

Evolutionary pressures on primate intertemporal choice*

Jeffrey R. Stevens[†]
Department of Psychology
Center for Brain, Biology, and Behavior
University of Nebraska-Lincoln

May 15, 2014

Abstract

From finding food to choosing mates, animals must make intertemporal choices that involve fitness benefits available at different times. Species vary dramatically in their willingness to wait for delayed rewards. Why does this variation across species exist? An adaptive approach to intertemporal choice suggests that time preferences should reflect the temporal problems faced in a species' environment. Here, I use phylogenetic regression to test whether allometric factors (relating to body size), relative brain size, and social group size predict how long 13 primate species will wait in laboratory intertemporal choice tasks. Controlling for phylogeny, a composite allometric factor that includes body mass, absolute brain size, lifespan, and home range size predicted waiting times, but relative brain size and social group size did not. These findings support the notion that selective pressures have sculpted intertemporal choices to solve adaptive problems faced by animals. Collecting these types of data across a large number of species can provide key insights into the evolution of decision making and cognition.

Keywords: allometry, brain size, decision making, intertemporal choice, primates, social group size

Introduction

Should a hungry baboon stop to eat a few nearby seeds or continue on to the larger but more distant fruit patch? Should a female manakin accept her current mate or search around for a better one? From finding food to choosing a mate, animals must make intertemporal choices

*Published as: Stevens, J.R. (2014). Evolutionary pressures on primate intertemporal choice. *Proceedings of the Royal Society of London, Series B*, 281, 20140499. DOI:[10.1098/rspb.2014.0499](https://doi.org/10.1098/rspb.2014.0499)

[†]Correspondence concerning this article should be addressed to Jeffrey R. Stevens, B83 East Stadium, University of Nebraska-Lincoln, Lincoln, NE 68588-0156, USA, E-mail: jeffrey.r.stevens@gmail.com

that involve fitness benefits available at different times [1, 2]. Species vary dramatically in their willingness to wait for delayed rewards. Though pigeons, rats, and tamarins wait just a few seconds for three times as much food, bonobos and chimpanzees can wait 1-2 minutes [3]. Why does this variation across species exist?

An adaptive approach to intertemporal choice suggests that time preferences should reflect the temporal problems faced in a species' environment [1, 4, 5]. A species' ecology may involve specific temporal requirements, such as the need to wait to acquire food. Ambush predators such as praying mantids, for instance, must wait motionless for minutes on end to capture prey wandering by. This foraging strategy may favor the ability to wait for long time periods to acquire food in general. Therefore, species that experience delays when foraging in the wild may have evolved decision mechanisms that allow them to wait for delayed food rewards in laboratory intertemporal choice tasks.

Pairwise species comparisons support this notion that animal intertemporal choices are shaped by evolutionary pressures. For example, common marmosets (*Callithrix jacchus*) frequently chew on tree bark and wait for sap to exude, a foraging technique that involves a time delay. In contrast, the closely related cotton-top tamarins (*Saguinus oedipus*) do not rely on gum, instead focusing on quickly snatching nearby insects [6, 7]. In laboratory intertemporal choice tasks in which individuals choose between a smaller food reward now vs. a larger food reward after a delay, the gum-eating marmosets also wait longer than the tamarins [8]. As another example, chimpanzees (*Pan troglodytes*) hunt monkeys and other small mammals much more frequently than does the closely related bonobo (*Pan paniscus*). These hunts require waiting on average 21 minutes (range 1-120 minutes) between initiating a hunt and capturing the prey [9]. Likewise, chimpanzees wait longer than bonobos in laboratory intertemporal choice tasks [10, 11]. Thus, performance on laboratory intertemporal choice tasks reflects the temporal demands observed in some natural foraging situations.

Pairwise comparisons allow researchers to hold constant many potential factors that may influence choices and only manipulate a small set of potential factors. These studies, however, tend to focus on a single hypothesis at a time. Recent data provide measures of intertemporal choice using similar methodologies for 13 species of primates. This offers, for the first time, the ability to use phylogenetic comparative methods [12] to test multiple hypotheses simultaneously and explore larger-scale factors that may underlie temporal preferences. In this study, I investigate three hypotheses, testing whether allometric, cognitive, and social factors influence intertemporal choices in primates.

Allometric relationships describe how morphological, physiological, and behavioral measures scale with body size [13]. Stevens & Mühlhoff [3] showed that waiting times increased with mean species body mass. This could occur because metabolism allometrically scales with body size: species with lower body mass also tend to have faster metabolic rates [14–16]. Shorter wait times would provide adaptive benefits for individuals with faster metabolic rates, because they simply cannot wait to replenish the energy burned by metabolism [1, 17]. Similarly, lifespan scales with body size [16], which also may provide adaptive benefits. Short-lived species should also have shorter waiting times because they might not live long enough to reap the future rewards [1, 18]. If we use body size as a proxy for these allometric relationships, the *body size hypothesis* predicts that larger species should wait longer than smaller species.

In humans, the ability to wait for delayed rewards correlates with higher performance

in cognitive measures such as IQ, academic success, standardized tests scores, and working memory capacity [19–21]. The *cognitive ability hypothesis* predicts that species with higher levels of cognition should wait longer than those with lower levels. Unfortunately, we do not have reliable data on general cognitive abilities across all of these primate species [for a subset, see 22, 23]. Brain size is often used as a proxy for more sophisticated cognition. Researchers have found that aspects of cognition such as behavioral innovation (developing new behaviors to solve problems) [24], tactical deception (the strategic manipulation of behavior in others) [25], and general cognitive ability [26] positively correlate with absolute and relative brain size (brain size scaled to body size). Thus, we can test the cognitive ability hypothesis using these two measures of brain size as proxies of cognition. This hypothesis predicts that larger brain sizes should result in longer wait times for intertemporal choice.

Researchers have proposed social complexity as a key selective pressure on decision making [27, 28]. Amici *et al.* [29] suggested that primate species exhibiting more fission-fusion social dynamics (a fluid splitting and joining of groups) demonstrated longer waiting times in an intertemporal choice task. They argued that the constant social flux associated with fission-fusion systems would select for individuals that carefully attend to the presence and absence of dominants and subordinates and inhibit impulsive responses based on this knowledge. The *social brain hypothesis* predicts that species living in more socially complex groups should adaptively wait longer than those in less complex groups. Though we do not have measures of fission-fusion dynamics for primates, we do have measures of group size. Therefore, the social brain hypothesis predicts that wait times should increase with group size.

To investigate these hypotheses, I aggregated data from the literature on intertemporal choice, variables related to body size (body mass, lifespan, home range size), brain size (absolute and relative), and group size, for 13 species of primates: black lemurs (*Eulemur macaco*), red-ruffed lemurs (*Varecia rubra*), black-and-white-ruffed lemurs (*Varecia variegata*), cotton-top tamarins (*Sagwinus oedipus*), common marmosets (*Callithrix jacchus*), brown capuchins (*Sapajus apella*), black-handed spider monkeys (*Ateles geoffroyi*), long-tailed macaques (*Macaca fascicularis*), rhesus macaques (*Macaca mulatta*), orangutans (*Pongo pygmaeus*), lowland gorillas (*Gorilla gorilla*), bonobos (*Pan paniscus*), and chimpanzees (*Pan troglodytes*). I then conducted phylogenetic regression analysis to assess which variables predicted intertemporal choices.

Methods

I collected intertemporal choice, body size, and socio-ecological data from the literature using original sources when possible. Therefore, most of the data use individuals (indifference points, body mass, brain volume, home range size, lifespan) or the groups/populations (group size) as the unit of data. If only aggregated information was published, I collected mean, median, standard deviation, range, and sample size when available. Data S1 includes all data used in this analysis. Table S1 summarizes and includes the references for all data.

I collected intertemporal choice data from delay choice experiments with adjusting delays or amounts (Figure S1). Most data were collected using a standard procedure in which subjects initially chose between two and six food rewards both available immediately [3, 8, 10, 30, 31]. Then, if the subject chose the larger reward consistently across a session, the

experimenter increased the delay to the large reward in the next session. The experimenter continued to adjust the delay until the subject chose equally (i.e., established indifference) between the two options. Other studies either used different rewards amounts [one vs. three food rewards, 29] or used other adjusting procedures to calculate discounting functions from which I could estimate an indifference point [32, 33]. Rhesus macaque experiments [32, 33] used liquid food rewards (water or juice), whereas all other experiments involved solid food rewards. For each subject, I used the mean delay to the larger reward as the dependent variable representing intertemporal choice.

I collected body mass, home range size, and group size data from numerous sources from the literature. When possible, I used body mass data for the subjects who were tested in the delay choice task [8]. For absolute brain size, I used Isler’s [34] endocranial volume measurements based on filling the endocranial cavity of skulls with sand, seeds, or beads. For relative brain size, I used the residuals from a phylogenetic generalized least squares regression [35, 36] with log body mass predicting log absolute brain size [37]. Lifespan data included the single maximum age recorded in the literature for each species (captive or wild).

I calculated mean values for each measure (indifference points, body mass, brain volume, home range size, lifespan, group size) for each species (Table S1). In some cases, only aggregated rather than individual data were available. Therefore, I calculated weighted means for each measure by weighting the values by the published sample sizes. If no sample sizes were available, I treated the data as individual cases and assigned a sample size of 1. Mean values of the measures generally agreed with values found in the PanTHERIA data base of mammalian life history and ecological traits [38]. I log-transformed all raw measures for this analysis to facilitate linear regression analyses. Permutations of these raw measures (principal components analysis scores, residuals from regressions) were not transformed.

Large-scale comparative studies suffer from lack of statistical independence due to varying degrees of phylogenetic relatedness [36, 39]. More closely related species share more recent common ancestry, rendering their traits nonindependent. Phylogenetic generalized least squares analyses [35, 36] conduct a statistical model that includes phylogenetic relationships in the variance-covariance matrix to account for this nonindependence problem. To employ this analysis, I estimated a phylogeny of the primates included in this analysis (Figure S2), using 10kTrees version 3 ([http:// 10ktrees.fas.harvard.edu/index.html](http://10ktrees.fas.harvard.edu/index.html)) [40]. I then used phylogenetic generalized least squares to conduct a multiple regression that accounted for phylogeny.

