Stepwise evolution of stable sociality in primates

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Although much attention has been focused on explaining and describing the diversity of social grouping patterns among primates[1–3], less effort has been devoted to understanding the evolutionary history of social living[4]. This is partly because social behaviours do not fossilize, making it difficult to infer changes over evolutionary time. However, primate social behaviour shows strong evidence for phylogenetic inertia, permitting the use of Bayesian comparative methods to infer changes in social behaviour through time, thereby allowing us to evaluate alternative models of social evolution. Here we present a model of primate social evolution, whereby sociality progresses from solitary foraging individuals directly to large multi-male/multi-female aggregations (approximately 52 million years (Myr) ago), with pair-living (approximately 16 Myr ago) or single-male harem systems (approximately 16 Myr ago) derivative from this second stage. This model fits the data significantly better than the two widely accepted alternatives (an unstructured model implied by the socioecological hypothesis or a model that allows linear stepwise changes in social complexity through time). We also find strong support for the co-evolution of social living with a change from nocturnal to diurnal activity patterns, but not with sex-biased dispersal. This supports suggestions that social living may arise because of increased predation risk associated with diurnal activity. Sociality based on loose aggregation is followed by a second shift to stable or bonded groups. This structuring facilitates the evolution of cooperative behaviours[5] and may provide the scaffold for other distinctive anthropoid traits including coalition formation, cooperative resource defence and large brains.

Anthropoids differ from other social vertebrates in the prevalence of stable groups and bonded relationships between individuals[6]. Explaining how primate social systems evolved is central to understanding the evolution of our closest relatives and the emergence of early human social behaviour[7]. Conventional explanations have appealed more to adaptive reasoning than phylogenetic history to account for patterns of sociality[4]. Adaptive arguments often invoke the socioecological model[8], which predicts that individuals readily alter patterns of aggregation in response to ecological conditions[3,9]. This focus has resulted in less emphasis on the historical processes and phylogenetic constraints that have informed other areas of evolutionary biology[10].

However, behaviour, like morphology, physiology and life history, is heritable[11] and shaped by historical processes. Primate social behaviour is no exception; Old World primates, particularly cercopithecines, have highly inflexible social structures, and social traits cluster according to taxonomic grouping across the order[4]. Strong historical constraints make it crucial to incorporate phylogeny when testing adaptive explanations, but also create the possibility of explicitly modelling the evolutionary pathways leading to extant primate grouping patterns.

To evaluate the evolution of stable sociality in primates, we mapped the composition of foraging groups (solitary, family groups, harems or multi-male; see Supplementary Information for further discussion of alternative classification schemes) for 217 species onto a primate consensus tree (Fig. 1 and Supplementary Information) derived from genetic data[12]. We then evaluated the strength of phylogenetic inertia

in the data (historical non-independence) using Pagel's lambda (λ)[13]. A λ value of 0 implies evolution independent of the phylogenetic tree, whereas a value of 1 indicates that the probability of shared inheritance between species is proportional to their relatedness. Social grouping patterns showed a strong phylogenetic signal ($\lambda_{max} = 0.983$, maximum likelihood (LL_{max}) = -150.038) (significantly different from a λ value of 0 ($LL_0 = -332.63$, $P < 0.001$), but not significantly different from a λ value of 1 ($LL_1 = -141.12$, $P = 0.189$)). Flexible social structure is characteristic of only two groups, the Callitrichidae and Lemuridae (Fig. 1).

This strong phylogenetic signal allows a reconstruction of the evolutionary pathways leading to extant primate grouping patterns. Theoretical models suggest two possibilities. First, the socioecological model posits that grouping patterns are driven by individual responses to resource availability[3,9]. Under this 'unstructured' model, if grouping patterns are facultative, transitions between all possible social states (and polymorphic states within species) should be equally likely. Second, primate social complexity has been proposed to increase in a stepwise fashion from solitary individuals, through small groups to large, socially complex groups[14–16]. From this 'increasing complexity' model we would predict that pair-living was the earliest form of social group, followed by more complex grouping patterns. Support for such a model of social evolution through pair-bonds has been found in birds[17,18] and insects[19].

