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Primate social organization evolved from a flexible pair-living ancestor

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Edited by Anthony Di Fiore, The University of Texas at Austin, Austin, TX; received September 9, 2022; accepted October 26, 2023

Explaining the evolution of primate social organization has been fundamental to understand human sociality and social evolution more broadly. It has often been suggested that the ancestor of all primates was solitary and that other forms of social organization evolved later, with transitions being driven by various life history traits and ecological factors. However, recent research showed that many understudied primate species previously assumed to be solitary actually live in pairs, and intraspecific variation in social organization is common. We built a detailed database from primary field studies quantifying the number of social units expressing different social organizations in each population. We used Bayesian phylogenetic models to infer the probability of each social organization, conditional on several socioecological and life history predictors. Here, we show that when intraspecific variation is accounted for, the ancestral social organization of primates was inferred to be variable, with the most common social organization being pair-living but with approximately 10 to 20% of social units of the ancestral population deviating from this pattern by being solitary living. Body size and activity patterns had large effects on transitions between types of social organizations. As in other mammalian clades, pair-living is closely linked to small body size and likely more common in ancestral species. Our results challenge the assumption that ancestral primates were solitary and that pair-living evolved afterward emphasizing the importance of focusing on field data and accounting for intraspecific variation, providing a flexible statistical framework for doing so.

social system | social structure | monogamy

Significance

Was the ancestor of all primates a solitary-living species? Did more social forms of primate societies evolve from this basic and simple society? Until now, the dogmatic answer was yes. We used a modern statistical analysis, including variations within species, to show that the ancestral primate social organization was most likely variable. Most lived in pairs, and only 10 to 20% of individuals were solitary. Living in pairs was likely ancient and caused by reproductive benefits, like access to partners and reduced competition within the sexes.

Understanding primate social evolution is central to understanding our own social ancestry. Numerous comparative studies have inferred that the ancestor of all primates was nocturnal, small, arboreal, and solitary (1–5). Previous research explained transitions from solitary living to pair- and group-living by various ecological factors and life history traits (1–3, 6, 7). The inferred ancestral solitary stage hinged largely on Strepsirrhines (among the extant primates), which are understudied and previously often assumed to be solitary living (8). However, several field studies over the last decades indicate Strepsirrhines to be more social (1, 8) and often pair-living (9).

Social systems are composed of different components including the social organization (composition of social units), social structure (interactions between individuals), care system (who cares for infants), and mating system (who mates with who) (10, 11). It has been argued that these components should be studied independently from each other to understand social evolution, especially in primates (1, 12–14). For example, pair-living as a form of social organization has often been equated with monogamy, even though monogamy refers to a mating system (1, 12, 13, 15–17). Importantly, pair-living species can vary significantly in their mating system, e.g., in the degree of extra-pair paternity (18, 19). Similarly, primate social organization varies greatly between (1, 3) but also within species (8, 20). Previous studies were statistically limited by assigning a single type of social organization to each species, such that the analysis could only consider between but not within species variation (2, 3, 21).

Here, we examined whether taking intraspecific variation in social organization (IVSO) into account and focusing on data from field studies, including many recent studies on nocturnal strepsirrhines, but excluding assumptions about nonstudied species, changes our estimate of the ancestral primate social organization. Intraspecific variation in primate social behaviour has long been recognised (22), and a few studies were successful in incorporating it into phylogenetic comparative studies (23). For example, considering intraspecies variation in primate group size did not alter conclusions of the social brain hypothesis predicting larger neocortex ratios in species with larger groups (24), but it remains to be tested whether intraspecific variation influenced other aspects of social

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Author contributions: L.H. and C.S. designed research; C.-A.O., J.S.M., C.P., P.A., C.K., L.H., A.V.J., and C.S. performed research; J.S.M., A.V.J., C.-A.O., and C.S. contributed new reagents/analytic tools; J.S.M. analyzed data; and C.-A.O., J.S.M., L.H., A.V.J., and C.S. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2215401120/-/DCSupplemental.

Published December 28, 2023.

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evolution. Primate social evolution is assumed to largely depend on ecology and life history (25, 26). For example, small nocturnal species living in forests are generally assumed to be solitary and large diurnal species living in open habitat to be group-living, with group composition (one or multimale groups) depending on diet (3, 10, 25). Species living in heterogeneous habitats are predicted to have a more variable social organization (27). Therefore, we tested whether these ecological and life history factors influenced primate social organization (*SI Appendix*, Table S3).

We assembled a database on the social organization of 493 populations of 215 primate species observed in the field, as published in the primary peer-reviewed literature. A population consists of individuals of a species that live in the same geographic area and can potentially mate and interact with each other. For our study, a population refers to the animals studied at one particular field site, even though in most cases the population would have consisted of many more social units than those observed in the study area. A social unit consisted of individuals being observed consistently together either during foraging or at sleeping sites, and which were sharing the same home range (home range overlap >50% during the study period). Studies varied considerably in duration and research effort, and species varied in life history (e.g., lifespan), making it difficult to find a definition of being "consistently together" that could apply to all studies. Consistently therefore means consistently within the duration of the study, which in most cases varied from months to years.

Rather than selecting a single social organization per species, we treated each study population as the unit of analysis. Within each population, we counted the number of social units exhibiting different social organizations, allowing us to quantify within-population variation (Fig. 1). Therefore, our statistical approach allowed us to consider variation in social organization i) between species, ii) between populations of the same species, and iii) between social units within populations. We developed a flexible Bayesian phylogenetic GLMM framework to partition this extensive variation in social organization across populations, species, and superfamilies, as well as to evaluate its phylogenetic and socioecological determinants. Using a multinomial likelihood, we modelled the relative frequency of each social organization being observed within each population, adjusting for phylogeny and research effort within superfamilies (a more direct measure of the effects of research effort per se, independently of unbalanced sampling across superfamilies).

