An Agent-Based Model of the Effects of a Primate Social Structure on the Speed of Natural Selection

Gideon M. Gluckman
University of Bath
Bath, UK
BA2 7AY
ggluckman@gmail.com

Joanna Bryson
University of Bath
Bath, UK
BA2 7AY
jjb@cs.bath.ac.uk

ABSTRACT

The rate of speciation is in most mammals an order of magnitude faster than in most other vertebrates. It is faster still in the social mammals. The apparent association between complex modes of sociality and high rates of evolutionary change might provide an answer to the question of why these rates differ so markedly. Using an individual based model of a population with a social structure mimicking the one common to cercopithecine primates and a simple model ecology, we investigate the effects of social structures on the rates at which natural selection operates. The results of the model indicate that the specific social structure modelled does affect the rate at which natural selection operates within the modeled population.

Categories and Subject Descriptors

H.4 [**Information Systems Applications**]: Miscellaneous

1. INTRODUCTION

The rate of speciation in most mammals is an order of magnitude faster than in most other vertebrates, and faster still in social mammals [9, 2]. The Primate order is amongst the fastest-speciating orders of mammals. The most speciose family of Primates, and also the youngest, is the Cercopithecidae [19], [18].

Species across this Family share at least the outlines of a common social system [10]. This outlined system includes linear sex-segregated dominance hierarchies with female philopatry and male dispersal, inherited female dominance, and reproduction limited to within the social group [12, 13, 20, 6]. The apparent association between complex modes of sociality and high rates of evolutionary change has been investigated as a causal relationship by a number of researchers using genetic and phylogenetic methods [5, 2] but these studies did not permit investigation into the mechanisms by which social modalities influence rates of evolution.

The present article attempts to establish whether any consistent effect on the action of natural selection can be ob-served in a population of agents in a social structure based on that typical to the cercopithecine primates within a simple set of ecological constraints. We use an agent-based model (ABM) that represents both the social relations (including dominance) and the resource constraints of a troop of Cercopithecine primates. This model does not attempt to make predictions about the rates of speciation or evolution in any specific animal species. Rather we seek to establish a more general point — that if a species maintains the described social structure, it is plausible to suggest that anomalously high rates of speciation could be caused by that structuring.

2. BACKGROUND

That accelerated adaptation might exist as a plausible outcome of the cercopithecine social system has been suggested by earlier work in modeling the effects of variability in the primary sex ratio of cercopithecine primates, on the basis of dominance rank, in population dynamics and matriline persistence [1]. Genetic investigations into the degree of relatedness in cercopithecine social groups, and the distributions of genetic diversity in the same, also point in the this direction [16]. However, neither study can provide a clear answer to the question of whether or not specific social systems can speed the process of evolution. Phylogenetic analyses across 225 genera of vertebrates has established the relative rates of adaptation and speciation across the Animal kingdom [5, 2] but such methods cannot isolate the effects of the various components of the social systems from which primates seem to benefit. The Altmanns' model operated at the level of single social groups and did not attempt to model the action of natural selection, while the genetic investigations by Melnick were not maintained for a period of time sufficient to observe selective effects.

In modeling the effects of selection, comparability of modeled populations requires that they operate in identical ecological circumstances and with shared life-history parameters and population dynamics. As the issue at hand is the possible effects of social structures on the pace of natural selection, no attempt to reproduce the values for those parameters observed in actual primate species is included in the current work. The intent is to create a knowledge-falsifying model [15] rather than a predictive one, to rule out the possibility of such an effect [17]. However, because the action of natural selection is greatly affected by the dynamics of the population under selection, what we require is a framework ecology to drive those dynamics in a consistent fashion, while allowing us to vary social parameters.

The simplest population dynamic regime to model is ex-

ponential growth at a common rate across the varied social parameters [7]. However, even an extremely slow exponential increase, maintained across an evolutionarily-relevant time span requires computational resources unavailable for the current work, as the population sizes involved become very large. A stable population regime is the solution to this problem. Modeling the action of natural selection adds additional requirements that the model act in a stochastic fashion and that some inherited variability in inclusive fitness, through variability in reproductive or mortality rates amongst the agents in the model, be included.

3. METHODS

Because the Cercopithecine primates live in such a wide range of ecological niches and in social systems with varying ecological effects of their own, we present three variations of our ABM. In each of these, the relationship between social-group size and ecological efficiency also varies, as a product of the calculation of the relationship between social dominance and reproduction probability. These represent differing relationships between social-group size and the social-group's average reproduction rate; species in which larger groups translate to greater and lesser average reproductive output and species in which the group size does not affect average reproductive output.