We used a Bayesian framework, implemented in BayesTraits[20], to evaluate four alternative models of social evolution (Fig. 2), including the two described above, on a posterior distribution of primate trees. The simplest model estimates a single rate of transition between all social states, representing an unstructured 'null' model of social change in which all state changes occur at the same underlying rate. We contrast this with a second, parameter-rich model in which rates are allowed to vary across all transitions. This model implies that some transitions are more likely than others, for example the rate from solitary to pair-living may be different from the rate from pair-living to solitary or to some other state—but does not make assumptions about what this structure will be. The third model simulates increasing complexity by restricting possible transitions to stepwise changes up and down a chain linking solitary to pair-living, to small harem groups and finally to large multi-male/multi-female groups. The fourth model is derived from the data and identifies likely transitions using the reversible-jump procedure in BayesTraits, which searches the posterior distribution of possible models by linking (setting to equal) or removing (setting to zero) transition rate parameters.

The model with the highest posterior support in the reversible-jump analysis (Supplementary Table 1) suggests that social evolution proceeds from solitary to multi-male/multi-female groups and then either to pair-living or harems. Back transitions occur from harems to multi-male groups, whereas transitions between pair-living and harems do not occur. Transitions from solitary to social are not reversed; such that once a lineage becomes social it remains so. We used Bayes Factors[20–22] to test whether there is sufficient signal in the primate sociality data to support decisively any of the four alternative models. Table 1 shows that the reversible-jump-derived model is not only the

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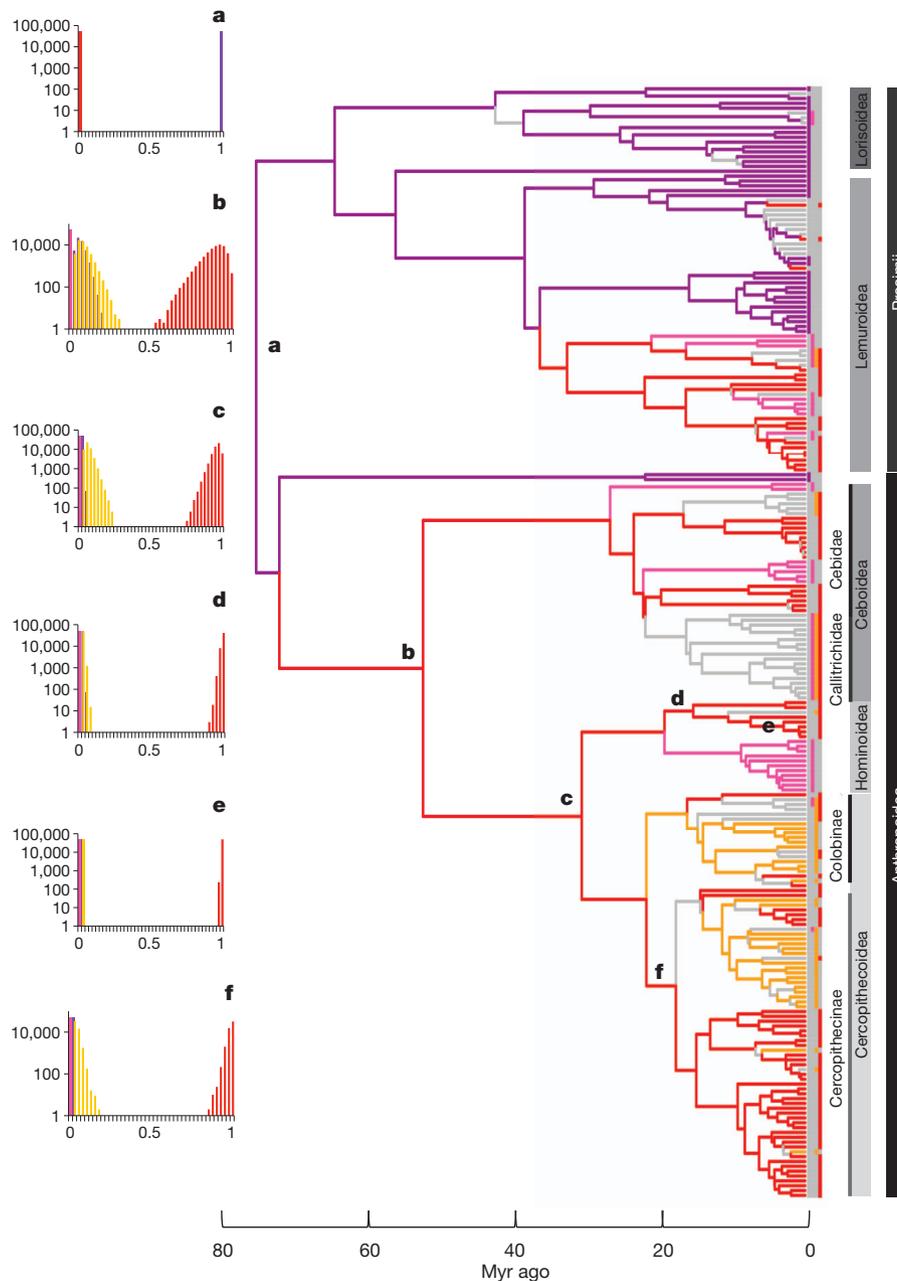
Figure 1 | Primate phylogeny showing ancestral state reconstructions for sociality under the reversible-jump Markov chain Monte Carlo-derived model of evolution. The tree topology is the maximum clade credibility tree from the 10kTrees Project[12] posterior distribution with branch lengths drawn proportional to time. Branches and tips are coloured for solitary (purple), uni-male (orange), multi-male (red), pair-living (pink) where the combined probability of the state and the branch is greater than or equal to 0.7. Where the combined probability is less than 0.7, the branch is grey. Histograms represent the posterior probability distribution of each social state at the nodes indicated (**a**, primate root; **b**, anthropoid root; **c**, catarrhine root; **d**, great ape root; **e**, *Pan–Homo* split; **f**, Old World monkey root).