The allometric variables of body mass, absolute brain volume, lifespan, and home range size were highly correlated (range: $r = 0.91-0.98$), though not correlated with relative brain size or group size (Figure S3). To avoid the problem of multicollinearity in multiple regression, I implemented a variable reduction strategy of aggregating these allometric variables into a single measure using principal component analysis. For the principal component analysis, I standardized the measures for the log-transformed values for each variable before generating a body size score for each species. This resulted in the absolute brain size measure being collapsed into the allometric variables, preventing its independent test for the cognitive ability hypothesis.

I analyzed the data using R statistical software version 3.1.0 [41], including the following R packages: caper [42], car [43], foreach [44], lattice [45], latticeExtra [46], and psych [47].

Results

In the principal component analysis on allometric variables, the first component accounted for 96% of the variance, with variable loadings ranged from 0.97-0.99. I used the values from the first principal component as my allometric score for the analyses.

Pairwise correlations between intertemporal choices and the predictor variables (Figure 1) showed correlations between allometric score and log-transformed waiting times ($r = 0.85$ [95% confidence interval: 0.56 - 0.95]) but not relative brain size ($r = -0.06$ [-0.59 - 0.51]) or log-transformed group size ($r = 0.4$ [-0.20 - 0.78]).

A multiple regression analysis tested whether allometric score, relative brain size or log-transformed group size predicted log-transformed waiting times. The analysis indicated that the three predictors produced an adjusted $R^2 = 0.71$, $F_{4,9} = 10.7$, $p < 0.01$. Allometric score predicted waiting times ($\beta = 0.82$, $p < 0.01$), but relative brain size ($\beta = -0.27$, $p = 0.13$) and group size ($\beta = 0.24$, $p = 0.11$) did not predict waiting times. An analysis using log-brain-volume-to-body-size ratio as a measure of relative brain size yielded similar results.

The phylogenetic least squares analysis generates a maximum-likelihood estimate of phylogenetic signal (λ), that is, whether phylogeny influences the traits under investigation. This analysis generated an estimate of $\lambda = 0.71$, which did not differ from 0 ($p = 0.15$). This finding does not provide support that phylogeny significantly influenced the traits, though this may result from low power due to the small sample size.

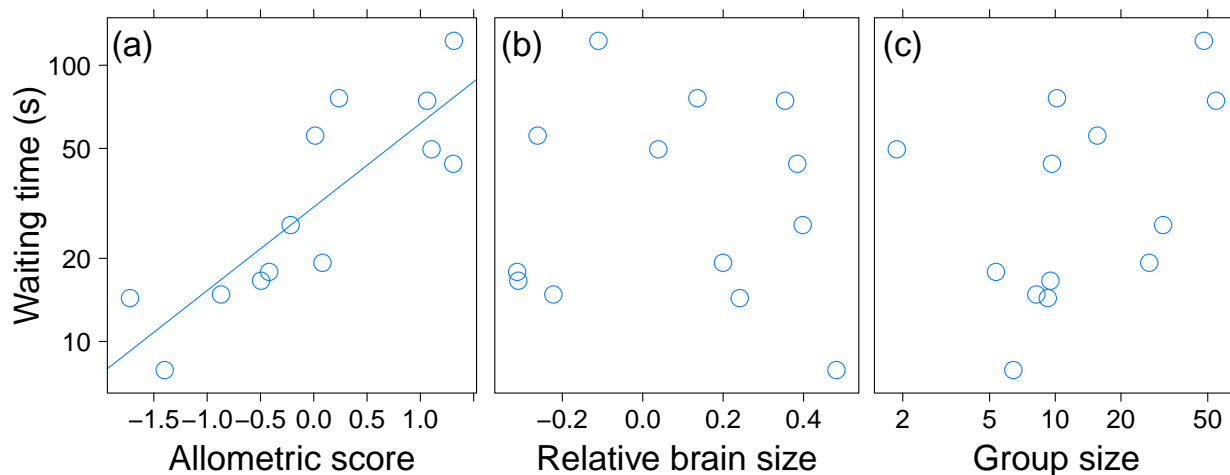


Figure 1: Relationship between waiting time and allometric score, relative brain size, and group size. Each data point represents the mean values for a species, and the lines represent statistically significant regression lines. Waiting time data are plotted on a log scale. (a) Allometric score (from principal component analysis including body mass, absolute brain size, lifespan, and home range size) significantly predicts waiting times ($R^2 = 0.72$). (b) Relative brain size (residuals from regressing log body mass and log absolute brain size) does not predict waiting time ($R^2 = 0.00$). (c) Group size (plotted on a log scale) does not predict waiting time ($R^2 = 0.16$).

Discussion

Allometric variables predicted the ability to wait for delayed rewards in a delay choice task across 13 species of primates (Figure 1a). I aggregated the allometric variables of body mass, absolute brain volume, lifespan, and home range size in this analysis using principal component analysis due to their high correlations. The high loadings of the variables in the first principal component provide evidence for a single allometric component for these data. Relative brain size and group size did not predict waiting times (Figure 1b&c). Intertemporal choices, therefore, demonstrate large-scale relationships with factors relating to body size but not cognitive or social variables.

The strong relationship between waiting times and allometry matches a previous result demonstrating that waiting times correlated positively with body mass [3]. This result supports the adaptive nature of the allometric scaling hypothesis because waiting times scale with two factors relevant to delays: lifespan and metabolic rate. Lifespan, or more precisely life expectancy, should shape temporal preferences [1, 18]. Low life expectancy means that an individual may not live long enough to receive a delayed payoff, so selection should favor choosing more immediate payoffs. This relationship occurs not just for species-level measures of longevity but also for individual expectations of survival. For instance, when female *Leptopilina* wasps detect cues of an impending and potentially life-threatening storm, they deposit more eggs, possibly in response to the decreased probability of survival [48]. Though lifespan may shape temporal preferences in some circumstances, it likely does not account for the pattern observed in the data presented here due to the large difference in time scales between the intertemporal choice data (measured in seconds) and lifespans (measured in decades).

Metabolic rate provides a factor highly correlated with lifespan but with more relevance to the time frames of the intertemporal choice task. Species with higher metabolic rates may have shorter waiting times for food because they need food sooner to meet energetic demands [1, 17]. Unfortunately, we do not have consistent metabolic rate data for most of the species in this analysis, so we could not test this factor. However, increases in waiting times are associated with larger body size and longer lifespans in this data set. Since body size and lifespan negatively correlate with metabolic rate [14–16], this finding aligns with the predictions of longer wait times with lower metabolic rates.

The cognitive ability hypothesis predicts that species with higher general cognitive abilities will wait longer. This hypothesis is based on the relationship between individual differences in intertemporal choice and cognitive ability demonstrated in the human literature. Children who wait longer for delayed rewards also have higher IQs ($r = 0.29-0.42$), grade-point averages ($r = 0.55-0.67$), and standardized tests scores ($r = 0.42-0.57$) [19, 20, 49, 50]. I used absolute and relative brain size as proxies for general cognition [26]. Because absolute brain size scaled with body size, it was subsumed into the allometric score to avoid problems associated with multicollinearity. Therefore, I did not test absolute brain size separately from the allometric variables. In the principal component analysis for allometry, brain volume had the highest loading of 0.99, highlighting the importance of absolute brain size for this analysis. It remains unclear whether absolute brain size contributes to species differences in intertemporal choice beyond other allometric variables. Despite the strong predictive power of absolute brain size via the allometric score, relative brain size did not

predict intertemporal choice. This is a bit surprising given that brain-to-body size ratio, encephalization quotient, and neocortex-to-whole brain size ratio correlate with aspects of cognition and social complexity [24, 25, 37, 51, 52]. Other evidence, however, corroborates this finding that absolute brain size more strongly relates to cognition than does relative brain size [26, 53–56].

The social brain hypothesis predicts that species living in more complex groups will wait longer. Group size did not predict intertemporal choice (Figure 1b), though visually inspecting the data suggests a weak pattern of longer waiting times in larger groups. Removing the potential outlier of the orangutan data results in a significant pairwise correlation with intertemporal choice ($r = 0.64$ [0.10 - 0.89]). However, a phylogenetic multiple regression omitting the orangutan data still does not show an effect of group size ($\beta = 0.29$, $p = 0.16$, $R^2 = 0.41$). A larger sample of species may clarify this relationship. This finding does not rule out the importance of other forms of social complexity on temporal preferences. Fission-fusion dynamics, for instance, may predict intertemporal choices [29] because the dynamics refer to the structure of the social group rather than simply the size of the group. Thus, social behavior may still have important influences on intertemporal choice, even though overall group size per se may not capture this relationship.

This study is limited in the number of species tested and in the phylogenetic distribution of species. Though all major groups (superfamilies) of primates are represented (except lorises and tarsiers), the sample is skewed toward great apes (four of six great ape species) with only 2-3 representatives from the other groups. Testing additional species would obviously improve our ability to test hypotheses about evolutionary influences on intertemporal choice. Given this initial work, we can use phylogenetic targeting [57] to select specific species that provide the most powerful tests of these hypotheses. Further work should not only add more representative or targeted species but also incorporate the within-species variation included in the current data set.

Another limitation of this study involves the methods used to measure intertemporal choice. A key advantage of the data set used here is that researchers used fairly consistent methods to measure intertemporal choice across species. It remains unclear, however, what exactly these methods measure. The repeated nature of the task likely engages foraging rate-based decision mechanisms [1, 4, 58], which differ substantially from the notion of patience or self-control in humans. Moreover, Stephens [59] has argued that some findings using these methods may result from constraints on information-processing abilities (e.g., discrimination abilities for various time delays and reward amounts). Thus, species differences in information processing may underlie some of the species differences observed in intertemporal choices. Finally, studies testing the same individuals in both the delay choice task used here and a related “delay maintenance” task showed limited evidence for a correlation between the two tasks, suggesting that they may not measure the same construct [60]. Therefore, validating the findings presented here requires using converging evidence by testing multiple methods across species.

