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Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain

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Socio-ecological models aim to predict the variation in social systems based on a limited number of ecological parameters. Since the 1960s, the original model has taken two paths: one relating to grouping patterns and mating systems and one relating to grouping patterns and female social structure. Here, we review the basic ideas specifically with regard to non-human primates, present new results and point to open questions. While most primates live in permanent groups and exhibit female defence polygyny, recent studies indicate more flexibility with cooperative male resource defence occurring repeatedly in all radiations. In contrast to other animals, the potential link between ecology and these mating systems remains, however, largely unexplored. The model of the ecology of female social structure has often been deemed successful, but has recently been criticized. We show that the predicted association of agonistic rates and despotism (directional consistency of relationships) was not supported in a comparative test. The overall variation in despotism is probably due to phylogenetic grade shifts. At the same time, it varies within clades more or less in the direction predicted by the model. This suggests that the model's utility may lie in predicting social variation within but not across clades.

1. Introduction

For many animals, particularly humans and other primates, social organization (i.e. group size, composition and cohesion), social structure (i.e. patterns of social interactions and relationships among individuals) and mating systems vary widely across species, within species and even within populations [1,2], with profound consequences for reproductive skew [3,4] and genetic population structure [5,6]. Examining the factors affecting this variation in social systems has been a major focus of ecological research since the 1960s [1,7].

Although these ideas have been central to research on non-human primates over the past decades, the initial spark goes back to John Crook's early works on birds [7] and was subsequently applied to non-human primates in his 1966 work with Gartlan [1]. This so-called 'socio-ecological model' assumed that a limited number of environmental factors affect population characteristics, leading to predictable differences in social systems. The flexibility in primate social systems was, therefore, considered a consequence of the variation in ecology. In the following years, this concept led to a host of tests of relationships between ecology, morphology and behaviour [8–14]. Although the original idea was intended to explain primate social systems using a single comprehensive (verbal) model, two different paths were subsequently pursued (figure 1): (i) models that relate to grouping patterns and mating systems [8–11,15] and (ii) models that relate to grouping patterns and female social structure [12–14]. Despite occasional calls for considering male and female strategies together, little progress has been made towards such a unified model [16,17]. Therefore, at present it seems justified to speak of at least two models, which

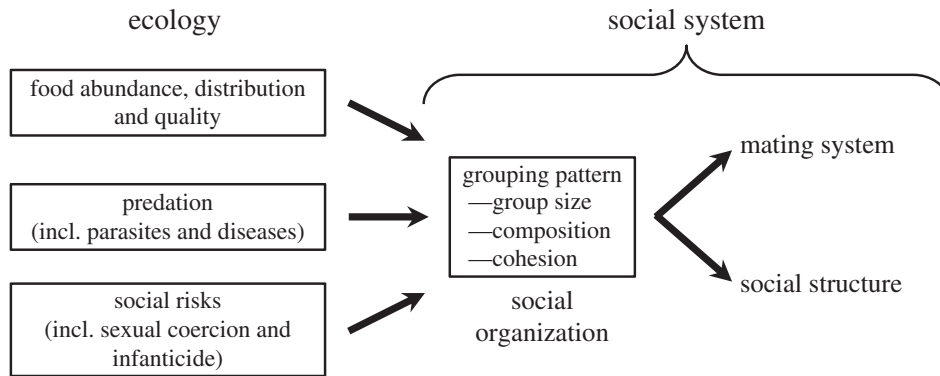


Figure 1. Flow-diagram of the two main strings of ideas both dubbed the ‘socio-ecological model’: a model relating to grouping patterns and mating systems [15] and to grouping patterns and female social structure [13].

are connected through the grouping pattern (figure 1), but have become essentially independent in their attempt to explain two basic but distinct aspects of social systems. The use of the term ‘socio-ecological model’ to simultaneously refer to both models has led to considerable confusion, however. Therefore, in the following, we will separately describe some core ideas of each model, review historical trends in the results and criticisms, present new results and point to some open questions. We will focus primarily on ecological factors, although phylogenetic, demographic and social ones shape social systems as well [18–21].