best fit to the data, but is also decisively better at explaining the data than the equal rates, the fully parameterized or the increasing complexity models.

We used the reversible-jump-derived model of social evolution to reconstruct the evolutionary history of social organization across the primate tree (Fig. 1). Ancestral node reconstructions reveal that the transition from solitary foraging at the primate root (74 Myr ago) to social aggregations was established at the anthropoid root (52 Myr ago) and the root of the Indriidae and Lemuridae (32 Myr ago) in prosimians. Other forms of social grouping evolved later in primates; harems appeared at the root of the Colobinae (16 Myr ago), followed soon after in the Cercopithecini (14 Myr ago). Pair-living arose at the root of the Callitrichidae (16 Myr ago), Hylobatidae (8.6 Myr ago), *Avahi* (6.4 Myr ago), hapalemurs (6.3 Myr ago), *Aotus* (4.8 Myr ago)

and *Callicebus* (4.5 Myr ago). Thus, the fundamental shift to sociality occurred with the appearance of aggregations, followed later by derived grouping structures, including pair-living.

We next examined two possible catalysts of primate social evolution. First, the switch to social living is presumed to occur under increased predation pressure[1] coinciding with the shift from nocturnal to diurnal activity. We used a test of co-evolution in BayesTraits[20] to assess whether changes in activity patterns predict the major transition to social living. There was decisive support[22] for the dependent model (that is, co-evolution between activity and sociality, Fig. 3a) over the independent model (mean $\mathrm{LL}_{\mathrm{D(dependent)}} = -33.03 \pm 0.08$ s.e.m. compared with $\mathrm{LL}_{\mathrm{I(independent)}} = -41.71 \pm 0.04$ s.e.m.; Bayes Factor 3.39; Supplementary Table 2), supporting the proposed link between the evolution of activity patterns and social living. Additionally, both
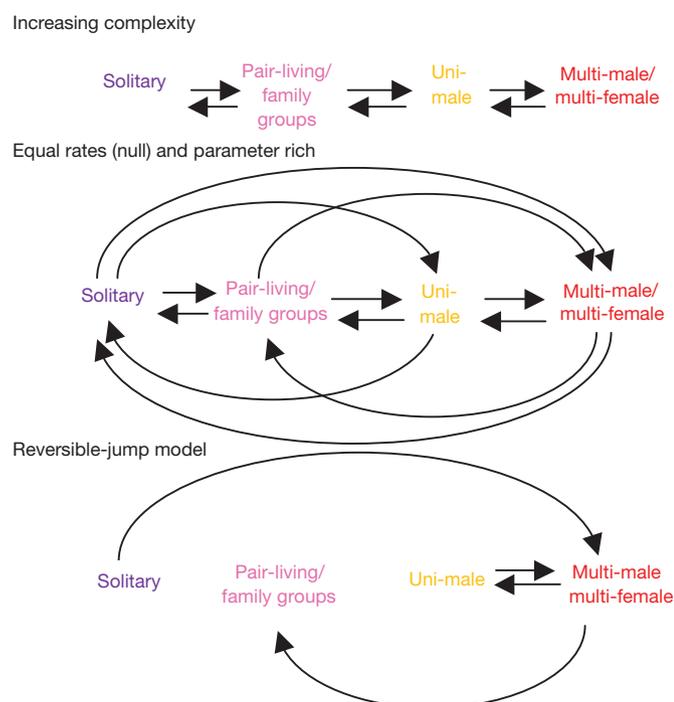
Figure 2 | **Alternative evolutionary models of primate social evolution.**
Arrows represent allowable transitions between modes of social living under
each model. Under the complexity and parameter-rich model, transition rates
represented by each arrow can vary. Under the equal rates model, all rates are
fixed to a single optimized rate parameter. The reversible-jump-derived model
is a significantly better fit to the data than the alternative models.

Figure 3 | **Estimated transition rates for co-evolution of social living.**
Estimated transition rates with (**a**) activity and (**b**) dispersal patterns. Thin
lines, an estimated median transition rate >0 but <0.01; heavy lines, a rate
>0.01; dashed lines, a median estimated zero transition rate. Full estimated
rates are reported in Supplementary Information.

intermediate states (social/nocturnal and solitary/diurnal) are unstable
as the transition rate from these states to social/diurnal is an order of
magnitude higher than any other transition. This suggests that the
switch from a solitary, nocturnal lifestyle to diurnal social living repre-
sents a major shift in the primate adaptive landscape. Group living has
long been argued to provide anti-predator benefits[1], and the shift to
diurnal social living in primates would have opened up a vast new
adaptive space in a highly visual world[23].

The second possible catalyst is the switch to sex-biased dispersal,
whereby one sex (typically males) disperses further from the natal range
than the other. This is assumed to be an ancestral or default mammalian
characteristic[24]. Changes in dispersal behaviour may be important in
the evolution of sociality because in its extreme form, philopatry, one
sex foregoes dispersal and remains in the natal range resulting in kin
structured groups. A switch to sex-biased dispersal could therefore
facilitate kin selection and the emergence of cooperative social
groups[25–27]. The extension of the mother–daughter bond to groups of
related females also has been proposed as the fundamental relationship
underpinning mammalian sociality[28]. We used Discrete to evaluate
whether sex-biased dispersal precedes the shift to sociality in primates.
Although we find support for co-evolution between social grouping
and dispersal patterns (mean $LL_D = -73.27 \pm 0.03$ s.e.m. versus
$LL_I = -74.66 \pm 0.05$ s.e.m.; Bayes Factor 1.21; Fig. 3b), the association
is much weaker than between sociality and activity patterns and inde-
pendent models are sampled above chance (Supplementary Table 3).