Given the time-span required for significant evolution to occur, direct observation of changes in gene frequencies in primates seems a difficult route to follow in search of an answer. Observations of the distribution of beneficial gene variants within a population might be profitably pursued, but the process of identifying specific genes and their effects on inclusive fitness presents problems of its own. Barring unforeseen advances in genetic technologies or the appearance of funding for the sorts of long-term traditional observational studies required, modeling natural selection in a population with the proper social structure seems the only immediate way forward. However, this modeling must operate at the individual level, rather than that of populations or social groups, as it is the interactions of these individuals that drives both the social and selective processes under inspection [8].

3.1 Environment

Most models of this sort used in biological investigations contain explicit spatial components. [14, 11, 4]. In some respects the current model does as well, but here the primary space represented is the social one and it is limited to tracking which social group an individual agent resides within. We use discrete time intervals in our models as well with a single clock in which each tick of the clock represents a single year.

Our ecologiy begins with the common construct of a carrying capacity(k_G), which allows for both stochastic events and the maintenance of comparability between populations with varying social parameters. Defined as the population size at which reproductive and mortality rates are in equilibrium, the application of a carrying capacity can be implemented as the outcome of linear differential equations defining the reproductive and mortality probabilities of individual members as total population size(n_G) varies [3]. Additional parameters in these linear equations, a base rate (b_R and b_M) of mortality and reproduction, allow finer control over population turnover rates by allowing the modeller

to set reproduction and mortality rates when the population size is at the carrying capacity(k_G).

$$P_R = (2 - (n_G/k_G))b_R \qquad (1)$$

$$P_M = (n_G/k_G)b_M \qquad (2)$$

Controlling reproductive variability is made essential by the need to maintain a constant number of social groups in the population, and the limitations that female philopatry and obligate male dispersal place on such maintenance. Because females can only join a social group by being born within it, and social group in which all the resident females die is rendered permanently non-viable. These requirements could be greatly ameliorated if the social groups being modelled were capable of self assembly if social group-fission could be used to maintain a constant number. However, such capacities are outside the scope of the current work. Self-assembling models of primate social grouping represent a technical and scientific challenge, in itself, significantly more complex than the task at hand.

The actual probabilities of reproduction and mortality, when the population is at carrying capacity, can be held as equal and constant, even if the effective carrying capacity changes due to the inclusion of an analog of natural selection acting on the carrying capacity the population operates under. This allows both the maintenance of comparability between runs of the model with varying social parameters and while under the effects of selection. The effect is analogous to density dependent rates of reproduction and mortality with an equilibrium at the population size set by the carrying capacity parameter and with parameters to determine the reproduction and mortality rates experienced at the population equilibrium point.

Within this common ecological framework, the social structure and parameters modulating the strength of its effects can be meaningfully compared. The social structure included in the current model contains the elements mentioned above; linear sex segregated dominance hierarchies with female philopatry and male dispersal, inherited female dominance, reproduction limited to within the social group and the assumption of a relationship between female reproductive success and dominance rank.

3.2 Agent Attributes and Behaviour

Each agent within our model has attributes of age, sex, social-group membership and genetic quality. 'Female' agents also possess a social dominance ranking within their social-group. Each tick of the model's clock represents one year, and the agents operate under a common life history based on their age and sex. In the current work, all agents have a maximum life-span of 10 years with weaning and sexual maturity beginning at age 2. At sexual maturity, male agents are moved from their natal social-group to another, randomly selected, one. Females remain in their natal group, and receive a dominance ranking one rank below their female parent. When a new agent is inserted into the dominance hierarchy, all lower-ranking agents are moved one rank further down the hierarchy.

During each clock tick, events occur in the following order; age-based mortality, ecologically-based mortality, male migration and reproduction. If a female agent dies for any reason, and she currently has an unweaned child, the offspring also dies.

3.3 Conditions

Three models of the relationship between reproductive success and dominance rank are included in the current work. The first, based on the earlier model suggested by the Altmanns [1], assumes an exponential relationship between female reproductive rates and dominance rank. The mathematical description of this relationship is expressed in the equation below for the reproduction probability(P_R) of a given female agent given her social rank (r_i) in which R is a social parameter, with a value between zero and one, meant to represent the fraction of the reproductive probability a group member experiences relative to the next higher ranked member. Dominance Hierarchy Strictness can then be thought of as $1 - R$.

$$P_R = R^{r_i - 1} \tag{3}$$

This can most easily be thought of as the extent to which more socially dominant animals exploit their dominance or the strictness of the dominance hierarchy. This model of the dominance/reproduction relationship poses a problem for maintaining comparability of populations with varying values for R, as the average reproduction rate of the social group will decrease with the parameter's value decreases and the group's current size increases. Expressed in ecological terms, this model might be held to represent primates with social behaviour that leads to ecological inefficiency that grows with group size;. Perhaps the larger the group, the more time wasted by increased social interaction or the less efficiently its members are able to forage. We refer to this model variant hereafter as the Top-Down Model, as the rank effect is calculated from the top ranked individual down to the bottom ranked one.

