaches fill this gap by modifying the sequences presented to primates and allowing the features within sequences to be investigated to identify how they respond to varying sequence structures. These experiments can also provide insights into the processes governing this learning and, by combining these methods with neuroimaging techniques, can identify brain regions important in sequence learning. However, due to the difficulty of running controlled experiments of this kind, the variety of species that these experiments have been conducted on is small compared to the observational methods described. Though they do potentially provide a deeper understanding of the mechanisms influencing sequence learning capacities in primates.

1.5.2 Cross species comparisons

Due to the large number of species and the diversity of primates, it is difficult to generalise too much regarding their sequence learning abilities. However, a few general themes are emerging. Across a diverse selection of primates, species are able to combine multiple discrete elements to create call sequences that provide information that conspecifics are able to identify and act upon. Wild communicative sequences, however are limited in the size of call sequences with meaningful combinations often being combinations of a small number of elements in simple configurations (Zuberbühler, 2018). Considering the evidence provided by Ghirlanda et al. (2017), this is not surprising, as the experimental evidence suggests that sequences of sizes greater than 3 elements are difficult for primates and other animals to learn. It is reasonable to predict that combinations of elements would be reasonably short in the natural communicative sequences commonly observed in wild primates. The development of these communicative sequences appears to be at least partially dictated by social learning across development, as highlighted by the evidence collected from marmosets and the extant hominids (Gultekin et al., 2021; Oller et al., 2019). Although the elements used in communication seem to be present from birth, the sophistication of these sequences is refined across development into adulthood.

An interesting parallel between species when looking at the ontogeny of learning sequences of behaviours, across varied contexts, is the presence of a stage where variable production of elements in random combinations aids in the learning of mature sequences. This is present in the babbling of pygmy marmosets (Snowdon & Elowson, 2001), the combinatorial exploration observed in the development of tool use in long tailed macaques (Tan, 2017) and the sequences of gestures used by chimpanzees that becomes refined to single gestures in adulthood (Hobaiter & Byrne, 2011). This may indicate that a common strategy in development is to practice with multiple redundant and often useless combinations of elements that the individual is then able to use to refine their abilities to develop the correct sequence of behaviours. This strategy may allow individuals to explore the possible combinations of elements and learn by reinforcement the correct sequences of elements to acquire the correct result.

Experimental work using playback experiments and false grammars have identified that primates are able to attend to and learn the adjacent dependencies between elements in sequences (Bowden et al., 2021). However, evidence gathered to date regarding their ability to learn non-adjacent dependencies is mixed. An explanation for these mixed results could be due to slight variations in experimental design, with the experiments identifying sensitivity to non-adjacent dependencies being predominantly using stimuli that only contained non-adjacent dependencies, whereas experiments using mixed grammars where both non-adjacent dependencies and adjacent dependencies do not detect sensitivity to non-adjacent dependencies. Potentially in mixed grammar experiments, processing of the adjacent dependencies is attended to first and obscures the learning of non-adjacent dependencies (B. Wilson et al., 2015). Neurophysiological evidence does point to primates being able to detect these non-adjacent dependencies, but proposed brain mechanisms highlight that more complex sequence learning must incorporate more brain regions than learning adjacent dependencies (Mueller et al., 2018; B. Wilson et al., 2017).

1.5.3 Comparisons to humans

A key goal motivating the exploration of sequence learning in primates is the potential for the information gained to inform our understanding of sequence learning in humans, with these insights potentially providing perspectives on human language, culture and tool use. The observation that gestural communication and manual tool use are predominantly observed in the great apes could point to these skills having been under co-selection in the ape lineage (Woll, 2014). Human neurophysiological evidence suggests that tool use and language learning share the same brain regions and therefore could point to the sequence learning skills necessary in both domains being attended to by a shared processing system that has been elaborated in the course of human evolution (Steele et al., 2012; Vandervert, 2016).

As mentioned previously, the expansion of the cerebellum has been implicated as potentially having important adaptative consequences in humans and great apes sequence learning abilities (Barton, 2012; Barton & Venditti, 2014). Cerebellum lesions experiments in primates seem to provide some support of the evidence found in human cerebral ataxia, with legions in the cerebellum not necessarily contributing to sequence cognition per se but being important in automating these abilities (Morgan et al., 2021; Nixon & Passingham, 2000). This may suggest that an increased capacity to automate sequences of behaviour in humans could explain some of humans unique capacities. With humans reliance on sequences of behaviour across a variety of contexts, having an increased ability to have behavioural sequences become automatic may allow humans to build complex sequence repertoires that can be performed without conscious effort. However studies in humans have identified that the cerebellum is likely to play an active role in sequence cognition by detecting and simulating repetitive events in the environment and forming internal models that allow for prediction of future events (Leggio & Molinari, 2015). Taken together these studies suggest that the cerebellum is likely to play multiple roles in sequence cognition.

Comparative fMRI studies related to sequence learning have identified that primates share a conserved system dedicated to sequence learning involving the ventral and dorsal lateral prefrontal cortex. The dorsolateral prefrontal cortex in the model proposed in these findings helps attend to non-adjacent dependencies and higher order sequence structures (B. Wilson et al., 2017). This may explain why during mixed grammar experiments with both adjacent and non-adjacent dependencies humans are able to attend to both relations between elements when primates are only able to attend to the adjacency relations (Attaheri et al., 2015). Comparisons between the event related potentials of non-adjacent dependencies in human adults and infants compared to macaques found that the primate event related potentials are similar to human infants, suggesting these abilities appear early in ontogeny in humans (Mueller et al., 2018).

In both the observational and experimental literature, the role of social learning in the acquisition of these abilities is highlighted suggesting that the acquisition of sequences during learning is importantly facilitated by exposure to conspecifics. An interesting parallel observed in a number of primate species is early primate behaviours homologues to human babbling in infants, suggesting that mechanisms that facilitate the acquisition of communicative sequences occurs early in our phylogeny (Gultekin et al., 2021; Oller et al., 2019). Specific adaptations that facilitate social learning of novel skills in humans could differentiate us from primates as although primates do seem to learn from each other, human children will actively engage with a novel sequence learning task as a collaborative exercise enhancing their ability to complete the task (Dean et al., 2012). This may point to humans having developed a selection of highly social adaptations that facilitate social learning that are not present in other primates, which could aid in the learning and memorisation of sequences of behaviour.

1.5.4 Future directions

Observational data provides evidence of structured and consistent sequences in a variety of contexts across primates. However, the main focuses of these experiments has been in the communicative domain and the use of tools. As highlighted by studies on gorillas' manual food processing skills (Neufuss et al., 2019), tool use is not the only physical domain where complex sequences can arise. A closer focus on a broader set of species manual abilities in relation to food extraction would potentially provide a broader perspective related to the evolution of manual abilities in sequential contexts. Similarly, in the experimental domain, tool use and puzzle box experiments have primarily focussed on the abilities of the great apes, with a handful of experiments investigating monkeys' abilities in this domain (Hihara et al., 2003). To better understand how manual abilities evolved, having a broader array of species attempt these kinds of tasks would allow for phylogenetic inferences about the evolution of these abilities to be made. Due to the recent interest in the link between tool use and language and with a number of hypothesis linking the cognitive aspects of tool use and language (Steele et al., 2012; Vandervert, 2016), more focus should be paid to whether the sequence learning abilities observed across visual and auditory domains from the false grammar experiments are also observed in tasks involving action sequences. Creating puzzle box or tool use experiments that focus on the sequential relations between elements could clarify how learning in these domains are linked.

Social learning mechanisms have been linked to the proliferation of sequences of behaviour (Vale et al., 2017). Studies in this area should begin to focus on the exact mechanisms of social transmission, for example investigating whether sequences are learnt by imitation or reinforcement learning could provide insight into the aspects of social behaviour that inform the development of these abilities. Increasing the number of species used in studies that track skill development across the lifespan would also provide a rich resource to aid in the understanding of sequence acquisition. In relation to tool use, the focus has predominantly been on the spread of these behaviours through social learning, but an important but neglected area of inquiry is the individual learning required to develop new skills in the first place (Bandini & Tennie, 2020). Clarifying the role of individual learning in the development of sequences of behaviour could therefore be another avenue of exploration.

Comparative neurophysiological studies are in their infancy in relation to sequence learning but have already provided unique insights (Barton & Venditti, 2014; B. Wilson et al., 2017). Understanding the biological aspects of sequence learning should therefore be a continuing effort. One of the potential approaches to do this would be to aim to understand how already implicated areas of the brain, such as the cerebellum and the ventral and dorsal lateral prefrontal cortex, link to each other and different brain regions to facilitate sequence learning. How these connections may vary between different primate species and humans would provide a complementary comparative perspective that could inform how selection acting on the brain influenced sequence learning abilities across primate evolution.

This review largely focussed on tool use in the observational chapter in relation to observations of sequence learning in relation to foraging. Compared to tool use, there is a relative lack of research on the potential sequences of behaviours used by primates in other foraging tasks. The exception is the manual processing abilities of gorillas which have been documented in relation to their processing of nettles and thistles (Byrne et al., 2001, 2011; Tennie et al., 2008). Chapter two of this thesis aims to directly compare the browse feeding behaviours of gorillas and the browse feeding behaviours of an understudied species, François' langur (*Trachypithecus francoisi*), as a way of identifying whether sequence learning abilities in feeding tasks are shared across a wider range of species and if not identify these differences. This study aims to use Markov chain analysis to identify sequential structures in these two species feeding behaviours, allowing for comparisons within a shared research framework. This will add to the existing literature on the sequences performed by these species outside of tool use contexts and potentially provide a framework for future comparative studies of this kind.

One suggestion made related to the experimental portion of this literature review is that the majority of experiments related to sequence learning have been performed on a relatively small number of species of primates. Therefore, chapter three of this thesis aims to present two understudied species, Francois Langurs and Black headed spider monkeys with a novel sequence learning task that assess sequence learning abilities in the physical domain. This study aims to increase our understanding of sequence learning in a broader range of species than those that we currently have literature on.

Chapter 2: Investigating Browse Feeding Behaviours Using Markov Chain Analysis in Gorillas (*Gorilla gorilla gorilla*) and François' Langurs (*Trachypithecus françoisi*)

2.1 Introduction

As illustrated in the previous chapter, one approach that can help elucidate the sequence learning abilities of primates is to identify sequences of behaviours performed by primates when engaging in tasks they perform naturally. Although observational studies are limited when trying to disentangle the underlying generative mechanisms that result in sequences of behaviours, establishing whether sequences of behaviour show evidence of hierarchical or structured organisation can provide supporting evidence that the execution of specific behavioural sequences is important to the organisms ability to function. This can be an important initial step in determining whether specific sequence learning strategies are likely to be necessary in learning these sequences of behaviours. Using Markov Chain Analysis this study aims to identify whether the moment to moment sequences of browse feeding behaviours of gorillas and François' langurs show evidence of higher order structure and whether the two species differ in the types of behavioural sequences they use when feeding. The use of Markov chain analysis allows for quantifiable comparisons to be made between the two species and provides a framework for understanding the structure of behavioural sequences used in the feeding context. This study will therefore provide novel comparative data on manual sequences, which will provide a richer understanding of the range of sequences of behaviours used by primates.

All organisms share the need to acquire energy from their environment in order to survive. Primates, as a diverse group of organisms, vary in their diets and are generally omnivorous -feeding on fruits, insects, hunting other small animals and extracting leaves and bark from branches (Chapman & Chapman, 1990). Most primate diets are predominantly herbivorous, meaning that the majority of their diet comes from plants (Milton, 1999). Primates must use a variety of behavioural strategies in order to extract food from plants. In this domain, previous research has focused on primates' use of tools, which has been documented in the great apes and a selection of other primate species (Haslam et al., 2009). Some primates will learn specific behavioural sequences to ensure successful manipulation of tools; for example orangutans (*Pongo pygmaeus*) will use sticks to extract the flesh and seeds of *Neesia* fruits (Van Schaik & Knott, 2001) and chimpanzees (*Pan troglodytes*) will use and modify stems of herbs to extract termites from termite mounds (Nishihara et al., 1995). Although tool use in primates is predominantly observed in the great apes, notable non-ape examples have also been observed in the genera *Cebus* and *Macaca* (Aguiar et al., 2014; Chevalier-Skolnikoff, 1990; Gumert et al., 2011). In wild feeding contexts, tool use is predominantly observed in chimpanzees and orangutans while being almost absent in bonobos (*Pan paniscus*) and gorillas (*Gorilla gorilla* and *Gorilla beringei*) (van Schaik et al., 1999). In captivity however, all great ape species have been observed using tools to acquire food, suggesting that great apes are generally endowed with the cognitive and manual capacities required to do so (Motes-Rodrigo & Tennie, n.d.). One study requiring gorillas, chimpanzees and orangutans to use assortments of tools in sequence, to reach food at a distance, identified that all three species were able to reach the food with the tools they were provided. Presenting evidence that great apes are able to develop novel behavioural sequences to reach a goal, with similar levels of sophistication, highlighting the potential importance of these cognitive abilities in these species survival (Martin-Ordas et al., 2012).

The prevalence of tool manipulation in the great apes is the basis of a number of hypotheses related to hominid cognitive evolution. For instance, the relative expansion of the cerebellum, a brain region related to learning sequences across a variety of contexts including tool use (Ueda et al., 2019) and language in humans (Starowicz-Filip et al., 2017), suggests that selection for increased sequence learning abilities make humans uniquely adept in these domains (Barton & Venditti, 2014; Vandervert, 2018). Other brain regions have also been found to overlap in activity in both tool use and language tasks. Overlapping activity in Broca's area has been observed when humans were perceiving language and when using tools (Higuchi et al., 2009) and the homologous brain region in chimpanzees has been identified as important in motor skills in tool use (Hopkins et al., 2017). A recent fMRI study also found that neural patterns in the basal ganglia are shared in tool use tasks and complex syntax tasks in humans. Behavioural evidence from this study also identified that training tool use abilities increased competence in a language learning task and vice versa (Thibault et al., 2021).Taken together, this evidence suggests that processing complex manual action sequences and processing structures present in language share processes in the brain. Both complex manual sequences and language share similar hierarchical structures, potentially indicating that both processes coevolved and share underlying cognitive mechanisms (Osiurak et al., 2021).

Great apes are also some of the only primates that integrate the use of gestures into their communicative repertoires (Fröhlich & Hobaiter, 2018). The use of gestures coupled with the preponderance of tool use in great apes has been used to suggest that the evolution of manual sequential actions co-evolved with communicative abilities in the great apes and humans (Hopkins & Cantero, 2003; Woll, 2014). The gestural origin hypothesis of language evolution suggests that the use of gestures acted as a precursor to vocal communication (Armstrong, 2008). Some evidence for this hypothesis has been suggested from the observation that in both humans and chimpanzees lateralisation of regions related to communication results in a bias towards the use of the right hand for gestures accompanied by vocalisation, which suggests that both the gestural communication and vocalisation are similarly lateralised in the left hemisphere of the brain (Hopkins et al., 2005; Hopkins & Cantero, 2003). These findings have been used to suggest that language lateralisation in the left hemisphere results from precursor lateralisation of manual abilities from a more evolutionarily ancient gestural precursor system. Neurophysiological evidence that communication related brain areas are multifunctional and are incorporated in a variety of sequential manual tasks like tool use (Higuchi et al., 2009; Stout & Chaminade, 2012), has led to the suggestion that these abilities share substantial processing and facilitated each other's evolution, with more general sequence processing capacities being shared across modalities. The current study therefore has the potential to identify sequential structures in primate manual feeding behaviours, which could indicate differences between a great ape and monkey species. Offering relevant data that can provide evidence of similar hierarchical structure in manual actions as are observed in sequential communication and language.

Compared to the other great apes, gorillas are somewhat of an outlier, rarely being observed using tools in the wild (Breuer et al., 2005) and being primarily folivorous for much of the year, increasing fruit consumption depending on seasonal availability (Fuh et al., 2022) and varying between the different subspecies (Doran & McNeilage, 1998). However, when given tools in captivity, gorillas are capable of learning to use them with comparable sophistication to the other great apes, suggesting that gorillas have comparable cognitive abilities in this domain (Pouydebat et al., 2005). Although gorillas rarely use tools in the wild, Byrne et al. (2001) identified that mountain gorillas will manipulate food items with their hands using multistage strategies to feed on a variety of plant types, including nettles and thistles, which have a number of defences that must be dealt with to efficiently eat them (Byrne et al., 2001). A more recent study investigating how mountain gorillas (*Gorilla beringei*) from the Bwindi Impenetrable National Park in Uganda process two species of hard-to-process plants and one species of unarmed plant. They identified that gorillas in this group used a repertoire of 19 distinct manual actions to process these three plant species with the harder to process species requiring more manual actions to process effectively. Processing of all plant species, including the species lacking protections, showed specific sequences of manual actions used by the gorillas (Neufuss et al., 2019). These studies suggest that gorillas use multistage methods to extract edible parts of these plants, allowing them to extract nutrients from a variety of sources in order to survive. Therefore, although gorillas don’t use tools in the wild, these findings indicate that these abilities are used in skilled manual activities more generally (Byrne, 2004). Understanding the nuances of these behaviours can therefore provide deeper insights into the evolution of manual sequence learning in great apes beyond tool use.

As complex manipulative abilities are likely not confined to tool use, it is necessary to broaden the investigation of these abilities in other primate species that haven’t been observed using tools in the wild. François’ langurs (*Trachypithecus françoisi*) are a semi-arboreal species of *Cercopithecidae* monkey, endemic to Southwest China and Vietnam, where they preside in the canopies of trees and rocky hillsides of the limestone cliffs common in their habitat (Yang et al., 2007; Zhou et al., 2013). François’ langurs are predominantly folivorous, spending on average, ninety four percent of their feeding time on leaves and six percent on fruit, flowers and twigs (C. Huang et al., 2008). As they predominantly feed on leaves, they make an excellent point of comparison to investigate potential species differences in their approach to extracting food from similar plant matter.

Investigating primate species with a diversity of diets and feeding behaviours is also relevant to understanding cognitive evolution more generally. The extractive foraging hypothesis suggests that complex cognition evolved to facilitate the extraction of nutrient rich foods that requires multiple processing steps to access (Parker, 2015). A cross species study by Decasien et al. (2017) aiming to identify the roles of diet and sociality in the evolution of brain size identified that primates with frugivorous diets had larger brains compared to folivorous primates. With this relationship potentially being due to the added complexity of feeding on fruits, where knowing their location, how to access them and their seasonal availability adds complexity to feeding on them (DeCasien et al., 2017). Increasing the range of primate species whose feeding behaviours are investigated in detail can help to elucidate the link between manual behavioural sequences and the evolution of complex cognition more generally.

Another important question when investigating the evolution of manual sequence learning abilities is understanding how they are honed across development and learning. Primates, like humans, have an extended developmental period before adulthood, where the infant must rely on their mothers and in some cases other group members to survive (Ross, 1998). A longitudinal study following chimpanzees across four years, with individuals varying in ages from infants to adults, identified that juvenile chimpanzees have similar foraging rates and foraging techniques to those of adults, suggesting that foraging skills are learnt early in development, with learning likely being aided due to cofeeding with their mother (Bray et al., 2018). Similar results have also been observed in gorillas (Nowell & Fletcher, 2008). In vervet monkeys (*Chlorocebus pygerythrus)* , increased synchrony in timing of mother and infants feeding bouts increased survivability of the infants suggesting that learning feeding techniques from the mother is key to early survival (Hauser, 1993). In these contexts, learning of simple foraging techniques occurred reasonably early in development. However, Estienne et al. (2019) followed the development of honey extraction techniques in juvenile chimpanzees and identified that the development of more complex extractive foraging techniques occurred more slowly. Finding that the full repertoire of relevant manual behaviours were observed at around six years of age, with successful extraction of honey being observed only twice at the ages of eight and eleven (Estienne et al., 2019). Unlike common foraging behaviours, more complex actions sequences therefore appear to take considerable time to acquire and hone (Carvajal & Schuppli, 2022). Understanding how behavioural sequences in relation to feeding are learnt across development can therefore provide insight into the incremental improvement of these skills across the lifespan and into the cumulative learning of these behaviours, as well as the contexts that facilitate this learning.

Outside of the importance of learning across development there is evidence to suggest that the learning of behavioural sequences in relation to feeding behaviours is facilitated by social learning more generally. Using network analysis to identify the proliferation of a novel variation on leaf sponge usage, where moss was used instead of leaves to create a moss sponge, identified that direct exposure to other individuals using the novel technique increased the probability of the observer acquiring the skill, suggesting that social learning is one mechanism for acquiring novel tool use behaviours (Hobaiter et al., 2014). Observation of two different groups of mountain gorillas, a wild population in Rwanda and a captive population at Port Lympne in the UK, identified that the two groups used different behavioural sequences to process nettles, but within groups there was considerable conformity at the process level (Byrne et al., 2011). This provides evidence of stable local traditions in the manual action sequences used in this task A separate experiment introducing a novel artificial fruit with three defences and gorillas watched each defence being removed in one of two ways by an experimenter. It was found that there was a tendency to copy the observed method of defence removal but the sequence of defence removals was not copied (Stoinski et al., 2001). In this experiment then, the copying of the individual methods was observed over learning of the process level sequence of techniques. Clarifying where and how social learning is relevant in the acquisition of new behavioural sequences is therefore an important aspect of understanding how sequences of behaviours develop in groups of primates.

Markov chain analysis is a technique that can be used to evaluate sequences to determine how different behavioural elements are stringed together to form more complex structures (Tweedie, 2001). In the behavioural domain, this methodology has predominantly been used in the investigation of animal communicative sequences (Kershenbaum et al., 2016). Recently however, Mielke and Carvalho (2022) used this method to identify sequential structures in play bouts observed in a group of chimpanzees. This analysis identified that strings of behaviours were significantly associated to each other, providing evidence that play behaviours are structured hierarchically. This analysis concluded that chimpanzee play bouts are structured with behaviours being used in specific contexts analogous to games (Mielke & Carvalho, 2022). Markov chain analysis therefore allows the moment to moment behaviours of organisms to be analysed and can be used in a variety of contexts where sequences can arise.

In this current study, we investigate the moment to moment sequences of feeding behaviours used in a group of captive housed western lowland gorillas (*Gorilla gorilla gorilla*) and a captive housed group of François' langurs. Recordings of individuals in these groups were gathered opportunistically during their feeding times and coded at a later date to generate sequences of feeding behaviours. To analyse this data, the approaches outlined by Mielke and Carvalho (2022) were used to investigate the sequences of feeding behaviours. The Markov chain analysis was used to identify whether behaviours were significantly associated, to determine potential structure in these behavioural sequences and to identify whether individuals and species differed in their behavioural approaches.

