R Analysis: Tool Use & Carnivory in Primates

INTRODUCTION

The order Primates contains an incredible array of diversity in terms of types of phenotypic appearance, diet, behavioral repertoire, ecological niche, etc. There has been a significant body of research which explores how these variables may drive brain expansion in specific primate lineages. This paper expands the discussion of these variables to include tool use. Tool use is a behavior that is typically only observed in primates with relatively large encephalization quotients such as humans, as well as other apes and some monkeys such as capuchins and macaques. There has been less research in the types of variables associated with primate participation in tool use behaviors yet tool use likely played a pivotal role in human evolution. For instance, tools enable more efficient nutrient extraction as tools can aid primates in extracting nutrients from hard exterior food sources such as nuts and some animal species like turtles and shellfish. Indeed, tooling primates often use tools for food processing, such as Capuchins who semi-regularly use stone tools to crack nuts (Izar, 2022). This project serves as an initial exploration into the interactions between tool use, proteinogenic diet, and other variables thought to have importance in primates, such as social groupings, body weight and brain size.

DATA ACQUISITION

Data on primate fruit consumption, brain size, body size, and social groupings was obtained in the supplemental materials of Decasien et al.'s publication exploring fruit as a driver of brain size increase (DeCasien et al., 2022). Meat consumption data was gathered from Watt's review of meat eating behaviors across primates (Watt, 2020). A peer-reviewed publication which reviewed tool use behaviors in primates with a semi-comprehensive list of tool-using species could not be found. However, Wikipedia (https://en.wikipedia.org/wiki/Tool_use_by_non-human_animals) provided a table that contained data on tool-using species as well as the publication that reported the tool-use behavior. I reviewed the table and randomly sampled multiple entries to confirm that they were peer-reviewed. Given that this project serves only as an initial exploration into the data, I determined that it would be appropriate to scrape the primate tool-use data from Wikipedia.

METHODS IN R

I downloaded the DeCasien et al. data set from the supplemental materials and directly imported the file into R to be cleaned. In the Watt's review of meat eating behaviors, there was not a downloadable file. As a result, the table was manually copied into a .csv file prior to being imported into R. To streamline data collection, I used the rvest library in R to scrape the Wikipedia table and stored the data as a dataframe. I cleaned the column data by removing spaces and standardizing the case within the column names, and also created new columns based on existing data. I used for-loops to fill in null values when appropriate (for example, if two rows contained the same value in the "family" column but one of them had a null value in the "infraorder" column then the value in the non-null row would be copied into the null value row). I merged all imported dataframes together except for the meat-eating dataframe, as the others had a unique species for each row while the meat-eating dataframe had multiple rows of the same species and I did not want to lose the data specificity from collapsing the other variable values into an mean. These dataframes

were saved as two separate .csv files and both imported into this .Rmd file. The following analysis contains summary statistics of this data as well as visualizations to explore the possible connections between these variables among primates.

ANALYSIS

CARNIVORY ACROSS PRIMATES

The review from Watts included a table of primates that participate in meat eating behaviors and the types of prey these primates have been observed eating. Watts provided a detailed analysis at the species level of meat intake, but the larger scale divisions among primate infraorders and families were less explored. The following summary table compares monkeys, apes and tarsiers (haplorhines) against lemurs and loirses (strepsirhines) in terms of the types of prey consumed and the number of times these primates have been observed eating that prey type according to Watts review.

```
## # A tibble: 6 x 3
## # Groups:   prey [6]
##   prey        haplorrhini strepsirrhini
##   <chr>            <int>         <int>
## 1 amphibia            47             3
## 2 aves               147            13
## 3 mammalia           156             4
## 4 squamata            65            10
## 5 teleostei           13             0
## 6 vertebrata           3             0
```

It is obvious from this table that haplorhines participate in meat eating behaviors at a much greater frequency than strepsirhines. Compared against strepsirhines, haplorhines have 11x more observations of eating aves, 6x more observations of eating squamata, 16x more observations of eating amphibia, and 39x more observations of eating mammalia. This does not include the vertebrata category as the specific prey type is unknown. Notably, there have not been observations of strepshirrhines eating fish and this appears to be a prey type unique to haplorrhine species. When looking at this data at the family level, it is clear that the higher frequency of carnivorous behaviors in haplorhines is largely due to hominidae, cercopithecididae, cebidae and callitrichidae. The dominance these families' prey consumption can be observed in the below chart:

Prey Type Diversity in Primate Families
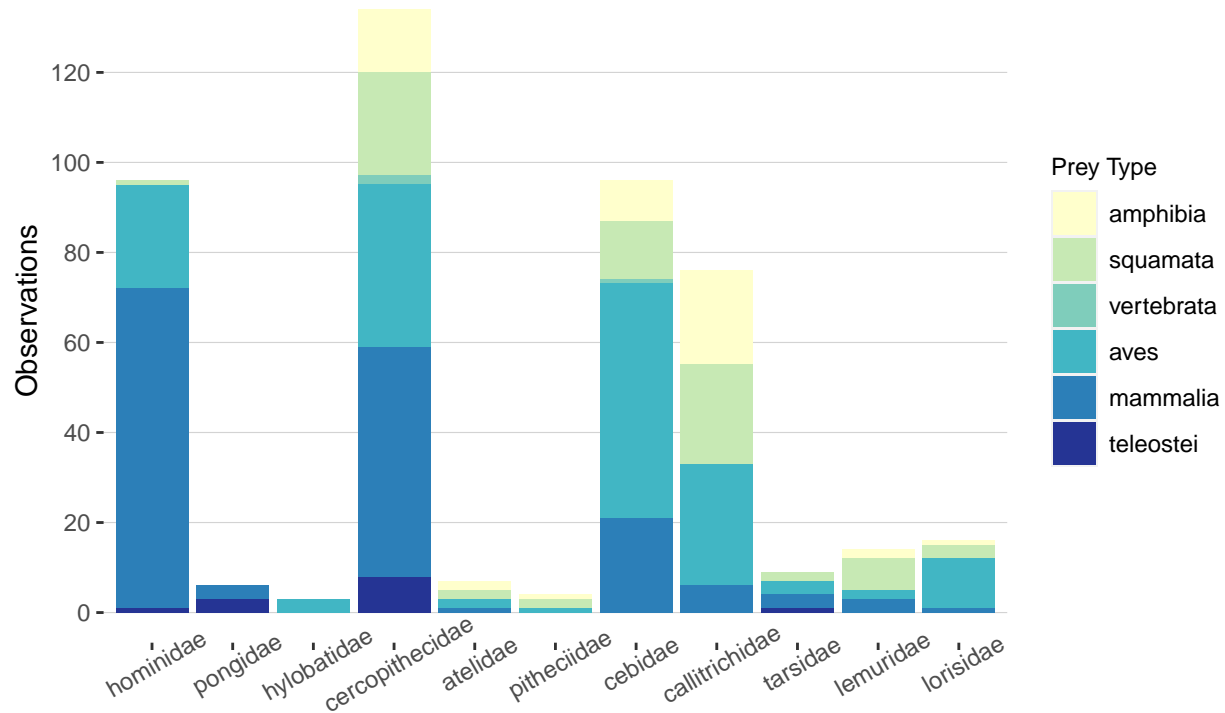
Interestingly, both hominidae and cercopithecidae appear to eat mammalia prey at much higher frequencies than cebidae or callitrichidae. Hominidae has the most observations of mammalia prey consumption compared to all other primate families. Cercopithecidae, cebidae and callitrichidae consume both squamata and amphibia as a sizable portion of their overall meat intake, however, consumption of these prey groups is rare in hominindae.

TOOL USE ACROSS PRIMATES

There are not any known tool-using strepsirrhine primates. Among haplorhines, there are 38 species who have been observed using tools. Unfortunately, there is not data readily available on the frequency of this tool use, therefore, these analyses are limited by a strict binary of known tooling primates versus non-tooling primates. Tool use does not occur evenly across haplorrhine primate families, but rather sporadically in only several primate families which are not always closely related. Of the 158 primate species represented within this dataset, the below graph shows the number of species by family who are known toolers (denoted as 1) versus non-toolers (denoted as 0):

```
## # A tibble: 9 x 3
## # Groups:   family [9]
##   family           '0'   '1'
##   <chr>          <int> <int>
## 1 aotidae            3     0
## 2 atelidae          10     2
## 3 callitrichidae    21     0
## 4 cebidae            9     6
## 5 cercopithecidae   56    23
```

```
## 6 hominidae          0      7
## 7 hylobatidae       11      0
## 8 pitheciidae       10      0
## 9 tarsidae           3      0
```