2. Ecology, social organization and mating systems

(a) Basic ideas and tests with non-human primates

The ecological model of social organization and mating systems (henceforth EMSOMS) suggests that resources (e.g. food and nest sites) and risks (e.g. predation, disease and infanticide) determine the spatio-temporal distribution of receptive females, which in turn affects the strategies available to males [8–10,15,22,23]. If resources are spatially dispersed, females may, depending on risks, live spatially isolated from other females. For males, this opens the options either for scramble competition polygyny, spatial polygyny or monogamy. Which strategy males pursue should depend on the economic defensibility of females and the requirements of infant care [10,15,22,24]. By contrast, if females form groups either temporarily or permanently, males may attempt to monopolize one or more clusters of females. Here, the monopolization potential will depend not only on the number of females, but also on the degree of spatial cohesion and/or temporal overlap in their receptive periods ([15,25]; for more details, see [10,22]).

In contrast to other mammals [8,9,26], in which ecological factors have been linked to grouping patterns and mating systems, studies of non-human primates have focused less on the environmental factors that underpin variation in mating systems (but see [27,28]). Rather they have examined the emergence of fission–fusion sociality [29,30] or constraints of group size, generally focusing on how predation avoidance and scramble competition for food set adaptive limits for minimum and maximum group size, respectively [31–35].

More recently, it has been argued that social organization in primates evolved from a solitary, nocturnal ancestor, but that—following a switch to a diurnal lifestyle—predation

avoidance favoured individuals in loose, diurnal aggregations of multiple males and females [36]. These loose aggregates are suggested to have then led to cohesive multi-male–multifemale groups, which in turn led to unimale groups and pairs in some taxa. These overarching trends were posited as evidence against the adaptive approach of the ‘socio-ecological model’ and its lack of accounting for phylogenetic history [36]. This criticism, however, is misplaced, as it focused only on ecological models of female social structure (see below) instead of studies of group formation and mating systems, which would be of more direct relevance to the authors’ analysis. Furthermore, the criticism falls short as the study does not incorporate primary factors such as competition for food [13,31] or social risks such as coercion and infanticide [37], even though the latter has been shown to be an especially important factor favouring male–female associations among prosimians [38]. At present, therefore, it remains unclear exactly how resources and risks affect female grouping patterns among non-human primates. While predators, food and infanticide clearly play a role, the relative importance of each factor and their contribution to the flexibility of grouping remain disputed [39].

In contrast, it seems clear that the spatio-temporal distribution of females is one of the main aspects underlying variation among primate mating systems, both across populations [40,41] and across species [42,43], at least among haplorrhines [44]. Additionally, strepsirrhine primates have recently been found to match the general expectations [45] that as the number of females and/or the overlap in sexual receptivity increases, so too does the number of males per group. Overall, therefore, most primates appear to live in a female defence polygyny system, which is probably the reason that little attention has been paid to potential ecological predictors of mating systems in primates.

(b) The roads less travelled

While female defence polygyny appears to be the most common mating system among non-human primates, the prevalence of other mating systems and their ecological bases are less clear. This is largely due to the paucity of comparable ecological data on a scale important to a primate [46,47] and the lack of comparable data on predation and social risks.

As in other mammals, the occurrence of spatially dispersed, solitary females seems to be linked to either scramble competition polygyny, as in some lemuroids and possibly orangutans [48,49], or spatial polygyny, as in some strepsirrhines [50,51]. Similarly, as in other mammals, spatial

dispersion of females [52] appears to be the best predictor for pair-living in primates, and permanent association and a monogamous mating system are probably related to the necessity for direct paternal care [53] or infanticide avoidance [38,54]. In these cases, the spatial dispersion of females seems to be determined by either the anti-predator benefits of crypsis (as in many small-bodied primates [33]), the dependence on non-divisible resources [55] or a low abundance of large resources [49]. Nevertheless, a comprehensive comparative analysis of the ecological factors affecting female primate distribution in space and time is lacking.