We tested several hypothesis's based on the existing literature. The existing evidence documenting gorillas feeding behaviours suggests that gorillas exhibit hierarchical processing of food, in line with apes enhanced cognitive capacities. Therefore, we tested the hypothesis that the gorillas show more complex structures in the behavioural sequences they use during feeding compared to François' langurs. The previous literature suggests that the structure of feeding techniques are potentially learnt by social learning mechanisms, so we tested the hypothesis that the use of feeding behaviours and sequences will show group level similarity in both species. As the existing literature has documented the importance of ontogeny in the learning of several food related behaviours, we hypothesised that juvenile individuals of each species will perform less complex feeding sequences compared to older group members. As well as the specific hypotheses derived above, which are based on Markov chain analysis, general information related to the lengths and variety of behaviours used were analysed to compare and describe general patterns of feeding behaviour across individuals and species. In this context the complexity of feeding structures will be discussed in reference to multiple measures, including whether a greater number of feeding behaviours were used during their feeding bouts and whether behavioural elements are connected in sequences. Differences between individuals, which are relevant when assessing whether these skills are learnt socially and whether these behaviours differ across development, will be measured by identifying differences in individuals uses of behaviours and any differences in how individuals form behavioural sequences from these behaviours.

2.2 Methods

2.2.1 Subjects:

This study was conducted by collecting observations from six captive western lowland gorillas and seven François' langurs located at Twycross Zoo, UK. Demographic information of the individuals is listed in table 1.

Table 1: Demographic information of the primates involved in the study:

Name	Species	Sex	Age (years)
Asante	*Gorilla gorilla gorilla*	Female	37
Biddy	*Gorilla gorilla gorilla*	Female	48
Lope	*Gorilla gorilla gorilla*	Male	9
Oumbi	*Gorilla gorilla gorilla*	Male	30
Ozala	*Gorilla gorilla gorilla*	Female	28
Shufai	*Gorilla gorilla gorilla*	Male	6
Chow Chow	*Trachypithecus Françoisi*	Male	12
Kaili	*Trachypithecus Françoisi*	Female	4
Lychee	*Trachypithecus Françoisi*	Female	16
Pak Choi	*Trachypithecus Françoisi*	Female	16
Shiitake	*Trachypithecus Françoisi*	Female	2
Shinji	*Trachypithecus Françoisi*	Male	4
Yalu	*Trachypithecus Françoisi*	Female	1

François' langurs and gorillas were housed in their usual enclosures, where they are fed communally, so all individuals had access to the same food. Leafy branches were provided to both species in combination with other fruits and vegetables. Gorillas and François' langurs were fed in different ways. The gorilla's food was placed directly into their enclosures by keepers whereas the François' langur's food was thrown onto the mesh on the top of their enclosure, where they would need to pull branches through to begin processing them. In both species, keepers would cut very large branches into smaller branches so they were easier for the keepers to transport, meaning that most branches were between one and two metres long. Compared to the gorillas, the branches given to the François' langurs were cut into smaller lengths of less than a meter to make sure they could pull the branches into the enclosure.

2.2.2 Behavioural Sampling and Coding

Materials

Recordings of these sessions were taken using a Panasonic HC-V770EB-K Full HD Camcorders mounted on a tripod.

Gorillas:

Video Sampling: Gorillas

Videos were collected from captive gorillas during their feeding periods in the morning from 9:30am to 11:00 am and 4:30 pm to 5:30 pm between the study period of the 20th of June and the 19th of August 2022. Individual gorillas were opportunistically focal followed with a video camera while feeding on branches, with individual videos generally being between three and ten minutes. Opportunistic sampling was used due to constraints on the ability to effectively follow individuals while feeding took place. This was due to the enclosures having many areas where it would be impossible to film them, coupled with the unpredictable movements of the gorillas often meaning individuals would be in positions that made it impossible to see their movements in relation to feeding. Opportunistic sampling was therefore decided upon to maximise the amount of data that could be collected, even though this method meant that some individuals were observed less. Due to the gorillas frequently moving, sometimes the very start or end of a feeding bout would be missed. For ease of coding, all of the individual focal feeding videos, from each session, were combined into a string of videos using the opensource video editing software Lightworks, so there was a montage of all subjects feeding videos in one continuous video for each session. Long periods of inactivity unrelated to browse feeding were cut out of the videos to decrease video lengths. Feeding videos were collected from the gorillas across a total of 33 separate sessions.

Behaviours used for Coding:

A behavioural ethogram was established to identify the different specific feeding behaviours. Previous studies have identified repertoires of hand motions used by gorillas in feeding tasks, with Neufuss et al. (2018) being the most comprehensive. However, coding using this scheme would have required higher quality videos and for the gorillas to be sat in an optimal position. Due to the constraints of working with a captive population and only being able to view and record them from the visitor areas, we adapted the ethogram to a simpler format. The gorillas' browse feeding were discreet and reasonably distinct so ambiguity between these motions was rare and potential ambiguities were highlighted in the coding scheme.

The ethogram for gorillas is provided in table 2.

Table 2: An ethogram describing the behaviours used by the captive gorillas during feeding bouts

Behaviour	Description	Potential ambiguity
Start Feeding Bout	A feeding bout starts when a gorilla picks up a branch and subsequently conducts a feeding behaviour on the branch. If a branch is picked up and no subsequent feeding behaviour is performed this is not the start of a bout (often individuals will collect branches to process later).	The start of a feeding bout is reasonably unambiguous but sometimes a branch will be picked up and put straight back down or picked up and the gorilla will continue to walk and collect food. This should not be counted as a start to the Feeding Bout.
End Feeding Bout	End of bout is when a gorilla puts down the branch it was feeding on. If they then pick up the same branch again this is counted as the start of another feeding bout. The only exception is when a branch is being propped up on a wall and being processed. In this case the gorilla might be feeding on a branch without actively holding it up. This is rare but when it happens the end of the feeding bout should be directly after the last feeding behaviour, when the gorilla moves away or starts feeding on a different branch.	Sometimes a gorilla will hold onto a branch with their feet. Often a gorilla will hold the branch in a downward position, while still holding onto it this can sometimes look like they have put the branch down, this should not be counted as the end of a feeding bout.
No Start	The video does not catch the start of a feeding bout.	It was sometimes difficult to catch the start of a feeding event while moving the camera

		into a good position to film. Where this is the case, No Start should be coded.
No End	The video cuts away before the end of a feeding bout.	Similar to No Start sometimes an individual would become completely obscured or the video would end before the end of a feeding bout. When this is the case, No End should be coded.
Pick Leaf/Leaves With Hand	The gorilla will pick a leaf or a bunch of leaves with their hand. This movement is a plucking motion and often removes more than one leaf.	This is a very common behaviour and is generally easy to differentiate. However, it could potentially be confused with snapping a small branch off. It is differentiated from this as, if a small leafy branch is pulled off and put directly into the mouth, (without any subsequent food processing steps) it should be counted under this behaviour.
Strip Leaves With Hand	The gorilla will slide their hand across a branch section to remove many leaves from a length of branch. This movement is a sliding motion. Resulting in a small bunch of leaves being ripped off.	This motion is distinctive but could potentially be confused with snapping a small/large branch off, however this motion will not result in a branch being removed. This motion is distinguished from Picking leaves as this motion involves the hand sliding across a section of a branch, not a plucking motion.
Pick Leaf/Leaves With Teeth	The gorilla will move the branch towards their mouth and pluck a leaf or bunch of leaves with their mouth.	This is a plucking motion versus stripping. This is a very quick motion and often happens multiple times in quick succession.
Strip Leaves With Teeth	The gorilla place a section of branch in their mouth and drag their mouth along the branch to remove leaves from a section of the branch.	This behaviour can potentially be confused with Stripping Bark with Teeth, but this motion does not pull off a section of bark. Stripping bark is a more effortful motion putting strain on the branch while bark is pulled off.
Strip Bark With Teeth	Pull off a string of bark. When putting the branch in their mouth the gorilla will often loosen bark by rolling the branch while chewing a single section before pulling a strip of bark off of the branch. This motion is very common towards the end of feeding bouts when there are no more leaves on the branch. This is not exclusively the case as gorillas will strip bark even when there are leaves still on the branch.	This motion can be confused with stripping leaves with Teeth. However, they can be differentiated as a string of bark is pulled off when stripping bark and will often hang from the Gorillas mouth. The motion also is more forceful and puts obvious strain on the branch, requiring the gorilla to perform a tugging motion. Stripping leaves is more of a raking motion across the branch.
Snap Small Branch Off	A small branch is snapped off using either hands or mouth and a subsequent food processing step/steps is conducted on this smaller branch, or the branch is dropped.	A small branch is defined as a branch with no smaller branches jutting off of it. It is a single straight branch with or without leaves on it, with no additional branches coming off of it.
Snap Large Branch Off	A large branch is snapped off using either hands or mouth and a subsequent food processing step/steps is conducted on this branch, or the branch is dropped.	A large branch is defined as a branch with at least one other branch jutting off from it. It is a branch that *has* additional branches coming off of it. The actual size of the branch is not necessarily indicative of the branch being classified as large or small, the classification is based on whether a branch has other branches jutting from it.
Rearrange Branch/Branches	A substantial rearrangement of the branches being eaten.	This is a reasonably rare behaviour and is delineated from the miscellaneous movements of the branch while conducting

	A substantial rearrangement of a branch is a 180º flip of the entire branch to change the orientation of the branch. This is a large deliberate motion and is not interrupted by other feeding behaviours. Sometimes a gorilla will be holding multiple large branches. If this is the case and the gorilla rearranges the branches between hands or switches which branch, they are feeding on this is also counted in this category.	other feeding behaviours. What sets this behaviour apart is that the branch is substantially moved or rearranged without conducting a feeding behaviour.

François' Langurs:

Behavioural Sampling:

Videos were collected from captive François' langurs during their feeding period in the afternoon from 12:45 pm to 2:00 pm between the study period of the 20th of June and the 19th of August 2022. To collect videos, focal videos were opportunistically collected of individuals feeding on branches, with these videos generally being between ten and twenty minutes. Opportunistic sampling was used for the François' langurs due to the same constraints, mentioned in relation to the gorillas, also being present when recording the langurs. As the François' langurs often fed in a group, it was usually possible to record multiple individuals feeding at the same time for an extended duration. For ease of coding, all of the individual videos from each session were combined into a single video using the opensource video editing software Lightworks, so there is one continuous video of focals for each session. Long periods of activity unrelated to browse feeding being cut out of the videos to decrease video lengths. Feeding videos were collected across five sessions. The ethogram of behaviours coded are described in table 3.

Table 3: An ethogram describing the behaviours used by the François' langurs during feeding bouts

Behaviour	Description	Potential ambiguity
Start Feeding Bout	A feeding bout starts when a François' langur pulled a branch through the mesh at the top of	The start of a feeding bout is reasonably unambiguous; however, langurs will

	their enclosure and subsequently fed or if it picked up a branch that had already fell or been pulled through the mesh. If a branch is pulled through the mesh or picked up and no subsequent feeding behaviour is performed this is not the start of a bout.	sometimes be unable to pull the branch through and be left with only a handful of leaves. This should not be counted as a Feeding Bout, as they have failed to pull the branch through the mesh. Although they may eat these leaves, we are interested in the sequence of behaviours used to process a full branch once it has been pulled into the enclosure properly.
End Feeding Bout	When a François' langur puts down the branch it was feeding on, this is the end of a bout. If they then pick up the same branch again this is counted as the start of its own feeding bout. The only exception to this is when a branch is being propped and being processed. In this case the langur might be feeding on a branch without actively holding it up. This is much more common in the langurs than with the gorillas, especially with smaller individuals. In these cases, the langur stopping feeding on that particular branch is the end of the feeding bout.	This is reasonably unambiguous but sometimes a François' langur will move their body around the branch they are processing (especially when they are small and the branch is being held by another individual or is laying on the platform they are sitting on.
No Start	The video does not catch the start of a feeding bout.	It was sometimes difficult to catch the start of a feeding event while moving the camera into a good position to film. Where this is the case, No Start should be coded.
No End	The video cuts away before the end of a feeding bout.	Similar to No Start sometimes an individual would become completely obscured or the video would end before the end of a feeding bout. When this is the case, No End should be coded.
Pick Leaf/Leaves With Hand	The François' langur will pick a leaf or a bunch of leaves with their hand. This movement is a plucking motion just like in the gorillas, however as the langurs are much smaller than the gorillas, they will often only pluck a single leaf or part of a leaf off.	This is a very common behaviour and is generally easy to differentiate.
Strip Leaves With Hand	The François' langur will slide their hand across a branch section to remove many leaves from a length of branch. This movement is a sliding motion resulting in a small bunch of leaves being ripped off.	This motion is reasonably distinctive but is a much smaller action than seen in the gorillas. This motion is distinguished from Picking leaves as this motion involves the hand sliding across a section of a branch, not a plucking motion.
Pick Leaf/Leaves With Teeth	For this motion, the François' langurs will move the branch towards their mouth and pluck a leaf with their mouth.	This motion is a plucking motion whereas, stripping leaves/bark is a stripping motion. This is a very quick motion and often happens multiple times in quick succession.
Move Around Branch	As the François' langurs would often feed on a branch that was resting on one of the platforms in their enclosure, they sometimes would move their body to a new position around the branch. This behaviour is very rarely observed as most feeding bouts are performed while sat in one position.	As mentioned in the row for End Feeding Bout this could be confused with the feeding bout ending. This is not the case as the movement is usually minimal and they continue feeding on the same branch after performing it.
Rearrange Branch	A substantial rearrangement of the branch being eaten. A substantial rearrangement of a branch is a 180º flip of the entire branch to change the orientation of the branch. This is a large	This is reasonably rare behaviour and is delineated from the miscellaneous movements of the branch while conducting other feeding behaviours. What sets this behaviour apart is that the branch is

	deliberate motion and is not interrupted by other feeding behaviours. As the François' langurs were smaller the branches were usually longer than their bodies and placed on the ground to eat. If they pulled the branch into a new position when this was the case this should also be coded under this category.	substantially moved or rearranged without conducting a feeding behaviour.

Coding conventions:

All videos for both species were coded using the BORIS (Friard & Gamba, 2016), an open-source behavioural coding software. All behaviours were discreet, thus were assigned a code and did not overlap. Each behaviour was coded as a point event at the point the behaviour occurred. Specific care was taken to ensure that the order of behaviours was documented accurately, as this information is key to the analysis.

Intercoder Reliability

To test intercoder reliability another coder was given the coding manual, four videos from different sessions and coded the behaviours they observed. This represented 6.67% of the total data set. The coded behaviours from both observers were aligned based on time, with missing observations (where one observer didn't code a behaviour the other did code) included in the analysis. As the comparison dataset included missing values a Krippendorff's Alpha statistic was calculated to ensure that the coding scheme is valid.

2.2.3 Statistical Analysis:

Dataset:

As the dataset for both species was relatively small, the bouts with their starts and ends cut off were also included in the analysis to increase the number of observations. This should not be problematic for our study given that the analysis relies on the moment to moment transitions between discrete behaviours, with our analysis being restricted to identifying patterns in short sequences of behaviour.

General Descriptive data and statistics:

Before conducting any inferential statistical, tests for normality were run and identified that none of the measures could be considered normally distributed (with Shapiro-Wilkes tests all returning p values lower than 0.05) therefore non-parametric tests were used. To identify the broad differences between the species and individuals in their feeding behaviours, the bout lengths measured in the number of behaviours performed, the number of unique behaviours used in each feeding bout and the proportion of usage of the feeding behaviours was calculated for each bout. An independent samples Mann-Whitney U test was conducted to determine whether the two species differed in the mean length of feeding bouts, measured in number of feeding behaviours across a bout. To determine within species differences, separate Kruskal-Wallis tests were run for both species. To determine differences between species in the average number of unique behaviours used in each feeding bout by each individual an individual samples t-test was conducted. For each bout this value was calculated by counting the number of unique behaviours performed in each bout and an independent samples Mann-Whitney U test was run to identify between species differences. A Kruskal-Wallis test for each species was also run to identify within species differences. The proportion that each behaviour was used in a bout was calculated for all bouts and separate Kruskal-Wallis tests were taken for each species to identify differences between individuals of the same species in the usage of each of the feeding behaviours. These statistical tests were conducted at the 0.05 significance level. General Descriptive and inferential statistics were calculated using the software SPSS version 27.

Markov Chain Analysis:

To run the Markov chain analysis, we replicated relevant aspects of the methods used by Mielke and Carvalho, which were provided open-access (2022,preprint). Copies of the code used and the raw graphical outputs are available in Appendix A and Appendix B respectively. All Markov Chain Analysis was performed in the programming language R version 4.2.1 using R studio build 554, with functions taken from the github repository, supplied in the supplementary materials of Mielke and Carvalho (2022).

First, to calculate the *transition probabilities* between the different elements, the conditional probabilities of the appearance of the possible combinations of Antecedent and Consequent feeding behaviours was calculated from the list of behaviours in each bout, for all the bouts identified. This was done for each individual in our analysis. This resulted in a table of transition probabilities for each pair of antecedent and consequent elements, for each individual (Mielke & Carvalho, 2022).

To test the significance of these transitions the elements per individual, feeding bouts were randomised based on the frequency the elements were present in the natural dataset and the length of the bouts. 10000 randomisations were performed to create a probability distribution that could be compared to the measured values for each individual. The significance of the transition probabilities was determined at the 0.01 significance level, which in our case would translate into less than 100 of the 10000 generated probabilities being higher than the measured transition probabilities. The average expected probability of each of the transitions was calculated by calculating the mean of these generated probabilities and a measure of magnitude of deviation from the expected values was calculated by dividing the observed transition value with the expected value (Mielke & Carvalho, 2022). This method has the benefit of controlling for any differences in the frequency of unique techniques used between the two species. This is because the randomisation step directly shuffles the sequences of behaviours fed into the analysis, which means expected transition probabilities are calculated with respect to the number of unique behaviours observed in the sequences. Therefore, the fact that the langurs have a smaller repertoire of coded behaviours should not lower the chance of finding significant transitions compared with the gorillas who have a larger repertoire of behaviours.

It was necessary to check the robustness of our results due to the reasonably small sample sizes and prevalence of certain behaviours. This was done by bootstrapping, where 1000 subsets of each individuals datasets were extracted and the transition probabilities calculated from these subsets. The results of this were represented graphically with the x-axis denoting how often the antecedent elements within the transition bigrams existed in the individuals dataset and the y-axis denoting the range of the transition probabilities calculated using the bootstrap.

Transition networks help visualise transitions and identify how elements cluster together and can therefore help to identify strategies used by individuals while feeding. Differences in these networks and how elements cluster helps to identify differences between species and individuals. From the transition data, network plots were generated in R, using ggplot2's built in network drawing capabilities, which indicated significant transitions between elements and how these behaviours clustered. These plots help identify how feeding behaviours are linked into larger structures. They also help in identifying similarities and differences in approach taken by the different species and between individuals of the same species. Raw networks outputs can be found in Appendix B, as these networks were redrawn from the outputs generated in R to aid visualisation and help with comparisons between individuals.

When looking for hierarchical structure in behavioural sequences, one way of identifying if these higher order structures exist is to identify whether increased knowledge of the system enhances one's ability to predict elements in the sequence (Mielke & Carvalho, 2022). This is a key aspect of hierarchical structure in sequences. A prediction analysis was therefore run, based on adding more antecedent elements to determine whether increasing knowledge of the sequence makes it easier to predict the next behaviour. To do this transitions were calculated for ninety five percent of the bouts and these transitions were used to predict consequent elements in the five percent of bouts not calculated. This was repeated 1000 times for each of the bouts and the prediction accuracy was averaged. For the null model the prediction accuracy was based on the probability of the occurrence of elements in the dataset. For 1st, 2nd, 3rd and 4th order predictions combinations of one, two, three and four behavioural elements were used as antecedents respectively, to identify whether increasing the number of elements included increases the accuracy of predictions. Two different methods of prediction accuracy were used, the raw predictions based off of the transition probabilities calculated and a Naïve Bayes classifier (Mielke & Carvalho, 2022). The mean prediction accuracy for all elements and bouts were calculated at each level and these values are presented.

2.3 Results:

Intercoder Reliability

Results from the Krippendorff's Alpha statistic revealed an α = 0.8652 with 610 pairs of behaviours being included in the analysis. This α level reveals a high degree of agreement in coders assignment of behaviours.

Overall data collected

Table 4: Summary counts of behaviours and bouts for N = 6 western lowland gorillas

	Asante	Biddy	Lope	Oumbi	Ozala	Shufai
Number of Observed Bouts	43	129	98	178	99	143
Pick Leaf With Hand	118	190	107	196	136	118
Strip Leaves With Hand	55	197	68	158	84	119
Pick Leaf with teeth	335	877	316	629	707	238
Strip leaves with Teeth	39	249	117	224	227	70
Strip Bark with Teeth	72	148	389	614	364	142
Snap small branch off	30	30	85	147	39	21
Snap Large Branch off	6	22	30	56	29	15
Rearrange Branch	13	18	17	37	42	22
Total Number of Behaviours	668	1731	1129	2061	1628	745

Table 5: Summary counts of behaviours and bouts for N = 7 François' langurs

	Chow Chow	**Kaili**	**Lychee**	**Pak Choi**	**Shiitake**	**Shinji**	**Yalu**
Number of Bouts Observed	30	13	15	14	24	8	12
Pick Leaf With Hand	133	68	123	87	28	5	25
Strip Leaves With Hand	41	17	57	21	6	0	0
Pick Leaf with teeth	207	121	231	154	193	57	135
Move around Branch	1	2	2	0	1	0	5
Rearrange Branch	5	8	6	1	2	0	2
Total Behaviours observed	387	216	419	263	230	62	167

Tables 4 and 5 depict the number of individual behaviours observed in both species. Overall, more data was collected from the gorillas compared to the François' langurs. This was largely due to changes in how the keepers fed the langurs restricting the number of observations that were able to be collected. Owing to this, Move Around Branch and Rearrange Branch were very rarely observed. As feeding behaviours were recorded opportunistically, individuals were not evenly represented in our dataset. In the gorillas, Asante often fed in areas concealed from public view meaning less observations were collected. Incidentally very few bouts were observed for the François' langur Shinji, with fewer than 100 behaviours being observed. Due to this, Shinji was included in the descriptive and inferential statistics based on frequencies of individual behaviours but, as the Markov chain analysis requires bigrams to be calculated, they were excluded for this analysis.