The second model provided attempts to remove the effect of the strictness of the dominance hierarchy on the average reproductive rate by rescaling each members individual reproduction rate to keep the average rate of the group unchanged, based on the size of the social group(n_G).

$$P_R = R^{r_i - 1} n_G (1 - R^{n_G})/(1 - R) \tag{4}$$

The range of values of R for which rescaling is effective, though, is limited the life-history traits of the agents, and the fact that they can only produce a single offspring at a time.

This Rescaled Model represents those primates in which the portion of time, spent socialising does not increase with group size, or in which foraging efficiency is unaffected. The third, Bottom-Up Model, calculates the effects of dominance rank from the lowest ranking member up to the highest ranked, the reverse of the Top-Down Model,

$$P_R = (1 + (1 - R))^{n_G - r_i} \tag{5}$$

This model serves to increase the average rate of reproduction in the group as group size or dominance/reproduction effect size increases, producing a larger stable population size. This represents probably the least likely ecological condition, a species of primates in which social costs decrease with increasing group size, or in which increasing group size also increases foraging efficiency.

All three of these models of social dominance and reproduction have effects on the reproduction rates and distributions of the social groups to which they are applied. In each case, reproductive probability is redistributed along a gradient within the group determined by the social dominance hierarchy, with relatively more reproductive probability being provided to those of higher social rank and less to those of lower rank. We refer to this as Reproductive Skew. When this skew is strong enough, it removes variability in the reproductive probabilities and thusly reduces stochasticity in the reproductive output of the social group by reducing the reproductive probability of low ranked members to zero and increasing the reproductive probability to certainty for highest ranks. We refer to this effect as Reproductive Skew Saturation [RSS]. As the saturative effect becomes stronger, overall reproductive output grows ever smaller as the applied gradient removes any chance for all but the most highly ranked group members lose all reproductive probability.

3.4 Selection

In our models, natural selection is modelled in a manner as simplified as the ecology. The inherited capacity on which selection acts in the model is a quantity that allows individual-level variation in the ecological constraints the agent operates under in the context of reproduction or mortality, which we call here genetic quality. We would expect such a value to correlate highly with fitness in most situations. Selection will always drive this inherited value to ever higher values, what we measure here (the dependent variable) is the *rate* of increase. An analog to mutation is also included in the form of a set of two parameters to control the frequency and size of the change induced by mutation to the genetic quality. To reduce the variability between individual runs of the model on the action of the selection analog, no variability in the genetic quality of the initial population is included. Instead, all such variability is the product of the mutation events during the model's run.

4. RESULTS

There are four relevant outputs of our model for investigating the effects of the Cercopithecine social-structure on the speed of selection; population size, total offspring produced, selection amount and selection index. For each of our three model types, we present graphs of these values across a range of values for the dominance hierarchy strictness $(1-R)$ from 1 to 0 in increments of 0.01. For each value of R, the model was run 1000 times with a Carrying Capacity parameter value(k_P) of 750 and 5 social groups. Only runs which ran for the full determined duration of 1000 clock-ticks without any of the social groups failing were included in the final results below. This is reflected in the size of the error bars as the model becomes less stable as R gets closer to 0 and dominance hierarchy strictness increases.

The amount of selection, as well as the ease with which the studied populations can be compared, depend in part on the population's mean size. Additionally, each of the three ecological models of dominance/reproduction relations affects the output population differently, as can be seen in the results below. The value presented is the arithmetic mean of the population's size at the end of each model run across all runs for a given value of R.

The amount of selection is calculated based on the population's average starting genetic quality value (always 0.5), subtracted from the final average quality score of the population when the model has run to completion. Even though all of the model runs last the same duration, because the mean population sizes differ this value will not suffice to provide

a measure of the speed of selection that can be compared across model types and values of R.

Instead, this selection amount is divided by the total number of offspring produced during each model run to produce the Selection Index value, the amount of selection per reproductive event. We've used this value, instead of the average population size because there may exist populations of the same size with differing rates of reproduction and mortality, population turn-over, that would evolve at different rates. However, these same populations will clearly produce a different number of offspring and may be, thusly, more comparable on this basis.