The data presented here allow us to test broad-scale factors that may influence intertemporal choice. The results support the notion that selective pressures have sculpted temporal preferences to solve adaptive problems faced by animals. In particular, waiting for delayed rewards may depend on whether metabolic demands can be met or whether the individual will live long enough to acquire the delayed reward. These general patterns do not, how-

ever, replace the smaller scale factors that influence preferences. Indeed, factors such as species-specific foraging ecology likely play a key role in intertemporal choice [1, 31], though broad-scale patterns may not exist to capture this relationship. Similarly, we would expect individual differences in temporal preferences based on sex, age, and dominance status, along with situational differences depending on hunger level, mating status, etc. Thus, numerous factors converge to determine an individual's choice for any particular decision. Nevertheless, broad-scale analyses can elucidate general evolutionary factors influencing intertemporal choice.

To conclude, the comparative analysis of intertemporal choice has included a broad range of primate species now that allows us to test evolutionary pressures on decision making. This opens up the possibility to test novel hypotheses that account for the phylogenetic relationships among species. Here, we see that the ability to wait for delayed rewards positively correlates with allometric variables but not relative brain size and group size. Collecting these types of data across a large number of species can provide key insights into the evolution of decision making and cognition [12].

Acknowledgments

I thank Jonathan Templin for statistical advice and Alan Bond, Juan Duque, Al Kamil, Bryce Kennedy, and Evan MacLean for comments on an early draft of the manuscript.

Data Accessibility

Data (Data S1) and R code (Data S2) are available in the Supplementary Materials and from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.0k37t>. The original L^AT_EX document, with Sweave-embedded R code [61] to allow reproduction of analyses [62], is available from the author.

References

- [1] Stevens, J. R. & Stephens, D. W. 2009 The adaptive nature of impulsivity. In *Impulsivity: The Behavioral and Neurological Science of Discounting* (eds. G. J. Madden & W. K. Bickel), pp. 361–387. Washington, DC: American Psychological Association.
- [2] Stevens, J. R. 2010 Intertemporal choice. In *Encyclopedia of Animal Behavior* (eds. M. D. Breed & J. Moore), vol. 2, pp. 203–208. Oxford: Academic Press.
- [3] Stevens, J. R. & Mühlhoff, N. 2012 Intertemporal choice in lemurs. *Behavioural Processes*, **89**(2), 121–127. doi:10.1016/j.beproc.2011.10.002.
- [4] Stephens, D. W. & Anderson, D. 2001 The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behavioral Ecology*, **12**(3), 330–339. doi:10.1093/beheco/12.3.330.

- [5] Fawcett, T. W., McNamara, J. M. & Houston, A. I. 2012 When is it adaptive to be patient? A general framework for evaluating delayed rewards. *Behavioural Processes*, **89**(2), 128–136. doi:10.1016/j.beproc.2011.08.015.
- [6] Snowdon, C. T. & Soini, P. 1988 The tamarins, genus *Saguinus*. In *Ecology and Behavior of Neotropical Primates* (eds. R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho & G. A. B. Fonseca), vol. 2, pp. 223–298. Washington, DC: World Wildlife Fund.
- [7] Stevenson, M. F. & Rylands, A. B. 1988 The marmosets, genus *Callithrix*. In *Ecology and Behavior of Neotropical Primates* (eds. R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho & G. A. B. Fonseca), vol. 2, pp. 131–222. Washington, DC: World Wildlife Fund.
- [8] Stevens, J. R., Hallinan, E. V. & Hauser, M. D. 2005 The ecology and evolution of patience in two New World monkeys. *Biology Letters*, **1**(2), 223–226. doi:10.1098/rsbl.2004.0285.
- [9] Mitani, J. C. & Watts, D. P. 1999 Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, **109**, 439–454.
- [10] Rosati, A. G., Stevens, J. R., Hare, B. & Hauser, M. D. 2007 The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and adult humans. *Current Biology*, **17**(19), 1663–1668. doi:10.1016/j.cub.2007.08.033.
- [11] Rosati, A. G. & Hare, B. 2013 Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PLoS ONE*, **8**(5), e63058. doi:10.1371/journal.pone.0063058.
- [12] MacLean, E. L., Matthews, L. J., Hare, B. A., Nunn, C. L., Anderson, R. C., Aureli, F., Brannon, E. M., Call, J., Drea, C. M. *et al.* 2012 How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition*, **15**(2), 223–238. doi:10.1007/s10071-011-0448-8.
- [13] Schmidt-Nielsen, K. 1984 *Scaling: Why Is Animal Size So Important?* New York: Cambridge University Press.
- [14] Rubner, M. 1883 Über den einfluss der körpergrösse auf stoff-und kraftwechsel. *Zeitschrift für Biologie*, **19**, 536–562.
- [15] White, C. R. & Seymour, R. S. 2003 Mammalian basal metabolic rate is proportional to body mass^{2/3}. *Proceedings of the National Academy of Sciences (USA)*, **100**(7), 4046–4049. doi:10.1073/pnas.0436428100.
- [16] Speakman, J. R. 2005 Body size, energy metabolism and lifespan. *Journal of Experimental Biology*, **208**(9), 1717–1730. doi:10.1242/jeb.01556.
- [17] Tobin, H. & Logue, A. W. 1994 Self-control across species (*Columba livia*, *Homo sapiens*, and *Rattus norvegicus*). *Journal of Comparative Psychology*, **108**(2), 126–133. doi:10.1037/0735-7036.108.2.126.

- [18] Daly, M. & Wilson, M. i. 2005 Carpe diem: adaptation and devaluing the future. *Quarterly Review of Biology*, **80**, 55–60.
- [19] Mischel, W., Shoda, Y. & Rodriguez, M. L. 1989 Delay of gratification in children. *Science*, **244**(4907), 933–938. doi:10.1126/science.2658056.
- [20] Duckworth, A. L. & Seligman, M. E. P. 2005 Self-discipline outdoes IQ in predicting academic performance of adolescents. *Psychological Science*, **16**(12), 939–944. doi:10.1111/j.1467-9280.2005.01641.x.
- [21] Shamosh, N. A., DeYoung, C. G., Green, A. E., Reis, D. L., Johnson, M. R., Conway, A. R. A., Engle, R. W., Braver, T. S. & Gray, J. R. 2008 Individual differences in delay discounting: relation to intelligence, working memory, and anterior prefrontal cortex. *Psychological Science*, **19**(9), 904–911. doi:10.1111/j.1467-9280.2008.02175.x.
- [22] Deaner, R. O., van Schaik, C. P. & Johnson, V. 2006 Do some taxa have better domain-general cognition than others? a meta-analysis of nonhuman primate studies. *Evolutionary Psychology*, **4**, 149–196.
- [23] Reader, S. M., Hager, Y. & Laland, K. N. 2011 The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society of London, Series B*, **366**(1567), 1017–1027. doi:10.1098/rstb.2010.0342.
- [24] Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. 2005 Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences (USA)*, **102**, 5460–5465. doi:10.1073/pnas.0408145102.
- [25] Byrne, R. W. & Corp, N. 2004 Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London, Series B*, **271**(1549), 1693–1699.
- [26] Deaner, R. O., Isler, K., Burkart, J. & van Schaik, C. 2007 Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution*, **70**(2), 115–124. doi:10.1159/000102973.
- [27] Dunbar, R. I. M. 2009 The social brain hypothesis and its implications for social evolution. *Annals of Human Biology*, **36**(5), 562–572. doi:10.1080/03014460902960289.
- [28] Stevens, J. R. & King, A. J. 2013 The lives of others: social rationality in animals. In *Simple Heuristics in a Social World* (eds. R. Hertwig, U. Hoffrage & the ABC Research Group), pp. 409–431. Oxford: Oxford University Press.
- [29] Amici, F., Aureli, F. & Call, J. 2008 Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, **18**(18), 1415–1419. doi:10.1016/j.cub.2008.08.020.
- [30] Tobin, H., Logue, A. W., Chelonis, J. J. & Ackerman, K. T. 1996 Self-control in the monkey *Macaca fascicularis*. *Animal Learning and Behavior*, **24**(2), 168–174.

- [31] Addessi, E., Paglieri, F. & Focaroli, V. 2011 The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition*, **119**(1), 142–147. doi:10.1016/j.cognition.2010.10.021.
- [32] Louie, K. & Glimcher, P. W. 2010 Separating value from choice: delay discounting activity in the lateral intraparietal area. *Journal of Neuroscience*, **30**(16), 5498–5507. doi:10.1523/jneurosci.5742-09.2010.
- [33] Pearson, J., Hayden, B. & Platt, M. 2010 Explicit information reduces discounting behavior in monkeys. *Frontiers in Psychology*, **1**, 237. doi:10.3389/fpsyg.2010.00237.
- [34] Isler, K., Christopher Kirk, E., 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. doi:10.1016/j.jhevol.2008.08.004.
- [35] Grafen, A. 1989 The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **326**(1233), 119–157. doi:10.2307/2396904.
- [36] Nunn, C. L. 2011 *The Comparative Approach in Evolutionary Anthropology and Biology*. Chicago: University of Chicago Press.
- [37] Barton, R. A. 1996 Neocortex size and behavioural ecology in primates. *Proceedings of the Royal Society of London, Series B*, **263**(1367), 173–177. doi:10.1098/rspb.1996.0028.
- [38] Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O’Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H. *et al.* 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, **90**(9), 2648–2648. doi:10.1890/08-1494.1.
- [39] Felsenstein, J. 1985 Phylogenies and the comparative method. *American Naturalist*, **125**(1), 1–15.
- [40] Arnold, C., Matthews, L. J. & Nunn, C. L. 2010 The 10ktrees website: a new online resource for primate phylogeny. *Evolutionary Anthropology*, **19**(3), 114–118. doi:10.1002/evan.20251.
- [41] R Development Core Team 2013 R: A language and environment for statistical computing.
- [42] Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. & Pearse, W. 2012 *caper: Comparative Analyses of Phylogenetics and Evolution in R*.
- [43] Fox, J. & Weisberg, S. 2011 *An R Companion to Applied Regression*. Thousand Oaks, CA: Sage, 2nd edn.
- [44] REvolution Computing 2009 *foreach: Foreach looping construct for R*. R package version 1.4.1.