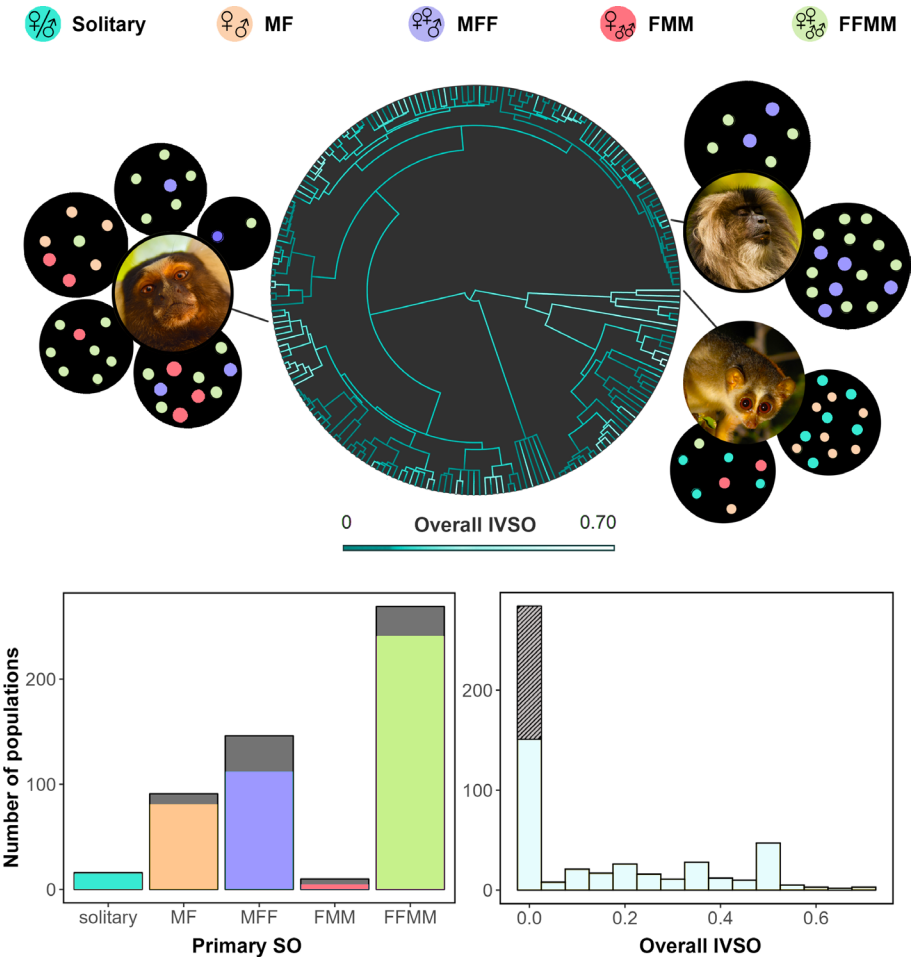


Fig. 1. The distribution of social organizations across extant primate populations. The *Top* panel demonstrates how we coded social organization per population as solitary, male-female (MF) or pair living, single male multifemale (MFF), single female multimale (FMM), or multimale and multifemale (MMFF). Three examples taken from field research on the slender loris (*Loris lydekkerianus*), common marmoset (*Callithrix jacchus*), and lion-tailed macaque (*Macaca silenus*) are shown. Large circles (*Middle*) around pictures represent different populations of the species. Smaller circles within each large circle represent a single social unit within a population, with color corresponding to the social organization observed. The phylogeny reflects a simple contour mapping of overall IVSO (# units deviating from primary social organization/total # units) across taxa in our database. Note that the branch lengths have been arbitrarily modified for visual clarity and should not be directly interpreted. The *Lower* panel shows the total number of populations in our dataset exhibiting each form of primary social organization, as well as overall IVSO (binwidth = 0.05). *Left*, primary SO: Dark gray bars represent uncertainty in the primary social organization for populations exhibiting two social organization with equally high frequency. *Right*, overall IVSO: Light gray hashed bars represent uncertainty in the level of IVSO due to studies including only a single social unit.

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We defined the "primary social organization" as the social organization with the greatest probability of being observed within a population. As a second response variable in the same model, we used a binomial likelihood to directly account for the degree of intrapopulation variation in social organization (IVSO) observed in each population, calculated as the proportion of social units deviating from the most frequent social organization (Fig. 1). This allowed us to estimate effects of socioecology and phylogeny on IVSO, irrespective of the relative probabilities of specific social organizations within a population. Both models accounted for the total number of social units, thus weighing larger studies more heavily.

Results

Distribution of Social Organization in Extant Primates. We observed relatively high rates of pair-living (primary social organization in 16% of populations and 23% of species) and low rates of solitary organization (primary social organization in 3% of populations and 6% of species) in our database (Fig. 1). Previous studies (1, 3, 7) counted many more species to be solitary living, as most solitary foragers were classified as having a solitary social organization. Our database challenges this assumption, showing that among 19 solitary foraging populations (from 17 species) only 9 had solitary living as the primary form of social organization, while in the remaining 10 populations pairs or groups shared the same home range and sleeping site (see also *SI Appendix*, Table S2). The most common form of social organization in extant primates is multimale multifemale groups, followed by one male multiple females groups and then by pairs, while one female multiple-male groups were rare (Fig. 1). Many species (64%) and populations (43%) exhibited more than one social organization, demonstrating that primate populations show substantial levels of variation in social organization (Fig. 1).

Variance Due to Phylogeny, Ecology, and Life History. We first wanted to know how much variation in primate social organization and IVSO is explained by phylogenetic history, current ecological conditions and life history, or unmeasured effects at the levels of populations, species, and superfamilies. Ecological conditions and life history included habitat heterogeneity (number of different habitats in which the population occurred), open vs. closed habitats, foraging strategy, substrate, activity pattern, body size, and dietary reliance on fruit, foliage, seeds, or animal protein. Using multiple imputation to leverage all predictors despite missing data (*SI Appendix*), we found that the ecological and life history variables considered explained only a small-to-moderate proportion of variation in social organization and IVSO (median R^2 range: 0.05 to 0.29; Fig. 2*A*; see *SI Appendix* for details on the direct and total effects of each predictor with and without imputation). Phylogeny explained a moderate to large proportion

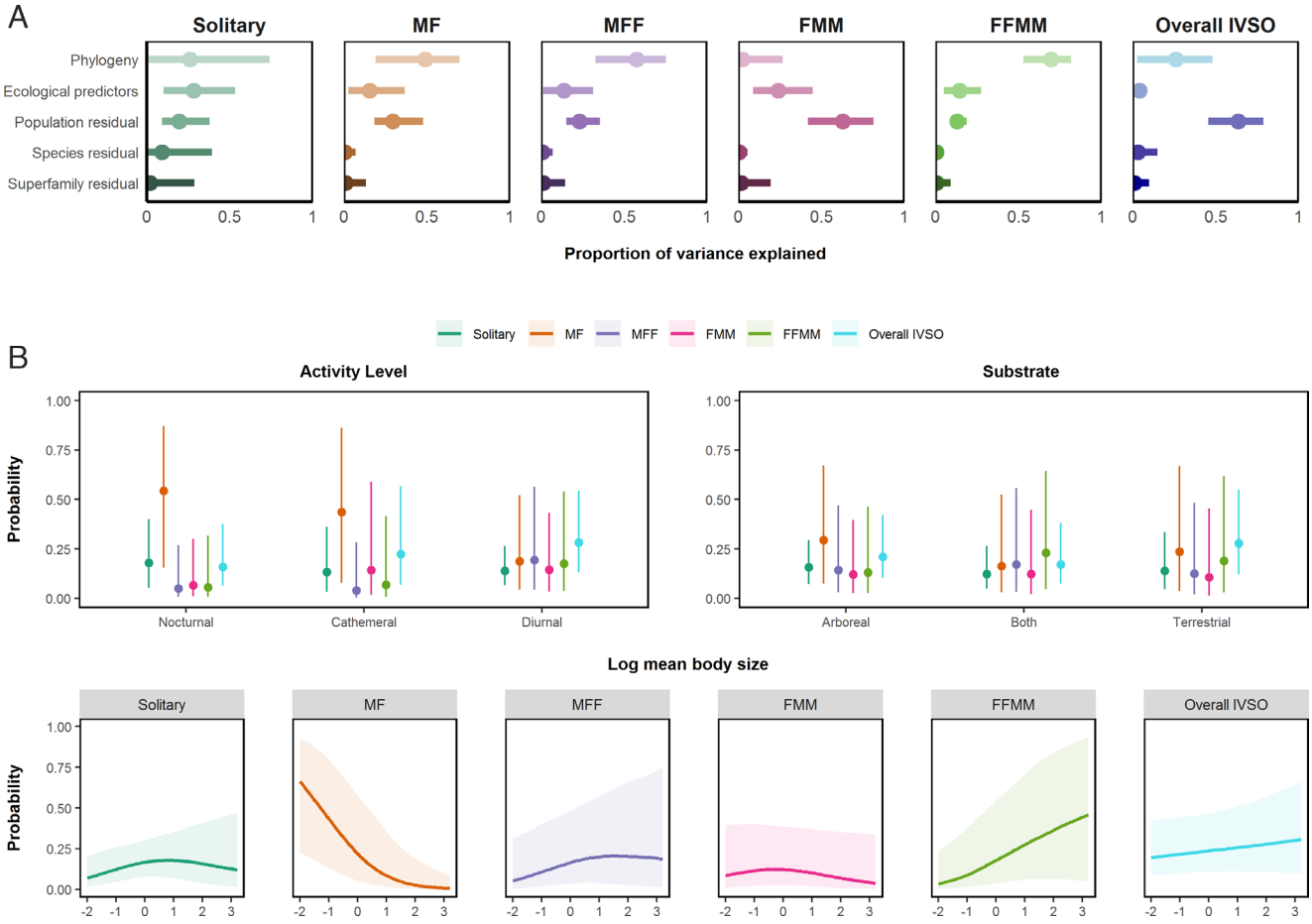


Fig. 2. Variation in social organization among extant primates. (*A*) The proportion of variation in each social organization and overall IVSO accounted for by phylogenetic history, ecological and life-history factors ("ecological predictors": habitat type and heterogeneity, diet, foraging style, substrate, activity pattern, and body size), as well as remaining residual (unexplained) variation among populations, species, and superfamilies. Dots indicate posterior medians, and lines indicate 90% Bayesian CIs. See *SI Appendix*, Table S4 for direct and total effect estimates for each predictor. (*B*) Total effects of the ecological and life history factors (activity level, substrate, and body size) used to predict ancestral social organization and IVSO. Thick lines indicate posterior medians, and ribbons indicate 90% Bayesian CIs.