2.3.1 General Descriptive and Inferential Statistics

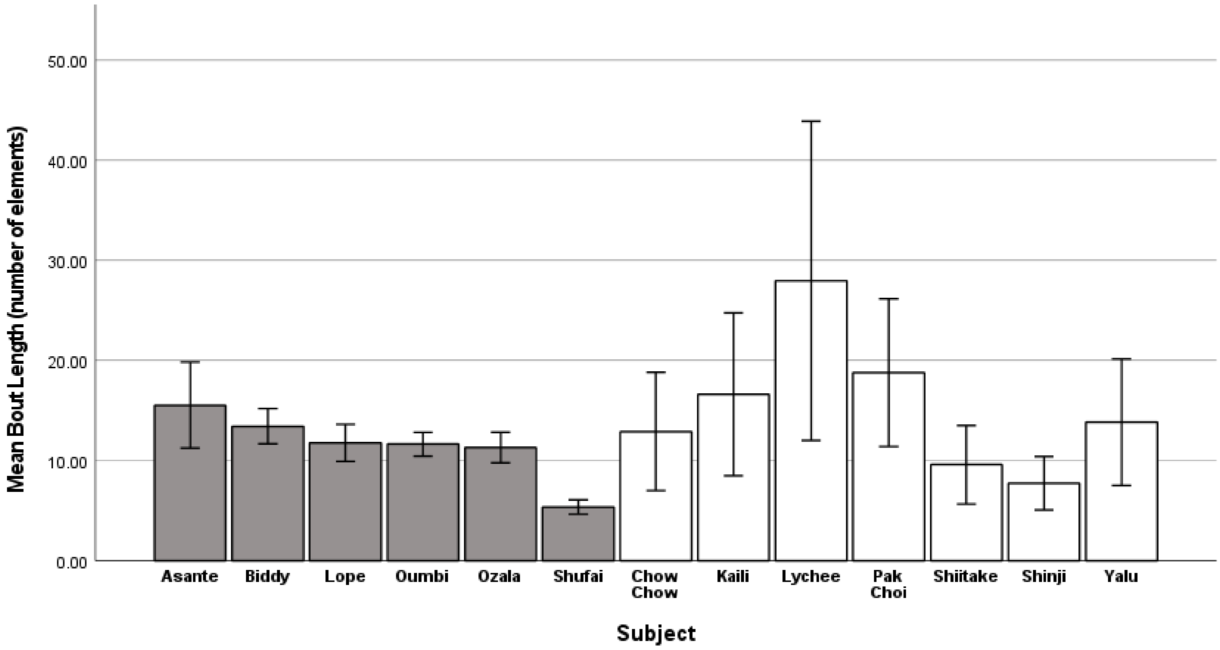


Figure 4: Mean bout lengths of individuals from both species. Grey bars = gorillas, White bars = François' langurs. Error bars depict standard error.

Figure 1 depicts the differences in average bout length between species and individuals. François' langurs feeding bouts were significantly longer (Mean= 15.03 SD= 17.08) compared to the gorillas (Mean = 10.94, SD= 9.16), U =2.160 , p = 0.031.

Regarding within species differences in bout lengths, there was significant variation in bout lengths of individual gorillas (H(5) = 98.865, p < 0.01). Bonferroni corrected Mann Whitney U tests were used to perform post hoc pairwise comparisons and these identified that Shufai's feeding bouts were significantly shorter than the feeding bouts of Ozala (p < 0.01), Oumbi (p < 0.01), Lope (p < 0.01), Biddy (p < 0.01) and Asante (p < 0.01). There was no significant difference found between the lengths of feeding bouts between the other individuals.

Among François' langurs, there was a significant difference between the bout lengths of individuals (H(6) = 15.628, p = 0.016). However after Bonferroni corrected Mann Whitney U tests were used to perform post hoc pairwise comparisons no differences between bout lengths retained significance.

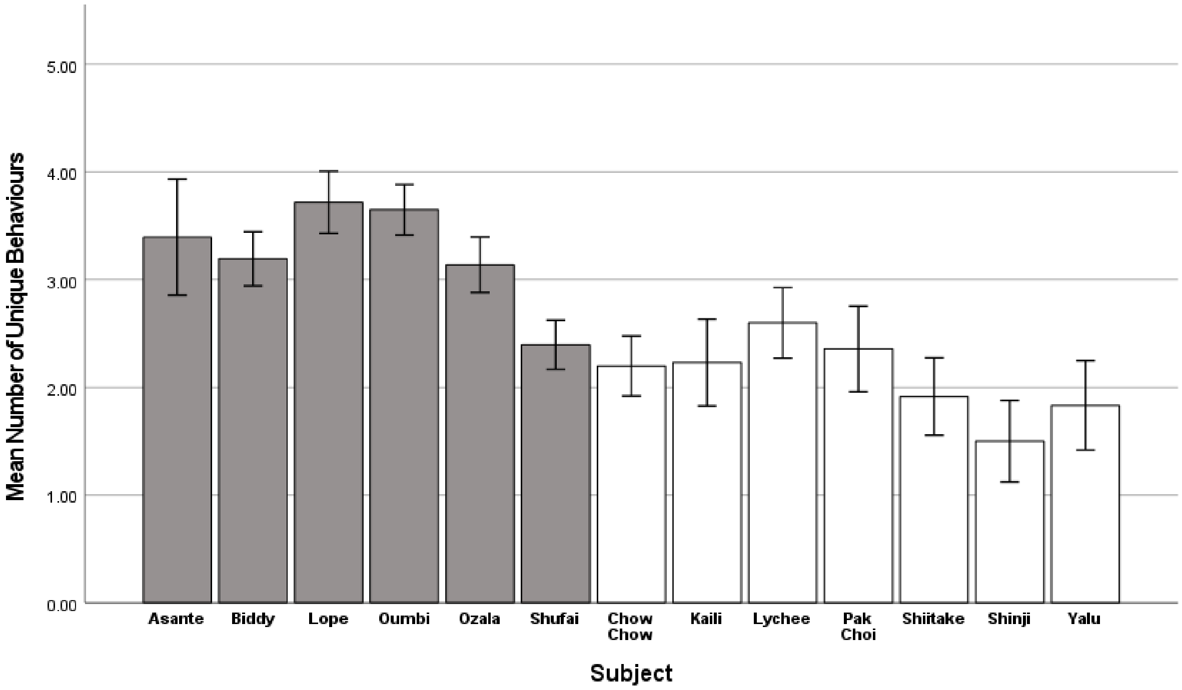


Figure 5: Mean number of unique behaviours of individuals from both species. Grey bars = gorillas, White bars = François' langurs. Error bars depict standard error.

As shown in Figure 2, the number of unique behaviours used by the gorillas (Mean = 3.22, SD= 1.55) was significantly larger than the number used by François' langurs (Mean = 2.12, SD= 0.79), U = -7.400, p < 0.001.

An analysis of within-species differences found that there was a significant difference between individual gorillas in the number of individually unique behaviours they used during feeding bouts (H(5) = 69.324, p < 0.001). Bonferroni corrected Mann Whitney U tests were used to perform post hoc pairwise comparisons and these identified that Shufai on average used less unique behaviours per bout compared to Asante (p < 0.01), Biddy (p < 0.01), Lope (p < 0.01), Oumbi (p < 0.01) and Ozala (p < 0.01). Ozala used significantly less unique behaviours compared to Oumbi (p = 0.002) and Lope (p = 0.002).

For the François' langurs, there was a significant difference between the number of individually unique behaviours used (H(6) = 15.594 , p = 0.016). Bonferroni corrected Mann Whitney U tests were used to perform post hoc pairwise comparisons and these identified that Shinji used significantly fewer unique behaviours on average during feeding bouts compared to Lychee (p= 0.032).

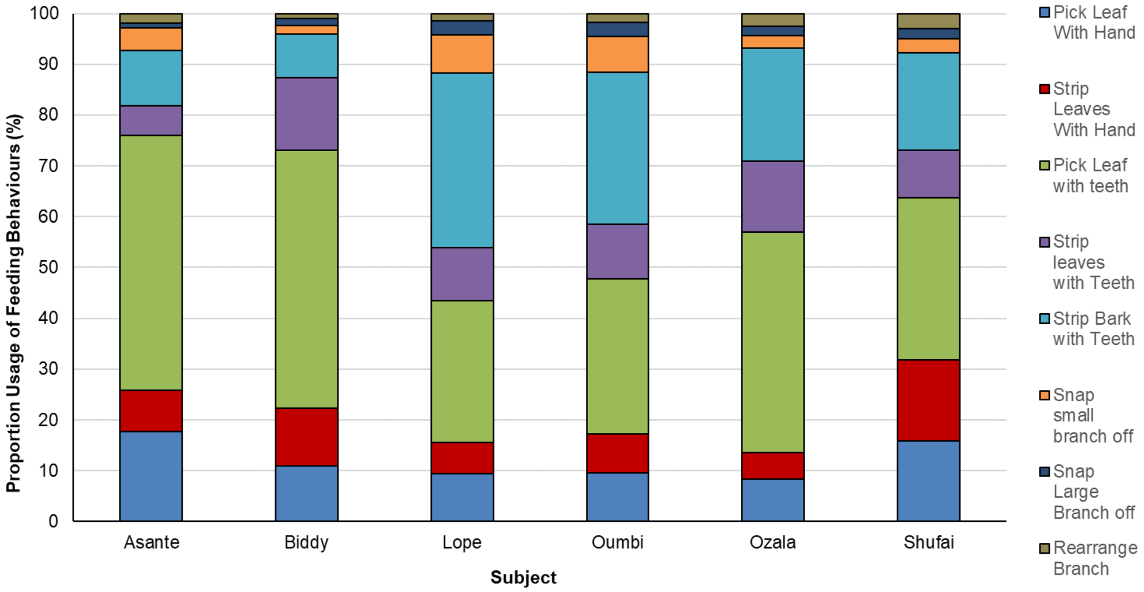


Figure 6: Stacked bar graph depicting the proportion usage of each element by individual captive western lowland gorillas (N = 6)

Figure 3 shows the overall percentages of each behaviours' usage across all bouts for gorillas (see Fig 4 for François' langurs). Kruskal Wallis tests with post-hoc Bonferroni adjusted pairwise Mann Whitney U tests were used for the different behaviours found that individual gorillas significantly differed in their usage of feeding behaviours, described below. The exception was for rearrange branches (H(5) = 8.534, p = 0.129). For brevity only significant comparisons will be mentioned, all other potential combinations were not significant.

For Pick Leaf With Hands (H(5) = 12.715, p = 0.026), Ozala’s usage was significantly lower than Shufai’s (p = 0.004).

For Strip Leaves With Hand (H(5) = 23.662, p < 0.01), Ozala’s usage of this behaviour was significantly lower than Shufai (p = 0.002), Biddy’s (p = 0.004) and Asante’s (p = 0.035).

For Pick Leaf With Teeth (H(5) = 38.740, p < 0.01) Lope’s usage of the behaviour was significantly lower than Ozala’s (p = 0.002), Biddy’s (p < 0.01) and Asante’s (p = 0.003). Shufai’s usage of this behaviour was significantly lower than Ozala’s (p = 0.031), Biddy’s (p = 0.001) and Asante’s (p= 0.023). Oumbi’s usage of the behaviour was significantly lower than Biddy’s (p = 0.012).

For Strip Leaves With Teeth (H(5) = 47.95, p < 0.01), Shufai’s usage was significantly lower than Oumbi’s (p < 0.01), Lope’s (p < 0.01), Ozala’s (p < 0.01) and Biddy’s (p < 0.01). Asante’s usage was significantly lower than Biddy’s (p = 0.005).

For Strip Bark With Teeth (H(5) = 81.625, p < 0.001), Biddy’s usage of this behaviour was significantly lower than Ozala’s (p< 0.01), Lope’s (p< 0.01) and Oumbi’s (p< 0.01). Asante’s usage was significantly lower than Lope’s (p<0.01), Oumbi’s (p = 0.004), and Ozala’s (p = 0.020). Shufai’s usage was significantly lower than Ozala’s (p = 0.014), Lope’s (p < 0.01) and Oumbi’s (p = 0.01). Ozala’s usage was significantly lower than Lope’s (p = 0.028).

For Snap Small Branch Off (H(5) = 53.988, p < 0.01), Shufai’s usage of the behaviour was significantly lower than Oumbi’s (p < 0.01) and Lope’s (p < 0.01). Ozala’s usage was significantly lower than Oumbi's (p < 0.01) and Lope's (p < 0.01). Biddys usage was significantly lower than Oumbi's (p = 0.02) and Lopes's (p < 0.01).

For Snap Large Branch Off (H(5) = 22.400, p < 0.01), Shufai's usage of this behaviour was significantly lower than Oumbi's (p < 0.001) and Lope's (p = 0.015).

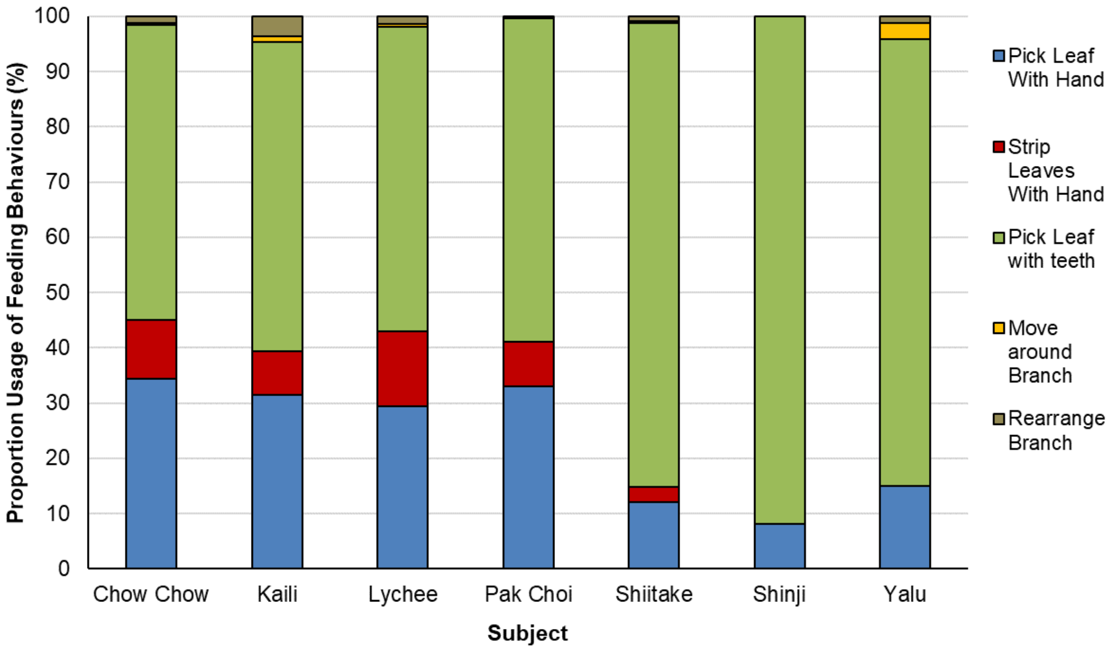


Figure 7: Stacked Bar Graph Depicting the Proportion usage of each element by individual François' langurs (N = 7)

Due to the extremely small number of observations made for Move Around Branch and Rearrange Branch these behaviours were excluded from comparisons in the langurs. Kruskal Wallis tests with post-hoc Bonferroni adjusted pairwise Mann Whitney U tests found that the François' langurs significantly differed in their usage of the feeding behaviours tested. For brevity only significant comparisons are mentioned.

For Pick Leaf With Teeth (H(6) = 27.953, p < 0.01), Lychee's usage of this behaviour was significantly lower than Shiitake's (p = 0.047) and Shinji's (p = 0.021). And Chow Chows usage of this behaviour was also significantly lower than Shiitake's (p = 0.011) and Shinji's (p = 0.010).

For Pick Leaf With Hands (H(6) = 19.716, p = 0.003), although the test was significant, after the Bonferroni correction no pairwise comparisons retained their significance.

For Strip Leaves With Hand (H(6) =21.172, p = 0.002), Lychee's usage of the behaviour was significantly higher than Shinji's (p= 0.027) and Yalu's (p= 0.006).

To summarise, the descriptive and inferential statistics show that François' langur feeding bouts were significantly longer than gorillas but the number of unique behaviours used in these bouts was, on average, less than the gorillas. Between individual François' langur's feeding bouts there was no statistically significant difference in the lengths of the feeding bouts between individuals. gorillas feeding bouts were all similar lengths except for the youngest in the group, the six year old male Shufai, whose feeding bout lengths were significantly shorter than all of the older gorillas. The number of unique behaviours used by François' langurs was also reasonably consistent, with the only significant difference being between the individual with the most unique behaviours per bout and the individual with the least. The number of unique behaviours used by the gorillas were also generally consistent. However, Shufai, the youngest individual, used significantly fewer unique behaviours during feeding bouts compared to all of the other individuals and Ozala, a 28 year old female with the second lowest number of behaviours per bout, used significantly fewer unique behaviours per bout on average than the two highest. The observation that François' langur feeding bouts contain significantly fewer unique feeding behaviours compared to gorillas shows that the François' langurs use a smaller repertoire of unique techniques during feeding bouts compared to the gorillas. As they use fewer types of behaviours, the complexity of the sequences of behaviours they use may therefore be more restrained than those produced by the gorillas. The within species observation that the youngest gorillas feeding bouts were significantly shorter than the adults and used significantly fewer behaviours may reflect a developmental difference in the feeding bouts performed by this individual.

When looking at the individual feeding behaviours, François' langurs did not significantly differ in their usage of Pick Leaf With Hands but differed in the other two behaviours tested. Lychee a sixteen year old female, was the individual that used Strip Leaves With Hand the most and used the behaviour significantly more than the two individuals that used it the least, Yalu a one year old female and Shinji a four year old male. This same individual as well as a 16 year old male named Chow Chow used Pick Leaf With Teeth significantly less than the two individuals that used it the most, the four year old male Shinji and the two year old female Shinji. As significant differences between behaviours was isolated to differences between some of the juveniles and some of the oldest individuals these differences could reflect differences in behavioural preferences related to development.

The gorillas differed significantly on all of the behaviours tested except for Rearrange Branch and showed a diversity of differences between individuals such that the average proportion of uses of these behaviours varied across the different gorillas. The variety of usage across the individual gorillas, in their preferences of the different behaviours gives a broad indication that the gorillas do not perform behaviours in feeding bouts uniformly and therefore differ in the techniques they prefer to use.

2.3.2 Markov Chain Analysis

Before conducting the analysis involving transitions, it was necessary to check the robustness of the transition statistics for each of the behaviours. Figures 5 and 6 depict the robustness plots for both species. These plots indicate that, for transition probabilities including rare elements, the range of transition probabilities is volatile in all individuals. This suggests that, for the gorillas, results including Rearrange Branches and Snap Large Branch

Off should be interpreted with caution. In the François langurs, results including Strip Leaves With Hands should be interpreted cautiously. Results including Move Around Branch and Rearrange Branch should be treated very cautiously due to the small number of observations.

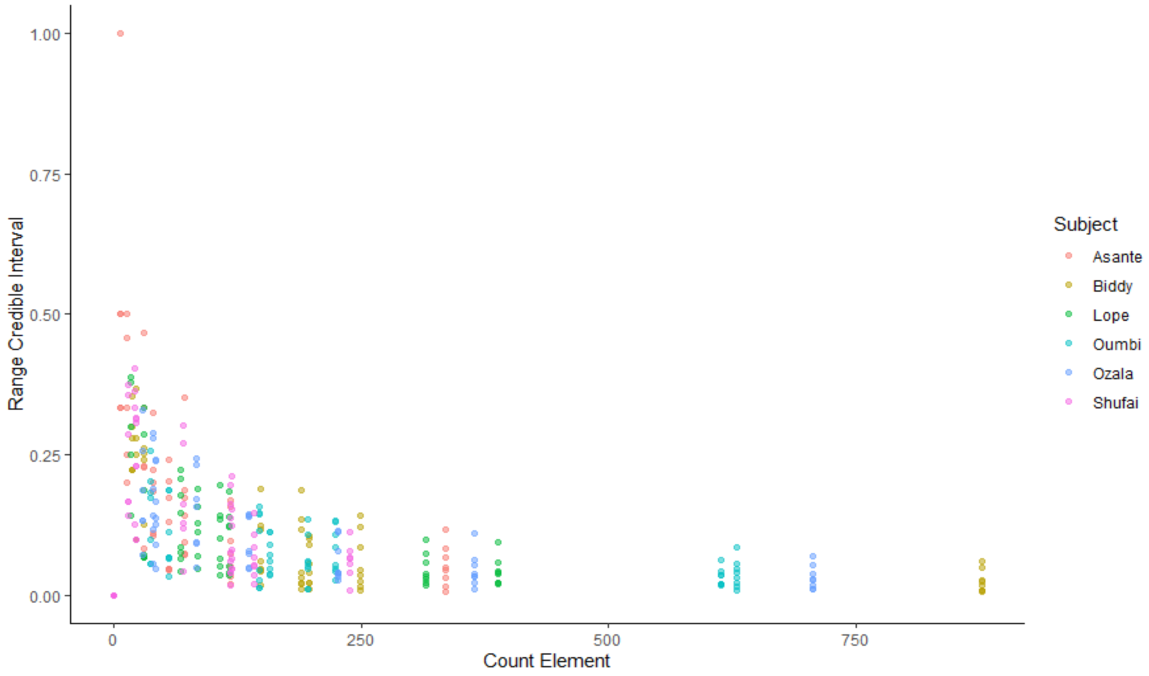


Figure 8: Graph to check robustness of gorillas data, created by generating a range of bootstrapped transition probabilities compared to the count of antecedent elements in bigrams

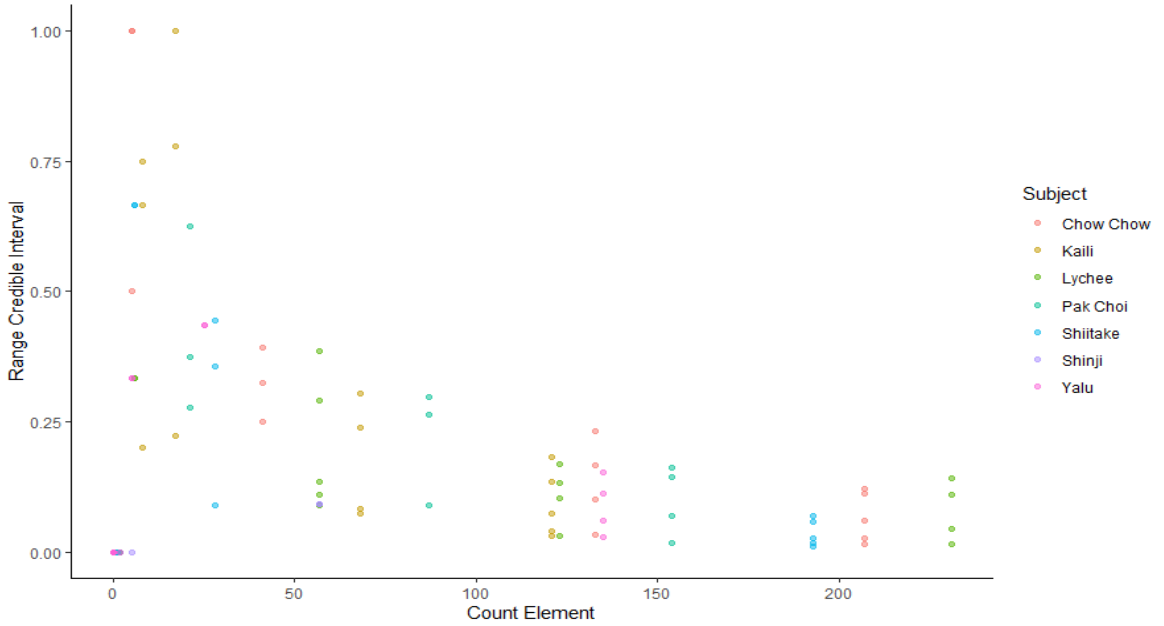


Figure 9: Graph to check robustness of François' langurs data, created by generating a range of bootstrapped transition probabilities compared to the count of antecedent elements in bigrams

Markov Transitions

Table 6: Increase in probabilities above expected values for antecedent and consequent behavioural elements in gorillas feeding bouts. Transitions that were not significant for any individuals are not listed. Significant transitions derived from the comparisons with expected values are highlighted, with magnitude being denoted in a gradient from green to yellow to red. Antecedents and consequent behaviours are highlighted grey to indicate significant transitions into the same behaviour.