- [45] Sarkar, D. 2008 *Lattice: Multivariate Data Visualization with R*. New York: Springer.
- [46] Sarkar, D. & Andrews, F. 2012 *latticeExtra: Extra Graphical Utilities Based on Lattice*.
- [47] Revelle, W. 2013 *psych: Procedures for Psychological, Psychometric, and Personality Research*. Evanston, Illinois. R package version 1.3.2.
- [48] Roitberg, B. D., Sircom, J., Roitberg, C. A., van Alphen, J. J. M. & Mangel, M. 1993 Life expectancy and reproduction. *Nature*, **364**, 108–108.
- [49] Mischel, W. & Metzner, R. 1962 Preference for delayed reward as a function of age, intelligence, and length of delay interval. *Journal of Abnormal Psychology*, **64**, 425–431.
- [50] Funder, D. C. & Block, J. 1989 The role of ego-control, ego-resiliency, and IQ in delay of gratification in adolescence. *Journal of Personality and Social Psychology*, **57**, 1041–1050.
- [51] Dunbar, R. I. M. 1992 Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, **22**(6), 469–493.
- [52] Marino, L. 1996 What can dolphins tell us about primate evolution? *Evolutionary Anthropology*, **5**(3), 81–86. doi:10.1002/(SICI)1520-6505(1996)5:3<81::AID-EVAN3>3.0.CO;2-Z.
- [53] Gibson, K. R., Rumbaugh, D. M. & Beran, M. J. 2001 Bigger is better: primate brain size in relationship to cognition. In *Evolutionary Anatomy of the Primate Cerebral Cortex* (eds. D. Falk & K. R. Gibson), pp. 79–97. Cambridge, UK: Cambridge University Press.
- [54] Sherwood, C. C., Stimpson, C. D., Raghanti, M. A., Wildman, D. E., Uddin, M., Grossman, L. I., Goodman, M., Redmond, J. C., Bonar, C. J. *et al.* 2006 Evolution of increased glia–neuron ratios in the human frontal cortex. *Proceedings of the National Academy of Sciences (USA)*, **103**(37), 13 606–13 611. doi:10.1073/pnas.0605843103.
- [55] Herculano-Houzel, S. 2011 Brains matter, bodies maybe not: the case for examining neuron numbers irrespective of body size. *Annals of the New York Academy of Sciences*, **1225**(1), 191–199. doi:10.1111/j.1749-6632.2011.05976.x.
- [56] MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E. *et al.* 2014 The evolution of self-control. *Proceedings of the National Academy of Sciences (USA)*, p. in press.
- [57] Arnold, C. & Nunn, C. 2010 Phylogenetic targeting of research effort in evolutionary biology. *American Naturalist*, **176**(5), 601–612. doi:10.1086/648329.
- [58] Kacelnik, A. 2003 The evolution of patience. In *Time and Decision: Economic and Psychological Perspectives on Intertemporal Choice* (eds. G. Loewenstein, D. Read & R. F. Baumeister), pp. 115–138. New York: Russell Sage Foundation.

- [59] Stephens, D. W. 2002 Discrimination, discounting and impulsivity: a role for an informational constraint. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 1527–1537. doi:10.1098/rstb.2002.1062.
- [60] Addessi, E., Paglieri, F., Beran, M. J., Evans, T. A., Macchitella, L., De Petrillo, F. & Focaroli, V. 2013 Delay choice versus delay maintenance: Different measures of delayed gratification in capuchin monkeys (*cebus apella*). *Journal of Comparative Psychology*, **127**(4), 392–398. doi:10.1037/a0031869.
- [61] Leisch, F. 2002 Sweave: dynamic generation of statistical reports using literate data analysis. In *Compstat 2002—Proceedings in Computational Statistics* (eds. W. Härdle & B. Rönz), pp. 575–580. Heidelberg: Physica Verlag.
- [62] de Leeuw, J. 2001 Reproducible research: the bottom line. Tech. rep., Department of Statistics Papers, UCLA, Los Angeles.

Electronic Supplementary Materials:
Evolutionary pressures on primate intertemporal
choice

Jeffrey R. Stevens

April 13, 2014

Table S1: Species intertemporal choice, allometric, relative brain size, and group size data

| Species | Indifference | | Body mass | | Absolute brain size | | Relative brain size (residuals) | | Lifespan | | Home range | | Group size | |
|----------------------------|-------------------------|--|-------------------------------------|--|-------------------------|--|---------------------------------|--|----------------------|--|---------------------------------|--|---|--|
| | point (s) | | (g) | | size (cm ³) | | size (residuals) | | (yrs) | | (ha) | | Group size | |
| <i>Eulemur macaco</i> | 14.8 ^[1] | | 2330.8 ^[2-5] | | 25.4 ^[6] | | -0.22 | | 28.0 ^[7] | | 13.6 ^[4,8-10] | | 8.2 ^[4,9,11,12] | |
| <i>Varecia rubra</i> | 16.6 ^[1] | | 3313.6 ^[2,13,14] | | 31.1 ^[6] | | -0.31 | | 35.0 ^[15] | | 37.3 ^[16-18] | | 9.5 ^[16-18] | |
| <i>Varecia variegata</i> | 17.9 ^[1] | | 3485.9 ^[2,3,19] | | 32.1 ^[6] | | -0.31 | | 34.0 ^[15] | | 86.0 ^[20-23] | | 5.3 ^[19,20,22-29] | |
| <i>Saguinus oedipus</i> | 7.9 ^[30] | | 396.8 ^[30] | | 9.7 ^[6] | | 0.48 | | 26.2 ^[15] | | 8.5 ^[31] | | 6.4 ^[31-33] | |
| <i>Callitrix jacchus</i> | 14.4 ^[30] | | 323.4 ^[30] | | 7.2 ^[6] | | 0.24 | | 23.0 ^[15] | | 2.3 ^[34-38] | | 9.2 ^[35,38-40] | |
| <i>Sapajus apella</i> | 55.6 ^[41,42] | | 3167.5 ^[43] | | 66.4 ^[6] | | -0.26 | | 45.1 ^[7] | | 182.6 ^[44-49] | | 15.6 ^[44,45,47-51] | |
| <i>Ateles geoffroyi</i> | 76.0 ^[41] | | 7435.6 ^[43,52] | | 107.3 ^[6] | | 0.14 | | 48.0 ^[7] | | 129.4 ^[53-59] | | 10.2 ^[53,57-63] | |
| <i>Macaca fascicularis</i> | 26.4 ^[41,64] | | 4928.0 ^[65-68] | | 64.4 ^[6] | | 0.40 | | 37.1 ^[69] | | 54.6 ^[65,66,70,71] | | 31.2 ^[65,66,70-79] | |
| <i>Macaca mulatta</i> | 19.3 ^[80,81] | | 6624.0 ^[65,82-84] | | 88.3 ^[6] | | 0.20 | | 40.0 ^[85] | | 202.6 ^[65,86,87] | | 27.0 ^[65,86-90] | |
| <i>Pongo pygmeus</i> | 49.6 ^[41] | | 54416.4 ^[43,91,92] | | 379.8 ^[6] | | 0.04 | | 59.0 ^[7] | | 770.2 ^[93-97] | | 1.9 ^[94,98,99] | |
| <i>Gorilla gorilla</i> | 44.0 ^[41] | | 145331.6 ^[100] | | 501.5 ^[6] | | 0.38 | | 54.0 ^[7] | | 1777.5 ^[101-108] | | 9.7 ^[103,104,109-115] | |
| <i>Pan paniscus</i> | 74.4 ^[116] | | 36585.0 ^[100,117] | | 344.3 ^[6] | | 0.35 | | 50.0 ^[15] | | 3860.0 ^[118-121] | | 54.6 ^[119-123] | |
| <i>Pan troglodytes</i> | 122.6 ^[116] | | 39348.6 ^[43,100,124-127] | | 367.6 ^[6] | | -0.11 | | 59.4 ^[7] | | 8910.1 ^[108,128-140] | | 48.0 ^[124,128-131,137,141-145] | |