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of variation in social organization [median phylogenetic signal (λ) range: 0.23 to 0.71], although single-female multimale social organization had much lower phylogenetic signal (median λ = 0.06). Species- or superfamily-level effects, independent of ecology and phylogeny, were weak (median R^2 range: 0.01 to 0.10), suggesting against grade shifts. However, population-level heterogeneity was consistently larger (median R^2 range: 0.13 to 0.63), indicating a sizable portion of unexplained variation among populations within the same species. These results suggest that while some forms of social organization are conserved within primate lineages, social organization often shows substantial variation among populations that remains unexplained by phylogeny or the ecological or life history variables we had included.

Ecological Predictors and Reconstruction of the Ancestral State. Next, we estimated the probability of each social organization and degree of IVSO for the last common ancestor of all primates, contingent on predictors. Evidence strongly suggests that ancestral primates were relatively small-bodied, arboreal, and nocturnal; hence, body size, substrate, and activity pattern can be used to make more informed inferences about ancestral states. Conversely, since the literature does not offer strong a priori expectations about ancestral habitat types, foraging strategies, or specific dietary patterns, we excluded these variables from this model, which had the added benefit of not requiring imputation.

The total effects of body size, substrate, and activity pattern on social organization are shown in Fig. 2*B*. Overall, pair-living was more common with nocturnal than diurnal activity [median difference (Δ) in probability of pair-living in nocturnal species compared to pair-living in diurnal species = 0.27, 90% CI (0.02, 0.56)]. Pair-living was more likely among smaller bodied species (−1 SD) compared to average-sized species [median Δ probability = 0.18, 90% CI (0.04, 0.34)] or larger species [+1 SD; median Δ probability = 0.30, 90% CI (0.07, 0.58)]. Multimale, multifemale groups were in turn more likely among larger-bodied species compared to average [median Δ probability = 0.10, 90% CI (−0.004, 0.28)] or small species [median Δ probability = 0.18, 90% CI (0.01, 0.50)]. No clear effects were observed for differences in substrate on the probability of social organization, and none of our predictors consistently explained variation in the overall proportion of IVSO across populations.

The oldest known primates were very small (28–30), making it important to account for body size when inferring ancestral states. As a first approximation, we assumed an ancestral body size of approximately 50 g (−2 SD log mean size relative to extant species; Fig. 2*B*), which is a slightly conservative estimate based on current fossil evidence indicating ancestral primates may have been as small as 30 g (19). We also assumed nocturnal activity and arboreal substrate as indicated by fossils from one of the oldest primates (31, 32). Under these assumptions, we found pair-living to be the most likely ancestral social organization [median probability = 0.77, 90% CI (0.31, 0.96)], compared to solitary [median Δ probability = 0.68, 90% CI (0.06 to 0.94)] and all forms of group living (all median Δ probabilities ≥ 0.70 and 90% CIs exclude zero; Fig. 3). In addition, there is support for a small proportion of solitary social units occurring in ancestral populations [median probability = 0.09, 90% CI (0.01, 0.30)], while little to no support is provided for the presence of group-living units (lower 90% CIs < 0.01). Note that these results were qualitatively robust to a wide range of ancestral body sizes, from −2 SD to −0.5 SD below the extant mean, as well as different activity patterns and substrate (*SI Appendix*, Table S6). In other words, pair-living was the most likely ancestral social organization so long as ancestral primates were smaller than average extant primates.

Our results infer that if we could sample 10 social units in an ancestral population, we would expect ~80 to 90% of those units to be pair-living, but also ~10 to 20% to be solitary. This pattern is supported by the overall IVSO model, which estimates that approximately 15% of social units [median probability = 0.16, 90% CI (0.06, 0.42)] should deviate from the primary social organization. Thus, the last common ancestor of all primates most likely had a variable social organization, with most individuals living in pairs but some being solitary.

Discussion

Like previous analyses (1, 3, 7), our results suggest that living in groups of multiple adults evolved late in primates' evolutionary history. However, our finding that pair-living was the ancestral primate social organization contrasts with previous studies which found solitary living to be ancestral (1, 3, 7). Our inference of ancestral pair-living was not because of an inflation of pair-living species (see agreement in our coding of pair-living with others, *SI Appendix*, Table S2), but is likely a consequence of our exclusive focus on primary field data and the exclusion of nonstudied nocturnal, cryptic species that have often been assumed to be solitary even in the absence of direct field observations (resulting in a much lower percentage of solitary species in our database compared to others). Multiple field studies revealed that few nocturnal Strepsirrhines actually exhibit solitary living, with pair-living instead being common (9, 33). Accordingly, we found pair-living to be more common in nocturnal Strepsirrhines than in diurnal Haplorrhines. Further, we focused exclusively on the composition of social units (social organization), while most previous studies combined the social organization of pair-living with the social structure of pair-bonding, biparental care, and a primarily monogamous mating system (3, 7). Similarly, we defined solitary living based on the social organization, while others had used a combination of mating system, social structure, and social organization to define solitary living (7). For example, many regarded all species that forage alone as solitary (1, 3), even when they share the same territory and sleeping sites (7). In contrast, we categorised a male and a female sharing a home range and sleeping site for extended periods with each other—but not with other adults—as pairs even when they forage alone, as has been done for many other mammalian taxa like elephant shrews (34), some carnivores such as red foxes (35), and many bird species. This demonstrates how differences in classifying social systems can influence the interpretation of social evolution. In addition, our ancestral state estimation accounted for body size, which is strongly associated with pair-living (Fig. 2*B*).

Here, we inferred that the ancestral social organization of primates was variable, with approximately 15% of the individuals in the population deviating from pair-living. Our analysis differs from previous studies by allowing IVSO rather than assigning a single social system to each species (3, 7). Intraspecific variation in primate social systems recently received more attention (8, 22–24). Kappeler and Pozzi (1) already considered IVSO in understanding primate social organization, but their statistical analysis used IVSO as one possible category and not as a continuous variable [as did several other studies on different mammalian taxa (34–37)].

Pair-living has often been regarded as a derived form of social system needing specific explanation (1, 3, 7). Thus, it might seem surprising that we found pair-living to be the most likely ancestral social organization. However, pair-living has also been suggested to be the ancestral form in other mammalian orders, including Artiodactyla (36), Eulipotyphla (38), and in Macroscelidea (34).