4.1 Top-Down

The Top-Down version of our model is the most ecologically probable. Larger social-groups are likely to pay efficiency costs as their size increases. The anticipated side-effect of this model of dominance/reproduction relations, a reduction in average population size, is clearly visible in our results. The total amount of selection appears to be driven by this factor. However, once the total number of reproductions is taken into account, our calculated selection index, the speed of selection clearly increases directly with dominance hierarchy strictness.

As can be seen in the results, the standard error values for Population Size and Total Offspring Produced do not increase as dominance hierarchy strictness increases, despite the decreased sample sizes. Selection Amount and Selection Index do not share this insensitivity and errors increase markedly as strictness increases.

This is caused by the increasing reproductive skew along the dominance hierarchy as strictness increases. Higher ranking agents become ever more likely to reproduce while the lower ranking agents become ever less likely to do so. As reproduction becomes more and more concentrated among the high dominance ranks, the variability in reproduction rates decreases until it is effectively no longer stochastic at all. Once this occurs, the Population Size and Offspring Produced begin to decrease along an exponential trajectory and the amount of selective pressure decreases as reproductive success depends less and less on genetic quality, relying entirely on rank instead. RSS effects are even more important in the other model versions as we will see below.

4.2 Rescaled

The results of the Rescaled version of our model are less easy to explain than the Top-Down version. While broadly similar in character, R values close to one initially produce an increased population size over the control value [1] with accompanying decreases in Selection Index and Amounts. The origin of the dynamics in this range of R are currently unexplained and will likely require data gathering at a lower level than population averages to explore fully. Once clear of this unexplained effect, Selection Index increase as R decreases much like the Top-Down Model.

The effects of RSS is visible again in these results, but the attempt at rescaling to avoid group-level reproductive effects seems to extend the skew-unsaturated range. This same rescaling also succeeds in increasing model stability across a larger range of R values, with visibly less increase in error sizes at given R values when compared to the Top-Down model results.

4.3 Bottom-Up

The Bottom-Up model results initially appear nearly meaningless. No dynamics of any sort are immediately apparent. This is a case of extreme RSS effects, combined with reproductive saturation as the average reproductive rate increases with decreasing values of R. However, by rerunning the model in a much smaller range of R values, between 1 and 0.991, more complex dynamics become visible.

Within this range, Population Size and Total Offspring Produced increase linearly with decreasing values of R, as expected. Selection Amount does not produce an obvious pattern, but Selection Index decrease almost linearly. This is the product of selection pressure decreasing along with R, as a result of the expected increased average reproduction rate.

5. DISCUSSION

It is clear that there is a complex relationship within our models, between the speed of evolution and social structuring. In all cases, the rate of evolutionary change varies with both the style and strictness of the dominance hierarchy. While it was only under the Top-Down version of the model that a clear acceleration of selection occurs, this case also seems the most likely to apply to actual ecological events where large social groups are likely less efficient exploiters of ecological resources.

Unfortunately, the limitations of the current model prevent us from exploring this phenomena more fully. Reproductive saturation, caused by implausibly large group sizes, and the need to maintain demographic viability across many model runs prevents us from being able to model more realistic scenarios. The same saturation effects also greatly reduce reproductive variability, likely limiting the pace of selection within the modelled population. Future work to improve the model populations long-term stability and perhaps allow self-assembly of the social groups should make exploration of these likely more fruitful areas of our parameter space accessible.

Perhaps equally exciting is the potential for applying some of the techniques invented in the current work to more practical pursuits. Evolutionary algorithms are a well established search technique, and systems designed to take advantage of the accelerated selection seen in our models might be used to significantly increase their efficiency. Clearly, structured populations of evolving agents are capable of solving problems with an efficiency that unstructured populations of the same size cannot match. Further refinements in producing these population structures and in layering them to greater complexity, should only extend the value of our techniques.