Additionally, contrary to the assumption of sex-biased dispersal being a
primate (and mammalian) default[24], the ancestral state for primates is
bi-sexual dispersal (posterior probability of 0.93) and the estimated
transition rates indicate that sex-biased natal dispersal follows the shift
to sociality rather than precedes it (Fig. 3b).

Dispersal changes, therefore, do not trigger social living, but as they
follow the emergence of social living they could be associated with a
secondary transition to stable groups. A similar suggestion was put
forward in a controversial model for the evolution of cooperative
sociality in eusocial insects[5]. The model argues that aggregating indi-
viduals first create population structure. Stable groups then emerge
secondarily through increased persistence resulting from silenced dis-
persal in at least one sex. To test whether this model explains the
evolution of stable primate groups, we classified species as solitary,
unstable social or stable social (the later defined as species with natal
philopatry coupled with no/limited secondary dispersal or those with
stable, long-term pair bonds). We then used the reversible jump pro-
cedure to identify the most likely model for the evolution of group
stability; our model suggests that solitary living is the ancestral state,
followed by unstable groups, and with a final transition to stable social
groups (marginal $LL = -65.2 \pm 0.019$, Supplementary Table 4). This
model is a better fit to the data than either an equal rates
($LL = -71.59 \pm 0.021$, Bayes Factor = 2.77) or a parameter-rich
model, where transitions are allowed between all states
($LL = -69.08 \pm 0.052$; Bayes Factor = 1.66; Fig. 4). It thus appears
that although the evolution of social groups does not occur through
increasing complexity as defined by group size, there is strong support
for a model of stepwise transitions leading from solitary living to
unstable social aggregations, followed by a second step to stable groups
based on either kinship or reproductive ties. Although transitions to
social grouping are not uncommon in vertebrates, this secondary
transition to stable grouping is, and may hold the key to the evolu-
tion of cooperative sociality characteristic of anthropoid primates,
particularly humans.

Our analyses demonstrate a model of primate social evolution,
which highlights the initial switch from solitary foraging to multi-
male/multi-female aggregations. Although we cannot directly test
adaptive explanations, our findings show this switch co-evolved with
a change from a nocturnal to a diurnal lifestyle, supporting the role of
predation in driving social evolution. Although group size has often
been used as a proxy of social complexity in primates, relationship
or group stability represents a more important indication of social

Table 1 | Comparison of alternative model performance

Model	Rank	Parameters	Mean likelihood	Log$_{10}$[Bayes Factor]
Reversible-jump Markov chain Monte Carlo-derived model	1	4	−64.84	-
Parameter-rich (unconstrained) model	2	12	−72.13	5.03
Equal rate 'null' model	3	1	−76.82	5.24
Increasing complexity	4	6	−77.55	6.5

Table shows number of model parameters, model rank, likelihood and log$_{10}$[Bayes Factors] (see Supplementary Information). The Bayes Factor indicates relative support for the reversible-jump-derived model
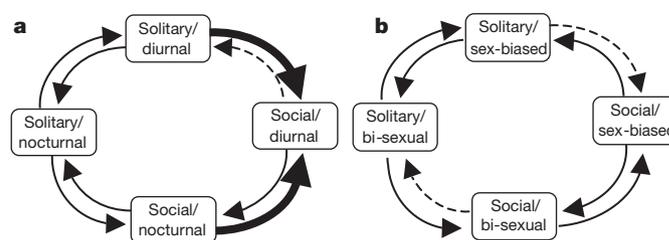over alternatives (0–0.5 minimal; 0.5–1.0 substantial; 1.0–2.0 strong; >2.0 decisive)[21].