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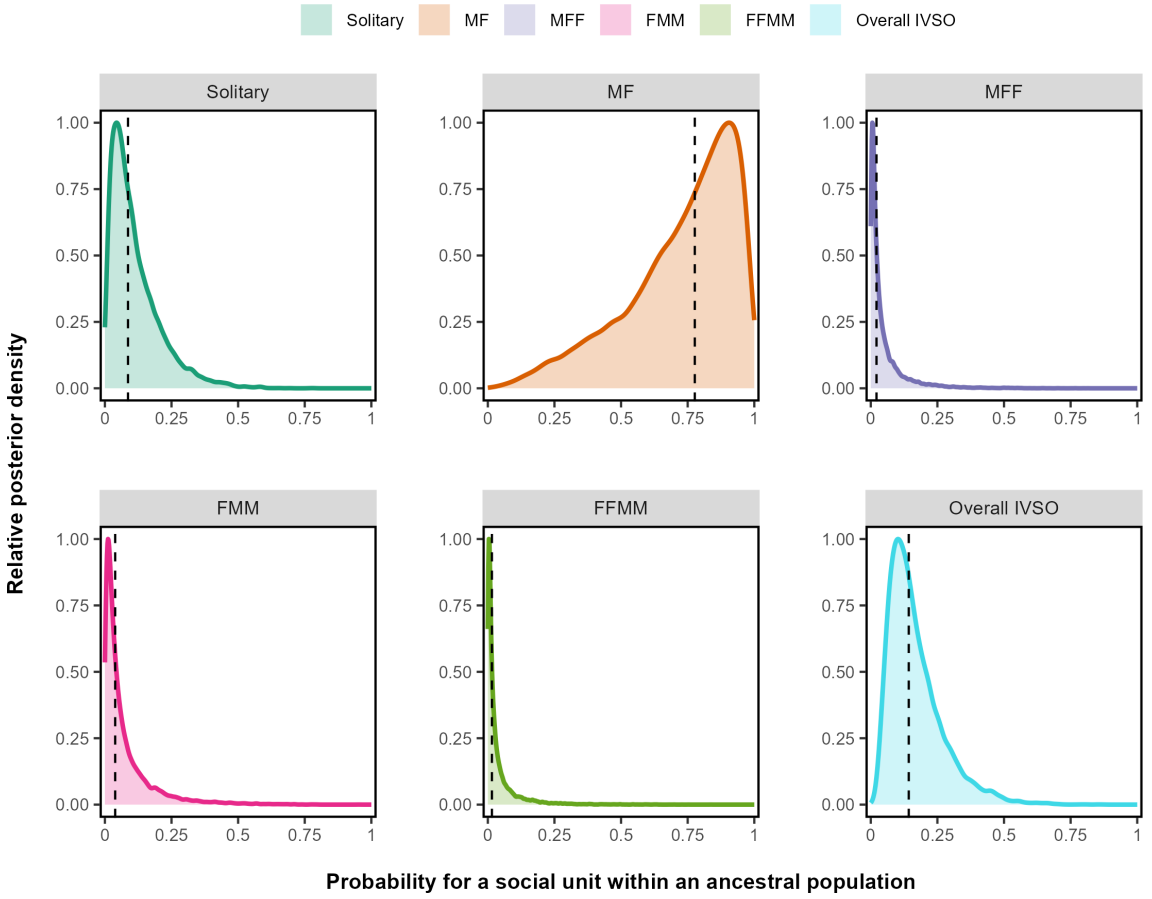


Fig. 3. Ecologically informed predictions of social organization in ancestral primate populations. Predicted probabilities of a social unit exhibiting each social organization and some form of IVSO within ancestral populations, assuming that the ancestral was primarily nocturnal, arboreal, and small-bodied (~50 g/−2 SD from the mean body size of extant species), as well as average within-superfamily sampling effort. See *SI Appendix*, Table S6 for predictions at different levels of ancestral body size, from −0.5 SD to −2 SD. Scaled posterior densities are shown, with posterior medians indicated by the dotted line.

In all of these analyses, pair-living was strongly related to small body size, and the fact that extant mammalian groups tend to be larger than their ancestors (39) might have biased previous ancestral state reconstructions that did not account for body size. We also note that the inference of pair-living as the most likely ancestral state holds across body sizes below the extant mean (Fig. 2 *B*, *Bottom* and *SI Appendix*, Table S6). Moreover, Kappeler and Pozzi (1) also suggested that pair-living is not a derived social organization in primates, but an ancestral form before the evolution of larger social groups.

Our results suggest that solitary living is a derived state and as such an adaptation to specific environmental conditions. Future studies will have to determine costs and benefits of solitary living as has been done for pair- and group-living (40). The socioecological model used in primatology would suggest that individuals become solitary living when food is rare and widely dispersed (not clumped) and when predation pressure is low (41), as seen, e.g., in orangutans (42). We further suggest that small nocturnal primates retain a pair-living social organization by reducing predation risk through solitary foraging. Here we show that pair-living is ancestral in primates, but we do not make statement about the evolution of other aspects of social system, such as the social structure (e.g., pair bonding), mating system (e.g., monogamy), or care system (e.g., biparental care); these other components of the social systems differ widely among extant pair-living primates, highlighting the importance of differentiating among them (11–15).

Materials and Methods

Materials.

Definition of social organization. Animal social systems can be characterized by variation in four inter-related components (11): social organization (composition and size of groups), social structure (social interactions), mating system (who mates and who reproduces with whom), and care system (who takes care of the offspring). Previous research has often used heterogeneous terminology to describe social systems across taxa, resulting in ambiguous definitions and confounding of distinct selection pressures (43). Here, we strictly focused on the composition of groups, a central aspect of social organization. Data for group composition were taken from the *Methods* and *Results* section of peer-reviewed field studies, avoiding any interpretations from the authors in the discussion. We defined social organization as solitary, pairs (MF), single male + multifemale (MFF), multimale + single female (FMM), multimale + multifemale (FFMM), and sex specific, where groups consisted of one sex only.

Database on social organization. We identified 450 species of primates using the IUCN database (International Union for Conservation of Nature) (44). We then conducted literature searches on social organization in Web of Science (Thomson Reuters) and in Google Scholar between January 2016 and September 2019. For each species, we initially searched the Latin name of the species and the term "social" (e.g., "*Alouatta caraya* AND social"; "*Gorilla gorilla* AND social"). If no literature on social organization was found, only the Latin name was searched. For several species, the Latin name changed over the years, in which case, we repeated the search with the previous versions of their names.

Searches on Web of Science were restricted to articles within one of the following three categories: "behavioral science", "zoology" and "environmental science/ecology". Only peer-reviewed literature from field studies was considered while reviews, laboratory-based studies, and captive studies were ignored to ensure that

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the social organization observed by a given species also occurred in their natural habitat (e.g., many species can be kept in pairs in captivity, but this does not mean that pairs occur in nature). For each study, we read the abstract, examined all figures and tables, and searched the following keywords throughout the papers: "social", "solitary", "group", and "pair". As such, our literature search focused on the data reported in *Methods* and *Results* sections of the peer-reviewed studies, not on the interpretation of the authors regarding the social organization in the introduction or discussion. This search yielded more than 2,000 articles that were scanned for information on social organization. Of these, a total of 977 papers contained useable data (83 for strepsirrhines, 247 for platyrrhines, 11 for tarsiers and 636 for catarrhines). Overall, data on social organization were found for 498 populations from 223 species (40 strepsirrhines, 6 tarsier, 64 platyrrhines, 93 catarrhines, and 20 hominoids). To determine the forms of social organization present in each population, we recorded the adult sex composition of all social units in a population using the classical definitions from Kappeler and van Schaik (including the differentiation between pairs and groups) (10) and adding "sex-specific group" as an additional category (*SI Appendix*, Table S1). Studies that did not report the sex of individuals were not included, following (45).