6. CONCLUSIONS

Despite the challenges of reproductive skew saturation and model demographic instability, we have clearly demonstrated that the our models of the Cercopithcine-typical social structure does affect the rate at which selection occurs in these populations. In the case of the Top-Down model, there is a clear pattern of acceleration of selection directly proportional to the strictness of the dominance hierarchy.
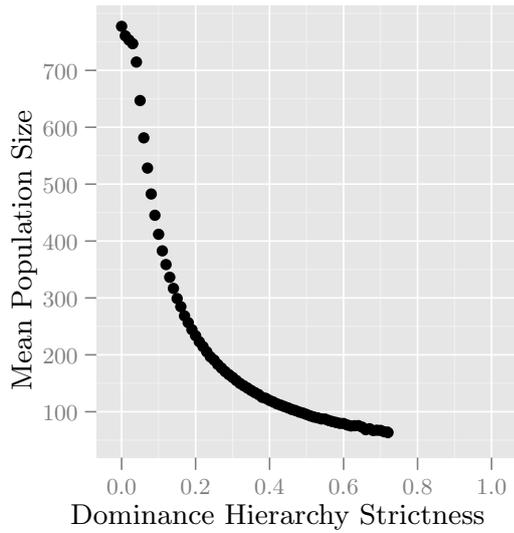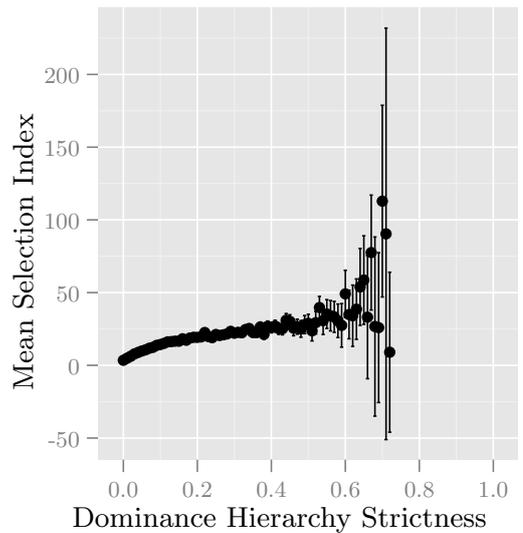
(a) Top-Down Model Population Size vs Dominance Hierarchy Strictness$(1 - R)$. As strictness increases, mean population size drops almost exponentially. This trajectory begins at the point where Reproductive Skew saturates out the stochasticity. Beyond this value almost all of the reproduction that occurs is deterministic, as the gradient removes most variability in reproductive probability.
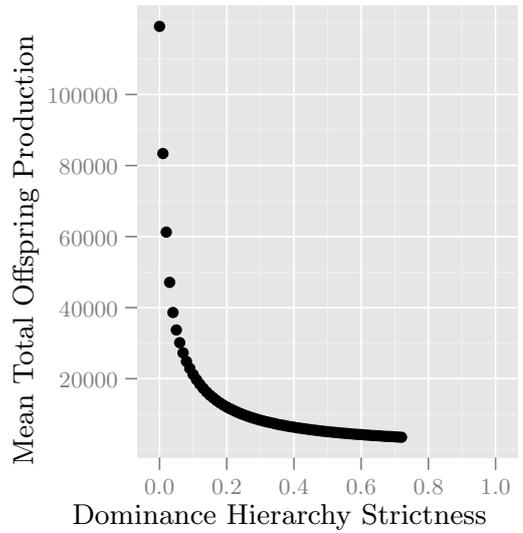
(b) Top-Down Model Total Offspring Produced vs Dominance Hierarchy Strictness$(1 - R)$. Again, as strictness increases, the average Total Offspring produced during a model run drops on a near exponential trajectory because of RSS.
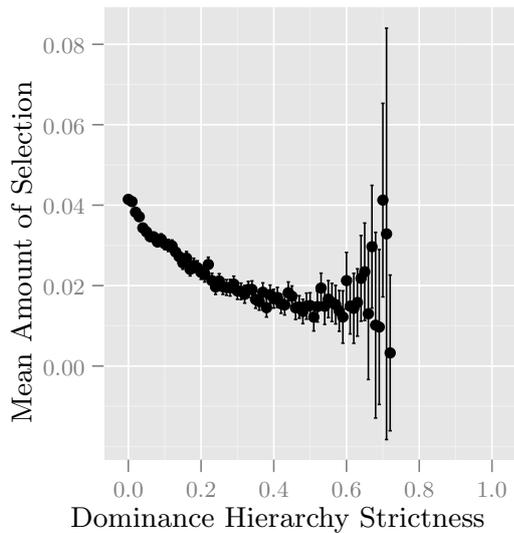
(c) Top-Down Model Selection Amount vs Dominance Hierarchy Strictness$(1 - R)$. The change in the population's average genetic quality value from the start to the end of a model run. The magnitude of this value is largely driven by the total number of reproductive events during a model run. Selection Index, the total amount of selection divided by the number of reproductive events allows comparison across differing population sizes.