ANTECEDENT	CONSEQUENT	Asante	Biddy	Lope	Oumbi	Ozala	Shufai
Pick Leaf With Hand	Pick Leaf With Hand	2.149	4.358	4.255	3.379	5.277	2.646
Pick Leaf With Hand	Snap Small Branch Off	1.711	1.912	1.75	1.275	2.712	1.469
Pick Leaf With Teeth	Pick Leaf With Teeth	1.341	1.397	2.133	1.774	1.498	1.727
Pick Leaf With Teeth	Strip Leaves With Teeth	1.276	1.139	1.25	1.45	1.115	1.5
Rearrange Branch	Snap Small Branch Off	3.5	8.538	1.709	4.325	3.042	6.8
Snap Large Branch Off	Snap Large Branch Off	23.857	2.8	1.4	1.732	1.991	1.743
Snap Small Branch Off	Strip Bark With Teeth	3.704	2.875	2.507	1.493	2.126	3.141
Snap Small Branch Off	Strip Leaves With Teeth	2.293	2.435	1.587	1.697	3.292	7.407
Strip Bark With Teeth	Strip Bark With Teeth	4.425	7.082	1.872	2.337	2.812	3.296
Strip Bark With Teeth	Rearrange Branch	2.474	2.882	1.4	1.444	1.5	2.357
Strip Leaves With Hand	Strip Leaves With Hand	4.37	2.136	6.424	4.289	2.47	3.165
Strip Leaves With Hand	Rearrange Branch	3.263	3.903	2.179	1.316	5.647	1.535
Strip Leaves With Hand	Snap Large Branch Off	2.333	2.059	1.84	1.111	3.056	1.167
Strip Leaves With Teeth	Snap Small Branch Off	2.467	1.615	2.621	1.958	1.906	3.936
Strip Leaves With Teeth	Strip Bark With Teeth	1.796	1.686	2	1.889	1.346	3.1
Strip Leaves With Teeth	Strip Leaves With Teeth	0.982	1.059	1.333	2.5	1.042	0.95

Table 6 shows that, in the gorillas, sixteen of a potential sixty four behavioural pairs significantly transitioned together in at least one of the observed gorillas. A 30 year old female, Asante showed the fewest significant transitions with only six significant transitions, whereas a 30 year old male, Oumbi showed the most with 13. All individuals perseverated on four distinct behaviours (with the behaviours significantly transitioning into themselves). These behaviours were Strip Leaves With Hand, Strip Bark With Teeth, Pick Leaf With Teeth, Pick Leaf With Hand. A significant transition shared between all individuals that did not involve perseverating on the same behaviour was when an individual snapped a small branch off and then stripped bark with their teeth. Although all individuals shared these transitions, each individual had patterns of significant transitions unique to them. Generally, significant transitions were observed in more than one individual although Ozala, a 28 year old female, was the only individual that significantly transitioned from stripping leaves with their hand and snaping large branches off. Oumbi, the 30 year old males, was also the only individual that significantly perseverated on stripping leaves with their teeth. The unique patterns of significant transitions for each individual potentially indicate that each individual uses a unique combination of processes to extract leaves and bark from branches.

François' Langurs

Table 7: Increase in probabilities above expected values for antecedent and consequent behavioural elements in François' langur Feeding Bouts. Transitions that were not significant for any individuals are not listed. Significant transitions derived from the comparisons with expected values are highlighted, with magnitude being denoted in a gradient from green to yellow to red. Antecedents and consequent behaviours are highlighted grey to indicate significant transitions into the same behaviour.

ANTECEDENT	CONSEQUENT	Chow Chow	Kaili	Lychee	Pak Choi	Shiitake	Yalu
Pick Leaf With Hand	Pick Leaf With Hand	1.73	1.702	1.873	1.906	2.718	2.84
Pick Leaf With Teeth	Pick Leaf With Teeth	1.344	1.226	1.347	1.358	1.043	1.072
Strip Leaves With Hand	Strip Leaves With Hand	3.298	8.108	3.933	5.921	0	0

Table 7 shows that, unlike the gorillas the François' langurs did not have any significant transitions beyond perseverating on the same behaviours. All individuals would repeatedly pick leaves with their hands and pick leaves with their teeth. All but the two youngest individuals perseverated when stripping leaves, with the association between repeating the stripping leaves with hand elements being much higher than expected.

Networks

Gorillas:

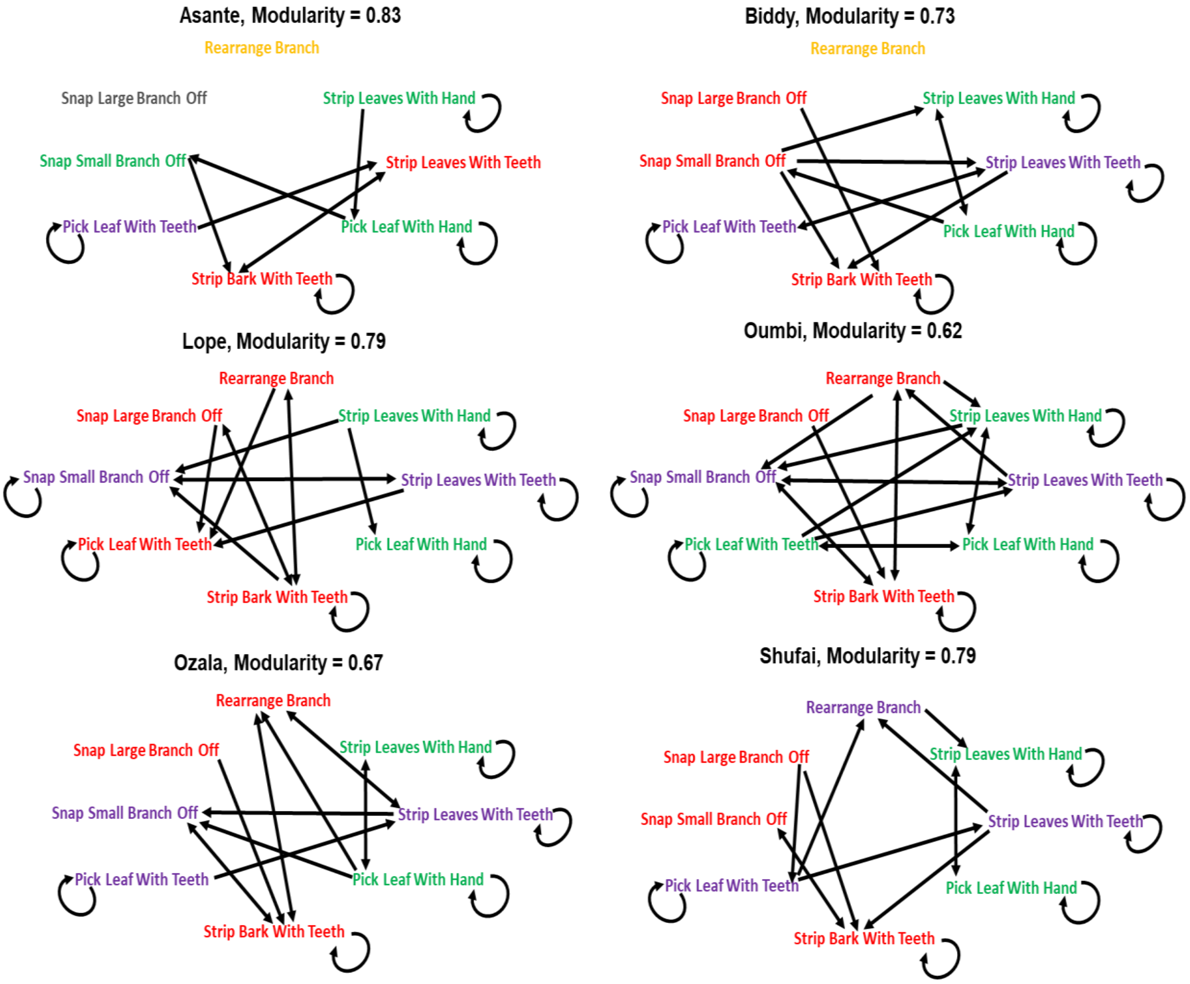


Figure 10: Network plots with unweighted edges for individual gorillas showing significant transitions between feeding behaviour elements. Colour Indicates cluster membership. Redrawn from output to aid clarity.

As shown in figure 7, the transition networks for the gorillas show that compared to the François' langurs (figure 8), they have more connections between behaviours beyond simple perseveration. Multiple behaviours cluster in the gorillas suggesting that certain behaviours are used in conjunction with each other indicating specific methods used during the processing of branches. High modularity scores greater than 0.6 suggest that these clustered behaviours were used in close conjunction with one and other compared to elements assigned to other clusters.

For all gorilla individuals, there were three of these clusters (excluding clusters from elements with no connections). These clusters showed some similarities, with the red cluster (see Figure 7) in Oumbi and Ozala being made up of the elements Strip Bark With Teeth, Rearrange Branch and Snap Large Branch Off. Lope’s red cluster was the same as Oumbi and Ozala but also included Pick Leaf With Teeth. In Shufai and Biddy, this red cluster was the same being made up of the elements Strip Bark With Teeth, Snap Small Branch off and Snap Large Branch Off. In Asante this Red Cluster on the other hand contained Strip Bark With Teeth and Strip Leaves With Teeth. In five of the six individuals this cluster contained the elements Strip Bark with Teeth and Snap Large Branch off.

As shown in Figure 7, The green cluster for Biddy, Lope, Ozala and Shufai contained the elements Pick Leaves with Hand and Strip Leaves with hand. This cluster also contained these elements in Oumbi and Asante but Oumbi’s green cluster also contained the Pick Leaf With Teeth Element, whereas Asante’s green cluster also contained the Snap Small Branch Off element. In all six individuals this cluster shared the Pick Leaf With Hand and Strip Leaves With Hands behaviours.

The purple cluster for Oumbi, Ozala and Lope contained the behaviours Strip Leaves With Teeth and Snap Small Branch Off, with Ozalas purple Cluster also containing Pick Leaves With Teeth. The purple clusters for both Biddy and Shufai contained the elements Strip Leaves with Teeth and Pick Leaves with Teeth, with Shufais also containing the behaviour Rearrange Branch. Asante’s purple cluster only contained the element Pick Leaf With Teeth. Five of the individuals shared the behaviour Strip Leaves With Teeth in this cluster and four of the individuals shared the behaviour Pick Leaves With Teeth. Clusters were not completely consistent however and individuals showed some variation in the assignment of behaviours.

François' Langurs:

Figure 11: Network plots for individual François' langurs, with unweighted edges showing transitions between feeding elements. Colour Indicates cluster membership. As these were technically not networks and could not be generated using the code, these were drawn directly.

Similar to the raw transitions in table 7, Figure 8 reveals that the transition networks for François' langurs identify that individuals perseverate on two or three behaviours, with no significant relationship between other elements. All of the observed behaviours were clustered into their own group as they had no interconnecting nodes, which shows that the individual behaviours were not strongly connected to one and other in structures beyond the repeating of the same elements.

Prediction Accuracy

Table 8: Prediction Accuracy of consequent elements in captive gorilla feeding bouts based on antecedent elements at different levels, where level is the number of antecedent elements used by the models. The basic transition probability distributions and a naïve bayes model were used.

		INDIVIDUAL GORILLAS PREDICTION ACCURACIES					
LEARNING MODEL	**Level**	**Asante**	**Biddy**	**Lope**	**Oumbi**	**Ozala**	**Shufai**
PROBABILITY DISTRIBUTION ACCURACY	0	0.282	0.346	0.273	0.229	0.242	0.100
	1	0.343	0.476	0.382	0.406	0.362	0.207
	2	0.454	0.613	0.561	0.556	0.489	0.223
	3	0.447	0.643	0.604	0.596	0.495	0.231
	4	0.443	0.682	0.642	0.605	0.483	0.220
ACCURACY NAIVE BAYES	0	0.436	0.543	0.509	0.119	0.388	0.292
	1	0.551	0.657	0.585	0.559	0.526	0.542
	2	0.547	0.641	0.646	0.627	0.565	0.526
	3	0.569	0.621	0.628	0.651	0.560	0.667
	4	0.565	0.623	0.590	0.629	0.527	0.692

In François' langurs, the only transition probabilities that were significant were perseverating on the same behaviour, therefore running the prediction accuracy analysis was neither possible nor informative. However, as the gorillas showed significant transitions across a variety of behaviours, identifying whether these transitions generate hierarchical structures is an important aspect when understanding if these sequences translate to higher-order structure. As shown in table 8, for all individuals, increasing the number of antecedent elements increased prediction accuracy. When using the transition probability distribution for each individual, Asante showed increased prediction accuracy with up to two antecedent elements. Ozala and Shufai showed increased prediction accuracy up to three antecedent elements. Biddy, Lope and Oumbi also increased prediction accuracy up to four antecedent elements. Shufai's prediction accuracies were generally lower when compared to the older group members when the raw prediction accuracy learning model was used, potentially suggesting that this juveniles feeding bouts contained more random variation compared to the adult gorillas. Using the Naïve Bayes method, accuracy of prediction increased for

Asante, Biddy and Shufai when there was one antecedent element. Prediction accuracy increased for Lope, Oumbi and Ozala with up to two antecedent elements. Shufai's prediction accuracy was comparable to the older group members when the Naïve Bayes model was used. Although the two methods generate slightly different results, in both cases increasing the number of antecedents increased prediction accuracy up to a point.

2.4 Discussion:

Results from the current study revealed that François' langur feeding bouts were significantly longer than those of gorillas but simpler and less idiosyncratic in structure. In the broadest sense, this is revealed by evidence that the number of unique behaviours used in each bout for François' langurs was significantly lower than the gorillas. Crucially, transition probabilities and their associated networks revealed that, unlike gorillas, François' langurs did not show higher order structure in combining behavioural elements as the only significant transitions were the transitions between the same behaviours (i.e. repeating the behaviour in a loop). The three repeated behaviours by François' langurs were to pick leaves with their hand, pick leaves with their teeth or strip leaves with their hands. The approach taken by the langurs therefore appears to be to perseverate on the same behaviour and then switch to a different behaviour and perseverate with that too. The youngest two langurs differed from the older individuals, as they did not significantly perseverate with stripping leaves with their hands, with the oldest of the two youngest only rarely using the behaviour in isolation and the youngest not using the behaviour at all.

Although gorillas performed significantly shorter feeding bouts, their feeding sequences were in line with the hypotheses of being more complex in regard to their sequential structure. Looking at the usage of behaviours, gorillas used significantly more unique behaviours per bout and individuals differed in the proportion usage of these behaviours. A closer examination of the usage of these behaviours by generating transition probabilities identified that gorillas, like François' langurs, perseverated on a number of behaviours, mainly those involved with picking and stripping leaves or bark with teeth or hands. However, gorillas also transitioned between behaviours beyond simple perseveration. Analysing the transition networks, as depicted in figure 7, identified that each individual had three clusters of behaviours (depicted in green, red and purple in the figure). The green cluster included the use of hands to pick and strip leaves, this cluster could be seen as the hand focused cluster. The red cluster included stripping bark with teeth in all cases so can be seen as the bark stripping cluster. The purple cluster varied more but always included stripping leaves with teeth so can be referred to as the teeth focused cluster. Due to the high modularity in the networks these clusters potentially suggest different approaches, which could be focussed on specific aspects of the feeding task.

Taking the stripping bark cluster as an example, qualitative observations indicated that stripping bark was most often left to the end once the leaves had been removed. The clusters suggest that a number of ‘branch processing’ steps are significantly associated with the stripping of bark in most individuals, such as snapping branches off and rearranging branches. These behaviours were often used to break the branch down into a short straight length that could easily and efficiently be stripped of all the bark without obstruction from small or large protrusions. The other two clusters are likely similarly context specific and potentially help to remove leaves efficiently in similar ways. Although there was reasonably broad agreement in the clusters individuals did differ in the use of behaviours and how they were connected, potentially indicating variation in individuals techniques. To test if these observations translated to hierarchical structure in their feeding bouts, we used prediction accuracy learning models and, although there was some variation between individuals and the models used, the overall trend showed that increasing the number of antecedent elements increased prediction accuracy between two and four antecedent elements. This analysis indicated that behaviours within feeding bouts were structured in sequence.

The results from this study support our hypothesis that gorillas have more complex structure to their feeding bouts compared to François’ langurs. The François’ langurs were found to perseverate on the same two or three feeding behaviours. By contrast, although the gorillas, often perseverated on the same behaviour, they showed significant transitions between different behaviours and the transition networks revealed that these clustered into distinct techniques. The increased prediction accuracy when the knowledge of antecedent elements increased provides further evidence that feeding bouts were structured hierarchically into more complex structures in all gorillas.

Although the hierarchical structures observed may indicate enhanced sequence learning abilities in the gorillas compared to the François' langurs it is also important to consider other factors that may have led to the differences in the observed behaviours. One of these factors is that the François' langurs were substantially smaller and weaker than the gorillas and therefore some behaviours involving major manipulations of the branches, such as snapping branches, may have been prohibitive and therefore constrained the potential behaviours that the langurs could perform in comparison to the gorillas. Relatedly the langurs would also not actively feed on the bark of the branches, which may again be due to physiological constraints, so the behaviours they performed were restricted to those related to removing leaves. The langurs were also supplied the branches slightly differently to the gorillas, with them first needing to pull the branches through the mesh of their enclosure. This may have resulted in the branches being more uniform than those provided to the gorillas and, although these branches had side branches like those presented to the gorillas, their more uniform shape may have required less processing when compared to the branches provided to the gorillas. In totality these constraint may have limited the variety of manipulations that were necessary for the langurs to perform on the branches to effectively feed and therefore resulted in limited opportunities for more elaborate sequences to be observed. As this was an observational study it is difficult to know how these factors influenced the differences observed between the species feeding behaviours.

It would also be erroneous to assume from these findings that the hierarchical organisation of behaviours observed in the gorillas was entirely due to a specific, elaborated hierarchical strategy on the part of the gorillas themselves. An important consideration is that the only possible actions, once leaves had been removed from a branch, was to remove the remaining bark, meaning that the final behaviours recorded in a bout would almost certainly be those involved in processing the remaining bark. Behaviours associated with bark stripping would therefore naturally cluster together at the end of feeding bouts once leaves had been removed and, without this context, this regular sequence could be seen as a sequentially based strategy on the part of the actor. Considering the specifics of the environment and the task itself can also provide alternative explanations related to the cognition that may be generating the observed behaviours. The evidence presented of hierarchical organised feeding behaviours in the gorillas may naturally lead to the hypothesis that an underlying sequence learning process, which deals with hierarchical organisation of behaviours, is needed to generate the strings of behaviours observed here. However, if one considers how the branch changes throughout the task an alternative hypothesis is that, at the start of the task the leaves are the primary affordance presented to the gorilla, so feeding on these is the natural starting point, as leaves are removed the bark becomes a more prevalent affordance to the gorilla, facilitating a change from feeding on the leaves to feeding on the bark. In this scenario a reliable string of behaviours would result and behaviours would cluster into specific strategies, with clusters associated with behaviours used in leaf eating and those used in bark eating. However, this would crucially arise from the specific interaction with the task as much as cognition on the part of the actor. This explanation draws from an embodied view of cognition (A. Wilson & Golonka, 2013), which provides an alternative cognitive account for the findings that does not necessarily involve hierarchical processing in the brain of the actor. Controlled experiments would be required to unravel the specific generative mechanisms underlying the organisation of the gorillas feeding behaviours in this and similar tasks.

It was predicted that the learning of feeding behaviours occurs socially in both species. The evidence presented here does not provide clear evidence for or against this prediction. All of the François' langurs used the same feeding behaviours at similar frequencies, particularly when looking at the oldest individuals, who did not differ in their use of the techniques and all used the same perseveration strategy with the same behaviours (treatment of the results for the youngest individuals will be discussed in relation to the final prediction). However, the simplicity of the feeding strategy and the small number of observed behaviours used by the langurs may mean that group-level similarity is to be expected even outside of social learning methods. The evidence in the gorillas is mixed, as individuals significantly differed in the individual behaviours they used in bouts and showed differences in the transition probabilities and cluster assignments of some of the behaviours. However, the clusters identified showed considerable similarity, which could indicate that these behaviours were learnt socially to some extent and modified at the individual level with experience. However, an alternative explanation as to why the clusters are similar could be that the behaviours are naturally likely to be associated. For example, movements involving removing leaves with hands, either by stripping or picking, could naturally flow together as they require similar movements with the same body parts. To help identify evidence of social transmission, further analysis should be conducted on different gorilla groups to identify between group variations in approach.