We searched for information in published papers aiming to determine social organization or that needed to know the social organization for research aims. There was no criterion for the length of study. Depending on the species, the study duration differed from months to years, to some extent reflecting variation in life history which differs greatly among species. To be included in our database, studies needed to include individual recognition of most adults (in the case of multimale multifemale groups not all individuals needed to be recognised individually), but not of juveniles and infants. We checked in the text in the *Methods* and *Results* sections which social units were reported by the researchers. We recorded social units when authors reported in the *Methods* or *Results* section the observed composition of social units (groups) in their study, most often in a table summarising the group composition of the study animals, or in the text by the number of solitary males, solitary females, pairs, or different groups having been observed. A social unit consisted of individuals being observed together either during travelling/foraging or at sleeping sites, and which were sharing the same home range. For animals being considered to form one social unit they had to be seen together for >50% of the time (though this was commonly >75% of the time). In cases where it was not evident from the original paper whether pairs/groups were consistently together or whether a pair was only observed during one occasion/a short period, the study was not included into our database. Our approach was in so far standardized as all these studies were peer-reviewed, which thus ensured that the social organizations had been reported adequately and corresponding to scientific standards. In other words, definitions were to our best knowledge appropriate for each species. We confirmed that our definition of pair-living was consistent with the terminology used by the scientists who studied these populations in the wild (*SI Appendix*, Table S2). We also found high consistency between our scoring for species with the main social organization of pair-living and the scoring of these species in two datasets generated by primatologists [Shultz et al. (3) and Kappeler and Pozzi (1)]. In contrast, our scoring of these species differed more from the scoring of Lukas and Clutton-Brock (7), which also differed considerably from the two other databases (*SI Appendix*, Table S2) and has been criticized for including information based on assumptions rather than direct observation (38; Schradin 2007). Based on these observations, we believe that our dataset is an accurate reflection of the natural inter- and intraspecific variation in primate social organisation.

From each paper, we recorded how often each category of social units was observed, e.g., how many solitary individuals, pairs, or different groups were recorded. We only recorded solitary living as a form of social organization when both sexes had been observed to be solitary, as single individuals of one sex may often represent dispersers. Whenever individuals were explicitly reported to be dispersers, they were not considered in the recording of social organization. Therefore, to record one social unit of solitary living, at least one solitary male and one solitary female were needed, to make the classification comparable to the criterion used for pair-living (one pair also consists of one male and one female). For example, when 5 solitary males and 4 solitary females were reported, we recorded 4 solitary social units. The same procedure was done with sex-specific groups. We only recorded sex-specific groups as a form of social organization when both sexes had been observed to live in unisex groups. This avoided that species with groups consisting of one adult male and multiple adult females were regarded to show IVSO because the remaining males were necessarily forming bachelor groups or were solitary, which would have led to an inflation of populations being scored as showing IVSO. To record one social unit of sex-specific groups, at least one group of males and one group of females were needed. For example, when 10 groups of males and 4 groups of females were reported, we recorded 4 sex-specific groups as social units. Overall, we only observed sex-specific groups in nine species, indicating that intersex units are the dominant form of social organization in group-living primates. This low count prevented us from drawing meaningful inferences about phylogenetic and ecological effects on the probability of sex-specific units occurring, and we therefore excluded these units from our analyses.

Data were collected at the population level by recording the total number of papers reporting a given social organization in a population. When the same individuals and their social units were included in more than one published paper, we considered only the most precise paper, e.g., papers where the precise number of social organizations and/or the sex of individuals was described, to avoid considering the social organization of the same individuals several times. The total number of peer-reviewed publications with nonoverlapping data reporting social organization per population was then recorded in the database as a crude measure of research effort. For example, populations with multiple studies over decades might be more likely to show variation in social organization than populations with only one single study. Similarly, taxa exhibiting greater (or lesser) variation in social organization may be more or less likely to be investigated by researchers.

The database records whether multilevel societies or fission-fusion societies occurred for each population. When multilevel societies (46) occurred within a population, indicating hierarchically structured social organization, we only recorded the composition of the core group defined in the study. We did this because the different core groups within primates' multilevel societies tend to maintain their social organization across interactions, such as the maintenance of the one male multiple female groups composing hamadryas baboon (*Papio hamadryas*) societies (47). In contrast, when populations with high fission-fusion dynamics (48) occurred in the population, suggesting a more fluid social organization, we recorded all forms of group composition observed, as this indicated that individuals of this population could exhibit multiple forms of social organization within their society over time.

Our study included data on only 30 of 119 nocturnal species versus 192 of 325 diurnal or cathemeral species. While nocturnal primates were previously often assumed to be solitary living, our review shows that most of them (16) are actually pair-living and that the scientists who studied them also categorized them as pair-living (*SI Appendix*, Table S2).

Intrapopulation variation in social organization (IVSO). IVSO was identified when different forms of social organization occurred within a population, indicating some degree of plasticity in a species' social organization. The social organization of a population describes in which social units both females and males are living. When only one sex had two or more forms of social organization without affecting the other sex this was also not recorded as IVSO. Bachelor groups or alternative reproductive tactics in one sex only (for example, male followers during the breeding season) are an interesting phenomenon by itself warranting study, but in these species, they are part of the main form of social organization and not a variation of it.

Environmental disruption such as the death of a dominant breeder or predation of group members can also change the social organization of a unit, but these changes do not reflect the evolved behavioral plasticity we want to explain (49). Thus, such environmental disruption events were not considered in our database but were recorded separately.

Previous studies have treated IVSO as a distinct category of social organization (1, 34, 36). However, given the wealth of data available for primate social organization, we were able to continuously measure IVSO at the population level as the proportion of social units deviating from the most frequently observed ("primary") social organization within a population. In the present study, we therefore conceptualized and measured IVSO as a distinct trait capturing the overall degree of variation in social organization, which may coevolve with the composition and frequency of specific social organizations within a population. This avoided the use of arbitrary thresholds for categorizing the presence or absence of IVSO, retaining the continuous information provided by the primary literature, and allowed us to consider how the evolution of specific forms of social organization and the overall degree of IVSO are related across species and populations.

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Predictors of social organization. We included the following predictors in our Bayesian model to account for potential social, ecological, life history, and methodological causes of variation in social organization: habitat heterogeneity, habitat type, body mass, diet, activity pattern, substrate, number of peer-reviewed publications with nonoverlapping data per population, and foraging strategy (*SI Appendix*, Table S3). Habitat type was recorded from the primary literature and categorized on IUCN classification and used to calculate habitat heterogeneity (total number of habitats per population). Further, we classified the different types of habitat as open, closed or open and closed. Populations were also categorized as having group- or solitary foraging individuals or both, depending on information in the primary literature used to categorize social organization.

We used two published databases (50, 51) for the predictors body mass, diet, activity pattern, and substrate (called "locomotion type" in these databases). First, we compared the two databases to see whether their information was similar. This was the case for substrate (terrestrial, arboreal, and both) and activity pattern (diurnal, nocturnal, and cathemeral). However, for body mass and diet, we found differences between the two databases, which could undesirably influence our statistical inferences. Body mass was recorded for males and females, with some studies only reporting average body mass across sexes. If for one species, more than one measurement for body mass was available for either sex, then we calculated the mean value and the SD. In our dataset, male and female mean body size across species were almost perfectly correlated, r = 0.97. Therefore, the choice of body size should not have any meaningful influences on our predictive inferences. For food, information was available at the species level for average diet composition, including percentage of fruits and foliage (composed of mature leaves, undefined leaves, and young leaves) as well as the percentage of seed and animal protein consumed. We took multiple steps to ensure that estimated effects for these variables were robust to variation in diet and body size results between the databases. Whenever there was a difference between the two databases, we checked whether their information was based on the same or on different published studies. If both databases reported the same primary study, we checked the publication ourselves and only utilized the data reported directly in the paper. If the two databases were not based on the same study, we then entered the average result across databases to account for potential heterogeneity and/or measurement error within taxa. We also conducted analyses of body size separately within each database to ensure that aggregated estimates were robust across datasets. No meaningful differences were observed between the databases in the main effects of body size on social organization and IVSO (all $\Delta\beta$ 90% CIs included zero), so we used the average species body size between databases for all reported analyses. Information on diet was also combined between the databases when possible to increase sample size, due to heterogeneous patterns of missing data across species.