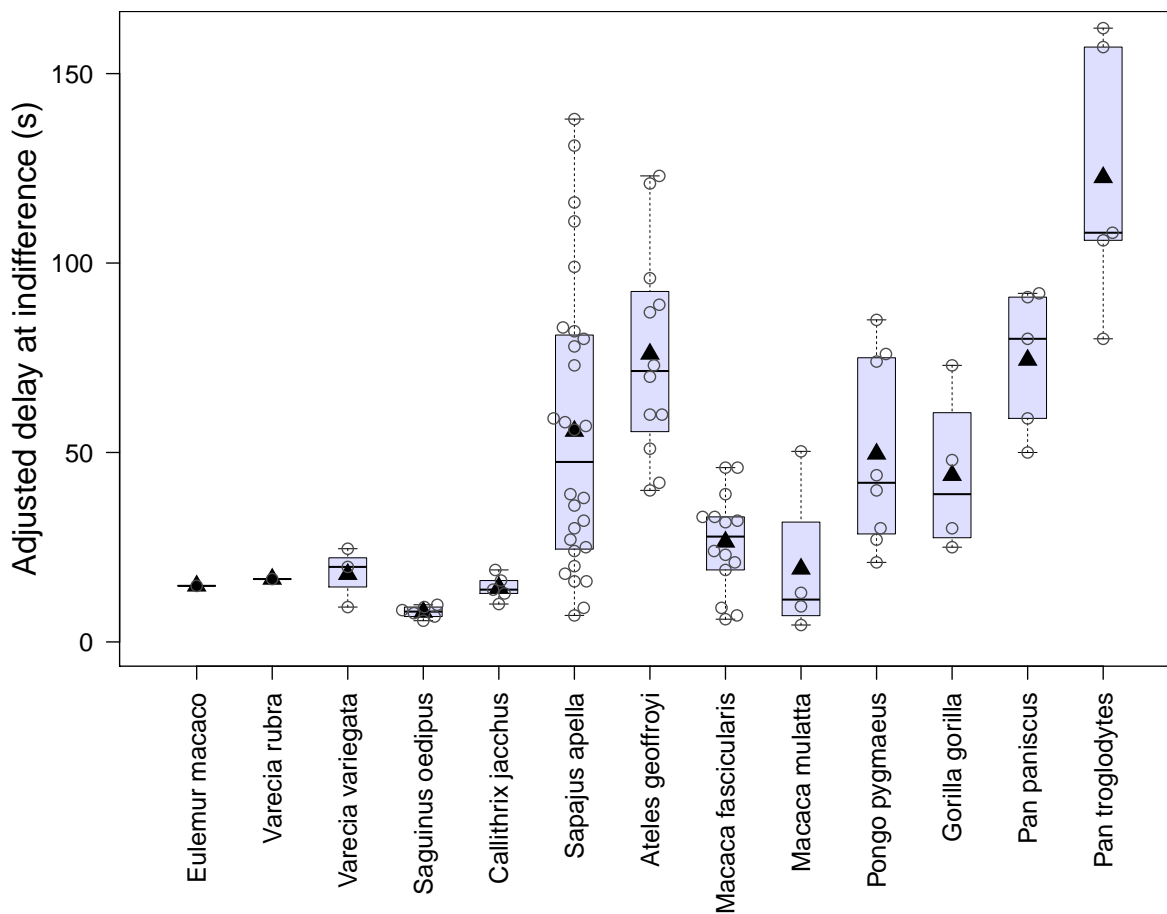


Figure S1: Intertemporal choice data. Thirteen species have been tested with adjusting intertemporal choice tasks: black lemurs (*Eulemur macaco*)^[1], red-ruffed lemurs (*Varecia rubra*)^[1], black-and-white-ruffed lemurs (*Varecia variegata*)^[1], cotton-top tamarins (*Saguinus oedipus*)^[30], common marmosets (*Callithrix jacchus*)^[30], brown capuchins (*Sapajus apella*)^[41,42], black-handed spider monkeys (*Ateles geoffroyi*)^[41], long-tailed macaques (*Macaca fascicularis*)^[41,64], rhesus macaques (*Macaca mulatta*)^[80,81], orangutans (*Pongo pygmaeus*)^[41], lowland gorillas (*Gorilla gorilla*)^[41], bonobos (*Pan paniscus*)^[116], and chimpanzees (*Pan troglodytes*)^[116]. The y-axis illustrates the indifference points representing the waiting time tolerated for three times as much food compared to an immediate reward. Circles represent data points for individual subjects, triangles represent the species mean, lines represent the median, boxes represent the interquartile range (25-75%), and whiskers represent the range.

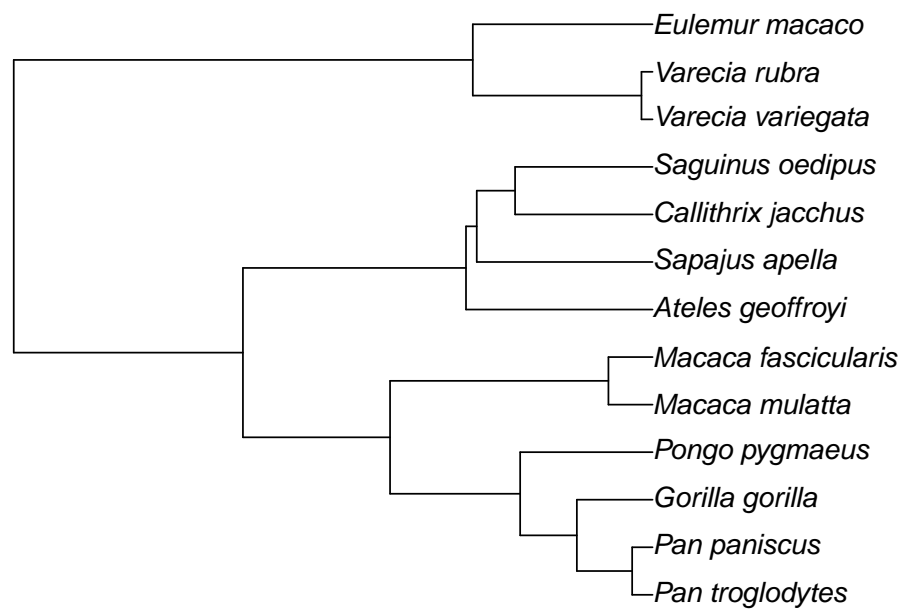


Figure S2: Phylogeny of species in comparative analysis. I used 10kTrees version 3^[146] to construct the weighted branch lengths of the primate phylogeny.

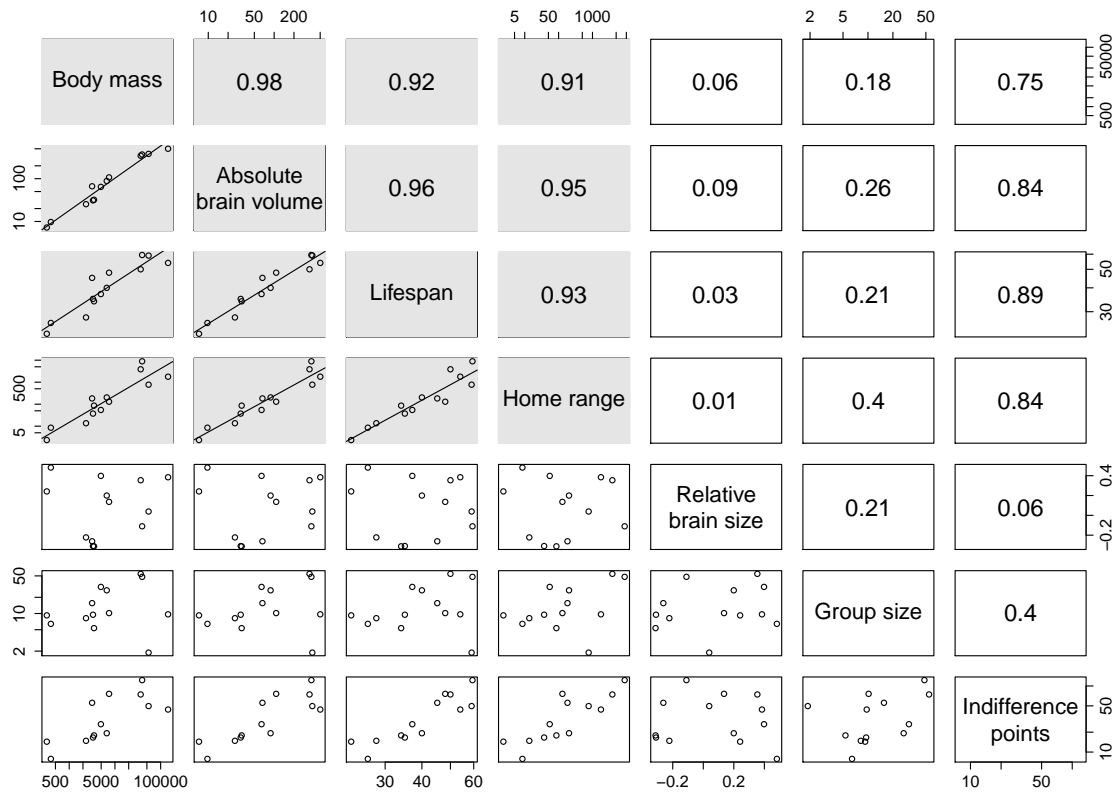


Figure S3: Correlation matrix for predictor variables and indifference points. All variables except relative brain size are plotted on log scale. Body mass, absolute brain volume, lifespan, and home range size (shaded panels) are highly intercorrelated. Upper panels show correlation coefficients.

References

- [1] Stevens, J. R. & Mühlhoff, N. 2012 Intertemporal choice in lemurs. *Behavioural Processes*, **89**(2), 121–127. doi:10.1016/j.beproc.2011.10.002.
- [2] Kappeler, P. M. 1991 Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica*, **57**(3), 132–146. doi:10.1159/000156575.
- [3] Terranova, C. J. & Coffman, B. S. 1997 Body weights of wild and captive lemurs. *Zoo Biology*, **16**(1), 17–30. doi:10.1002/(SICI)1098-2361(1997)16:1<17::AID-ZOO4>3.0.CO;2-E.
- [4] Bayart, F. & Simmen, B. 2005 Demography, range use, and behavior in black lemurs (*Eulemur macaco macaco*) at Ampasikely, northwest Madagascar. *American Journal of Primatology*, **67**(3), 299–312. doi:10.1002/ajp.20186.
- [5] Junge, R. E. & Louis, E. E. 2007 Biomedical evaluation of black lemurs (*Eulemur macaco macaco*) in Lokobe Reserve, Madagascar. *Journal of Zoo and Wildlife Medicine*, **38**(1), 67–76. doi:10.1638/06-006.1.
- [6] Isler, K., Christopher Kirk, E., 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. doi:10.1016/j.jhevol.2008.08.004.
- [7] Hakeem, A., Sandoval, G. R., Jones, M. & Allman, J. 1996 Brain and life span in primates. In *Handbook of the Psychology of Aging* (eds. J. E. Birren & K. W. Schale), pp. 78–104. Academic Press.
- [8] Jolly, A. 1972 *The Evolution of Primate Behavior*. New York: Macmillan.
- [9] Colquhoun, I. C. 1993 The socioecology of *Eulemur macaco*: a preliminary report. In *Lemur Social Systems and Their Ecological Basis* (eds. P. M. Kappeler & R. U. Ganzhorn), pp. 11–23. New York: Plenum Press.
- [10] Schwitzer, N., Randriatahina, G. H., Kaumanns, W., Hoffmeister, D. & Schwitzer, C. 2007 Habitat utilization of blue-eyed black lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in primary and altered forest fragments. *Primate Conservation*, **22**(1), 79–87. doi:10.1896/052.022.0106.
- [11] Jolly, A. 1966 *Lemur Behavior: A Madagascar Field Study*. Chicago: University of Chicago Press.
- [12] Andrews, J. R. 1990 *A preliminary survey of black lemurs, Lemur macaco in north-west Madagascar: the final report of the Black Lemur Survey 1988*.
- [13] Vasey, N. 2003 *Varecia*, ruffed lemurs. In *The Natural History of Madagascar* (eds. S. M. Goodman & J. Benstead), pp. 1332–1336. Chicago: University of Chicago Press.
- [14] Dutton, C. J., Junge, R. E. & Louis, E. E. 2008 Biomedical evaluation of free-ranging red ruffed lemurs (*Varecia rubra*) within the Masoala National Park, Madagascar. *Journal of Zoo and Wildlife Medicine*, **39**(1), 76–85. doi:10.1638/06-062.1.
- [15] Weigl, R. 2005 *Longevity of Mammals in Captivity: From the Living Collections of the World*. Stuttgart: Schweizerbart.