a

Solitary → Unstable social → Stable social

(Unstable social ← Stable social)

b

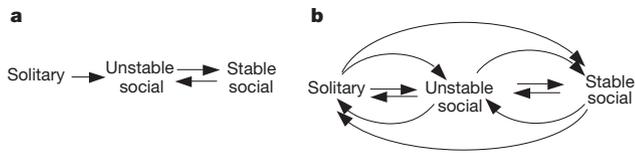Solitary ⇄ Unstable social ⇄ Stable social (with additional curved transitions between all states)

Figure 4 | Alternative evolutionary models for the evolution of stable grouping patterns. a, The model with the highest posterior support for the evolution of stable or bonded social groups. The model implies that stable social groups evolve from sociality through unstable social groups. **b**, Alternative models allow transitions between all possible states, either all constrained to the same rate (equal rates model) or allowed to vary (parameter-rich model).

complexity[6]. Our models suggest that the initial switch to sociality involved loose or unstable multi-male/multi-female aggregations (as exemplified in diurnal lemurs) followed by secondary transitions to bonded social relationships between mothers and daughters[28] (philopatry) or reproductive adults[6] (pair-living). This secondary transition may be a key step towards facilitating cooperative social behaviour. In non-primates, social structuring is most commonly characterized by aggregations, with bonding associated with pair-living (for example, birds, ungulates, carnivores), and kin-based groups limited to a few taxa such as elephants and cetaceans[6,29]. Kin-based structuring parallels that seen in eusocial insects. Testing these evolutionary models in other phyla would reveal whether the pathways suggested for primate evolution are more widely characteristic of cooperative sociality.

METHODS SUMMARY

To account for uncertainty in the underlying phylogeny, model testing was undertaken across a Bayesian posterior distribution of 10,000 ultrametric primate trees derived from genetic data as part of version 2 of the 10kTrees Project[12]. The maximum clade credibility tree we present was inferred from the complete 10kTrees sample using TreeAnnotator[30]. Pagel's lambda was estimated using the Ape and Geiger (see Supplementary Information) packages in R.

BayesTraits[20] uses an Markov chain Monte Carlo method to derive posterior distributions of log-likelihoods, the rate parameters of models of evolution, and trait values at ancestral nodes on the phylogeny. Transition rates between all states were constrained to be equal for the unstructured model (producing a simple one-parameter model). Rates were allowed to vary freely to parameterize the flexible model. All rates in the increasing complexity model except the forward and backward transitions between solitary/pair-living, pair-living/uni-male and uni-male/multi-male groups were restricted to zero. Model transition rates were also determined using the reversible-jump procedure in BayesTraits. Reversible-jump models were ranked in order of their posterior probability to identify the top ranked model. Model performance was compared using a $\log_{10}$[Bayes Factor][21]. Co-evolution between behavioural traits was assessed using the Discrete package in BayesTraits. Social organization was classed as solitary (0) or social (1) (including pair-living); activity pattern as nocturnal (0) and diurnal (1); natal dispersal as bi-sexual (0) or sex-biased (1) (see Supplementary Materials for further details).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Author Contributions S.S. designed the study, compiled the data and executed analyses. C.O. executed analyses. Q.A. was involved in study design and advised on statistical analyses. All authors contributed to the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to S.S. (susanne.shultz@anthro.ox.ac.uk).