Methods.

Statistical analyses. We employed multilevel phylogenetic models to investigate the evolution of social organization and IVSO across primates, and we conducted all analyses within a flexible Bayesian framework to account for non-Gaussian outcome measures, measurement error in social and ecological data within taxa, as well as uncertainty in phylogenetic relationships across taxa (52–54). Our analyses used one of the most recent and up-to-date mammalian phylogenies from the VertLife project (55), and results were robust to using a different phylogeny (*SI Appendix*, *Robustness Checks*). The phylogeny represented relationships among species, while variation among different populations of the same species was captured with an additional random effect (52, see below). Primary social organization was modelled as a multinomial response variable, appropriate for repeatedly measured categorical data (56), while IVSO was treated as a binomial response, representing the number of groups deviating from the primary social organization out of the total number of groups observed (i.e., each social group observed in a population was coded as either being "primary" = 0 or "nonprimary" = 1 in organization). Multiresponse models were estimated to simultaneously assess phylogenetic and ecological effects on these measures, as well as to conduct robust ancestral state reconstruction of the primary social organization and magnitude of IVSO expected in ancestral primate populations. We took multiple steps to integrate uncertainty in our phylogeny and empirical measures during these analyses, e.g., pooling the analyses over a random sample of phylogenies, which were supported by robustness checks to ensure appropriate inferential stability among models (*SI Appendix*, *Robustness Checks*). Conservative, weakly regularizing priors were also used to introduce more realistic assumptions into the estimators, as well as to reduce the risks of inferential bias caused by multiple testing and measurement and sampling error (54, 57). Code for all analyses described in the text along with the original database can be found at https://osf.io/tybfk/.

For all analyses, we estimated two generalized multilevel phylogenetic models, one for describing the probability of each social organization with a multinomial distribution and the other for describing overall IVSO with a binomial distribution. For population p for species s, the multinomial model predicted the number of units observed in category i as a function of the total number of units observed n_{ps} and a vector of parameters $\boldsymbol{\theta}_{ps}$ for the relative probabilities of each category compared to the base category, which in this case is solitary social organization.

$$\text{Social organization}_{ps} \sim \text{Multinomial}_{\text{K}}\left(n_{\text{ps}}, \boldsymbol{\theta}_{ps}\right),$$

$$\text{logit}\left(\theta_{ps}^{(i)}\right) = \mu_0^{(i)} + \boldsymbol{x}'_{ps}\boldsymbol{\beta}^{(i)} + \alpha_{\text{phylo(s)}} + \alpha_{\text{species(s)}} + \alpha_{\text{superfamily(s)}} + \alpha_{\text{population(p)}} \text{ for } i, \ldots, K-1.$$

The parameters $\boldsymbol{\theta}_{ps}^{(i)}$ for each category i (MF, MFF, FMM, and FFMM) as compared to category K (Solitary) were predicted on the transformed logit scale by a category-specific intercept $\mu_0^{(i)}$, fixed effects $\boldsymbol{\beta}^{(i)}$ (research effort and ecological predictors), where $\boldsymbol{x}'_{ps}$ is the transposed vector of population- and/or species-specific predictors, and by the random effects $\boldsymbol{\alpha}$, which capture Brownian Motion phylogenetic effects $\boldsymbol{\alpha}_{\text{phylo(s)}}$ as well as any deviations from these phylogenetic predictions at the superfamily, species, and population level. The term $\boldsymbol{\alpha}_{\text{population(p)}}$ is an observation-level random effect capturing overdispersion from the expected variance. Note that because this is a multilevel or mixed-effects model, we were able to specify phylogenetic effects across species while simultaneously accounting for population variation within species, removing the need to average over or otherwise ignore uncertainty in species-typical patterns (see refs. 52, 58, and 59). This also allowed us to partition how much of the observed differences in population-level measures of social organization could be explained by within- versus-between species variation.

By adjusting for any species-level effects, the K-1 intercepts $\boldsymbol{\theta}_{ps}$ provide appropriate relative probabilities of nonsolitary compared to solitary social organization for an average ancestral population. These values can be transformed to the absolute scale using the logistic function, which facilitates calculating the probability of social units in an average ancestral population showing each of the K social organizations. In particular, for solitary and any other social organization i

$$\Pr\left(\text{Solitary}\right) = \frac{1}{1 + \sum_i^{K-1} \exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)}$$

$$\Pr(i) = \frac{\exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)}{1 + \sum_i^{K-1} \exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)}.$$

Note that this standard parameterization of the multinomial model can be equivalently specified with K intercepts, where $\theta_0^{\text{Solitary}} = -\sum_{i \neq \text{Solitary}}^{K-1} \theta_0^{(i)}$. This approach allows for modelling predictors directly on the probability of each category, as shown in Fig. 2*A*, and can be implemented manually in the Stan statistical programming language (60).

The variance explained in social organization by each set of effects can be calculated on the transformed scale using model predictions for the fitted data. Specifically, the total latent variance for social organization i is given by

$$V_{T^{(i)}} = V_{\boldsymbol{\beta}^{(i)}} + V_{\alpha_{\text{phylo}}^{(i)}} + V_{\alpha_{\text{species}}^{(i)}} + V_{\alpha_{\text{superfamily}}^{(i)}} + V_{\alpha_{\text{population}}^{(i)}} + \left(\frac{\pi}{\sqrt{3}}\right)^2,$$

where $\left(\frac{\pi}{\sqrt{3}}\right)^2$ is the theoretical variance of the logit scale. The latent variance explained (R^2), also known as the repeatability or phylogenetic signal (λ), can then be estimated by

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$$R^2_{\beta^{(i)}} = \frac{V_{\beta^{(i)}}}{V_{T^{(i)}}},$$

$$R^2_{\alpha^{(i)}} = \frac{V_{\alpha^{(i)}}}{V_{T^{(i)}}},$$

$$\lambda_{(i)} = \frac{V_{\alpha_{phylo}{}^{(i)}}}{V_{T^{(i)}}}.$$

Note that when using a multilevel or mixed-effects model to estimate phylogenetic effects, the quantity $\frac{V_{\alpha_{phylo}{}^{(i)}}}{V_{T^{(i)}}}$, sometimes referred to as "phylogenetic heritability", is equivalent to the lambda parameter λ more commonly known from phylogenetic generalized least squares regression (see ref. 52). To make this equivalence clear, we therefore use the same symbol $\lambda_{(i)} = \frac{V_{\alpha_{phylo}{}^{(i)}}}{V_{T^{(i)}}}$ to refer to the magnitude of variance predicted by phylogenetic effects [i.e., phylogenetic signal, (61)].

The same approach is taken for predicting the total probability τ_{ps} of IVSO given the number of social units n_{ps} for population p of species s using a Binomial distribution

$$\text{Overall IVSO}_{ps} \sim \text{Binomial}\left(n_{ps}, \tau_{ps}\right),$$

$$\text{logit}\left(\tau_{ps}\right) = \mu_0 + \boldsymbol{x}'_{ps}\boldsymbol{\beta} + \alpha_{\text{phylo(s)}} + \alpha_{\text{species(s)}} + \alpha_{\text{superfamily(s)}} + \alpha_{\text{population(p)}}.$$

The probability τ_{ps} predicts the proportion of social units expected to deviate from the primary social organization observed in the population or, equivalently, the probability of deviating for a randomly selected social unit. As noted above, because this is a multilevel model with species-level phylogenetic effects, we are able to use our population-level measures of IVSO to partition and estimate sources of both within- and between-species variation in IVSO.