All species within hominidae (H. sapiens, P. troglodytes, P. paniscus, G. gorilla, G. beringei, P. abeli and P. pygmaeous) are observed tool users, although there is a known variability in frequency of tool use which is not evaluated within this exploration. Notably, hylobatidae does not have known tool users despite being the group most closely related to hominidae. Cercopithecidae has the highest number of tooling species out of all represented primate families, although the majority of species within this group are not known to use tools. Outside of hominidae and cercopithecidae, only cebidae and atelidae primates have been observed using tools.

## AN EXPLORATION OF TOOLING & PROTEINS IN PRIMATES

Research supports ties between diet and brain size, such as DeCasien's work linking increased fruit consumption to relatively larger brains across primates (DeCasien, 2017). Additionally, tool use is typically only employed by relatively larger brained primates, as demonstrated in the discussions of tool use across primates above. Given the support for both of these ideas, it is likely that there would also be associations between diet and tool use. Tool use is a complex behavior observed sporadically across only several primate groups and, when it is observed in a primate species, it is frequently for the purpose of nutrient extraction, although this depends on the primate species. This prompts the question: are the diets of tooling species different from non-tooling primate species? The below chart divides primates into tooling species and non-tooling species. Each primate species represents one count on the y-axis and the bars of this chart are colored by the type of dietary range in meat-eating for each of these primates.
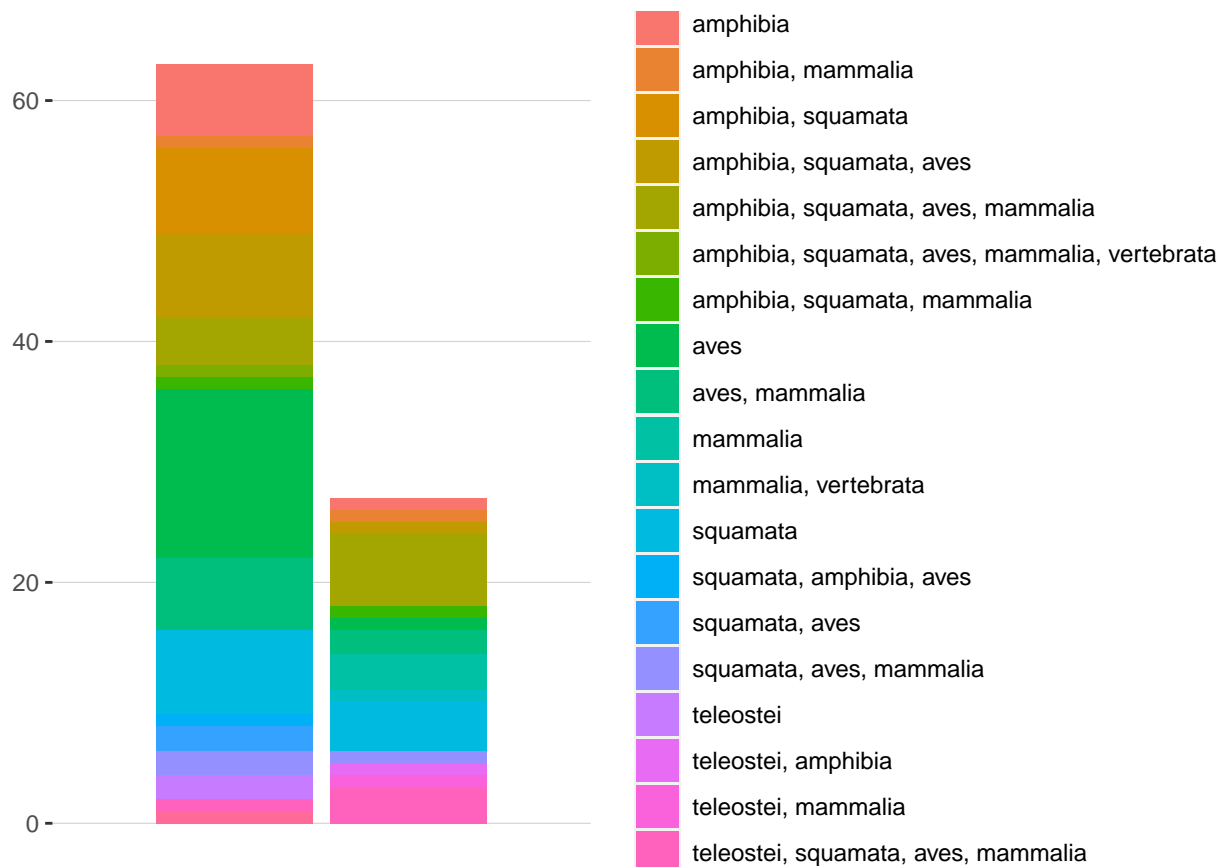
Although the effectiveness of this visualization is limited due to the large number of categories it depicts, it does showcase a couple interesting features. Firstly, the bottom, pink-colored region which represents the inclusion of fish in the primate diet is expanded in tooling species as opposed to non-tooling species. Secondly, primates whose observed meat consumption is exclusively birds as shown by the middle green category compose a sizable portion of the non-tooling species' meat intake but, in tooling species, this category has one of the smallest number of occurrences. According to this data, there are only 38 tool-using primates while there are 91 primate species known to eat meat, yet the tool-using primates make up almost half of the instances of meat eating behaviors.