METHODS

Primate data. Primates were classified as solitary, pair-living and group-living[9]; group-living were further split into single and multi-male groups (Supplementary Fig. 1). Data were compiled mainly from secondary literature or review articles[3,16,31–35] and several online sites (pin.primate.wisc.edu, www.theprimata.com). The species were coded as follows: solitary ($n = 40$), pair-living ($n = 53$), single-male, multi-female ($n = 67$) or multi-male, multi-female ($n = 121$). Dispersal was classified as male-biased ($n = 86$), female-biased ($n = 14$) or bi-sexual dispersal ($n = 105$). Recent papers have argued that dispersal is more flexible than classification schemes acknowledge[36]. However, here we attempt to capture the characteristic dispersal behaviour for each species. Activity was classified as diurnal or nocturnal; cathemeral species were classed as polymorphic for activity. Species were also classified in multiple states when variation between or within populations was reported. One classification decision we faced was how to categorize species that spent most of their time foraging solitarily but were either known to have extended and stable social groups or had stable sleeping associations (for example, *Loris*, *Microcebus*, *Galago*, *Pongo*). Although no primate is truly solitary, these species are particularly problematical as a few well-documented studies suggest stable community structures in nocturnal species, yet they do not form stable foraging parties[37]. The same discussion about whether orang-utans are social or solitary has longed plagued primatologists. For this reason, we used multiple classifications for these species: (1) solitary foragers, (2) polymorphic (solitary foraging plus social category), and (3) solitary foraging except for *Pongo*. This way we were able to evaluate the impact their classification had on model performance. The classification scheme that primarily relied on social grouping classification, with the exception of *Pongo*, had the highest mean likelihood (LL = −64.80), followed by the polymorphic classification scheme (LL = −66.14), and finally the scheme that classified *Pongo* as solitary (LL = −71.71). *Pongo* classification affects model fit as they would be the only example of an anthropoid primate to revert from social to solitary living. We evaluated the posterior probability of predicted rate classes (zero versus non-zero) for each transition across all three classification schemes (Supplementary Fig. 2). Finally, we classified stability based on reported adult dispersal or migration events for both males (typically secondary dispersal after joining new groups) and females (classified as post-partum dispersal). This classification is more subjective than the previous traits as the data are limited and often descriptive. We classified pair-living species as stable if group turnover events were typically associated with death or severe injury to one of the adults (rather than regular emigration by resident adults). For group-living species, we defined stability as at least one sex typically remaining in the group throughout adulthood (resulting in kin-based groups). The primary references that the classifications are based on are found in the Supplementary Table 6.

Tree. The primate phylogeny was based on a sample of 10,000 ultrametric trees from version 2 of the 10kTrees Project[12]. This provides a posterior distribution of phylogenies using Bayesian inference from six mitochondrial (CYTB, COX1, COX2, 12S rRNA, 16S rRNA and a gene cluster) and three autosomal genes (MC1R, CCR5, SRY) for 230 primate species. The nodes of the consensus tree are dated using mean molecular branch lengths from the Bayesian analysis and six known fossil calibration points[12]. The consensus tree is a maximum credibility tree and was inferred from the complete 10,000 tree sample using TreeAnnotator[30]. As BayesTraits[20] (http://www.evolution.rdg.ac.uk/SoftwareMain.html) allows missing data, we included all species from the tree block rather than pruning the tree to fit the data.

Phylogenetic signal. Phylogenetic signal in data indicates that related species are more similar in a particular trait than would be expected by chance (that is, the trait of a daughter species is not independent of that of the parent). To quantify phylogenetic signal in our primate sociality data, we used the fitDiscrete function in the Geiger[38] package in R to calculate the maximum likelihood value of Pagel's lambda[13,39] on the maximum credibility tree. A λ value of 1 is consistent with a model of evolution along the phylogeny (that is, a probability of shared inheritance proportional to relatedness), whereas a λ value of 0 suggests evolution independent of the phylogenetic tree[40]. A likelihood ratio test was used to compare the fitted maximum likelihood value of λ with a model implying no phylogenetic signal ($\lambda = 0$) to a model of evolution along the tree ($\lambda = 1$). The likelihood ratio test follows a χ^2 distribution, with one degree of freedom. Polymorphisms were collapsed such that flexible species were assigned an additional flexible social category.