Heterogeneous patterns of missing data were present for our ecological and life-history measures across species. As a consequence, a few populations lacked data for foraging style (1%), primary substrate (3%), body size (2%), while many lacked data on the proportion of dietary reliance on fruits (18%), foliage (28%), seeds (60%), and animal protein (51%). Best practice for statistical estimation from a nonexperimental dataset such as ours is to use some form of multiple imputation to account for nonrandom missingness across observations (54). Therefore, when seeking to assess the aggregate average effects of ecological predictors across species (Fig. 2*A*), we used the mice R package (62) to impute missing ecological and life-history values across predictors and obtain more reliable population statistics in our full model. However, for biological inferences about the effects of specific predictors (Fig. 2*B*) and the overall ancestral state (Fig. 3), we relied only on observed values taken from primary literature, excluding any rows containing missing data. *SI Appendix*, Table S4 provides sample sizes and posterior estimates for all predictors in the full model with and without imputation, as well as in univariate models capturing the total effect of each predictor.

Ancestral state reconstructions are commonly carried out with intercept-only random effects models, in which the global model intercept is interpreted as the expected ancestral state after marginalizing over any species-level phylogenetic or stochastic effects; multiple regression models are then used separately to identify relevant selection pressures across the sample (52, 63). However, as the size and depth of the sampled phylogenetic tree grows, so too does the potential bias introduced into a reconstruction by unmeasured temporal trends and processes of nonrandom convergent evolution. These concerns are particularly acute for our dataset, which contains unbalanced samples across all major clades within the primate order and covers a span of approximately 69 My. Therefore, we conducted our reconstruction of primate social organization in the context of a broader multiple regression model accounting for the effects of key social and ecological factors thought to be relevant to understanding the adaptive niche of ancestral primates, and which may also be associated with directional change in social organization and IVSO across extant primates. In particular, we assumed that ancestral primates were of relatively small body size [~50 g or −2 SD z-score log mean body size (4, 5, 64)], largely arboreal in their substrate, and nocturnal in their activity pattern. Inferences were robust under varying assumptions of ancestral body size, from −2 SD to −0.5 SD (*SI Appendix*, Table S6). We also adjusted our reconstruction for biased sampling caused by differential research effort within primate superfamilies by averaging over the main effect for number of peer-reviewed publications with nonoverlapping data conducted relative to the mean number of peer-reviewed publications with nonoverlapping data per superfamily (i.e., centered within superfamilies).

Given that our analyses were conducted in a fully Bayesian framework, we avoided the limitations of null-hypothesis testing (65), and instead relied on multiple sources of information provided by posterior distributions of model parameters and predictions. Median posterior estimates and median absolute deviations were used to characterize the central tendency and relative dispersion of estimated effects, while 90% Bayesian credible intervals (CIs) and posterior probabilities of positive or negative effects (i.e., *P*+ or *P*−) were used to gauge uncertainty in the magnitude and direction of these effects. Note that a 90% Bayesian CI excluding zero indicates greater than 0.95 posterior probability (*P*+ or *P*−) in support of a directional effect. These posterior probabilities *P*+ or *P*− directly quantify support for substantive rather than null hypotheses, so that values closer to 1 indicate greater support for the directional effect (+, −) and values closer to 0 indicate greater support for the opposite directional effect (−, +). Within this Bayesian framework, we were also able to directly test hypotheses about *differences* in the absolute probability of social organizations (reported as Δ probabilities), such as whether pair living was more probable than solitary living, by simply subtracting their posterior distributions. All models were estimated in the Stan statistical programming language (60) using R (R Core Team 2020) and the brms package (66).

Data, Materials, and Software Availability. Code for all analyses described in the text along with the original database have been deposited in OSF (https://osf.io/tybfk/) (67). All other data are included in the manuscript and/or *SI Appendix*.

ACKNOWLEDGMENTS. We thank the CNRS, the University of Strasbourg, and the University of Zurich. Comments by S.F. Dobson improved the significance statement.

1. P. M. Kappeler, L. Pozzi, Evolutionary transitions toward pair living in nonhuman primates as stepping stones toward more complex societies. *Sci. Adv.* **5**, eaay1276 (2019).
2. D. Lukas, T. Clutton-Brock, Evolution of social monogamy in primates is not consistently associated with male infanticide. *Proc. Natl. Acad. Sci. U.S.A.* **111**, E1674–E1674 (2014).
3. S. Shultz, C. Opie, Q. D. Atkinson, Stepwise evolution of stable sociality in primates. *Nature* **479**, 219–222 (2011).
4. M. T. Silcox, J. I. Bloch, D. M. Boyer, S. G. B. Chester, S. López-Torres, The evolutionary radiation of plesiadapiforms. *Evol. Anthropol.* **26**, 74–94 (2017).
5. M. Dagosto, D. Gebo, X. Ni, T. Smith, Estimating body size in early primates: The case of Archicebus and Teilhardina. *J. Hum. Evol.* **115**, 8–19 (2018).
6. C. Opie, Q. D. Atkinson, R. I. M. Dunbar, S. Shultz, Male infanticide leads to social monogamy in primates. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 13328–13332 (2013).
7. D. Lukas, T. H. Clutton-Brock, The evolution of social monogamy in mammals. *Science* **341**, 526–530 (2013).
8. P. Agnani, C. Kauffmann, L. D. Hayes, C. Schradin, Intra-specific variation in social organization of Strepsirrhines. *Am. J. Primatol.* **80**, e22758 (2018).
9. P. M. Kappeler, Lemur behaviour informs the evolution of social monogamy. *Trends Ecol. Evol.* **29**, 591–593 (2014).
10. P. M. Kappeler, C. P. van Schaik, Evolution of primate social systems. *Intern. J. Primatol.* **23**, 707–740 (2002).
11. P. M. Kappeler, A framework for studying social complexity. *Behav. Ecol. Sociobiol.* **73**, 13 (2019).
12. M. Huck, A. Di Fiore, E. Fernandez-Duque, Of apples and oranges? The evolution of "monogamy" in non-human primates. *Front. Ecol. Evol.* **7**, 472 (2020).
13. E. Fernandez-Duque, M. Huck, S. Van Belle, A. Di Fiore, The evolution of pair-living, sexual monogamy, and cooperative infant care: Insights from research on wild owl monkeys, titis, sakis, and tamarins. *Am. J. Phys. Anthropol.* **171**, 118–173 (2020).
14. A. Di Fiore, D. Rendall, Evolution of social organization: A reappraisal for primates by using phylogenetic methods. *Proc. Natl. Acad. Sci. U.S.A.* **91**, 9941–9945 (1994).
15. S. R. Tecot, B. Singletary, E. Eadie, Why "monogamy" isn't good enough. *Am. J. Primatol.* **78**, 340–354 (2016).
16. P. A. Garber, L. M. Porter, J. Spross, A. Di Fiore, Tamarins: Insights into monogamous and non-monogamous single female social and breeding systems. *Am. J. Primatol.* **78**, 298–314 (2016).
17. C. Kvarnemo, Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy: Causes and consequences of monogamy. *Biol. Rev.* **93**, 1795–1812 (2018).
18. A. Cohas, D. Allainé, Social structure influences extra-pair paternity in socially monogamous mammals. *Biol. Lett.* **5**, 313–316 (2009).
19. L. Brouwer, S. C. Griffith, Extra-pair paternity in birds. *Mol. Ecol.* **28**, 4864–4882 (2019).
20. C. A. Chapman, A. Corriveau, V. A. M. Schoof, D. Twinomugisha, K. Valenta, Long-term simian research sites: Significance for theory and conservation. *J. Mammal.* **98**, 652–660 (2017).