- [16] Rigamonti, M. M. 1993 Home range and diet in red ruffed lemurs (*Varecia variegata rubra*) on the Masoala Peninsula, Madagascar. In *Lemur Social Systems and Their Ecological Basis* (eds. P. M. Kappeler & J. U. Ganzhorn), pp. 25–39. New York: Plenum Press.
- [17] Vasey, N. 2007 The breeding system of wild red ruffed lemurs (*Varecia rubra*): a preliminary report. *Primates*, **48**, 41–54.
- [18] Martinez, B. T. 2010 Forest restoration in Masoala National Park, Madagascar: The contribution of the red-ruffed lemur (*Varecia rubra*) and the livelihoods of subsistence farmers at Ambatoladama. Ph.D. thesis, University of Minnesota, Minneapolis, MN.
- [19] Morland, H. S. 1991 Preliminary report on the social organization of ruffed lemurs (*Varecia variegata variegata*) in a northeast Madagascar rain forest. *Folia Primatologica*, **56**(3), 157–161. doi:10.1159/000156540.
- [20] White, F. J. 1991 Social organization, feeding ecology, and reproductive strategy of ruffed lemurs, *Varecia variegata*. In *Primate Today: Proceedings of the 13th Congress of the International Primatological Society* (eds. A. Ehara, T. Kimura, O. Takenaka & M. Iwamoto), pp. 81–84. New York: Elsevier.
- [21] Britt, A. 1996 Environmental influences on the behavioural ecology of the black-and-white ruffed lemur (*Varecia variegata variegata*, kerr, 1792). Ph.D. thesis, University of Liverpool, Liverpool, UK.
- [22] Balko, E. 1998 The behavioral plasticity of *Varecia variegata* in Ranomafana National Park, Madagascar. Ph.D. thesis, SUNY College of Environmental Science and Forestry, Syracuse, NY.
- [23] Baden, A. L. 2011 Communal infant care in black-and-white ruffed lemurs (*Varecia variegata*). Ph.D. thesis, Stony Brook University, Stony Brook, NY.
- [24] Petter, J.-J. 1962 *Recherches sur l'écologie et l'éthologie des lémuriers malgaches*. Paris: Editions du Muséum.
- [25] Pollock, J. 1979 Spatial distribution and ranging behaviour in lemurs. In *The Study of Prosimian Behaviour* (eds. G. A. Doyle & R. G. Martin), pp. 359–409. New York: Academic Press.
- [26] Welch, C. & Katz, A. 1992 Survey and census work on lemurs in the natural reserve of Betampona in eastern Madagascar with a view to restocking. *Dodo: Journal of the Jersey Wildlife Preservation Trusts*, **28**, 45–58.
- [27] Balko, E. A. & Underwood, B. H. 2005 Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Primatology*, **66**(1), 45–70. doi:10.1002/ajp.20127.
- [28] Overdorff, D. J., Erhart, E. M. & Mutschler, T. 2005 Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? *American Journal of Primatology*, **66**, 7–22.
- [29] Ratsimbazafy, J. 2007 Diet composition, foraging, and feeding behavior in relation to habitat disturbance: implications for the adaptability of ruffed lemurs (*Varecia variegata editorium*) in Manombo Forest, Madagascar. In *Lemurs* (eds. L. Gould & M. L. Sauther), pp. 403–422. New York: Springer.
- [30] Stevens, J. R., Hallinan, E. V. & Hauser, M. D. 2005 The ecology and evolution of patience in two New World monkeys. *Biology Letters*, **1**(2), 223–226. doi:10.1098/rsbl.2004.0285.

- [31] Neyman, P. F. 1977 Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In *The Biology and Conservation of the Callitrichidae* (ed. D. G. Kleiman), pp. 39–71. Washington, DC: Smithsonian Institution Press.
- [32] Hershkovitz, P. 1977 *Living New World Monkeys (Platyrrhini), Volume 1: With an Introduction to Primates*. Chicago: University of Chicago Press.
- [33] Savage, A., Giraldo, L. H., Soto, L. H. & Snowdon, C. T. 1996 Demography, group composition, and dispersal in wild cotton-top tamarin (*Saguinus oedipus*) groups. *American Journal of Primatology*, **38**, 85–100.
- [34] Maier, W., Alonso, C. & Langguth, A. 1982 Field observations on *Callithrix jacchus jacchus* L. *Zeitschrift für Säugetierkunde*, **47**, 334–346.
- [35] Hubrecht, R. C. 1985 Home-range size and use and territorial behavior in the common marmoset, *Callithrix jacchus jacchus*, at the Tapacura Field Station, Recife, Brazil. *International Journal of Primatology*, **6**, 533–550.
- [36] Stevenson, M. F. & Rylands, A. B. 1988 The marmosets, genus *Callithrix*. In *Ecology and Behavior of Neotropical Primates* (eds. R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho & G. A. B. Fonseca), vol. 2, pp. 131–222. Washington, DC: World Wildlife Fund.
- [37] Alonso, C. & Langguth, A. 1989 Ecologia e comportamento de *Callithrix jacchus* (Primates: Callitrichidae) numa ilha de floresta Atlântica. *Revista Nordestina de Biologia*, **6**(2), 105–137.
- [38] Scanlon, C. E., Chalmers, N. R. & Monteiro da Cruz, M. A. O. 1988 Changes in the size, composition, and reproductive condition of wild marmoset groups (*Callithrix jacchus jacchus*) in north east Brazil. *Primates*, **29**(3), 295–305. doi:10.1007/BF02380953.
- [39] Stevenson, M. F. 1978 The behaviour and ecology of the common marmoset (*Callithrix jacchus jacchus*) in its natural environment. *Biology and Behaviour of Marmosets*, p. 298.
- [40] Koenig, A. 1995 Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, **35**(4), 311–317. doi:10.1002/ajp.1350350407.
- [41] Amici, F., Aureli, F. & Call, J. 2008 Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, **18**(18), 1415–1419. doi:10.1016/j.cub.2008.08.020.
- [42] Addessi, E., Paglieri, F. & Focaroli, V. 2011 The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition*, **119**(1), 142–147. doi:10.1016/j.cognition.2010.10.021.
- [43] Smith, R. J. & Jungers, W. L. 1997 Body mass in comparative primatology. *Journal of Human Evolution*, **32**(6), 523–559. doi:10.1006/jhev.1996.0122.
- [44] Izawa, K. 1980 Social behavior of the wild black-capped capuchin (*Cebus apella*). *Primates*, **21**(4), 443–467. doi:10.1007/BF02373834.
- [45] Freese, C. & Oppenheimer, J. 1981 The capuchin monkey, Genus *Cebus*. In *Ecology and Behavior of Neotropical Primates* (eds. A. F. Coimbra-Filho & R. A. Mittermeier), vol. 1, pp. 331–390. Washington, DC: World Wildlife Fund.
- [46] Terborgh, J. 1983 *Five New World Primates: A Study in Comparative Ecology*. Princeton, N.J.: Princeton University Press.

- [47] Robinson, J. & Janson, C. 1987 Capuchins, squirrel monkeys, and atelines: socioecological convergence with Old World primates. In *Primate Societies* (eds. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker), pp. 69–82. Chicago: University of Chicago Press.
- [48] Di Bitetti, M. S. 2001 Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. *Journal of Zoology*, **253**(1), 33–45. doi:10.1017/S0952836901000048.
- [49] Izar, P., Verderane, M. P., Peternelli-dos Santos, L., Mendonça-Furtado, O., Presotto, A., Tokuda, M., Visalberghi, E. & Fragaszy, D. 2012 Flexible and conservative features of social systems in tufted capuchin monkeys: comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. *American Journal of Primatology*, **74**(4), 315–331. doi:10.1002/ajp.20968.
- [50] Thorington, R. 1967 Feeding and activity of *Cebus* and *Saimiri* in a Colombian forest. In *Progress in Primatology* (eds. D. Stark, R. Schneider & H. J. Kuhn), pp. 180–184. Stuttgart: Gustav Fischer Verlag.
- [51] Fragaszy, D. M., Visalberghi, E. & Fedigan, L. M. 2004 *The Complete Capuchin: The Biology of the Genus Cebus*. Cambridge: Cambridge University Press.
- [52] Stephan, H., Frahm, H. & Baron, G. 1981 New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologica*, **35**(1), 1–29.
- [53] Dare, R. J. 1974 The social behavior and ecology of spider monkeys, *Ateles geoffroyi*, on Barro Colorado Island. Ph.D. thesis, University of Oregon, Eugene, OR.
- [54] Coehlo, A., Coehlo, L., Bramblett, C., Bramblett, S. & Quick, L. 1976 Ecology, population characteristics and sympatric associations in primates: a bioenergetic analysis of howler and spider monkeys in Tikal. *Yearbook of Physical Anthropology*, **20**, 96–135.
- [55] Fedigan, L. M., Fedigan, L., Chapman, C. & Glander, K. E. 1988 Spider monkey home ranges: a comparison of radio telemetry and direct observation. *American Journal of Primatology*, **16**(1), 19–29. doi:10.1002/ajp.1350160104.
- [56] Chapman, C. A. 1990 Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behavioral Ecology and Sociobiology*, **26**(6), 409–414. doi:10.1007/BF00170898.
- [57] Campbell, C. J. 2000 The reproductive biology of black-handed spider monkeys (*Ateles geoffroyi*): Integrating behavior and endocrinology. Ph.D. thesis, University of California, Berkeley, Berkeley, CA.
- [58] Ramos-Fernández, G. & Ayala-Orozco, B. 2003 Population size and habitat use of spider monkeys in Punta Laguna, Mexico. In *Primates in Fragments: Ecology and Conservation* (ed. L. K. Marsh), pp. 191–209. New York: Springer.
- [59] Wallace, R. B. 2008 Towing the party line: territoriality, risky boundaries and male group size in spider monkey fission–fusion societies. *American Journal of Primatology*, **70**(3), 271–281. doi:10.1002/ajp.20484.
- [60] Carpenter, C. R. 1935 Behavior of red spider monkeys in Panama. *Journal of Mammalogy*, **16**(3), 171–180. doi:10.2307/1374442.
- [61] Eisenberg, J. F. & Kuehn, R. E. 1966 The behavior of *Ateles geoffroyi* and related species. *Smithsonian Miscellaneous Collections*, **151**(1-63).