It was also hypothesised that these skills develop across ontogeny, such that juveniles will exhibit less complex feeding bouts as compared to older individuals. There was some evidence for this in the François' langurs, as the two youngest individuals never or rarely used the strip leaves with hand technique and there was no significant perseveration with this technique as seen in the older individuals. This suggests that these individuals have not yet developed this technique beyond rarely using it randomly during feeding bouts. Potentially, this could suggest that the learning of the individual feeding behaviours must be refined during development. In the gorillas the evidence is less clear. There was only one juvenile in the gorilla group and, similar to the older gorillas, the three distinct clusters were present in the juveniles feeding bouts. However, during the prediction accuracy, although the predictions increased with more antecedent elements, the prediction accuracy was lower when using the raw probability distribution compared to the adults. This may suggest that, although these clusters appeared and there was evidence of hierarchical structure observed, the juveniles feeding bouts contained more randomness. However, the Naïve Bayes prediction accuracies for the juvenile were similar to those of the adults making this interpretation less robust. Interesting to note, is that the juvenile feeding bouts were significantly shorter than the adults, which may suggest that the clusters identified here are only one level of complexity and that the higher order sequences of behaviours during longer feeding bouts are still yet to be learned. Investigating these higher order sequences is beyond the scope of the present study as Markov Chain Analysis is best equipped to identify moment by moment sequences of behaviour across short spans. Analysis that incorporates both descriptions of higher order sequences of behaviours as well as the moment to moment sequences can bridge this gap and provide insight into sequences of behaviours at different resolutions.

Although gorillas and François' langurs have never been directly compared with respect to feeding behaviours, the species level differences observed in this study are consistent with the existing literature for each species. The previously described studies on gorillas identified that gorillas showed consistent sequences of behaviour when processing difficult to feed on plants (Byrne et al., 2001; Byrne & Byrne, 1993; Neufuss et al., 2019) and even when processing plants without protections (Neufuss et al., 2019). These previous studies have primarily focussed on documenting the process level feeding techniques of gorillas in detail. This study differs however in that it identified structure in the moment to moment feeding behaviours of the gorillas with the aid of a Markov chain approach (Mielke & Carvalho, 2022, preprint). This study has identified sequential structure in the moment to moment feeding behaviours of gorillas at a finer scale. Taking these results together suggests that gorillas may learn and perform structured behavioural sequences at both scales. As the focus on manual ability has primarily focussed on the great apes and tool use (Byrne, 2004), the data presented here is some of the first of its kind in a monkey species, as previous studies have generally focussed on the acquisition of knowledge related to the types and location of foods and the development of individual behaviours (Hauser, 1993; C. Huang et al., 2008; Rapaport & Brown, 2008).

The indication that the François' langurs use a very simple strategy of perseverating on a few feeding behaviours when extracting leaves on branches suggests that, compared to gorillas, they do not form more complex sequences to facilitate their feeding. It should be noted though that the technique of perseverating on a single behaviour by the langurs could be a reasonably efficient and yet computationally conservative way of feeding on branches with leaves. Allowing them to feed effectively without requiring energy intensive cognitive resources. This would be in line with the extractive foraging hypothesis (Parker, 2015), which indicates that species that rely on energy rich food items that require more complex food processing steps, compared to browse feeding, will have evolved enhanced cognitive capacities to deal with the added challenges of feeding on these food items. Compared to omnivorous species, langurs predominantly feed on leaves and therefore they may not need to develop more complex feeding patterns to effectively feed. In fact, due to the energy constraints of feeding predominantly on leaves, energetically intensive cognitive abilities may even be selected against (DeCasien et al., 2017). If this is true, across evolutionary relevant spans of time, selection for more complex cognitive faculties aimed at feeding more efficiently would not occur. However, sequence complexity is not the only source of complexity in manual actions and although the langurs did not exhibit complex sequential structure in their feeding bouts, the behaviours themselves may require sophisticated cognitive features not evaluated in this experiment. For example, as we used reasonably broad categories to delineate different behaviours there may be more subtle characteristics of the feeding behaviours involving hand eye coordination and control of hand movements that are unable to be evaluated here. So, although these results are suggestive of the feeding behaviours of langurs being less complex in their sequential structure than those performed by the gorillas, this study does not necessarily provide evidence that langurs lack complex cognition more generally.

Gorillas are also generally folivorous so, based on the extractive foraging hypothesis (Parker, 2015), one may initially predict that their feeding bouts would be similarly lacking in sequential complexity. However, fruits and other foods are seasonally important aspects of their diet, meaning that the cognitive capacities necessary for more complex sequential behaviours used in extractive foraging were likely selected for in gorillas (Fuh et al., 2022). Also, due to their increased physical size compared to most primates the calories required to survive necessitates that they feed on larger volumes of food, particularly in the case of leaves and bark which contain relatively few calories compared to other food sources. This is particularly the case in comparison to the langurs, which have evolved foregut fermentation (Stewart et al., 1987), which may allow them to extract more calories from leaves compared to gorillas. Browse feeding is generally considered a simple form of feeding, as the food source is abundant and removing leaves from branches is a simple task. However, selection for more efficient feeding methods that require more complex behavioural sequences would potentially be important for gorillas compared to other folivorous primates. As developing feeding strategies involving more complex behavioural sequences may ensure that enough calories are eaten, even when the food available does not require specialised manipulations to access. The fact that we identified hierarchical structure in gorilla feeding behaviours when eating branches, whereas not in the langurs, may suggest that the development of sequence learning could be as important in increasing the efficiency of their feeding, as it is for accessing hard to extract foods. Although, as previously discussed, other generative mechanisms may be involved in these behavioural differences so these results should be interpreted with this in mind.

The observation that the youngest François’ langurs did not exhibit one of the feeding behaviours used by the adults fits with the existing evidence on the ontogeny of feeding behaviours in primates that suggests these behaviours must be learnt across development

(Hauser, 1993). Anecdotally, the youngest female, who was one year of age while the study was being conducted, would very often feed at the side of her mother, potentially supporting the role of vertical learning from mother and child, which plays an important role in other primate species (Jaeggi et al., 2010; van de Waal et al., 2014). Although our results regarding the gorillas are mixed, it should be noted that the juvenile gorilla was six years old during this study, which is approaching the end of infancy and moving into adolescence (Bray et al., 2018). It is therefore potentially unsurprising that this juvenile has already learned the sequences observed in the adults. Previous research has identified that in chimpanzees and gorillas, the feeding behaviours observed in adulthood are relatively quickly learned and almost adultlike around the time of weening (Bray et al., 2018; Nowell & Fletcher, 2008). These moment to moment physical sequences may therefore be learnt reasonably early in development.

When more complex behaviours have been studied the effective development of tool use skills took much longer to learn and become adept with (Carvajal & Schuppli, 2022; Estienne et al., 2019). In these studies, the behavioural elements necessary to perform the correct tool use were learned much earlier and putting them together to form the overall tool use sequence took substantially longer. One of the results relating to the juvenile in our study was that his feeding bouts were substantially shorter than those performed by adults. This could be because the moment to moment sequences captured in this study have already been learnt by this individual, but putting these sequences together into even larger structures may be beyond his grasp. A recent study investigating the development of hierarchical action sequences in humans identified that success at a main goal in a task with subgoals improved with age between the ages of three and five (Schröer et al., 2021). Viewing the clusters observed here as analogous to subgoals in larger processes, it may be that similar developmental processes occur in both species. Investigating this would require the use of techniques that can interrogate the development of overall sequence structures, beyond what Markov chain analysis is capable of. Combining a number of techniques that facilitate this would be a natural progression beyond this study. Alternatively, it could also reflect differences in attentional resources, with Shufai being more likely to become distracted by other factors in the environment while feeding than the older group members and therefore perform shorter sequences. It may also be the case that there are explanations for this difference unrelated to cognition. Being the smallest gorilla meant Shufai was also low ranking, with the two other males often aggressing towards him during feeding and competing for food. This may have meant that Shufai was left with only smaller, less desirable, branches to feed on, which would therefore need fewer behaviours to process. As this was an observational study disentangling which of these factors is relevant is difficult and would require more controlled conditions than those available.

Assessing these findings against previous theories related to sequence learning in primates more generally, the more complex structures identified in the sequences of gorillas compared to the François' langurs falls in line with what would be predicted based on the rapid evolution of the cerebellum observed in great apes and humans (Barton & Venditti, 2014; Vandervert, 2018). The ability to develop these sequences may have been selected for in the ancestors of great apes to increase their ability to innovate manual sequences, resulting in more complex action sequences that aided survival. This study has identified that, compared to a monkey species feeding on a similar food item, gorillas performed more complex, hierarchically organised sequences to aid in extracting food from their environment. The development of these sequence learning abilities may therefore be a feature that sets apart the great apes from the other primates. However, as this is a small study with only two species, further testing of this kind would provide a firmer basis to assess this. The Markov chain method used here provides a useful framework for future investigation that can provide a basis for directly comparing the structure of behavioural sequences produced by primates across a variety of behavioural contexts. Using this approach to investigate the grammars of action (Pastra & Aloimonos, 2012) involved in numerous contexts could provide a uniform approach to investigate commonalities and differences in the sequential structure of behaviours between species.

Identifying the existence of hierarchical structures in manual action sequences also has potential relevance in understanding the evolution of language in humans. Due to hierarchical processing's central importance in language, identifying where sequence processing is most likely to be important can provide insight into the challenges that would have selected for enhanced sequence cognition in the course of primate evolution. The use of gestures in communication has been documented in the great apes (Genty et al., 2014; Pollick & de Waal, 2007) with their use showing intentionality (Cartmill & Byrne, 2010) and flexibility (Pollick & de Waal, 2007) which are important aspects of language. These findings have been used as evidence of the gestural theory of language origins, which suggests that gestures were an initial precursor for language in our own lineage (Armstrong, 2008). Therefore, understanding whether there are links between communicative sequences involving manual action and manual sequence learning capacities in other tasks, such as foraging and tool use, would help establish whether sequence learning abilities are likely to have enhanced these precursor gestural communication systems. Providing insight into whether sequential processing involved in forming communicative sequences of gestures, as well as manual sequences involved in foraging behaviours, co-evolved and share common learning processes in the brain. Neurophysiological links between tool use and language related areas of the brain have already been documented in both humans and in other primates (Higuchi et al., 2009; Thibault et al., 2021), which provides evidence that there is a link between the mental processes observed in language and in other physical domains. A suggestion for these findings is that the common factor between these domains is the ability to hierarchically organise behaviours into sequences (Steele et al., 2012). Therefore, identifying whether similar structures are seen in the manual and communicative sequences performed by primates is an important step in determining at what point in our evolution these abilities got exapted for use in other domains.

In our experiment we identified evidence that the sequences of feeding behaviours used by the gorillas shows hierarchical structure, whereas the langurs feeding behaviours didn’t. If similar organisational principals are shared across the domains of communication and manipulative sequences, it would be reasonable to predict that similar sequential structures may be present in the gestural communication of gorillas. Gorillas, like the other great apes, use a large range of gestures to communicate and these gestures are intentional and used flexibly (Genty et al., 2009). However, no specific work on gestural communication has been performed on langurs and evidence for intentional gestural communication in monkeys is scarcer than in the great apes. However, recent research on red capped mangabeys (Schel et al., 2022), bonnet macaques (Gupta & Sinha, 2019) and olive baboons (Molesti et al., 2020) suggests that intentional gestural communication does occur in monkeys, although the repertoires and amount of flexibility seems to be lower (Schel et al., 2022). The existence of gestural communication in primates beyond the apes suggests that gestural communication may be more common in primates than previously thought, however, the difference in flexibility and repertoire size may suggest that their use is less adaptable than in apes. Research on gestural sequences in apes does not suggest that structured combinations of gestures are used regularly in communicative contexts, beyond repetitions of a gesture when the recipient does not initially respond (Hobaiter & Byrne, 2011) or instances where sequences of redundant gestures are used by younger individuals until they achieve the desired response (Pika et al., 2003). Research specifically on gorillas finds that gestural sequences don’t show evidence of sequence structure during communicative bouts (Genty & Byrne, 2010), which may indicate that processes involved in learning structured sequences during feeding behaviours are not employed when learning their gestural communication system. As this appears to be true of the great apes more generally (Byrne et al., 2017), and there is evidence that great apes can perform hierarchically structured manual tasks (Hayashi & Takeshita, 2022), this may suggest a limited role of sequence processing in the early evolution of the gestural aspects of primate communication systems. Although the use of gestures may have played an important role in the evolution of some aspects of language in humans, such as intentionality and flexible use of elements (Prieur et al., 2020), the absence of adult organised gestural sequences suggests a limited role in the evolution of language relevant sequence learning processes.

However, as this is just an observational study the generative mechanisms underlying the feeding behaviours of the gorillas cannot be inferred and therefore substantial further work is necessary to unpick the roles different aspects of behaviour may have had in facilitating the evolution of human language. It would be useful then if more work was conducted on the sequential use of behaviours across a breadth of activities in a wider range of primates, to identify which activities exhibit evidence of hierarchical structure and which species are more likely to exhibit hierarchical sequences of behaviours when performing these activities. As this will help elucidate which tasks may require specific sequence learning abilities, while identifying which species are most likely to be more capable of performing tasks where sequence learning is required. Coupling this with controlled experimental studies that provide insight into the cognitive processes involved in these tasks could substantially improve our understanding of the evolution of sequence learning abilities in humans and the context in which these abilities are likely to have evolve.

Chapter 3: Investigating Manual Sequence Learning in François' Langurs (*Trachypithecus françoisi*) and Black Headed Spider Monkeys (*Ateles fusciceps*) Using A Novel Puzzle Box Task

3.1 Introduction

The study described in the previous chapter used observations of natural behaviours, exhibited by the two species studied, to identify differences between sequences of behaviours used while feeding. However, observational studies of this kind are limited in providing insight regarding how these skills are learnt and what specifically is being learnt to aid in task completion. An important follow up is to therefore use experimental approaches, to identify how different species learn the behaviours necessary to efficiently perform sequential behaviours. The relevance of understanding how other species differ in these learning processes is that it can provide insights into how other species are differently adapted to survive in their environments. It also has the potential to inform us about differences that are relevant to humans' unique cognitive abilities. A cross species review of sequence learning data performed by Ghirlanda et al. (2017) identified that compared to humans other animals, including two species of monkey, failed to discriminate sequences longer than three elements unless they had extensive training. Humans on the other hand are able to learn to distinguish sequences of up to eight elements or longer in fewer than ten trials (Ghirlanda et al., 2017). Although the experimental set ups reviewed may have been biased towards humans, the stark contrast potentially suggests that humans have evolved enhanced sequence learning abilities compared to other animals. These enhanced sequence learning abilities may be a fundamental cognitive faculty that allows humans to develop complex cultural knowledge, language and tool use (Stout & Chaminade, 2012).

To investigate this further, understanding sequence learning abilities in non-human primates can provide insight into the evolution of these abilities in humans, as identifying species differences in these abilities can indicate important evolutionary pressures that may have selected for enhancements in sequence learning abilities. The cerebellum is an important brain region involved in the learning of sequences, as this brain region is arranged to form internal representational models of repetitive structures in events (Leggio & Molinari, 2015). Cross species comparisons, between primate species investigating the evolution of cerebellum size, have identified that this brain region has shown enhanced expansion in the great apes and humans in recent evolutionary history. This finding suggests that humans and the great apes have evolved enhanced sequence learning abilities compared to other primates (Barton & Venditti, 2014). Therefore, it is important to clarify differences in primate species' sequence learning abilities using behavioural experiments, as a way of helping establish how these abilities evolved differently across the primate order.

In primates, studies aiming to test their ability to learn and develop behavioural sequences have been conducted using several experimental paradigms. These have been reviewed more extensively in chapter 1, so will only be briefly summarised here. Sequence learning experiments conducted on great apes have identified that great apes are able to sequentially use tools (Lonsdorf et al., 2009; Martin-Ordas et al., 2012; Tecwyn et al., 2012) and complete tasks involving the comprehension and learning of visual and auditory sequences (Endress et al., 2010; Ohshiba, 2002; Renner et al., 2016). These studies highlight that these abilities have been identified in the manual, visual and auditory domains, suggesting that great apes are able to learn relations between elements in simple sequences of action to achieve novel goals. In monkeys, sequence learning studies have predominantly focussed on the learning of auditory or visual sequences, using playback or touchscreen based experimental methods (Milne et al., 2018). Experiments in these domain have identified the ability of monkey species to attend to the relationships between elements in sequences by attending to adjacency relationships between elements (Heimbauer et al., 2018; Milne et al., 2018; B. Wilson et al., 2013), with there being mixed evidence that monkeys are able to learn non-adjacent dependencies between elements (Milne et al., 2018; Mueller et al., 2018; Newport et al., 2004). This evidence suggests that primates are able to attend to relations between adjacent elements in sequences and may be able to attend to relationships between non-adjacent elements in a more limited capacity.

From the summary of results above and the review in chapter 1, data on sequence learning abilities appear to exist across a diversity of domains in the great apes, but data addressing monkeys' manual sequence learning abilities relatively sparse in comparison. A few experiments that have been conducted to this end and do indicate that it is possible for monkeys to learn to use tools in sequence to reach food goals (Hihara et al., 2003), as well as put manual elements together in experimental settings to learn novel behavioural sequences (Beran & Parrish, 2012; Hikosaka et al., 2002). However, the number of monkey species used in manual sequence learning tasks is low. This gap is likely due to the lack of evidence of tool use outside of the great apes and a small selection of monkey species (Biro et al., 2003; Fragaszy et al., 2011; Hobaiter et al., 2014; Musgrave & Sanz, 2018), which has potentially biased the focus of manual sequence learning towards primate species where these skills have been observed, owing to their presumed relevance in understanding the evolution of human tool use (Steele et al., 2012). However, evidence from gorillas in the study presented in the previous chapter, as well as the studies on their manual sequences while feeding on difficult to process food items (Byrne et al., 2011; Byrne & Byrne, 1993; Neufuss et al., 2019) and their ability to learn complex tool interactions in captivity (Lonsdorf et al., 2009; Martin-Ordas et al., 2012), suggests that the absence of observed tool use in the wild does not necessarily mean that the cognitive apparatus necessary for generating complex manual sequences are absent (Byrne, 2004). The scope of manual sequence learning studies must go beyond the species already represented, to give a broader perspective on these skills across a diverse range of primates. Therefore, this study aims to provide data to fill this gap by providing data on the manual sequence learning abilities of two species of primates that have never been tested in this kind of task.

The species chosen for this study were partially selected based on their availability. However, from the species available to us, François' langurs (*Trachypithecus françoisi*) and black headed spider monkeys (*Ateles fusciceps)* were a sensible choice. In the previous chapter it was observed that François' langurs, when extracting leaves to feed on from branches, used sequences of behaviours that did not show higher order structures compared to the western lowland gorillas (*Gorilla gorilla gorilla*). This species of monkey may therefore have relatively deficient sequence processing abilities compared to great apes. The previous study was limited however, due to the study relying entirely on observation meaning this conclusion can only be inferred. Therefore, collecting primary data on the François' langurs using a manual sequence learning task can help identify the limits of this species abilities to learn manual sequences. Comparing this to the relatively rich experimental data on manual sequence learning in great apes (Keller & Delong, 2016; Martin-Ordas et al., 2012; Tecwyn et al., 2012) can provide novel data on the differences between monkeys and great apes sequence learning abilities. Including another understudied monkey species by also testing the black headed spider monkeys will enhance these comparisons by potentially identifying similar differences in a distinct monkey species' sequence learning abilities, that can be incorporated into this comparison.

Black headed spider monkeys are platyrrhine primates that, like the François' langurs (Yang et al., 2007), are arboreal, spending almost the entirety of their lives in rainforest canopies (Roosmalen & M, 1985; Rosenberger et al., 2008; Wallace, 2006). Unlike the langurs however, this species of spider monkeys is frugivorous, feeding on a diversity of calorie rich fruits. This contrast with the François' langurs, whose diet consists almost entirely on leaves (Yang et al., 2007), may be important in explaining any potential differences in the two species manual sequence learning abilities. As highlighted by the extractive foraging hypothesis, differences in feeding adaptations may be relevant to the evolution of cognitive abilities that aid in foraging for food. This hypothesis predicts that enhanced cognitive abilities relating to foraging are predicted to arise, to overcome the challenges of processing and locating energy rich food items (Parker, 2015). These two species therefore can provide comparative data on differently adapted monkey species to identify whether between species differences in these abilities arise due to differences in foraging adaptations. As neither species are apes, this comparison could yield interesting results beyond predictions made based on the divide between the great apes and other primates, which can provide a more nuanced insights where this divide is less clear cut (Amici et al., 2010).

To provide data on previously understudied species of primates, in their ability to solve manual sequence related problems, a puzzle box was designed with multiple difficulties and was introduced to captive François' langurs and black headed spider monkeys using a voluntary approach paradigm. The puzzle box used was specifically designed for this experiment and has not been used with other species of primates prior to this study. A novel design was chosen as previous manual sequence learning tasks often involved the use of tools in task completion (Hihara et al., 2003; Lonsdorf et al., 2009), which may involve several cognitive and physical constraints that are not necessarily themselves related to sequence cognition. The design used in this study therefore aimed to minimise this, by ensuring the interactable elements only require simple discrete movements. Our design also aimed to more explicitly extract whether the sequence is being comprehended, as the third difficulty requires the subject to appreciate the order of behaviours necessary to complete the task. A more detailed descriptions of the task can be found in the methods section, which further elaborates on this point.

Previous experiments on captive monkeys have shown that monkeys are capable of completing similar manual tasks with simple relations between elements (Hihara et al., 2003), based on these findings it is therefore reasonable to hypothesise that the monkeys in our study will also be able to complete manual tasks with simple relations between elements.