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21. J. H. Crook, J. S. Gartlan, Evolution of primate societies. *Nature* **210**, 1200–1203 (1966).
22. J. M. Kamilar, A. L. Baden, What drives flexibility in primate social organization? *Behav. Ecol. Sociobiol.* **68**, 1677–1692 (2014).
23. K. B. Strier, P. C. Lee, A. R. Ives, Behavioral flexibility and the evolution of primate social states. *PLoS One* **9**, e114099 (2014).
24. A. A. Sandel *et al.*, Assessing sources of error in comparative analyses of primate behavior: Intraspecific variation in group size and the social brain hypothesis. *J. Hum. Evol.* **94**, 126–133 (2016).
25. T. Clutton-Brock, C. Janson, Primate socioecology at the crossroads: Past, present, and future. *Evol. Anthropol.* **21**, 136–150 (2012).
26. R. I. M. Dunbar, "Socio-ecological systems" in *Primate Social Systems*, R. I. M. Dunbar, Ed. (*Studies in Behavioural Adaptation*, Springer, US, 1988), pp. 262–291.
27. C. Schradin, L. D. Hayes, N. Pillay, C. Bertelsmeier, The evolution of intraspecific variation in social organization. *Ethology* **124**, 527–536 (2018).
28. X. Ni *et al.*, The oldest known primate skeleton and early haplorhine evolution. *Nature* **498**, 60–64 (2013).
29. L. Van Valen, R. E. Sloan, The earliest primates. *Science* **150**, 743–745 (1965).
30. M. A. O'Leary *et al.*, The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* **339**, 662–667 (2013).
31. S. G. B. Chester, J. I. Bloch, D. M. Boyer, W. A. Clemens, Oldest known euarchontan tarsals and affinities of Paleocene Purgatorius to Primates. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 1487–1492 (2015).
32. C. F. Ross, Into the Light: The origin of Anthropoidea. *Annu. Rev. Anthropol.* **29**, 147–194 (2000).
33. P. M. Kappeler *et al.*, Long-term field studies of lemurs, lorises, and tarsiers. *J. Mammal.* **98**, 661–669 (2017).
34. C. Olivier, A. V. Jaeggi, L. D. Hayes, C. Schradin, Revisiting the components of Macroscelidea social systems: Evidence for variable social organization, including pair-living, but not for a monogamous mating system. *Ethology* **128**, 383–394 (2022).
35. F. Dalerum, Phylogenetic reconstruction of carnivore social organizations. *J. Zool.* **273**, 90–97 (2007).
36. A. V. Jaeggi, M. I. Miles, M. Festa-Bianchet, C. Schradin, L. D. Hayes, Variable social organization is ubiquitous in Artiodactyla and probably evolved from pair-living ancestors. *Proc. R. Soc. B: Biol. Sci.* **287**, 20200035 (2020).
37. J. Qiu, C. A. Olivier, A. V. Jaeggi, C. Schradin, The evolution of marsupial social organization. *Proc. R. Soc. B: Biol. Sci.* **289**, 20221589 (2022).
38. M. Valomy, L. D. Hayes, C. Schradin, Social organization in Eulipotyphla: Evidence for a social shrew. *Biol. Lett.* **11**, 20150825 (2015).
39. M. Pagel, C. O'Donovan, A. Meade, General statistical model shows that macroevolutionary patterns and processes are consistent with Darwinian gradualism. *Nat. Commun.* **13**, 1113 (2022).
40. T. Clutton-Brock, Social evolution in mammals. *Science* **373**, eabc9699 (2021).
41. E. H. M. Sterck, D. P. Watts, C. P. van Schaik, The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* **41**, 291–309 (1997).
42. C. Schuppli *et al.*, The effects of sociability on exploratory tendency and innovation repertoires in wild Sumatran and Bornean orangutans. *Sci. Rep.* **7**, 15464 (2017).
43. D. R. Rubenstein, P. Abbot, "Social synthesis: Opportunities for comparative social evolution" in *Comparative Social Evolution*, D. R. Rubenstein, P. Abbot, Eds. (Cambridge University Press, ed. 1, 2017), pp. 427–452.
44. IUCN, The IUCN Red List of Threatened Species (Version 2022-2). IUCN Red List. https://www.iucnredlist.org. Accessed 1 January 2022.
45. L. Makuya, C. Olivier, C. Schradin, Field studies need to report essential information on social organisation–Independent of the study focus. *Ethology* **128**, 268–274 (2021).
46. C. C. Grueter *et al.*, Multilevel organisation of animal sociality. *Trends Ecol. Evol.* **35**, 834–847 (2020).
47. H. Kummer, *Social Organization of Hamadryas Baboons* (Karger Book, 2023) (27 April 2023).
48. F. Aureli *et al.*, Fission-fusion dynamics: New research frameworks. *Curr. Anthropol.* **49**, 627–654 (2008).
49. C. Schradin, Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Phil. Trans. R. Soc. B: Biol. Sci.* **368**, 20120346 (2013).
50. C. Galán-Acedo, V. Arroyo-Rodríguez, E. Andresen, R. Arasa-Gisbert, Ecological traits of the world's primates. *Sci. Data* **6**, 1–5 (2019).
51. N. Rowe, M. Myers, "All the world's primates" in *The International Encyclopedia of Primatology,* Pogonias Press, Ed. (John Wiley & Sons, Ltd., 2017), pp. 1–4, 10.1002/9781119179313.wbprim0086.
52. J. D. Hadfield, S. Nakagawa, General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J. Evol. Biol.* **23**, 494–508 (2010).
53. T. Currie, A. Meade, "Keeping yourself updated: Bayesian approaches in phylogenetic comparative methods with a focus on markov chain models of discrete character evolution" in *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology,* L. Z. Garamszegi, Ed. (Springer Berlin Heidelberg, 2014), pp. 263–286.
54. R. McElreath, *Statistical Rethinking: A Bayesian Course with Examples in R and STAN* (Chapman and Hall/CRC, ed. 2, 2020), 10.1201/9780429029608.
55. N. S. Upham, J. A. Esselstyn, W. Jetz, Inferring the mammal tree: Species–level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**, e3000494 (2019).
56. J. Koster, R. McElreath, Multinomial analysis of behavior: Statistical methods. *Behav. Ecol. Sociobiol.* **71**, 138 (2017).
57. N. P. Lemoine, Moving beyond noninformative priors: Why and how to choose weakly informative priors in Bayesian analyses. *Oikos* **128**, 912–928 (2019).
58. L. Z. Garamszegi, "Uncertainties due to within-species variation in comparative studies: Measurement errors and statistical weights" in *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology,* L. Z. Garamszegi, Ed. (Springer Berlin Heidelberg, 2014), pp. 157–199.
59. L. Z. Garamszegi, Ed., *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice* (Springer Berlin Heidelberg, 2014), 10.1007/978-3-662-43550-2 (28 January 2021).
60. B. Carpenter *et al.*, Stan: A probabilistic programming language. *J. Stat. Softw.* **76**, 1–32 (2017).
61. M. Symonds, S. Blomberg, "A primer on phylogenetic generalised least squares" in *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*, L. Z. Garamszegi, Ed. (Springer Berlin Heidelberg, 2014), pp. 105–130.
62. S. van Buuren, K. Groothuis-Oudshoorn, mice: Multivariate imputation by chained equations in R. *J. Stat. Softw.* **45**, 1–67 (2011).
63. T. Garland, A. R. Ives, Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* **155**, 346–364 (2000).
64. G. P. Wilson Mantilla *et al.*, Earliest Palaeocene purgatoriids and the initial radiation of stem primates. *R. Soc. Open Sci.* **8**, 210050 (2021).
65. B. B. McShane, D. Gal, A. Gelman, C. Robert, J. L. Tackett, Abandon statistical significance. *Am. Stat.* **73**, 235–245 (2019).
66. P.-C. Bürkner, brms: An R package for Bayesian multilevel models using stan. *J. Stat. Softw.* **80**, 1–28 (2017).
67. C.-A. Olivier, J. S. Martin, Primate-SO-analysis. OSF. https://osf.io/tybfk/. Deposited 14 November 2023.

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