(d) Top-Down Model Selection Index vs Dominance Hierarchy Strictness$(1 - R)$. The average Selection Amount divided by the total number of reproductive events in a model run. This value represents the average amount of selection per reproduction, the rate of evolution. For the Top-Down model of Dominance Reproductive Relations, this value is lowest at the control and rises roughly linearly as hierarchy strictness increases.
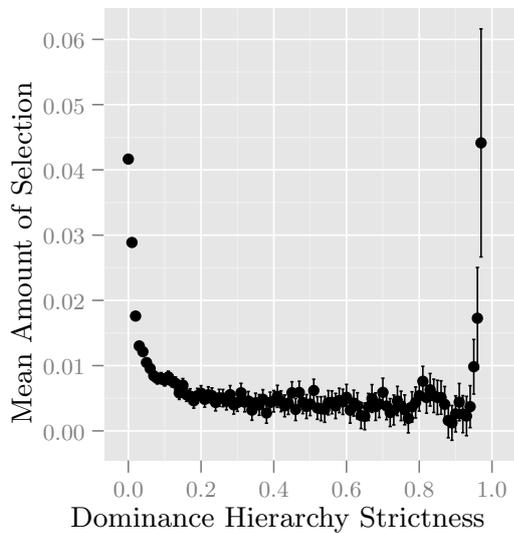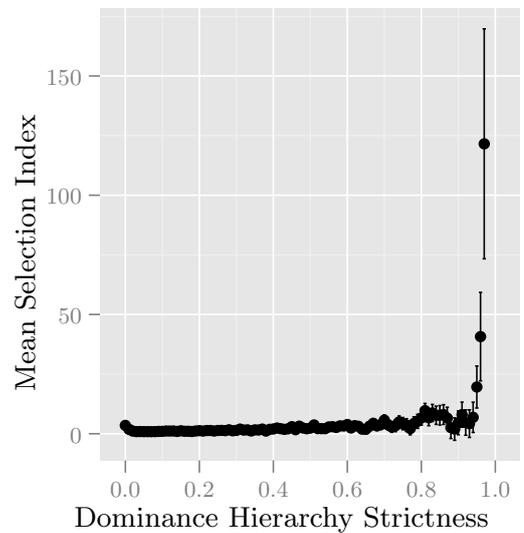
Figure 1: Top-Down Model Results
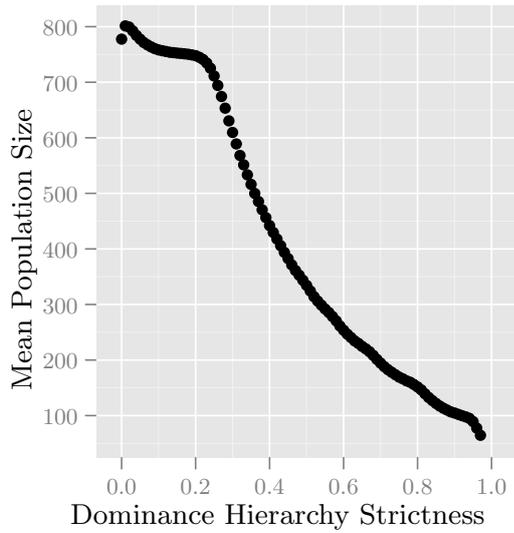
(a) Rescaled Model Population Size vs Dominance Hierarchy Strictness$(1 - R)$. Like the Top-Down model as strictness increases, mean population size drops almost exponentially. The point where Reproductive Skew saturates out the stochasticity, is lowered as rescaling flattens the reproductive probability gradient while strictness is low.
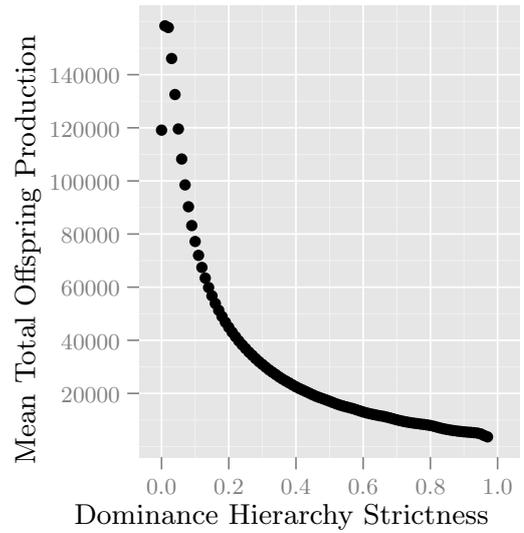
(b) Rescaled Model Total Offspring Produced vs Dominance Hierarchy Strictness$(1 - R)$ Again, as strictness increases, the average Total Offspring produced during a model run drops on a near exponential trajectory because of Reproductive Skew saturation. The markedly higher values of offspring produced for strictness values just greater than 0 appear to be caused by increased population turnover. The source of this increase is not yet understood.