In order to explore both tool use and meat eating behavior in the context of primate brain evolution, I ran a Welch Two Sample T-test on some of the variables of interest. There was not a difference in average primate brain size when comparing meat eaters versus non-meat eaters (p-value = 0.2499), although there was a difference when comparing tool users versus non-tool users (p-value = 0.001626). As brain size is negatively allometric to body size in primates, I created a new column called scaled_brain_body_size which was based on research suggesting a regression line with a slope of 0.0646 best described the brain-body relationship across primates (Isler, 2008). These results held when evaluating the difference in scaled brain size in meat eaters versus non-meat eaters (p-value = 0.9216), as well as scaled brain size in tool users versus non-tool users (p-value = 0.003476).

Finally, to explore the relationship between scaled brain size, observed meat eating behavior, observed tool use and the added variable of primate group size, a scatterplot was created:
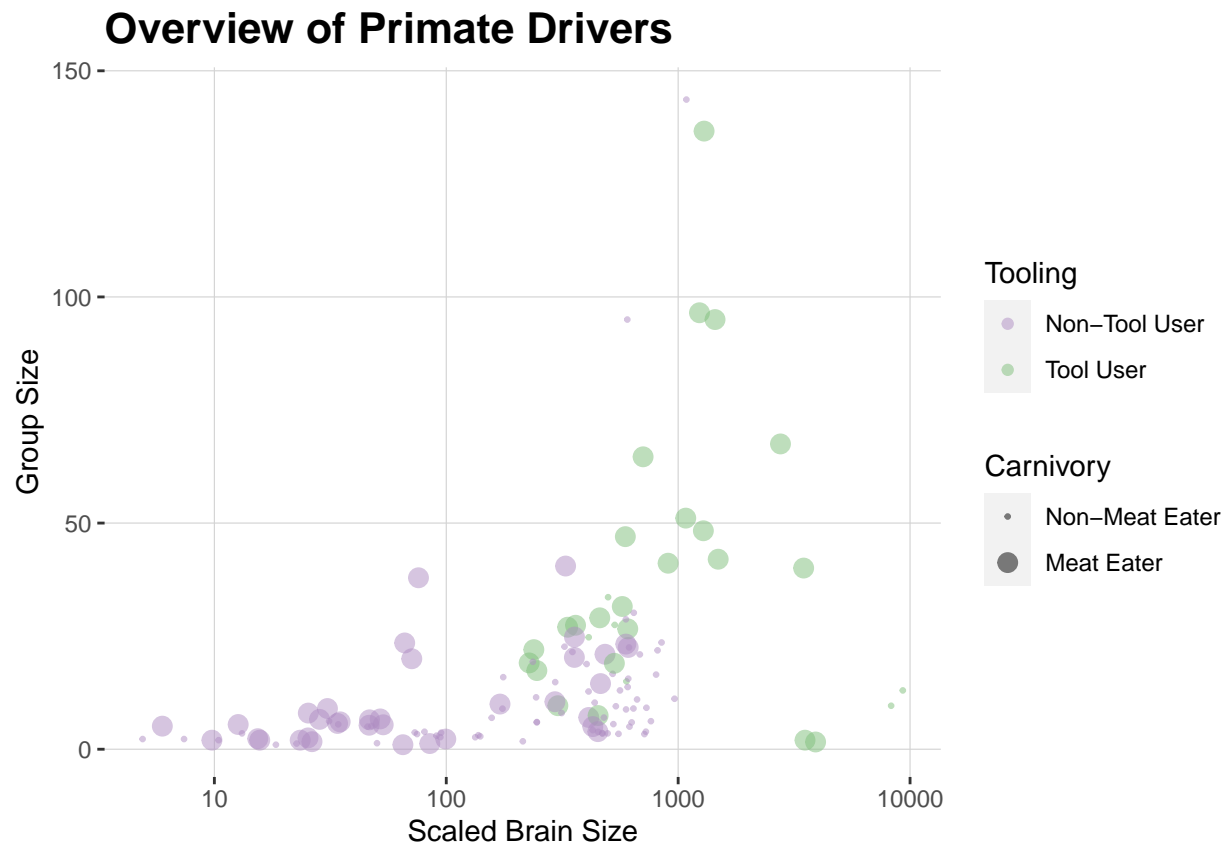
Scaled brain size represents the x-axis, while average primate group size represents the y-axis. In this plot, the difference in circle size reflects if the primate is known to eat meat (large circle) or is not known to eat meat (small circle), while the color indicates if the primate is a tooling species (green) or a non-tooling species (purple). There is an obvious association with scaled brain size and tool use. Interestingly, almost all tooling species, as represented by the color green, have large circles which indicates meat eating behavior with the exception of two small green dots which represent Gorilla species.