Furthermore, in recent years, it has become clear that, across the primate order, certain populations or species living in multimale–multifemale groups may not fit the pattern observed in female defence polygyny [56]. Some non-phylogenetic comparative studies suggest that risk of predation and/or infanticide may be associated with the number of males per group [37,57]. In addition, although heavily disputed and long considered absent among primates [58], some multimale primate societies may indeed exhibit mating systems that can be characterized as resource defence (or territorial) polygyny [10,15,26]. In contrast to Emlen & Oring's [15] original idea of solitary females being attracted to individual males that defend territories or resources, however, in non-human primates multiple males jointly defend a group's territory, and this may occur with either female dispersal or philopatry [27,59].

At present, such a cooperative male resource defence polygyny seems to be the best characterization of the mating system for common chimpanzees, in which males patrol and defend an area [59]. The lethal aggression and intercommunity killings that have been observed at multiple sites [60,61] may ultimately help to expand a group's area [61], which can benefit female reproductive performance [59]. Similarly, cooperative male resource defence polygyny appears to be the mating system of Phayre's leaf monkeys, a mid-sized Asian colobine we studied in Thailand [56,62]. Although it remains unclear whether males benefit reproductively from the size or quality of an area, males jointly defended territories with little overlap between neighbouring groups [56,62]. While home range size generally increased with group size, the multimale group was able to defend and maintain a larger territory than the similarly-sized and even the larger one-male group (figure 2).

More generally, cooperative male resource defence polygyny can be found in platyrrhines (lion tamarins and some tamarins [63,64], capuchin monkeys [27,65–68], spider monkeys [69,70]), cercopithecines (mangabeys, guenons [71]), colobines (colobus monkeys [72]; Phayre's leaf monkeys, see above) and hominoids (polyandrous gibbons [73]; chimpanzees, see above). Additional cases in point are male resource defence polygyny in one-male groups of platyrrhines (saki monkeys [74]), monogamous/polygynous strepsirrhines (bamboo lemurs [75]), and resource defence monogamy in hylobatids ([76], but see [77]). Thus, although less common than female defence polygyny, male resource defence occurs in all major radiations of primates.

Among these species, the nature of between-group encounters seems to relate to ecological variables (e.g. the availability of certain foods [78]), although the occurrence and outcome of aggression between groups may be mediated by the numerical asymmetry in male group size or encounter location [78,79]. As in other cases in which individuals benefit through group augmentation [80], multimale groups

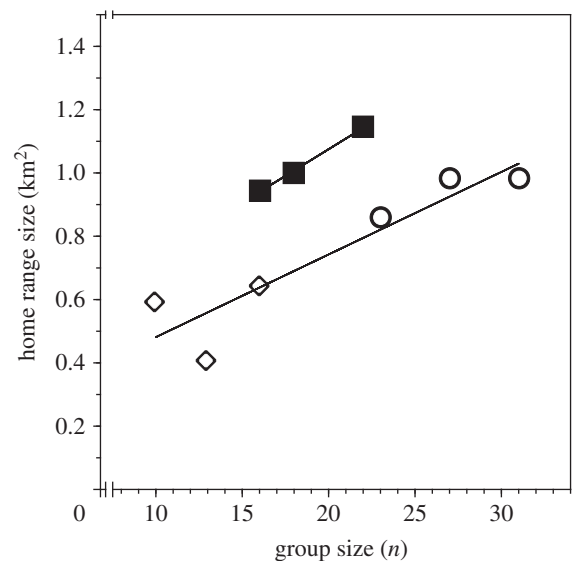


Figure 2. Home range size of Phayre's leaf monkeys in relation to group size and number of adult males. Depicted are annual home ranges in 2004, 2005 and 2006 for three groups (two one-male groups, one multimale group). Regression lines added for demonstration purpose only. One-male groups: $y = 0.22 + 0.03 \times x$ (circles and diamonds), multimale group: $y = 0.40 + 0.03 \times x$ (filled squares).

might be beneficial in these systems if they increase the group's competitive ability. Some of these additional males are likely to defect during collective aggression against other groups [81], however, given the indirect nature of the benefits to male reproductive success [17,82]. Moreover, the presence of additional males could increase the frequency or effectiveness of paternal care (including infant protection) and the options for male protectors, decreasing predation and infanticide risk and increasing female mate choice options (discussion in [23]). Thus, while the costs to males of shared reproduction will increase with the presence of additional competitors, both males and females might ultimately benefit from males defending resources. To date, however, the conditions—ecological, demographic or social—that have led to the evolution of male resource defence among non-human primates remain unknown, as are the factors that help overcome the potential collective action problems [82].