(c) Rescaled Model Selection Amount vs Dominance Hierarchy Strictness$(1-R)$. Like the Top-Down model this value decreases with dominance strictness as RSS lowers the average reproductive output.
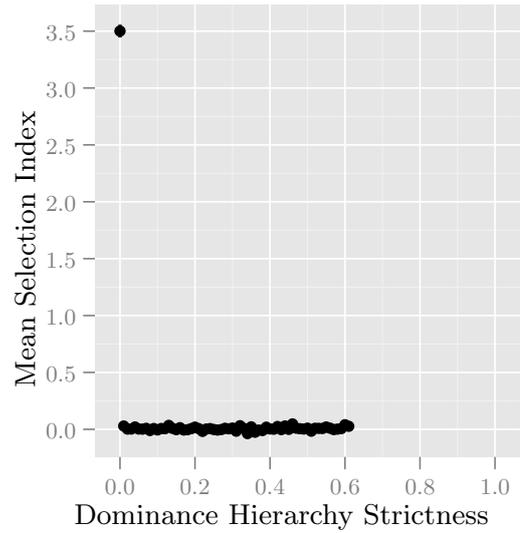
(d) Rescaled Selection Index vs Dominance Hierarchy Strictness$(1-R)$. For the Rescaled model, this value still rises roughly linearly as hierarchy strictness increases but only after the initial hump of increased population turnover is traversed.
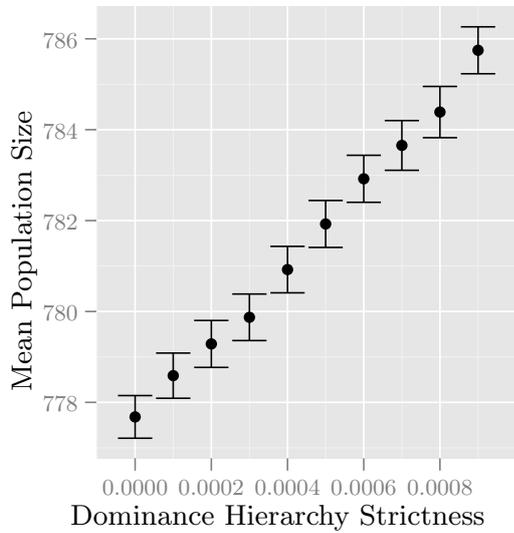
Figure 2: Rescaled Model Results
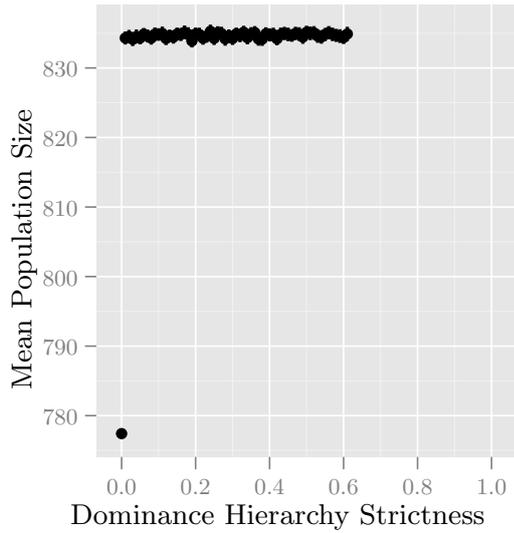
(a) Bottom-Up Model Population Size vs Dominance Hierarchy Strictness$(1 - R)$. Unlike the earlier two models, as dominance hierarchy strictness increases, mean population size remains near constant. This occurs because reproductive skew saturates the model and all of the population are producing offspring at their maximum possible rate almost immediately.
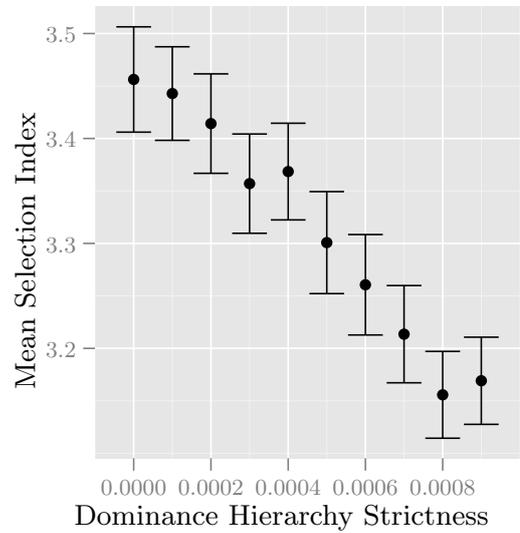
(b) Bottom-Up Selection Index vs Dominance Hierarchy Strictness$(1-R)$. The average Selection Amount divided by the total number of reproductive events in a model run. As with earlier values, charted, the Selection Index appears to remain constant.

Figure 3: Bottom-Up Model Results

(a) Bottom-Up Model Population Size vs Dominance Hierarchy Strictness$(1 - R)$. When dominance strictness is low, reproductive skew saturation is not yet dominant and a clear relationship between average Population Size can be observed, with population size increasing linearly as dominance strictness increases. The number of offspring produced follows the same pattern, but is not displayed here.