- [62] Milton, K. 1993 Diet and social organization of a free-ranging spider monkey population: the development of species-typical behavior in the absence of adults. In *Juvenile Primates* (eds. M. Pereira & L. Fairbanks), pp. 173–181. Oxford: Oxford University Press.
- [63] Estrada, A., Luecke, L., Belle, S. V., Barrueta, E. & Meda, M. R. 2004 Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan sites of Calakmul and Yaxchilán, Mexico and Tikal, Guatemala. *Primates*, **45**(1), 33–39. doi:10.1007/s10329-003-0062-8.
- [64] Tobin, H., Logue, A. W., Chelonis, J. J. & Ackerman, K. T. 1996 Self-control in the monkey *Macaca fascicularis*. *Animal Learning and Behavior*, **24**(2), 168–174.
- [65] Roonwal, M. L. & Mohnot, S. M. 1977 *Primates of South Asia: Ecology, Sociobiology, and Behavior*. Cambridge, MA: Harvard University Press.
- [66] MacKinnon, J. & MacKinnon, K. 1978 Comparative feeding ecology of six sympatric primates in West Malaysia. In *Recent Advances in Primatology* (eds. D. Chivers & J. Herbert), vol. 1, pp. 305–321. New York: Academic Press.
- [67] Bakar, A., Amir, M. & Marshal 1981 Morphological studies on crab eating monkey in Indonesia. *Kyoto University Overseas Research Report of Studies on Indonesian Macaque*, **1**, 11–14.
- [68] Fooden, J. 1995 Systematic review of southeast Asian longtail macaques, *Macaca fascicularis* (Raffles, 1821). *Fieldiana Zoologica*, **81**, 1–206.
- [69] Jones, M. L. 1982 Longevity of captive mammals. *Zoologische Garten*, **52**(2), 113–128.
- [70] Kurland, J. A. 1973 A natural history of kra macaques (*Macaca fascicularis* Raffles, 1821) at the Kutai Reserve, Kalimantan Timur, Indonesia. *Primates*, **14**(2-3), 245–262. doi:10.1007/BF01730823.
- [71] van Schaik, C. P., van Noordwijk, M. A. v., de Boer, R. J. & den Tonkelaar, I. 1983 The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology*, **13**(3), 173–181. doi:10.2307/4599622.
- [72] Furuya, Y. 1965 Social organization of the crab-eating monkey. *Primates*, **6**(3-4), 285–336. doi:10.1007/BF01730354.
- [73] Bernstein, I. S. 1967 A field study of the pigtail monkey (*Macaca nemestrina*). *Primates*, **8**, 217–228.
- [74] Medway, L. 1969 *The Wild Mammals of Malaya and Offshore Islands including Singapore*. Oxford University Press.
- [75] Fooden, J. 1971 Report on primates collected in western Thailand, January-April, 1967. *Fieldiana Zoology*, **59**, 1–62.
- [76] Poirier, F. E. & Smith, E. O. 1974 The crab-eating macaques (*Macaca fascicularis*) of Angaur Island, Palau, Micronesia. *Folia Primatologica*, **22**(4), 258–306. doi:10.1159/000155631.
- [77] Angst, W. 1975 Basic data and concepts on the social organization of *Macaca fascicularis*. *Primate Behavior*, **4**, 325–88.

- [78] Crockett, C. M. & Wilson, W. L. 1980 The ecological separation of *Macaca nemestrina* and *M. fascicularis* in Sumatra. In *The Macaques: Studies in Ecology, Behavior and Evolution* (ed. D. G. Lindburg), pp. 148–181. New York: Van Nostrand Reinhold.
- [79] Wheatley, B. P. 1980 Feeding and ranging of East Bornean *Macaca fascicularis*. In *The Macaques: Studies in Ecology, Behavior and Evolution* (ed. D. G. Lindburg), pp. 215–246. New York: Van Nostrand Reinhold.
- [80] Louie, K. & Glimcher, P. W. 2010 Separating value from choice: delay discounting activity in the lateral intraparietal area. *Journal of Neuroscience*, **30**(16), 5498–5507. doi:10.1523/jneurosci.5742-09.2010.
- [81] Pearson, J., Hayden, B. & Platt, M. 2010 Explicit information reduces discounting behavior in monkeys. *Frontiers in Psychology*, **1**, 237. doi:10.3389/fpsyg.2010.00237.
- [82] Altmann, S. A. 1962 A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Sciences*, **102**(2), 338–435. doi:10.1111/j.1749-6632.1962.tb13650.x.
- [83] Napier, P. H. 1981 *Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles*. London: British Museum (Natural History).
- [84] Fitch, W. T. 1997 Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America*, **102**(2), 1213–1222. doi:10.1121/1.421048.
- [85] Mattison, J. A., Roth, G. S., Beasley, T. M., Tilmont, E. M., Handy, A. M., Herbert, R. L., Longo, D. L., Allison, D. B., Young, J. E. *et al.* 2012 Impact of caloric restriction on health and survival in rhesus monkeys from the NIA study. *Nature*, **489**(7415), 318–321. doi:10.1038/nature11432.
- [86] Neville, M. K. 1968 Ecology and activity of Himalayan foothill rhesus monkeys (*Macaca mulatta*). *Ecology*, **49**(1), 110–123. doi:10.2307/1933566.
- [87] Teas, J., Richie, T., Taylor, H. & Southwick, C. 1980 Population patterns and behavioral ecology of rhesus monkeys (*Macaca mulatta*) in Nepal. In *The Macaques: Studies in Ecology, Behavior and Evolution*, pp. 247–262. New York: Van Nostrand Reinhold.
- [88] Southwick, C. H., Beg, M. A. & Siddiqi, M. R. 1961 A population survey of rhesus monkeys in villages, towns and temples of Northern India. *Ecology*, **42**(3), 538–547. doi:10.2307/1932240.
- [89] Southwick, C. H., Beg, M. A. & Siddiqi, M. R. 1965 Rhesus monkeys in north India. In *Primate Behavior: Field Studies of Monkeys and Apes* (ed. I. DeVore), pp. 111–159. New York: Holt.
- [90] Seth, P. K. & Seth, S. 1986 Ecology and behaviour of rhesus monkeys in India. In *Primate Ecology and Conservation* (eds. J. G. Else & P. C. Lee), vol. 2, pp. 89–103. Cambridge, UK: Cambridge University Press.
- [91] Eckhardt, R. B. 1975 The relative body weights of Bornean and Sumatran orangutans. *American Journal of Physical Anthropology*, **42**(3), 349–350. doi:10.1002/ajpa.1330420303.
- [92] Rodman, P. S. 1984 Foraging and social systems of orangutans and chimpanzees. In *Adaptations for Foraging in Nonhuman Primates* (eds. P. S. Rodman & R. G. H. Cant), pp. 134–160. New York: Columbia University Press.

- [93] Horr, D. A. 1975 The Borneo orang-utan: population structure and dynamics in relationship to ecology and reproductive strategy. *Primate behavior*, **4**, 307–323.
- [94] Rijksen, H. D. 1978 *A Field Study on Sumatran Orang-utans (Pongo pygmaeus abelii Lesson 1827)*. *Ecology, Behaviour and Conservation*. Wageningen: H. Veenman & Zonen.
- [95] Rodman, P. S. & Mitani, J. C. 1987 Orangutans: sexual dimorphism in a solitary species. In *Primate Societies* (eds. B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker), pp. 148–154. Chicago: University of Chicago Press.
- [96] Galdikas, B. M. F. 1988 Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology*, **9**(1), 1–35. doi:10.1007/BF02740195.
- [97] Singleton, I. & van Schaik, C. P. 2001 Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, **22**(6), 877–911. doi:10.1023/A:1012033919441.
- [98] Rodman, P. S. 1973 Population composition and adaptive organisation among orang-utans of the Kutai Reserve. In *Comparative Ecology and Behaviour of Primates* (eds. R. P. Michael & J. H. Crook), pp. 171–209. New York: Academic Press.
- [99] MacKinnon, J. 1974 The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour*, **22**(1), 3–74. doi:10.1016/S0003-3472(74)80054-0.
- [100] Jungers, W. L. & Susman, R. L. 1984 Body size and skeletal allometry in African apes. In *The Pygmy Chimpanzee* (ed. R. L. Susman), pp. 131–177. New York: Springer.
- [101] Remis, M. J. 1994 Feeding ecology and positional behavior of western lowland gorillas (*Gorilla gorilla gorilla*) in the central african republic. Ph.D. thesis, Yale University, New Haven, CN.
- [102] Tutin, C. E. G. 1996 Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In *Great Ape Societies* (eds. W. C. McGrew, L. F. Marchant & T. Nishida), pp. 58–70. New York: Cambridge University Press.
- [103] Yamagiwa, J., Maruhashi, T., Yumoto, T. & Mwanza, N. 1996 Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In *Great Ape Societies* (eds. W. C. McGrew, L. F. Marchant & T. Nishida), pp. 82–98. New York: Cambridge University Press.
- [104] Bermejo, M. 2004 Home-range use and intergroup encounters in western gorillas (*Gorilla g. gorilla*) at Lossi forest, North Congo. *American Journal of Primatology*, **64**(2), 223–232. doi:10.1002/ajp.20073.
- [105] Cipolletta, C. 2004 Effects of group dynamics and diet on the ranging patterns of a western gorilla group (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *American Journal of Primatology*, **64**(2), 193–205. doi:10.1002/ajp.20072.
- [106] Doran-Sheehy, D. M., Greer, D., Mongo, P. & Schwindt, D. 2004 Impact of ecological and social factors on ranging in western gorillas. *American Journal of Primatology*, **64**(2), 207–222. doi:10.1002/ajp.20075.
- [107] Robbins, M. M., Nkurunungi, J. B. & McNeilage, A. 2006 Variability of the feeding ecology of eastern gorillas. In *Feeding Ecology in Apes and Other Primates* (eds. G. Hohmann, M. M. Robbins & C. Boesch), vol. 48, pp. 25–47. Cambridge, UK: Cambridge University Press.