DISCUSSION

This work is only an initial exploration into this topic, although I am interested in expanding the dataset in terms of primate species representation as well as including more high quality data. For example, it would be more informative to have frequency data, rather than dividing primates into binaries which cannot capture variation in behaviors. The largest barrier to this work is, while there is a large amount of research within this field on tool use behaviors and diet composition, it has not been synthesized into a larger dataset across primates. Instead, this information usually exists in publications focusing on a specific species and, as a result, someone would need to manually go through numerous publications to extract individual species information and do this hundreds of times over to create a comprehensive dataset. I am interested in pursuing a project which uses web scraping techniques to help automate this process and use existing primatology research to create novel, more comprehensive datasets in order to evaluate macroevolutionary trends in primates and I intend to work towards this goal during the summer.

REFERENCES

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. Nature ecology & evolution, 1(5), 0112.

Isler, K., Kirk, E. C., Miller, J. M., Albrecht, G. A., Gelvin, B. R., & Martin, R. D. (2008). Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. Journal of Human Evolution, 55(6), 967-978.

Izar, P., Peternelli-dos-Santos, L., Rothman, J. M., Raubenheimer, D., Presotto, A., Gort, G., ... & Fragaszy, D. M. (2022). Stone tools improve diet quality in wild monkeys. Current Biology, 32(18), 4088-4092.

Watts, D. P. (2020). Meat eating by nonhuman primates: a review and synthesis. Journal of human evolution, 149, 102882.

APPENDIX

I. Table of Variables in Dataframe1 This table contains the variable names and their associated definitions for all columns within the first dataframe.