In sum, the past primary focus on female defence polygyny among non-human primates has painted a picture of a rather impoverished and inflexible mating system across the primate order. This has been further exaggerated by the use of simplistic categories when attempting to reconstruct the evolution of primate sociality [36]. In contrast, the more recent results summarized above indicate that primate mating systems are more flexible than has been acknowledged. The EMSOMS provides one framework that, in addition to phylogenetic, demographic and social factors [18–21], allows for the examination of this flexibility and its underlying ecological factors.

3. Ecology, competition and female social relationships

(a) Basic ideas and critique of the model

With the ecological model of female social relationships (henceforth EMFSR), a new dimension was introduced to the

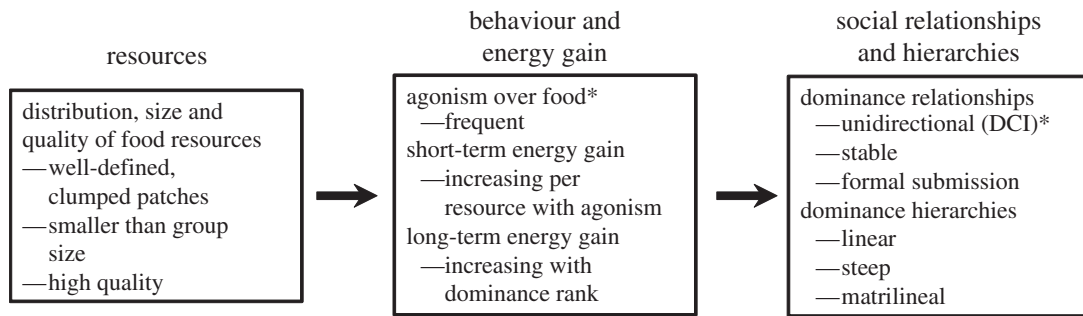


Figure 3. Ecological conditions for within-group contest competition and predictions for behavioural responses and energetic consequences, as well as their social outcomes for dominance relationships and hierarchies. Predictions do not consider conditions for between-group competition as they concern a separate prediction for tolerance (for details of other competitive regimes, see [13,83,85,101]). Asterisks (*) represent variables used in the current comparative analysis.

socio-ecological model [1]. Wrangham [14] reasoned that food availability and distribution should have major effects not only on the grouping and dispersal patterns of females, but also on their agonistic and affiliative relationships within and between groups. This idea was extended by van Schaik and colleagues to include predation risk as an ecological factor [13] and later infanticide as a social factor favouring grouping [17,38,83]. In the following, we restrict the discussion of the EMFSR to suggestions specifically incorporating cost–benefit approaches, while not considering more qualitative approaches and those based on behavioural indicators of competition [12,84].

The EMFSR suggests that ultimately females may form groups due to predation pressure, a defendable distribution of high-quality resources and/or social benefits via infanticide avoidance [13,14,83]. Among group-living females, the availability of high-quality patches that can be monopolized (or usurped) by a subset of residents will affect social relationships. Because these resources may promote within-group contest competition, females may form either despotic–nepotistic or despotic–nepotistic–tolerant relationships to maximize access and inclusive fitness benefits, with tolerance being predicted when between-group competition is strong [83]. In case such resources are rare or absent, females should either form egalitarian relationships and disperse or remain philopatric, if strong between-group competition favours kin-based coalitions to defend group-controlled resources [83].

Over the past years, this verbal model has been criticized for a variety of reasons [18,21,39]. Some critiques have related to re-evaluations of hypotheses and predictions [72,85], incorporating formal (mathematical) modelling [86], incorporating phylogenetic relationships to capture phylogenetic similarity and constraints [87,88], excluding dispersal patterns [18,85] or extending the model to incorporate cooperative actions [89,90]. Others criticized the overemphasis of competition and underemphasis of affiliation and cooperation [91]. Importantly, mismatches between predictions and results have been pointed out [92,93] and the lack of phylogenetic methods and the presence of correlations among social variables [94,95] have resulted in calls to abandon the model altogether [21] or to investigate different components separately [18].