It is predicted then that both species will be able to complete the first two difficulties. However, both species will take a significantly larger numbers of trials to learn the third difficulty compared to the number of trials necessary to learn the first two difficulties (with both species potentially failing this difficulty) due to the third difficulty requiring an appreciation of sequence order. Unlike Francois Langurs, black headed spider monkeys rely on extractive foraging for a large part of their diets (Wallace, 2006). Therefore, in line with the extractive foraging hypothesis (Parker, 2015), it is also hypothesised that black headed spider monkeys will have enhanced manual sequence learning abilities compared to the Francois Langurs. Based on this hypothesis it is predicted that the black headed spider monkeys will figure out the task difficulties in fewer trials compared to the François' langurs and reach harder difficulties then the Francois Langurs are capable of.

3.2 Methods

3.2.1 Subjects

This study was conducted by collecting experimental data from five captive black headed spider monkeys and seven François' langurs located at Twycross Zoo in the summer of 2022. Demographic information of the individuals is listed in table 9.

Table 9: Demographic information of the primates involved in the study

Name	Species	Sex	Age (years)
Ernie	*Ateles fusciceps*	Female	3
Jamundi	*Ateles fusciceps*	Female	14
Moa	*Ateles fusciceps*	Female	14
Monty	*Ateles fusciceps*	Male	28
Neiva	*Ateles fusciceps*	Female	4
Chow Chow	*Trachypithecus françoisi*	Male	12
Kaili	*Trachypithecus françoisi*	Female	4
Lychee	*Trachypithecus françoisi*	Female	16
Pak Choi	*Trachypithecus françoisi*	Female	16
Shiitake	*Trachypithecus françoisi*	Female	2
Shinji	*Trachypithecus françoisi*	Male	4
Yalu	*Trachypithecus françoisi*	Female	1

François' langurs and black headed spider monkeys were housed in their usual enclosures' so all individuals had equal access to the puzzle box. The puzzle box was set up in an easily accessible area of their enclosure, where all monkeys were able to reach it. As this was a voluntary approach experiment individuals were able to approach the puzzle box at will and engage with the task as they pleased.

3.2.2 Apparatus

To test the two species manual sequence learning abilities a puzzle box was designed and built by the technical team in Durham Universities psychology department. A picture of this puzzle box is presented in figure 9a with the overall design in diagrammatic form depicted in Figure 9b. This puzzle box was designed with three difficulty levels, which could be pre-set at the start of the experiment and adjusted to increase or decrease the difficulty as needed. The body of the Puzzle box was built using transparent Perspex and metal was used for the moving elements. Moving elements were attached to springs so that they would reset into their initial position after being moved. This was important because once the puzzle box had been put into position the ability for the experimenter to interact with it was limited, so the box needed to auto reset between attempts. During the experiment food would be fed into the puzzle box using two 1 meter long transparent tubes, which were duct taped together and could be inserted into the back of the box (Shown in figure 11c). This allowed food to be placed into the box and replaced as needed during the experiment. The food would roll down the tube and enter from the back of the box and rest on the platform in the box.

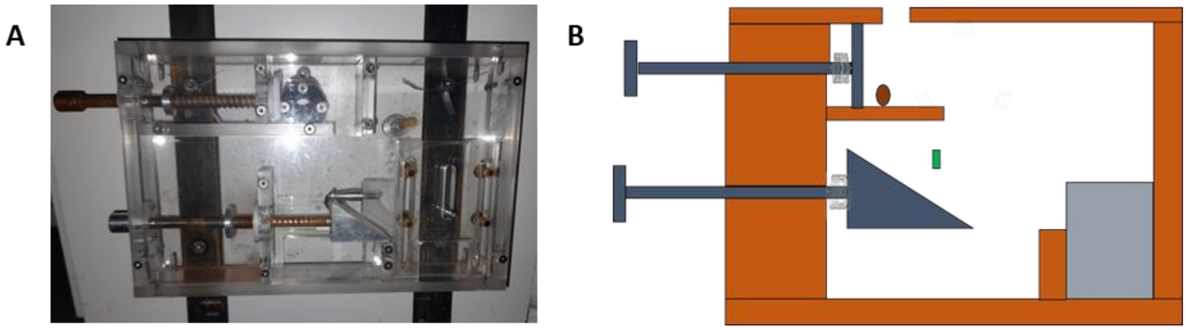


Figure 9 A) A picture of the final puzzle box B) A diagram of the final puzzle box.

The three difficulties are described using diagrams in figure 10. For the first difficulty the monkeys only needed to push a plunger to knock the food onto the wedge below, where it would roll into an access area where the monkeys could reach in to collect the food (Figure

10a). For the second difficulty a door to the food collection point would be closed, meaning after pushing the plunger the monkeys would need to also lift the door to access the food (Figure 10b). For the third difficulty the wedge is offset so that if the monkey pushes the plunger the food will fall into an inaccessible part of the box. The monkey must therefore first push the wedge into position, then push the plunger and then open the door (Figure 10c). The wedge mechanism is connected to the door such that it latches when pushed into place, lifting the door lifts a latch allowing the spring to reset the wedge and therefore must be performed last. In the first two difficulties the actions follow naturally from the position of the food and elements of the task can be learnt from the position of the food during the task. However, the hardest difficulty requires the monkeys to learn the sequence of steps and the relation between the order of steps, therefore more explicitly challenging the monkeys' sequence learning abilities.

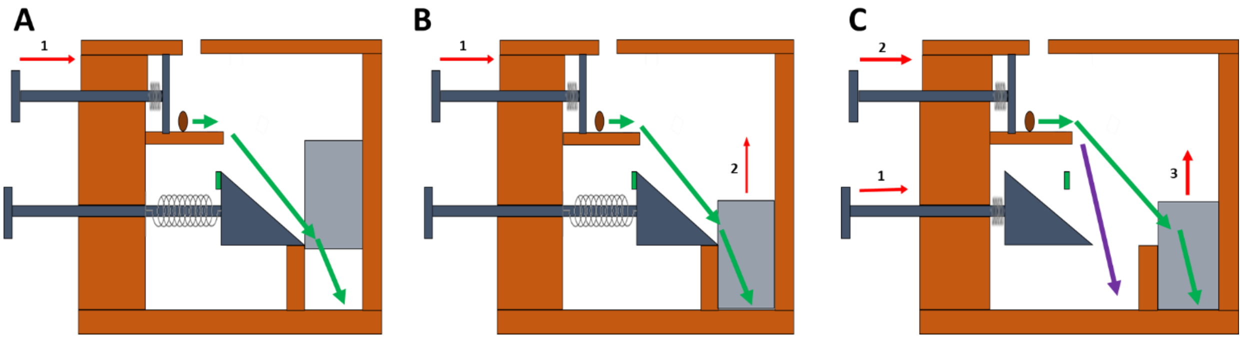


Figure 10 Diagrams depicting the different difficulties of the puzzle box. The red arrows indicate the movements that the monkeys must perform, with numbers indicating the order. The green arrows indicate the correct movement of food when movements have been correctly performed. The purple arrow indicates where the food falls if performed incorrectly. A) First difficulty B) Second difficulty C) Third difficulty.

For both species the puzzle box was set up by attaching the puzzle box to wooden framings against the widest mesh on the enclosure. For both species the puzzle box was placed in an area where individuals could easily access it (Shown in Figure 11). For the François' langurs a small platform was directly underneath the mesh allowing individuals to sit while performing the task. Due to the large width of the mesh, langurs were able to reach their hands through to interact with the box reasonably uninhibited.

Figure 11 Pictures depicting the placement of the puzzle box. A) Francois langur sat on the platform with access to the puzzle box B) Puzzle box position for the François' langurs C) Puzzle box position for the Spider Monkeys, with spider monkeys climbing down the mesh to interact with the box. The connecting tube that allowed food to be fed into the box is also present in the image.

The puzzle box was attached against the mesh of the black headed spider monkeys' enclosure in a similar way but, due to their greater strength and longer reach, a smaller mesh boarder was placed behind the puzzle box to ensure that individuals couldn't reach and grab at the tube. The mesh that the puzzle box was set against was also large in width allowing the monkeys to reach through and interact with the puzzle box elements. Unlike the langurs the spider monkeys did not have a platform to sit on but would instead climb down to reach the box and would hang from the mesh using their prehensile tails.

3.2.3 Experimental Procedure

The puzzle box was set up how it was described previously and was left up continuously, as putting it up at the start and removing it after each session was not practical. The François' langurs were tested across three weeks between the dates of the 18th of July to the 4th of August for twenty sessions. The black headed spider monkeys were tested across two weeks between the dates of 8th of August to the 19th of August and were tested across nineteen sessions. Sessions were conducted for an hour between 9:30 and 10:30 in the morning and between 14:00 and 15:00 in the afternoon. For the François' Langurs' 11 sessions were conducted in the afternoon and nine were conducted in the morning. For the black headed spider monkeys 9 sessions were conducted in the afternoon and 10 were conducted in the morning.

Although the puzzle box was left up continuously food was only put into the box, using the tubes, during the sessions. If there was any food left at the end of sessions was removed by keepers so that food was not left in when sessions were not being performed. Because of this, interest in the apparatus was likely restricted to the session durations. These sessions were recorded using two Panasonic HC-V770EB-K Full HD Camcorders, with one filming directly behind the puzzle box and the other filming from a different angle to aid with coding and identification. For the François' langurs the food used was butternut squash and the food used for the spider monkeys was sweet potatoes. Keepers confirmed that both of these food items were high value foods in the respective species and therefore was a sufficiently salient reward. Food was portioned into 1.2cm diameter balls using a small melon baller, as single balls were an extremely small reward three balls made up one portion of rewards so three balls would be placed in at the start of each session. Rarely, one of the food balls would fall off of the platform into the collection area. When this happened, the fallen item would be replaced.

At the start of each session cameras would be set up and the tube would be inserted into the back of the box. The cameras would then begin recording and the initial food pieces would be placed into the box. The tube was left in the back of the box for the duration of the recording and if an individual managed to extract the food the food would be replaced. Due to this experiment being a voluntary approach task, monkeys were able to interact with the task whenever they chose to. Five minutes before the end of the session the tube would be removed and the last five minutes would be recorded without it, after which the cameras would stop recording. Remaining food in the box would then be removed from the box.

The difficulty was initially set at the first difficulty level with the increase in difficulty only being performed when more than half of the individuals in the groups were able to complete that difficulty. Which would mean three individuals for the black headed spider monkeys and four individuals in the François' langurs. As well as this, to ensure that individuals had interacted with the task all individuals would need to interact with each difficulty level at least eight separate times.

3.2.4 Coding

The software BORIS (Friard & Gamba, 2016) was used to code the session videos. To do this for each session behaviours were coded as described in the ethogram below.

Ethogram:

Difficulty: As previously described the difficulty of the box was determined at the start of the experiment, being set physically by the experimenter at the start of a block of sessions. This was defined as an independent variable for entire sessions within the coding software.

Approach*: In the case of the François langurs, an approach towards the box was defined when they sat in front of the box on the platform directly underneath the puzzle box position. In the black headed spider monkeys, due to the set up being slightly different individuals would need to climb down or across the mesh of the enclosure to reach the box. The wooden framing directly surrounding the puzzle box (seen in figure 11c) can be used as a point of reference, such that an approach is defined as when a spider monkey climbs into the framed area around the box.

Retreat*: In the case of the François' langurs a retreat is defined as the langur moving off of the platform directly underneath the puzzle box. Similar to the approach behaviour defined above, for the spider monkey a retreat was defined as moving out of the area delineated by the wooden framing surrounding the puzzle box.

Puzzle Box Attempt:

Start Attempt: After an approach the François langur or spider monkeys' first touch of the box is defined as the start of an attempt.

End Attempt: The final touch of the box including touches involved in the retrieval of any food item they were able to extract before retreating is the end of an attempt for both species.

Success or Failure: After an attempt, whether the monkey was able to successfully remove the food by performing the correct action should be coded.

***:** Neither approach nor retreat are explicitly coded behaviours in their own right due to being quite different in the two species, but are described to help define the start and end of attempts.

Coding Convention:

A Puzzle Box Attempt should be coded continuously from start to finish (defined above), so that the time spent with the box for each attempt can be measured. In the Software this would therefore be coded as a state event. Touches of the box are so short they were coded as discrete events. In the Software these were therefore coded as point events.

3.2.5 Measures and Statistical Analysis

From the behaviours documented for each video using the coding scheme, the time spent on the attempt, whether the attempt was successful or a failure and the touches used in each attempt was documented. For each session the percentage of attempts successfully completed can be calculated for each individual to identify how success changes across the sessions at the different box difficulties. With this information, separate generalised linear mixed models can be used to identify species and individual level differences in their ability to complete the task based on investigating whether these parameters influence these measurements. These generalised linear mixed models identify the attempt number as the repeated measure, except for in the case of the percentage of attempts successfully completed, where the session number would be used as the repeated measure.

To ascertain if there were differences between the species' general interest in the box, every time an individual would touch the box, this would be coded. To identify species differences between interest across the sessions a rate of touches per minute was calculated for each individual for each session. To identify differences in interactions within the sessions, the sessions were split into twelve five minute time bins and the total number of touches were calculated for each time bin, for each individual. In both cases linear mixed models were used to identify species level differences and the general trend across time in interactions within and between sessions. Statistical analysis was performed using SPSS version 27.

3.3 Results

Across both species none of the monkeys were able to complete even the first difficulty of the task, meaning the analysis that can be conducted are extremely limited. The only analysis we are able to reasonably conduct is to analyse the rate of interaction measures for the individuals of both species.

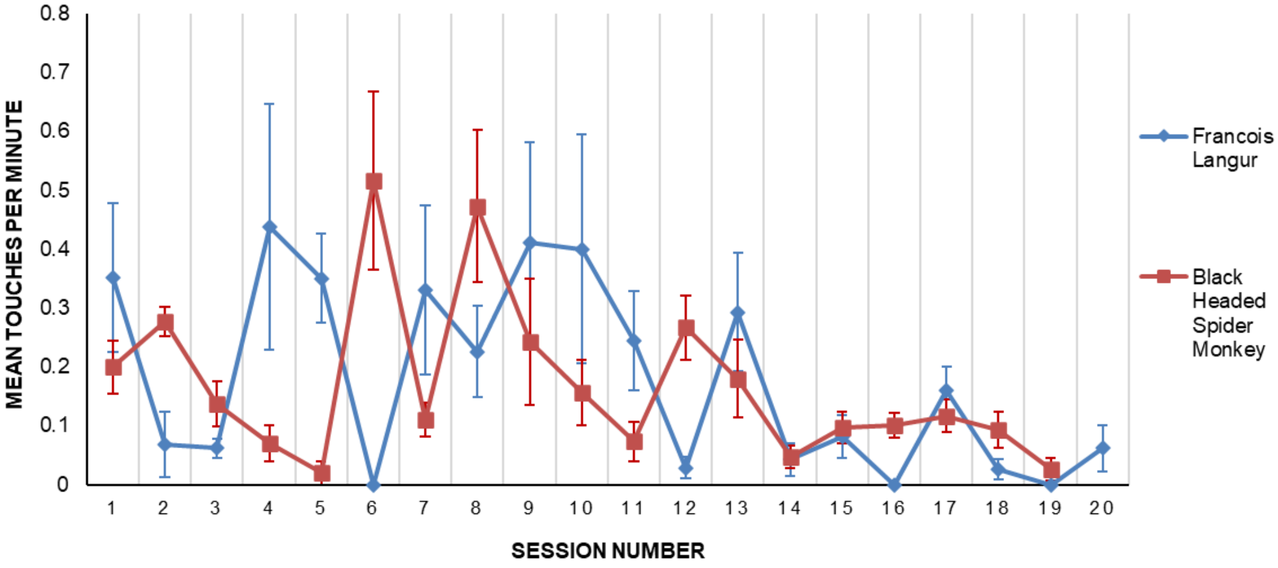


Figure 12 The Average number of box touches for both species across the session. Error bars represent standard error.

To ascertain the two species overall interactions towards the box across sessions the number of times individuals touched the box was measured in each session and a rate measure was calculated for the number of touches per minute. The averages for these are presented in figure 12. A linear mixed model was run to identify whether the two species differed in their interaction with the box across the sessions. The model therefore contained Species as a fixed effect and Subject as a random effect, with the repeated measure being the number of sessions. Whether there was an interaction effect between Species and Session was also tested. This identified that there was no significant effect of species (F[1,12.6] = 0.784, p = 0.377) and there was no significant interaction effect between sessions and species (F[1,223.3] = 0.562, p = 0.454). suggesting there was no significant difference between the two species rates of touching across trials. However, there was a significant effect of session number on touch rates (F[1,223.3] = 16.516, p< 0.01), with the model estimate for the impact of session number being calculated as -0.008520. This means there was a significant decrease in touch rate across the sessions in both species.

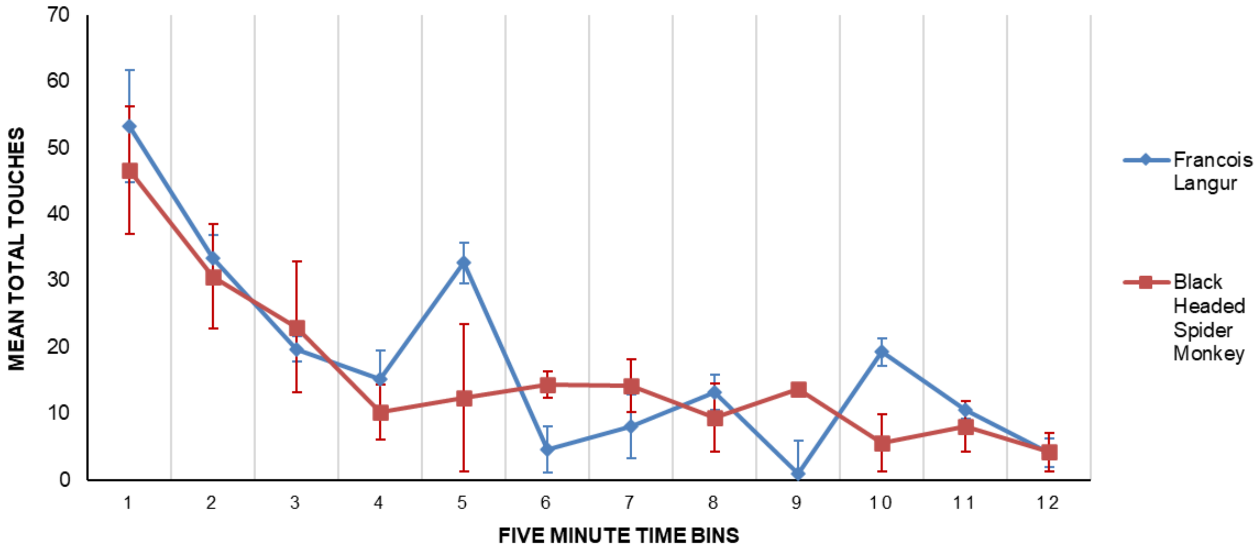


Figure 13 Average of the total touches calculated for each individual across the first 19 sessions, with touches being organised into twelve five minute time bins. Error bars represent standard error.

To identify the species interactions with the box within the sessions, the total number of touches for each five minute segment of the first 19 sessions were calculated. The 20th was excluded as only 19 sessions were run with the black headed spider monkeys so that both species totals were taken from the same number of sessions. The averages of these totals across the individuals is illustrated in figure 13. A linear mixed model was conducted to identify whether the species differed in their interactions with the task within sessions. The model therefore contained Species as the fixed effect and Subject as a random effect, with the repeated measure being the five minute time bins. Whether there was an interaction effect between species and time bins was also tested. This identified that there was no significant effect of species (F[1,86.8] = 0.457, p = 0.501) and there was no significant interaction effect between species and time bin (F[1,132] = 0.187, p = 0.666). suggesting there was no significant difference between the two species frequency of touches of the box within trials. However, there was a significant effect of time bin number on touch rates (F[1,132] = 58.62, p< 0.01), with the model estimate for the impact of the time bin count being calculated as -2.74. This means there was a significant decrease in number of touches within the sessions in both species.

To summarise, there was no significant effect of species on the interaction rates and frequencies across sessions and within sessions and there were no significant interaction effects. Between sessions touch rate showed a significantly negative correlation with session number, meaning that touch rate showed a trend of decreasing across the sessions in both species. Within the sessions the frequency of touches was at the highest during the start and decreased significantly across the time bins. Therefore, both species showed similar patterns of touching the puzzle box.

3.4 Discussion

The fact that neither species was able to complete the task, at even the easiest difficulty level, means that interpreting these results in reference to sequence learning abilities specifically is extremely limited. Beyond the superficial observation that they were not able to learn the first action in the sequence. In relation to the hypothesis this study aimed to investigate, the prediction that both species would be able to complete the first two difficulties was found to be false. As both species failed to complete the task, the hypothesis that the black headed spider monkey's would learn to complete the task more quickly and achieve harder difficulties compared to the François langurs was also not confirmed.

Instead of focussing further on these hypothesis, it is worth evaluating what about the task provided a barrier to the species ability to complete the task. With any voluntary approach task, one potential issue is whether the species are sufficiently engaging with the task, which could potentially explain individuals inability to complete the task. The evidence from the interaction measures presented in the results section suggests that both species engaged with the task, which makes this explanation less likely. Their interest was concentrated at the start of sessions and decreased across the sessions, likely as their interest waned from the initial novelty of the box. From observations while running the experiment individuals of both species were sufficiently motivated and attempted to access the food in the box multiple times. However, it should be noted that due to the use of a tube to insert food into the box, sometimes the food would fall into the collection point unintentionally, which potentially inflated their interest in the box beyond their interest in extracting the trapped food items.

As it seems unlikely that lack of motivation was the factor stopping both species from completing the task it may be the case that even the first difficulty of the task was too cognitively demanding. When looking at the first difficulty in more detail the participating primates must use a plunger to push the food. This could be considered a very controlled form of tool use, which has not been observed in either of the two species (although tool use has been observed in a very limited capacity in the genus Ateles (Lindshield & Rodrigues, 2009). Beyond the already discussed sequence cognition requirements, tool use is hypothesised to be a cognitively complex activity with multiple aspects, which is why it is rarely observed in primates, only being observed regularly in the great apes and in select monkey species (Musgrave & Sanz, 2018). Using a tool requires a level of cognition where the individual represents the tool as an item that is functional in helping extract the food item (Baber, 2006). When primates feed without using tools, they are directly in contact with the food item they are eating, forming these representations of objects may be a cognitive capacity less well formed in these species meaning that the use of the plunger is particularly difficult to grasp.