(b) Bottom-Up Selection Index vs Dominance Hierarchy Strictness$(1-R)$. Again, unlike the larger set of runs, Selection Index is not constant across the R values displayed. However, as saturation increases and reproductive rates increase, the speed of selection drops under reduced selective pressure.

Figure 4: Bottom-Up Model Low Strictness Results

Additionally, the consistent effects of these structures on population size may also point in the direction of further benefits to populations structured in this manner, as a way to control population independently of the usual ecologically imposed constraints. That a mechanism driven by socially learned behaviour, the adoption of maternal dominance rank, interacts with evolutionary selection in such a complex way provides strong support for the idea that complex sociality is responsible for the observed pattern of frequent speciation in social vertebrates. Further investigation into these mechanisms may lead to advances in our understanding of evolutionary processes and the ability to harness these phenomena in creating evolved software.

7. ACKNOWLEDGMENTS

8. REFERENCES

[1] M. Altmann and J. Altmann. Models of status-correlated bias in offspring sex ratio. *American Naturalist*, 137(4):542–555, 1991.

[2] M. Baker and P. Marler. *Evolution of social behavior - hypotheses and empirical tests : report of the Dahlem Workshop on Evolution of Social Behavior - Hypotheses and Empirical Tests, Berlin 1980, Feb. 18-22 / Hubert Markl, ed. ; rapporteurs : Marc Feldman ... [et al.] ; [Dahlem-Konferenzen].* Verlag Chemie, Weinheim, 1980.

[3] M. Begon. *Ecology : from individuals to ecosystems.* Wiley-Blackwell, 2006.

[4] L. Bian. Object-oriented representation for modelling mobile objects in an aquatic environment. *International Journal of Geographical Information Science*, 14(7):603–623, 2000.

[5] G. L. Bush, S. M. Case, A. C. Wilson, and J. L. Patton. Rapid speciation and chromosomal evolution in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 74(9):3942, 1977.

[6] B. Chapais. The role of alliances in social inheritance of rank among female primates. *Coalitions and alliances in humans and other animals*, pages 29–60, 1992.

[7] L. Cole. The population consequences of life history phenomena. *The Quarterly Review of Biology*, 29(2), 1954.

[8] L. e. a. DeAngelis, D.L. Gross. *Individual-based models and approaches in ecology : populations, communities, and ecosystems.* Chapman, 1992.

[9] A. Di Fiore and D. Rendall. Evolution of social organization: A reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences*, 91:9941–9945, 1994.

[10] A. Di Fiore and D. Rendall. Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences of the United States of America*, 91(21):9941, 1994.

[11] H. S. He, D. J. Mladenoff, and J. Boeder. An object-oriented forest landscape model and its representation of tree species. *Ecological Modelling*, 119(1):1 – 19, 1999.

[12] S. Kawamura. The matriarchal social order in the Minoo-B group. *Primates*, 1(2):149–156, 1958.

[13] N. Koyama. On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. *Primates*, 8(3):189–216, 1967.

[14] M. Makela, G. Rowell, W. S. IV, and L. Wilson. An object-oriented intracolonial and population level model of honey bees based on behaviors of european and africanized subspecies. *Ecological Modelling*, 67(2-4):259 – 284, 1993.

[15] C. C. Maley and H. Caswell. Implementing i-state configuration models for population dynamics: an object-oriented programming approach. *Ecological Modelling*, 68(1-2):75 – 89, 1993. Theoretical Modelling Aspects.

[16] D. Melnick. The genetic consequences of primate social organization: a review of macaques, baboons and vervet monkeys. *Genetica*, 73(1):117–135, 1987.

[17] W. M. Mooij and M. Boersma. An object-oriented simulation framework for individual-based simulations (osiris): Daphnia population dynamics as an example. *Ecological Modelling*, 93(1-3):139 – 153, 1996.

[18] P. Perelman, W. E. Johnson, C. Roos, H. N. SeuÃąnez, J. E. Horvath, M. A. M. Moreira, B. Kessing, J. Pontius, M. Roelke, Y. Rumpler, M. P. C. Schneider, A. Silva, S. J. O'Brien, and J. Pecon-Slattery. A molecular phylogeny of living primates. *PLoS Genetmal*, 7(3):e1001342, 03 2011.

[19] A. Purvis. A composite estimate of primate phylogeny. *Philosophical Transactions: Biological Sciences*, 348(1326):405–421, 1995.

[20] A. Pusey and C. Packer. Dispersal and philopatry. *Primate Societies*, 1987.