The importance of the mismatches is currently difficult to judge because large-scale, cross-species comparisons of wild, unprovisioned primates are lacking [85]. Instead, comparative approaches have used primarily captive or provisioned populations [87,88] or included only a few wild, unprovisioned populations or species [96–98]. To date, only two broader

comparisons have been conducted with wild, unprovisioned primates [91,99], and both studies were restricted to agonistic behaviour. Unfortunately, one of these analyses has serious conceptual and analytical flaws [100], and neither directly tested predictions of the model or controlled for phylogeny. As noted previously, the assumption of independence of species' responses to local ecological conditions, which is implicit in the model, is a serious problem that should be incorporated in comparative studies [85]. Nevertheless, given the paucity of data for certain aspects of the model [85], it is clear that a general test is currently unfeasible. It therefore seems that investigating individual aspects of the model is indeed the most viable route [18].

(b) Testing links between agonism and social structure

Central to the EMFSR is the idea that there is a link between (i) the abundance, distribution, size and quality of resources; (ii) the frequency and form of agonistic behaviour and its energetic consequences; and (iii) characteristics of the dominance relationships of females (figure 3). Specifically, if contestable resources predominate, females should exhibit high rates of agonism over food and energy gain should positively correlate with aggression rate in a given patch (i.e. short-term consequence) and be skewed by dominance rank overall (i.e. long-term consequence) [13,83]. If this so-called within-group contest competition prevails, females are expected to form despotic dominance relationships characterized by stable and unidirectional (i.e. consistent) relationships that are strong (i.e. high steepness) and arranged in a transitive pattern (i.e. linear hierarchies). In addition to despotism, the rank order should exhibit a nepotistic pattern (i.e. matrilineal hierarchies [13,83]; figure 3).

Individual studies of food distribution and agonism have supported parts of these predictions (overview in [86,101]), including widespread evidence that monopolizable resources elicit increased rates of agonism [102–107]. Broader comparisons across a large number of species have been hampered by the paucity of studies that incorporate measures of contestability on a scale that is relevant to the study animals [46,47,108]. Such a 'consumer-centred measure' is represented by Lloyd's Extended Index, which can incorporate data on resource size, quality and abundance [109]. So far, however, it has been incorporated in only a single study, which facilitated successful prediction of agonistic behaviour in one population of capuchin monkeys [108]. Future progress in testing the link between food and agonism depends on more studies using this method to quantify food

distribution. Less direct testing using broad dietary categories (e.g. frugivory or folivory) as proxies for the distribution or contestability of resources [12,13] has proved unsatisfactory, because food categories do not appear to accurately capture the spatio-temporal heterogeneity of food quality [47,84,98]. Nevertheless, the widespread use of dietary categories to make inferences about social relationships (e.g. in a recent review [18]), and the strong link between diet and various aspects of primate behaviour [110] make it important to conduct a comparative study of the presumed link between diet and agonism.

Another crucial step in testing the model is to investigate the link between agonism, skew in energy gain or fitness and social relationships (figure 3). Unfortunately, relatively few studies have provided data on either energy gain or fitness in relation to agonism or dominance rank [101]. Thus, at present, only the predicted link between rates of agonism and dominance relationships (i.e. higher rates of agonism occur in association with more despotic dominance relationships) can be tested. Here, we present such a test using published and unpublished data for 22 groups from 19 populations representing 16 primate species, including two platyrrhines, 10 cercopithecines, three colobines and one hominoid (see the electronic supplementary material, figure S1 and table S2).

(i) Data selection and methods

We selected studies that provided data on rates of agonism among adult females that were collected exclusively using focal animal continuous recording [111]. Because we were unable to find sufficient data for agonism over food, we used data from all contexts. We tested the predicted link of these rates to one component of despotism, the directional consistency of dominance relationship, quantified via the 'Directional Consistency Index' DCI [112]. In contrast to both linearity and steepness [47,113], DCI has not been demonstrated to be sensitive to unknown relationships and currently seems to be the most accurate measure of despotism. Data for dominance matrices to characterize DCI usually came from the same groups as the agonistic rates (for details see the electronic supplementary material, table S2), but were collected via focal and ad libitum sampling [111] and included either all types of agonistic behaviours or only submissive behaviours. DCI values were calculated from dominance matrices using MATMAN, v. 1.1 [114] or taken from the literature. Because of the effect of small group sizes on dominance characteristics [47], analysis was limited to groups with at least six adult females.