Beyond potential cognitive shortcomings, another potential issues that obscured the monkeys ability to learn the task was that the pressing action required to complete the first step is not a natural motion for these monkeys, so it was difficult for them to naturally perform this action. When interrogating the box a few times individuals would place their hands on the correct part and grasp it, sometimes even attempting to pull it. As the plunger was set in place with a spring a small amount of force was necessary to push the plunger to successfully complete the action. Even though individuals would touch the plunger they would never attempt to push it. Effectively this meant that it was difficult for the monkeys to figure out the first step by trial and error as nothing about the boxes basic affordances would suggest these elements would move from their position. It is therefore very difficult to conclude that the issues these species had completing the task was due to cognitive issues. This may have been a particularly unsuitable set up for the two species used in this study as both species are mainly arboreal (Roosmalen & M, 1985; Zhou et al., 2013), meaning that their manual abilities are adapted differently to the ape species commonly used in these studies, which are terrestrial (Gebo, 1996; Heldstab et al., 2016). Both of these species are likely specifically adapted to grasping and pulling motions, due to both species being arboreal and therefore specifically adapted to arboreal locomotion (Vanhoof et al., 2021). This is particularly evident in the spider monkeys, which have extremely diminished thumbs and whose hand and limb morphology show extensive adaptation necessary for navigating their environment (Emura et al., 2020; Preuschoft, 2019; Rosenberger et al., 2008). It may therefore be more reasonable to suspect that the issues exhibited by these species in this task were based on physical constraints.

As the experiment garnered a sparsity of interpretable results the rest of the discussion will be dedicated to offering suggestions on how experiments of this kind may be improved in the future. The previous discussion highlights an issue beyond the present study in the comparative literature, when using physical abilities to assess cognitive abilities, as it is often difficult to know the physical constraints species may have that inhibit their ability to complete tasks. This makes studies of this kind more difficult to interpret as there is very often the confounding variable of species differences unrelated to cognitive capacities. If one of the goals of follow up research on sequence learning abilities in primates is to address manual sequence learning abilities in a wider range of primates, this is an important issue that needs to be addressed. Due to the primary importance of complex tool use in humans success, uncovering the evolution of manual sequence learning abilities is an important feature in the evolution of these abilities and therefore, suggestions that help to design experiments that are more likely to garner interpretable results would be useful.

Some studies address this with extensive training to ensure that individuals have learnt the basic elements of a task prior to increasing difficulty (Calapai et al., 2017; Conway & Christiansen, 2001; Westlund, 2015). However, this is an unsatisfactory solution in a lot of contexts as it requires extended access to animals, often in a one on one capacity, and is potentially expensive and unfeasible. It also may cause ethical issues due to needing to train individuals one on one, which could cause undue stress on the animal participants. It is also worth considering that the majority of captive primates are kept in zoological parks, where a large diversity of species are housed, which usually have reasonably limited accommodations for experiments. Methods that require considerable hands on effort and personal time with the animals being tested are therefore unreasonable to run in a large portions of captive primate populations. It would therefore be extremely useful to develop a way in which experimenters can assess the manual abilities of the species they wish to conduct further experiments on as part of a pilot study that can help aid subsequent puzzle box development.

For this I have designed a potential apparatus that could be presented to captive primates, which would help assess these abilities prior to designing more elaborate puzzle boxes that aim to assess sequence learning in a wider range of species (Figure 14).

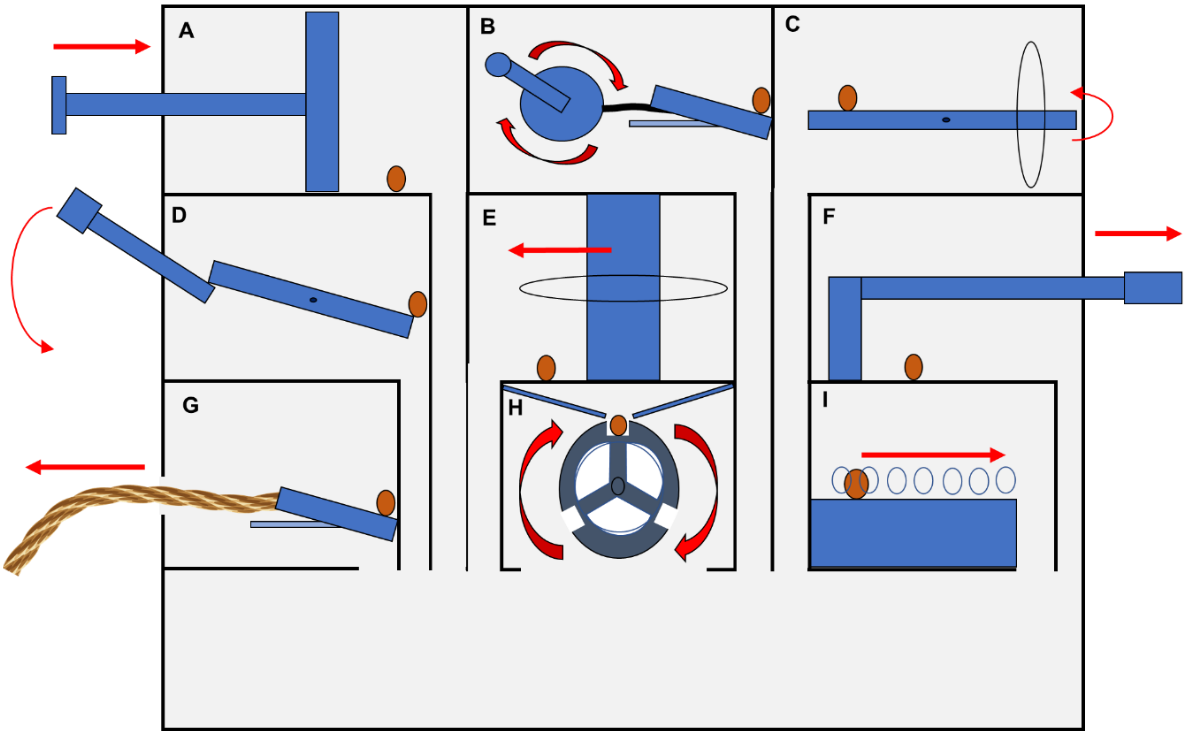


Figure 14 An example of a manual ability assessment box that could be piloted prior to designing tasks aimed at investigating manual sequence learning skills. The example box contains nine different manual actions that once completed would give the monkey a food reward. Red arrows indicate the movements required by the monkeys. A) The monkey must push a plunger B) a crank is attached to a spool which must be turned C) A seesaw element in the box must be rotated D) a lever must be pulled down E) A solid block must be slid to push the food item F) A tool must be pulled to drag the food item G) A rope must be pulled H) A cog must be turned I) The food can be directly pushed by pushing fingers through holes in the box.

This apparatus is a relatively simple box that could be set up against the mesh of an enclosure in a similar set up to the puzzle box used in this study. The box contains a variety of different manual actions that, when completed food will be dispensed. These manual actions include pulling and pushing motions with a variety of different tools and handles that could be manipulated by the monkeys to access the food items in the compartments. The puzzle box should be built from either transparent acrylic or Perspex to allow experimenters to record the interactions by the monkeys. Documenting How often the food is removed from each area could allow for a repertoire of preferred manual actions to be determined across a variety of species. This would allow for species tailored sequence learning tasks to be designed more effectively, diminishing the risk that the differences in physical abilities, unrelated to the cognitive capacities that experimenters are generally interested in, confounding the results. Independently it will also provide data on the manual abilities of different primates which is interesting in its own context, related to how different primate species manual abilities have evolved differently across a variety of ecological contexts, where previous studies have focused on the adaptations related to hand morphology in hominins related to tool use (Kivell, 2015; Marzke, 2013).

Although the results from this study failed to provide evidence regarding the two species abilities to learn manual sequences, an appraisal of the techniques used has allowed us to identify guidance towards investigating these capacities in future experiments. Going forward this could help future research to escape one of the potential pitfalls present when working with captive, zoo housed primates.

Chapter 4: General Conclusions

4.1 Overall conclusions:

Evaluating the sequence learning abilities of primates holds the potential to provide insights into how these abilities evolved in humans, by highlighting differences between species of primates. Helping to unravel the proximate and ultimate mechanisms that have led to any differences across this diverse group of organisms. Due to sequence learning being fundamentally important in a variety of human specific skills, such as language, complex tool use and cumulative culture, understanding humans enhanced abilities in this cognitive ability may hold the key to understanding uniquely human cognition.

The observational study presented in chapter two provided evidence that the feeding behaviours of a great ape species showed sequential hierarchical structure where the monkey species studied didn’t. This finding provides potential insight into differences in cognitive abilities of great apes compared to other primates, with great apes potentially showing enhanced sequence cognition in the domain of manual sequence learning. However, there were multiple potential explanations for why these behaviours differed. Using two very different species of apes allowed us to explore a range of potential generative mechanisms underlying the difference in the observed sequences used. Contributing to our understanding of the complex factors that generate consistent patterns in sequences of behaviours. The Markov chain analysis used allowed us to actively compare the two primates approaches to the task in an informative manner giving us a foundation to make comparisons. As an illustration of the utility of this method the study therefore illustrates that Markov chain analysis and other mathematical approaches to formalise the relations between sequence elements in a way that makes results readily comparable. This framework then could help guide future studies by allowing more direct comparisons between the different sequences used by different species across a wider set of contexts.

The aim of the third chapter was to increase the range of species which we have experimental manual sequence learning data on. Data on a more diverse range of primates can ultimately aid in finding broader phylogenetic comparisons between primates, enhancing our understanding of the evolution of sequence learning abilities. However, the experiment described in chapter three failed to provide results that were easy to interpret in the context of sequence learning. Instead, the experiment highlights the importance of increasing the breadth of species studied in these kinds of experiments, as neither of the species tested were represented in similar experiments meaning that designing appropriate tasks was made more difficult. The key finding of this experiment then is that, to generate reliable experimental sequence learning results in the manual domain, a keener focus must be taken when considering the physical constraints present in the specific species being worked with. In the experiment conducted here both species were arboreal with their hand physiology potentially being highly adapted to climbing which may have made the movements necessary in the task particularly difficult. As a diverse taxa it is likely that primate species have diverse adaptations that influence the range of movements they can achieve and are likely to be able to form when completing experimental tasks.

One approach would be to ensure that the movements necessary are universally appropriate by ensuring they are extremely easy to perform, such that physical constraints that differ between species are eliminated. This approach would ensure consistency between species but has the potential to lose the essence of manual sequence learning. Making the movements so trivial as to be manual in an extremely minimal sense and therefore unlike the diverse range of movements the species being tested are actually capable of. An alternative approach would be to ensure these tests take advantage of the capabilities of the specific species being tested and by developing experiments that incorporate these into the tasks. A natural criticism of this approach may be to point out that if the manipulations used between species differs the ability to generalise across tasks may be made more difficult. However, one could analogise the use of different manipulations for different species as being similar to a scenario where a person gives a translated version of a written test to different test takers based on their native language. The test is asking the same questions but in a way that has been modified to be comprehensible to the test taker. Similarly, in manual sequence learning experiments, it should be possible to retain the sequential aspect of tasks while substituting specific manipulation to be more species specific. The difficulties encountered herein would point to this approach being worth considering and elaborating on, where the goal is to extend our understanding of the cognitive processes underlying manual sequence learning across diverse primate species.

4.2 Future Directions:

The literature review section highlighted that further investigations into the neurophysiological basis of sequence cognition, focusing on potential species differences between primates, will help elucidate the neuronal mechanisms that facilitate sequence learning. Sampling from a greater variety of primates would also be beneficial, particularly in manual sequence learning tasks, where there is a sparsity of studies conducted on species outside of the great apes.

The study described in the second chapter presented interesting differences between species in the sequential behaviours of a great ape and a monkey species when performing a comparable manual task. These results highlight the importance of considering the learning of manual sequences outside of tool use in understanding the evolution of sequence learning abilities. Using Markov Chain Analysis helped reveal the structure of these feeding behaviours, so using this methodology across a greater diversity of manual behaviours could aid in identifying structure in a diversity of manual behaviours outside of feeding contexts. Markov chain analysis is limited in that it is best suited to identify structures between discrete behaviours within a limited range, so combining this method with tools that are able to analyse sequences as a whole could provide a rich picture of the sequential structure of these behaviours at multiple scales. The discussion of this chapter also illustrated that there were multiple potential explanations for these behaviours, including physical constraints and constraints related to interactions with the environment. Controlling for these more firmly in future observational tasks may help better discern the relevant factors related to generating any sequential behaviours observed.

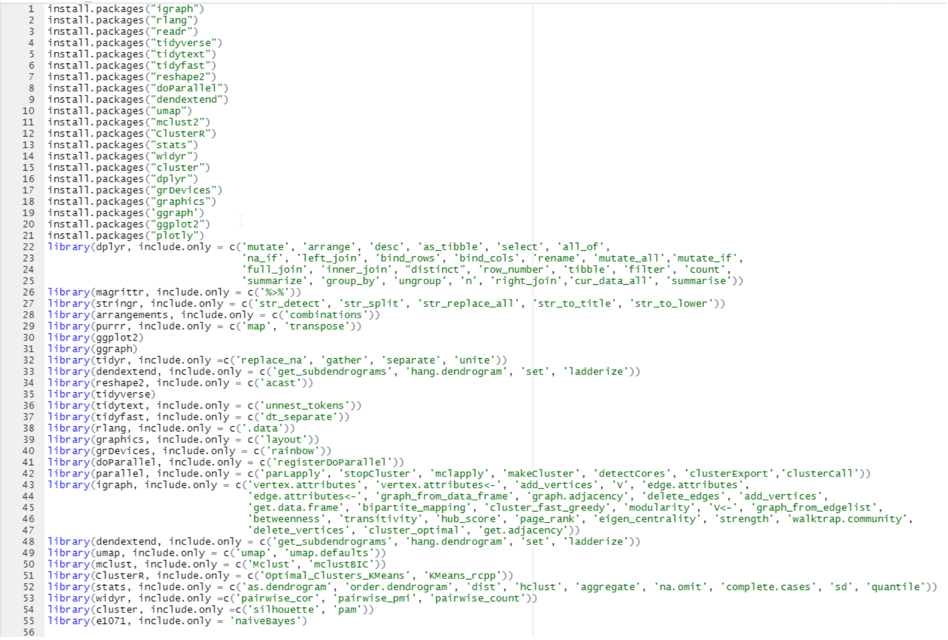
The experiment conducted in the third chapter, involving the use of a novel puzzle box, failed to produce results useful in assessing the two species manual sequence learning abilities. However, this highlighted that, an important consideration going forward, must be to ascertain the manual abilities of a greater diversity of primates prior to attempting similar data collection. This will allow investigators to design species specific apparatus that can interrogate the sequence learning abilities of primates, while limiting other confounding physical factors unrelated to their abilities to learn manual sequences. One way of enhancing our understanding of these manipulative abilities would be by first performing observational studies of the kind described in chapter two that could provide a basis for deciding which manual behaviours the species is likely to be able to perform. Another possible approach would involve pretesting using an apparatus specifically designed to ascertain general manual abilities in understudied species. Performing these approaches prior to designing sequence learning tasks in the future would therefore be useful in informing the design of these tasks in a more diverse range of primate species.

Appendices:

Appendix A - Markov Chain Code

All functions used in relation to the code below were loaded as a package can be found in the github repository related to the paper (Mielke & Carvalho, 2022). The direct link for which is below.

https://github.com/AlexMielke1988/Mielke-Carvalho_Chimpanzee-Play



```r
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install.packages("rlang")
install.packages("readr")
install.packages("tidyverse")
install.packages("tidytext")
install.packages("tidyfast")
install.packages("reshape2")
install.packages("doParallel")
install.packages("dendextend")
install.packages("umap")
install.packages("mclust2")
install.packages("ClusterR")
install.packages("stats")
install.packages("widyr")
install.packages("cluster")
install.packages("dplyr")
install.packages("grDevices")
install.packages("graphics")
install.packages('ggraph')
install.packages("ggplot2")
install.packages("plotly")
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                                'full_join', 'inner_join', "distinct", 'row_number', 'tibble', 'filter', 'count',
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library(umap, include.only = c('umap', 'umap.defaults'))
library(mclust, include.only = c('Mclust', 'mclustBIC'))
library(ClusterR, include.only = c('Optimal_Clusters_KMeans', 'KMeans_rcpp'))
library(stats, include.only = c('as.dendrogram', 'order.dendrogram', 'dist', 'hclust', 'aggregate', 'na.omit', 'complete.cases', 'sd', 'quantile'))
library(widyr, include.only =c('pairwise_cor', 'pairwise_pmi', 'pairwise_count'))
library(cluster, include.only =c('silhouette', 'pam'))
library(e1071, include.only = 'naiveBayes')

```
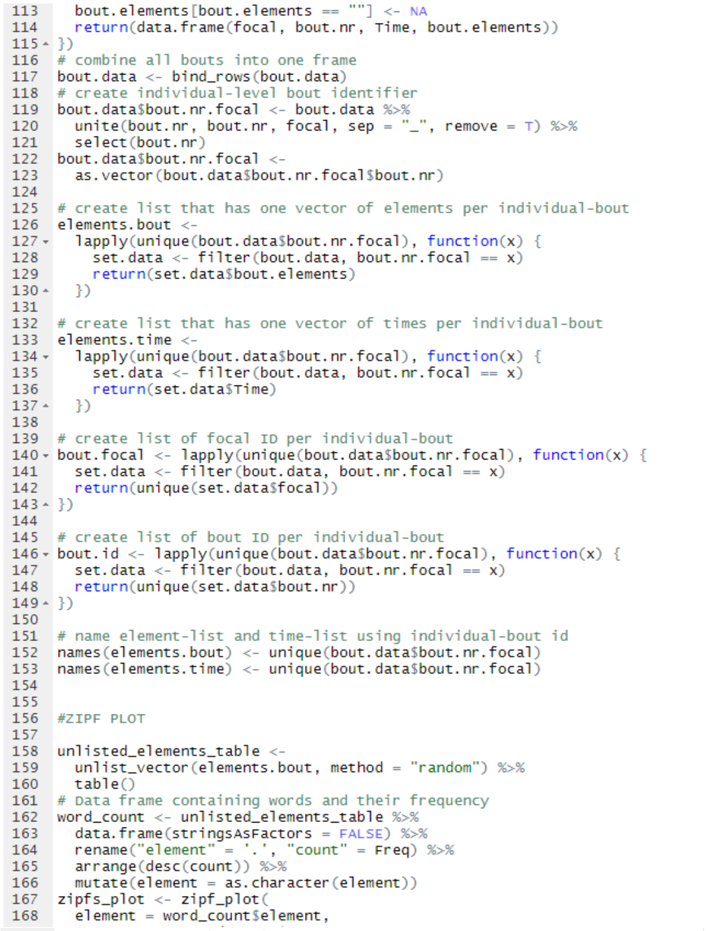
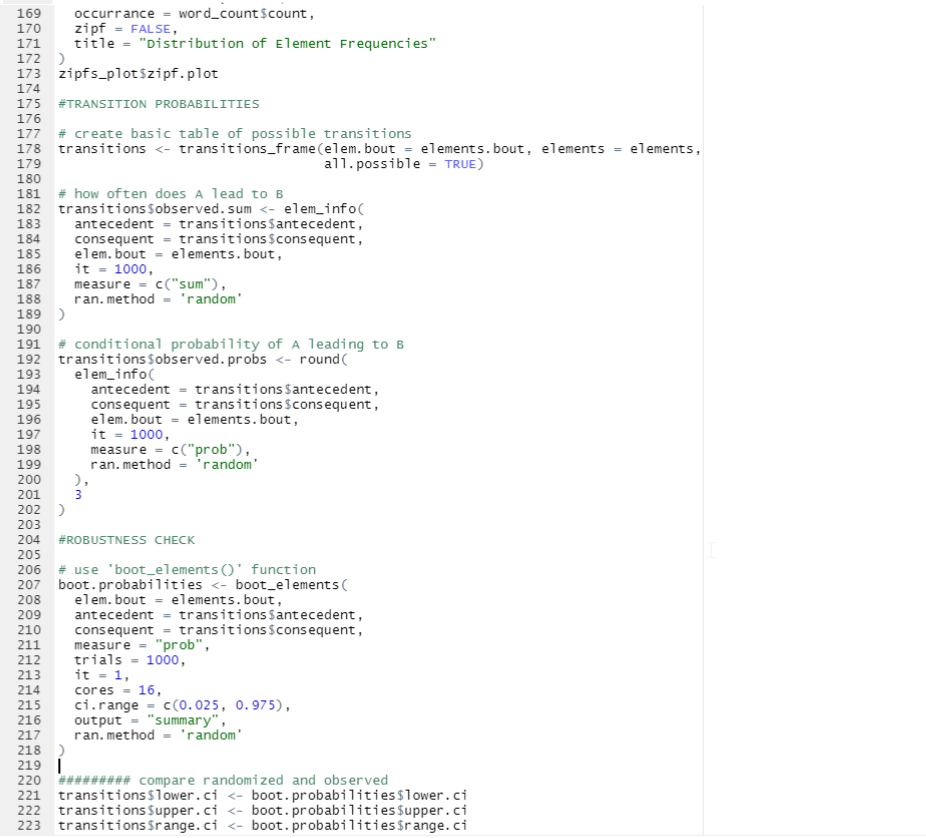

```r
#DATA MANIPULATION

element_table <-
  read_csv('E:/Sequence Learning Study/Data/Gorilla Data/Ethogram.csv', show_col_types = FALSE)
elements <- element_table$elements

video_data <-
  read_tsv("E:/Sequence Learning Study/Data/Gorilla Data/Gorilla Data For Code.tsv")

Oumbi <- video_data[video_data$Subject == "Oumbi", c("ObservationIDnum", "bout.nr" ,"Behavior","Time", "Subject")]
Lope <- video_data[ video_data$Subject == "Lope", c("ObservationIDnum", "bout.nr" ,"Behavior","Time", "Subject")]
Shufai <- video_data[video_data$Subject == "Shufai", c("ObservationIDnum", "bout.nr" ,"Behavior","Time", "Subject")]
Ozala <- video_data[video_data$Subject == "Ozala", c("ObservationIDnum", "bout.nr" ,"Behavior","Time", "Subject")]
Asante <- video_data[video_data$Subject == "Asante", c("ObservationIDnum", "bout.nr" ,"Behavior","Time", "Subject")]
Biddy <- video_data[video_data$Subject == "Biddy", c("ObservationIDnum", "bout.nr" ,"Behavior","Time", "Subject")]

#Name of Subject changed here to create outputs for each individual below example is Asante

Subject <- Asante

data <- subset(Subject, Behavior!="StartFeedingBout" & Behavior!="EndFeedingBout" & Behavior!="NoStart" & Behavior!="NoEnd")

# go through each bout, remove useless information
bout.data <- lapply(unique(data$bout.nr), function(x) {
  # select bout and sort by subject and time
  set.data <-
    filter(
      data,
      bout.nr == x,
      !"Behavior" %in% c(
        "NoStart",
        "NoEnd",
        "StartFeedingBout",
        "EndFeedingBout")
    ) %>%
    arrange("bout.nr", "Time")
  # vector with focals
  focal <- set.data$Subject
  # bout nr
  bout.nr <- sub(".*/", "", unique(set.data$bout.nr))
  # vector with time
  Time <- set.data$Time
  # put elements into list
  bout.elements <- list()
  for (i in 1:nrow(set.data)) {
    yy <-
      as.vector(unlist(strsplit(
        unlist(set.data[i, ]),
        split = ",", fixed = T
      )))
    yy <- intersect(yy, elements)
    bout.elements[[i]] <- yy
  }
  # elements that co-occur in event are combined by % symbol
  bout.elements <- sapply(bout.elements, paste, collapse = "%")
  # empty cells (i.e. those not containing a recognised element) get NA
```