Glossary of Terms

Term

Definition

species

The taxonomic name of the primate

mean_brain

The primate's average brain size

diet_category

The type of diet in terms of frugivory, folivory and omnivory

per_fruit

The percent of fruit intake relative to other dietary elements

mean_groupsize

The average groupsize of the primate

social_system

The type of social system used by primate

mating_system

The type of mating system used by primate

tool_type

Provides info about the type of tool use by tooling primates

body_weight

The average body weight of the primate

infraorder

The taxonomic infraorder of the primate

superfamily

The taxonomic superfamily of the primate

family

The taxonomic family of the primate

prey

The taxonomic group of primate prey

prey_order

The taxonomic order of primate prey

prey_family

The taxonomic family of primate prey

use_tools

Binary of observed tool use in primate. 0=no tool use; 1=tool use

genus

The taonomic genus of the primate

meat_eater

Binary of observed meat eating in primates. 0=no meat-eating; 1=meat-eating

II. Summary of Variables in Dataframe1

```
##     species              mean_brain       diet_category           per_fruit
##   Length:205        Min.   :    1.778   Length:205           Min.    : 0.00
##   Class :character   1st Qu.:   15.561   Class :character     1st Qu.:22.25
##   Mode  :character   Median :   61.197   Mode  :character     Median :49.00
##                      Mean   :   78.568                        Mean    :45.91
##                      3rd Qu.:   96.606                        3rd Qu.:67.08
##                      Max.   : 1274.881                        Max.    :92.00
##                      NA's   :40                               NA's    :115
##   mean_groupsize     social_system       mating_system        tool_type
##   Min.   : 1.000    Length:205          Length:205           Length:205
##   1st Qu.: 3.882    Class :character    Class :character     Class :character
##   Median : 9.167    Mode  :character    Mode  :character     Mode  :character
```

7

```
##   Mean    : 17.578
##   3rd Qu.: 21.860
##   Max.   :143.640
##   NA's    :48
##    body_weight        infraorder        superfamily         family
##   Min.   :     48.39  Length:205         Length:205         Length:205
##   1st Qu.:    862.07  Class :character   Class :character   Class :character
##   Median :   4516.32  Mode  :character   Mode  :character   Mode  :character
##   Mean   :   7767.46
##   3rd Qu.:   7842.66
##   Max.   :136212.60
##   NA's   :61
##      prey             prey_order        prey_family        use_tools
##   Length:205         Length:205         Length:205         0:167
##   Class :character   Class :character   Class :character   1: 38
##   Mode  :character   Mode  :character   Mode  :character
##
##
##
##
##      genus            meat_eater  scaled_brain_body_size
##   Length:205         0:114       Min.   :    4.904
##   Class :character   1: 91       1st Qu.:   72.629
##   Mode  :character               Median :  357.059
##                                  Mean   :  586.020
##                                  3rd Qu.:  604.333
##                                  Max.   : 9308.293
##                                  NA's   :69
```

III. Table of Variables in Dataframe2 This table contains the variable names and their associated definitions for all columns within the second dataframe which contained the specific detail on diversity of prey type in meat eating primates.

Glossary of Terms

Term

Definition

species

The taxonomic name of the primate

mean_brain

The primate's average brain size

diet_category

The type of diet in terms of frugivory, folivory and omnivory

per_fruit

The percent of fruit intake relative to other dietary elements

mean_groupsize

The average groupsize of the primate

social_system

The type of social system used by primate

mating_system

The type of mating system used by primate

tool_type

Provides info about the type of tool use by tooling primates

body_weight

The average body weight of the primate

infraorder

The taxonomic infraorder of the primate

superfamily

The taxonomic superfamily of the primate

family

The taxonomic family of the primate

prey

The taxonomic group of primate prey

prey_order

The taxonomic order of primate prey

prey_family

The taxonomic family of primate prey

use_tools

Binary of observed tool use in primate. 0=no tool use; 1=tool use

genus

The taonomic genus of the primate

meat_eater

Binary of observed meat eating in primates. 0=no meat-eating; 1=meat-eating

scaled_brain_body_size

Brain size scaled to body size based on regression line thought to best represent the relationship between brain and body size in primates

IV. Summary of Variables in Dataframe2

```
##   infraorder          superfamily                    family        species
##  Length:461           Length:461        cercopithecidae:134    Length:461
##  Class :character    Class :character   hominidae      : 96    Class :character
##  Mode  :character    Mode  :character   cebidae        : 96    Mode  :character
##                                         callitrichidae : 76
##                                         lorisidae      : 16
##                                         lemuridae      : 14
##                                         (Other)        : 29
##          prey       prey_order       prey_family        parvorder
##  amphibia  : 50    Length:461        Length:461         Length:461
##  squamata  : 75    Class :character  Class :character   Class :character
##  vertebrata:  3    Mode  :character  Mode  :character   Mode  :character
```

```
##  aves      :160
##  mammalia  :160
##  teleostei : 13
##
```