Model settings and performance. To identify the model best supported by the data for each analysis (social evolution, stability, social-activity and social-dispersal models, plus the social-stability data sets), we used the Discrete and Multistate option in BayesTraits[20]. We began with the reversible-jump procedure, using a uniform hyper before seed exponential rate priors with mean and variance ranging between 0 and 2 (ref. 41). We initially explored using a uniform hyper-prior to seed exponential rate priors with mean and variance ranging between 0

and 2. Model performance was robust to choice of hyper prior. 'Rate dev' settings were set to achieve acceptance values within 20–40% (for most models this was 0.02, 0.05 or 0.1). To establish whether the models had converged, we evaluated the posterior distribution and trace of harmonic mean log-likelihoods; we assumed convergence when this distribution was approximately normal, the likelihood traces did not show large jumps across runs. Models visited by the Markov chain were run in order of their posterior probability (Supplementary Tables 1–4). The posterior sample of transition rates for the social evolution model is shown in Supplementary Fig. 3.

Each Markov chain Monte Carlo simulation was run five times for 30 million iterations sampled every 100, with the first 25 million iterations discarded as the burn-in period. Examination of the post-burn-in log-likelihood and rate parameters across the Markov chain plotted in Tracer[21] indicated that runs had reached convergence by this time (25 million iterations) and effective sample sizes for the parameters of interest were all above 2,000. We report the posterior distribution for rate parameters, marginal log-likelihoods[21] and states at ancestral nodes from the run with the median likelihood.

Model comparison: social evolution. We constructed four different models of social organization. First, all rates were set equal, simulating equal likelihood for all transitions. Second, rates were allowed to vary freely without constraint to produce a 'flexible' model. Third, we ran a 'complexity' model where transitions were restricted so that movements were only allowed between solitary and pair-living, pair-living and uni-male harems, and uni-male harems and multi-male social organization. Finally, the model structure with the highest posterior support from the reversible-jump analysis was run, allowing transitions from solitary to multi-male and from multi-male to pair-living and to uni-male and back. All other rates were set to zero. Final models were run using uniform rate priors (0–0.3) across a range informed by either the reversible-jump analyses for the data driven models or maximum likelihood analyses for theoretical models. Examination of posterior distributions indicated that the rates were well within the prior bounds. Stability of the models was checked by evaluating variance in the mean log-likelihood values over five iterations of the final analyses.

To compare alternative models of social evolution, we calculated both the marginal likelihood and Bayes Factor (the ratio of the marginal likelihoods) using Tracer[21]. The Bayes Factor (BF) shows the weight of evidence to support one model over another, from 0 to 0.5 (minimal), to 0.5–1.0 (substantial), to 1.0–2.0 (strong), to greater than 2.0 (decisive)[22].

Ancestral states. We used BayesTraits to infer the posterior probability of social behaviours at each ancestral node in the primate tree under the model with the highest posterior probability from the reversible-jump analysis. Although the results presented in Supplementary Fig. 1 are drawn on the maximum clade credibility tree, the analysis was performed across the posterior distribution of 10,000 primate trees. The ancestral state probabilities for each branch of the tree are the combined posterior probability of each state on that branch with the posterior probability that the branch itself exists.

Correlated evolution. The Discrete package in BayesTraits enables analysis of the co-evolution of two binary traits over a phylogeny. We ran two Discrete analyses to test the hypotheses that either dispersal or activity patterns determine social organization in primates by investigating the correlation and relative timing of changes in social organization with those in dispersal and activity. We ran the Discrete analysis with social organization as solitary (0) or social (1) (including pair-living), dispersal as bi-sexual (0) or either female or male (1) and activity as nocturnal (0) or diurnal (1) with cathemeral as (01). Model parameters and performance were established using the procedures described above. Exponential rate priors were seeded from a uniform hyper prior with mean and variance ranging between 0 and 2 (ref. 41). The posterior sample of reversible-jump Markov chain Monte Carlo models for social-activity analyses is shown in Supplementary Table 2, and for social-dispersal analyses in Supplementary Table 3. A Bayes Factor[21] comparison was made between the independent and the dependent reversible-jump hyperprior model runs such that independent evolution could be rejected if there was support for the dependent model. In addition to a Bayes Factor comparison, we also investigated the number of visits to independent models in the dependent run to assess whether this was above chance[20]. Mean and median transition rates for the two dependent analyses are reported in Supplementary Table 5.

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