- [108] Yamagiwa, J. & Basabose, A. K. 2006 Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi-Biega National Park. *Primates*, **47**(1), 74–90. doi:10.1007/s10329-005-0147-7.
- [109] Fay, J. M. 1989 Partial completion of a census of the western lowland gorilla (*Gorilla g. gorilla* (Savage and Wyman)) in southwestern Central African Republic. *Mammalia*, **53**(2), 203–215. doi:10.1515/mamm.1989.53.2.203.
- [110] Tutin, C. E. G., Fernandez, M., Rogers, M. & Williamson, E. 1992 A preliminary analysis of the social structure of lowland gorillas in the Lopé Reserve, Gabon. In *Topics in Primatology: Behavior, Ecology, and Conservation* (eds. N. Itiogawa, Y. Sugiyama, G. P. Sackett & R. K. R. Thompson), vol. 2, pp. 245–254. Tokyo: University of Tokyo Press.
- [111] Mitani, M., Yamagiwa, J., Oko, R., Moutsambote, J., Yumoto, T. & Maruhashi, T. 1993 Approaches in density estimates and reconstruction of social groups in a western lowland gorilla population in the Ndoki forest, northern Congo. *Tropics*, **2**, 219–229.
- [112] Nishihara, T. 1994 Population density and group organization of gorillas (*Gorilla gorilla gorilla*) in the Nouabale-Ndoki National Park, Congo. *Africa Kenkyu*, **44**, 29–45.
- [113] Remis, M. J. 1993 Nesting behavior of lowland gorillas in the Dzanga-Sangha Reserve, Central African Republic: implications for population estimates and understandings of group dynamics. *Tropics*, **2**(4), 245–255.
- [114] Magliocca, F., Querouil, S. & Gautier-Hion, A. 1999 Population structure and group composition of western lowland gorillas in North-Western Republic of Congo. *American Journal of Primatology*, **48**(1), 1–14. doi:10.1002/(SICI)1098-2345(1999)48:1<1::AID-AJP1>3.0.CO;2-2.
- [115] Parnell, R. J. 2002 Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology*, **56**(4), 193–206. doi:10.1002/ajp.1074.
- [116] Rosati, A. G., Stevens, J. R., Hare, B. & Hauser, M. D. 2007 The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and adult humans. *Current Biology*, **17**(19), 1663–1668. doi:10.1016/j.cub.2007.08.033.
- [117] Deschner, T., Kratzsch, J. & Hohmann, G. 2008 Urinary C-peptide as a method for monitoring body mass changes in captive bonobos (*Pan paniscus*). *Hormones and Behavior*, **54**(5), 620–626. doi:10.1016/j.yhbeh.2008.06.005.
- [118] Kano, T. 1982 The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates*, **23**(2), 171–188. doi:10.1007/BF02381159.
- [119] Badrian, A. & Badrian, N. 1984 Social organization of *Pan paniscus* in the Lomako Forest, Zaire. In *The Pygmy Chimpanzee: Evolutionary Biology and Behavior* (ed. R. L. Susman), pp. 325–346. New York: Springer.
- [120] Kano, T. & Mulavwa, M. 1984 Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In *The Pygmy Chimpanzee: Evolutionary Biology and Behavior* (ed. R. L. Susman), pp. 233–274. New York: Springer.
- [121] Hashimoto, C., Tashiro, Y., Kimura, D., Enomoto, T., Ingmanson, E. J., Idani, G. & Furuichi, T. 1998 Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, **19**(6), 1045–1060. doi:10.1023/A:1020378320913.

- [122] Kuroda, S. 1979 Grouping of the pygmy chimpanzees. *Primates*, **20**(2), 161–183. doi:10.1007/BF02373371.
- [123] White, F. J. 1988 Party composition and dynamics in *Pan paniscus*. *International Journal of Primatology*, **9**(3), 179–193. doi:10.1007/BF02737400.
- [124] Rahm, U. 1967 Observations during chimpanzee captures in the Congo. In *Progress in Primatology* (eds. D. Stark, R. Schneider & H. J. Kuhn), pp. 195–207. Stuttgart: Gustav Fischer Verlag.
- [125] Pusey, A. E. 1978 The physical and social development of wild adolescent chimpanzees: (*pan troglodytes schweinfurthii*). Ph.D. thesis, Graduate Division Special Programs, Ethology, Stanford University, Palo Alto, CA.
- [126] Wrangham, R. W. & Smuts, B. B. 1980 Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, **Suppl 28**, 13–31.
- [127] Uehara, S. & Nishida, T. 1987 Body weights of wild chimpanzees (*Pan troglodytes schweinfurthii*) of the Mahale Mountains National Park, Tanzania. *American Journal of Physical Anthropology*, **72**(3), 315–321. doi:10.1002/ajpa.1330720305.
- [128] Goodall, J. 1965 Chimpanzees of the Gombe Stream Reserve. In *Primate Behavior: Field Studies of Monkeys and Apes* (ed. I. DeVore), pp. 425–473. New York: Holt.
- [129] Reynolds, V. & Reynolds, F. 1965 Chimpanzees of the Budongo Forest. In *Primate Behavior: Field Studies of Monkeys and Apes* (ed. I. DeVore), pp. 368–424. New York: Holt.
- [130] Sugiyama, Y. 1968 Social organization of chimpanzees in the Budongo Forest, Uganda. *Primates*, **9**(3), 225–258. doi:10.1007/BF01730972.
- [131] Izawa, K. 1970 Unit groups of chimpanzees and their nomadism in the savanna woodland. *Primates*, **11**(1), 1–45. doi:10.1007/BF01730674.
- [132] Kano, T. 1971 The chimpanzee of Filabanga, western Tanzania. *Primates*, **12**(3-4), 229–246. doi:10.1007/BF01730413.
- [133] Kano, T. 1972 Distribution and adaptation of the chimpanzee on the eastern shore of Lake Tanganyika. *Kyoto University African Studies*, **7**, 37–129.
- [134] Nishida, T. & Kawanaka, K. 1972 Inter-unit-group relationships among wild chimpanzees of the Mahali Mountains. *Kyoto University African Studies*, **7**, 131–169.
- [135] Nishida, T., Uehara, S. & Nyundo, R. 1979 Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates*, **20**(1), 1–20.
- [136] Baldwin, P. J., McGrew, W. C. & Tutin, C. E. G. 1982 Wide-ranging chimpanzees at Mt. Assirik, Senegal. *International Journal of Primatology*, **3**(4), 367–385. doi:10.1007/BF02693739.
- [137] Tutin, C. E. G., McGrew, W. C. & Baldwin, P. J. 1983 Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates*, **24**(2), 154–173. doi:10.1007/BF02381079.
- [138] Ghiglieri, M. P. 1984 *The Chimpanzees of the Kibale Forest: A Field Study of Ecology and Social Structure*. New York: Columbia University Press.

- [139] Boesch, C. & Boesch, H. 1989 Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, **78**, 547–573.
- [140] Newton-Fisher, N. E. 2003 The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *African Journal of Ecology*, **41**(2), 150–156. doi:10.1046/j.1365-2028.2003.00408.x.
- [141] Kortlandt, A. 1967 Experimentation with chimpanzees in the wild. In *Neue Ergebnisse der Primatologie* (eds. D. Stark, R. Schneider & H. J. Kuhn), pp. 208–224. Stuttgart: Fischer.
- [142] Nishida, T. 1968 The social group of wild chimpanzees in the Mahali Mountains. *Primates*, **9**(3), 167–224.
- [143] Suzuki, A. 1971 Carnivory and cannibalism observed among forest-living chimpanzees. *Journal of Anthropological Society of Nippon*, **79**(1), 30–48. doi:10.1537/ase1911.79.30.
- [144] Wrangham, R. W. 1977 Feeding behavior of chimpanzees in Gombe National Park, Tanzania. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes* (ed. T. H. Clutton-Brock), pp. 503–538. New York: Academic Press.
- [145] Nishida, T. & Hiraiwa-Hasegawa, M. 1987 Chimpanzees and bonobos: cooperative relationships among males. In *Primate Societies* (eds. D. L. Cheney, R. M. Seyfarth, B. B. Smuts, T. T. Struhsaker & R. W. Wrangham), pp. 165–177. Chicago: University of Chicago Press.
- [146] Arnold, C., Matthews, L. J. & Nunn, C. L. 2010 The 10ktrees website: a new online resource for primate phylogeny. *Evolutionary Anthropology*, **19**(3), 114–118. doi:10.1002/evan.20251.