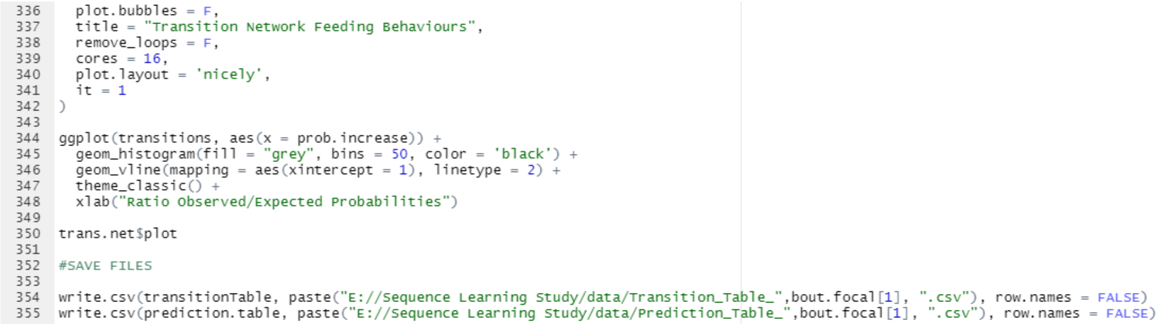


```r
  bout.elements[bout.elements == ""] <- NA
  return(data.frame(focal, bout.nr, Time, bout.elements))
})
# combine all bouts into one frame
bout.data <- bind_rows(bout.data)
# create individual-level bout identifier
bout.data$bout.nr.focal <- bout.data %>%
  unite(bout.nr, bout.nr, focal, sep = "_", remove = T) %>%
  select(bout.nr)
bout.data$bout.nr.focal <-
  as.vector(bout.data$bout.nr.focal$bout.nr)

# create list that has one vector of elements per individual-bout
elements.bout <-
  lapply(unique(bout.data$bout.nr.focal), function(x) {
    set.data <- filter(bout.data, bout.nr.focal == x)
    return(set.data$bout.elements)
  })

# create list that has one vector of times per individual-bout
elements.time <-
  lapply(unique(bout.data$bout.nr.focal), function(x) {
    set.data <- filter(bout.data, bout.nr.focal == x)
    return(set.data$Time)
  })

# create list of focal ID per individual-bout
bout.focal <- lapply(unique(bout.data$bout.nr.focal), function(x) {
  set.data <- filter(bout.data, bout.nr.focal == x)
  return(unique(set.data$focal))
})

# create list of bout ID per individual-bout
bout.id <- lapply(unique(bout.data$bout.nr.focal), function(x) {
  set.data <- filter(bout.data, bout.nr.focal == x)
  return(unique(set.data$bout.nr))
})

# name element-list and time-list using individual-bout id
names(elements.bout) <- unique(bout.data$bout.nr.focal)
names(elements.time) <- unique(bout.data$bout.nr.focal)


#ZIPF PLOT

unlisted_elements_table <-
  unlist_vector(elements.bout, method = "random") %>%
  table()
# Data frame containing words and their frequency
word_count <- unlisted_elements_table %>%
  data.frame(stringsAsFactors = FALSE) %>%
  rename("element" = '.', "count" = Freq) %>%
  arrange(desc(count)) %>%
  mutate(element = as.character(element))
zipfs_plot <- zipf_plot(
  element = word_count$element,
```



```r
  occurrance = word_count$count,
  zipf = FALSE,
  title = "Distribution of Element Frequencies"
)
zipfs_plot$zipf.plot

#TRANSITION PROBABILITIES

# create basic table of possible transitions
transitions <- transitions_frame(elem.bout = elements.bout, elements = elements,
                                 all.possible = TRUE)

# how often does A lead to B
transitions$observed.sum <- elem_info(
  antecedent = transitions$antecedent,
  consequent = transitions$consequent,
  elem.bout = elements.bout,
  it = 1000,
  measure = c("sum"),
  ran.method = 'random'
)

# conditional probability of A leading to B
transitions$observed.probs <- round(
  elem_info(
    antecedent = transitions$antecedent,
    consequent = transitions$consequent,
    elem.bout = elements.bout,
    it = 1000,
    measure = c("prob"),
    ran.method = 'random'
  ),
  3
)

#ROBUSTNESS CHECK

# use 'boot_elements()' function
boot.probabilities <- boot_elements(
  elem.bout = elements.bout,
  antecedent = transitions$antecedent,
  consequent = transitions$consequent,
  measure = "prob",
  trials = 1000,
  it = 1,
  cores = 16,
  ci.range = c(0.025, 0.975),
  output = "summary",
  ran.method = 'random'
)

######### compare randomized and observed
transitions$lower.ci <- boot.probabilities$lower.ci
transitions$upper.ci <- boot.probabilities$upper.ci
transitions$range.ci <- boot.probabilities$range.ci
```

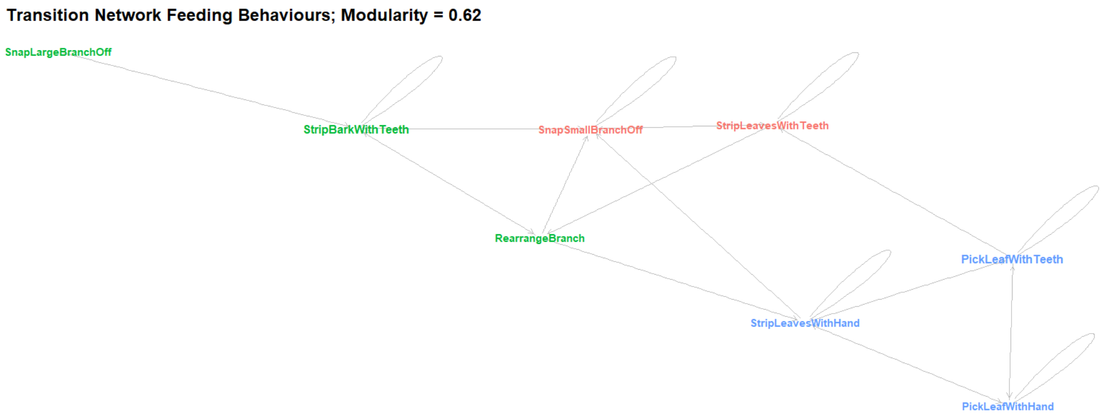
```r
transitions$range.ci <- boot.probabilities$range.ci
transitions$sd <- boot.probabilities$sd.ci
transitions$cv <- boot.probabilities$cv.ci

ggplot(data = transitions, aes(x = count.antecedent, y = range.ci)) +
  geom_point(alpha = 0.5) +
  theme_classic() +
  ylab("Range Credible Interval") +
  xlab("Count Element")

#STATISTICAL TESTS

randomizations <- randomized_elem_info(
  elem.bout = elements.bout,
  antecedent = transitions$antecedent,
  consequent = transitions$consequent,
  observed = transitions$observed.probs,
  it = 1,
  cores = 16,
  trials = 10000,
  type = "across",
  output = "expected"
)


transitions$expected.sum <- randomizations$sum
transitions$expected.probs <- round(randomizations$prob, 3)
transitions$pvalue <- round(randomizations$pvalue, 3)
transitions$z <- round(randomizations$z, 3)
transitions$prob.increase <-
  round(transitions$observed.probs / transitions$expected.probs, 3)

#Distribution of Transitional Probabilities

ggplot(transitions, aes(x = observed.probs)) +
  geom_histogram(fill = "grey", bins = 50, color = 'black') +
  theme_classic() +
  xlab("Conditional Transition Probabilities")

#Ratio Observed/expected

ggplot(transitions, aes(x = prob.increase)) +
  geom_histogram(fill = "grey", bins = 50, color = 'black') +
  geom_vline(mapping = aes(xintercept = 1), linetype = 2) +
  theme_classic() +
  xlab("Ratio Observed/Expected Probabilities")


#TABLE WITH RELEVANT DATA

transitionTable <- subset(transitions, select = c("antecedent", "consequent", "observed.probs", "expected.probs", "pvalue", "prob.increase"))

# PREDICTIONS

loo4 = prediction_loo(
  elem.bout = elements.bout,
  it = 1,
  trials = 100,
  cores = 8,
  lvl = 4,
  out = 20,
  prediction = 'product',
  ran.method = 'random'
)

prediction.table <-
  data.frame(level = seq_along(loo4)-1,
             prediction_accuracy =
               sapply(loo4, function(x){x$accuracy}),
             prediction_accuracy_naive_bayes =
               sapply(loo4, function(x){x$naivebayes.accuracy}),
             prediction_accuracy_forest =
               sapply(loo4, function(x){x$forest.accuracy})
  )

kableExtra::kbl(prediction.table,
                row.names = F,
                caption = "Prediction accuracy of applied transition probabilities at different levels: level 0 is the prediction based on
                the simple occurrence probability of each element, level 1 has one antecedent element, level 2 has two antecedents, etc",
                col.names = c('Level', 'Prediction Accuracy', 'Prediction Accuracy Naive Bayes', 'Prediction Accuracy Random Forest'),
                digits = 3)

## Warning in !is.null(rmarkdown::metadata$output) && rmarkdown::metadata$output
## %in% : 'length(x) = 4 > 1' in coercion to 'logical(1)'

#Similarity Cluster

similar.cluster <- similiarity_clusters(
  elem.bout = elements.bout,
  measure = c("prob"),
  k = NULL,
  it = 1,
  facet = FALSE,
  level = "bigram",
  ran.method = 'random',
  n_epochs = 8000,
  trials = 1000
)

similar.cluster$dendrogram.plot


# Transition Network

trans.net <- network_plot(
  elem.bout = elements.bout,
  edge.weight = "transition",
  min.prob = 0,
  min.count = 5,
  significance = 0.01,
  hide_unconnected = F,
  link = "unweighted",
  clusters = T,
```



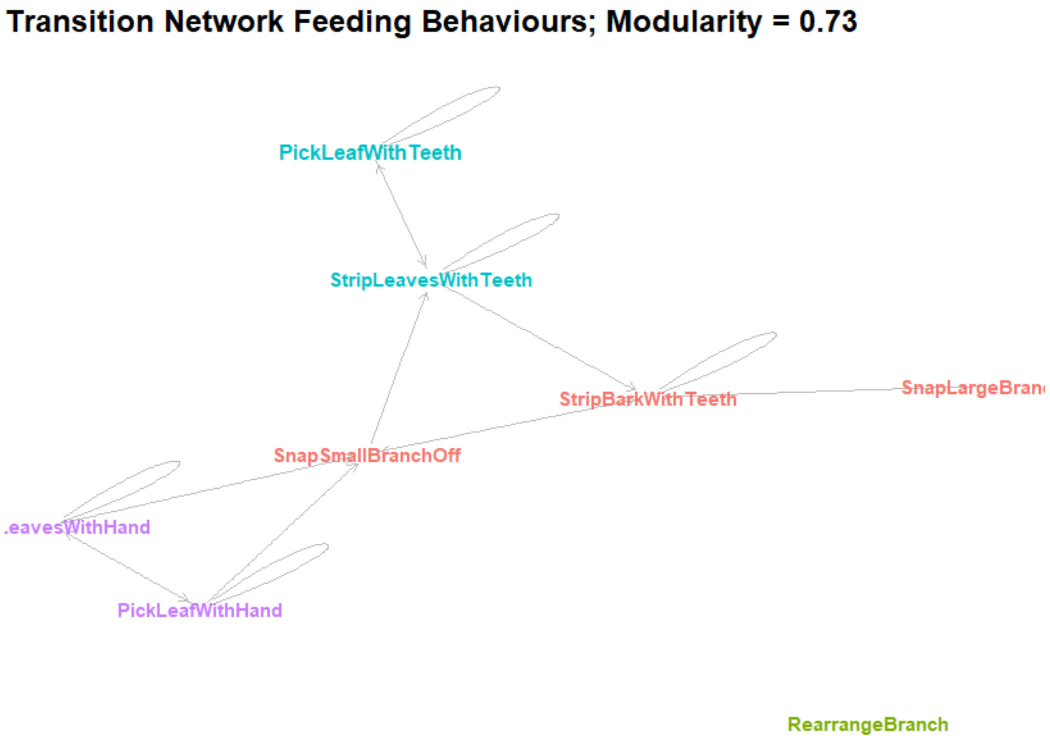
```r
  plot.bubbles = F,
  title = "Transition Network Feeding Behaviours",
  remove_loops = F,
  cores = 16,
  plot.layout = 'nicely',
  it = 1
)

ggplot(transitions, aes(x = prob.increase)) +
  geom_histogram(fill = "grey", bins = 50, color = 'black') +
  geom_vline(mapping = aes(xintercept = 1), linetype = 2) +
  theme_classic() +
  xlab("Ratio Observed/Expected Probabilities")

trans.net$plot

#SAVE FILES

write.csv(transitionTable, paste("E://Sequence Learning Study/data/Transition_Table_",bout.focal[1], ".csv"), row.names = FALSE)
write.csv(prediction.table, paste("E://Sequence Learning Study/data/Prediction_Table_",bout.focal[1], ".csv"), row.names = FALSE)
```

Appendix B - Raw Network Plots:

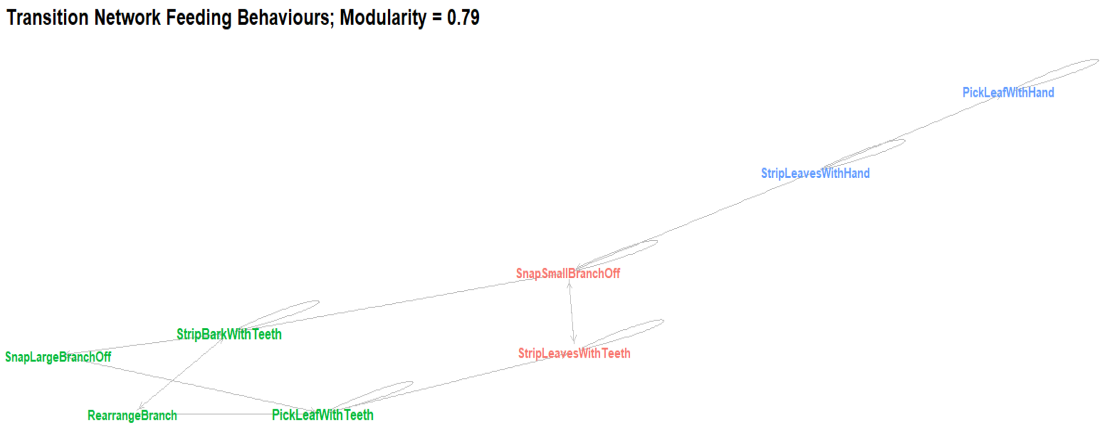
Oumbi



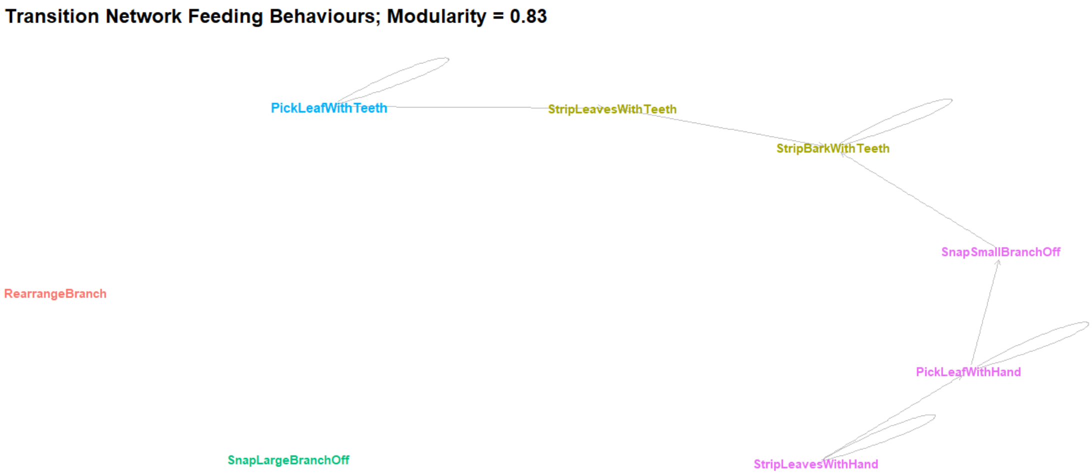
Biddy



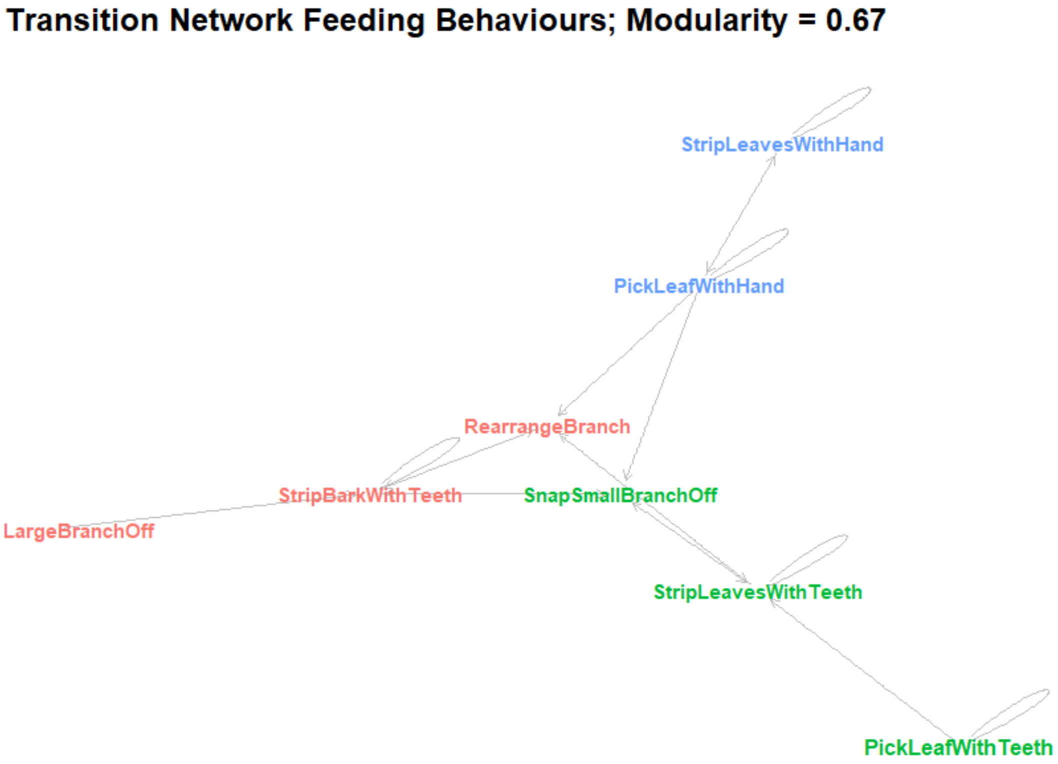
Lope


Transition Network Feeding Behaviours; Modularity = 0.79
PickLeafWithHand
StripLeavesWithHand
SnapSmallBranchOff
StripBarkWithTeeth
StripLeavesWithTeeth
SnapLargeBranchOff
RearrangeBranch
PickLeafWithTeeth

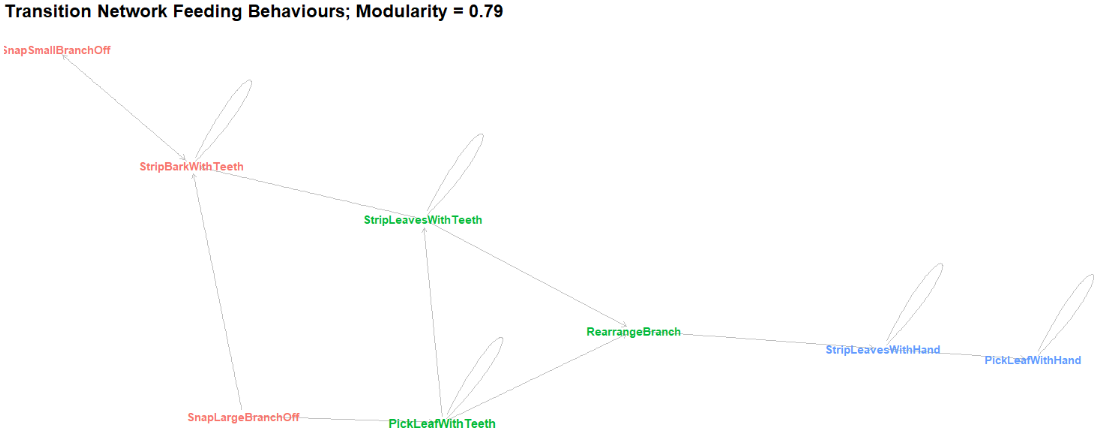
Asante


Transition Network Feeding Behaviours; Modularity = 0.83
PickLeafWithTeeth
StripLeavesWithTeeth
StripBarkWithTeeth
SnapSmallBranchOff
RearrangeBranch
PickLeafWithHand
SnapLargeBranchOff
StripLeavesWithHand

Ozala


Transition Network Feeding Behaviours; Modularity = 0.67

Shufai


Transition Network Feeding Behaviours; Modularity = 0.79

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