To test whether rates of agonism predicted DCI, we used standard least-square regression [115] as well as phylogenetic generalized least squares (PGLS; [116]) based on the consensus of 1000 phylogenetic trees obtained from the 10K Trees website [117] and the maximum likelihood of the phylogenetic signal in the relationship between agonism and despotism, using the 'pgls' function in the caper package [118] for the R statistical environment (see the electronic supplementary material, figure S1 and table S3). As the sample size was small, we repeated the comparison across the component phylogenetic trees to incorporate uncertainty in either the topology or branch lengths of the consensus tree (C. L. Nunn 2012, personal communication).

Because it is not clear *a priori* whether different clades follow similar scaling rules or are constrained and because

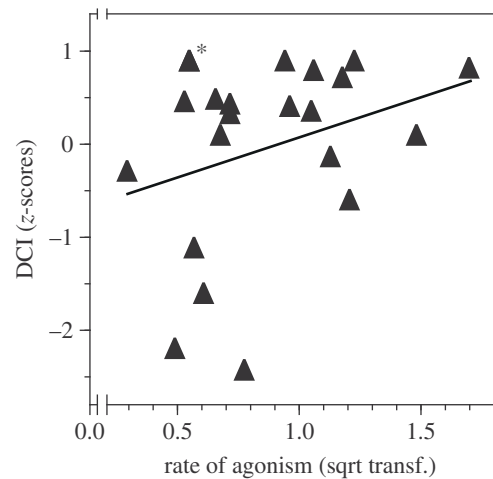


Figure 4. Rates of agonism among female non-human primates in relation to directional consistency (DCI) for standard least-square regression using all 22 groups representing 19 populations and 16 species. Note that one triangle (*) represents two cercopithecine groups. Regression line added for demonstration purpose only: $y = -0.79 + 0.87 \times x$.

grade shifts may occur, a single best fit model might not be appropriate [119]. We therefore tested for differences of DCI across radiations using a phylogenetic ANCOVA [120] with taxon as an independent variable and agonistic rates as a covariate. Because the sample size was small and data were unevenly distributed across clades, we compared cercopithecines ($n = 13$ populations) against all other taxa combined ($n = 6$). All analyses were conducted with transformed data (agonism: square-root transformation; DCI: z-scores [115]).

(ii) Results and discussion

In a standard least-square regression, we did not find the expected relationship between rates of agonism and DCI ($R^2 = 0.103$, $\beta = 0.91$, $t = 1.52$, $p = 0.144$, $n = 22$; figure 4). Similarly, for phylogenetic generalized least squares analysis DCI was not significantly associated with rate of agonism (adjusted $R^2 = 0.100$, $\beta = 1.08$, $t = 1.73$, $p = 0.101$, $\lambda = 0.650$, $n = 19$; figure 5). The high value of Pagel's λ reaffirms the necessity to employ phylogenetic methods [21]. The latter result did not change when we repeated the comparison across 1000 different phylogenetic trees. Except for one tree, in which the p -value was marginally below 0.1, all other 999 values were above (see the electronic supplementary material, figure S2 and table S4). Thus, based upon the data that are currently available, the model's prediction of an association of rates of agonism with despotism would appear unsupported.

Yet, inspection of figure 5 indicates that directional consistency varies tremendously across different primate clades, with the highest values shown by cercopithecines and the lowest for platyrrhines and colobines. Moreover, the relationship between agonism and DCI seemed to vary across clades, as well. A phylogenetic ANCOVA revealed that there is no main effect of the rate of agonism (phylogenetic $p = 0.786$) on DCI; however, both taxon (phylogenetic $p < 0.001$) and the interaction of agonism and taxon (phylogenetic $p = 0.012$; complete test values in the electronic supplementary material, table S5) significantly affected DCI. In both cases (i.e. cercopithecines and other primates), the

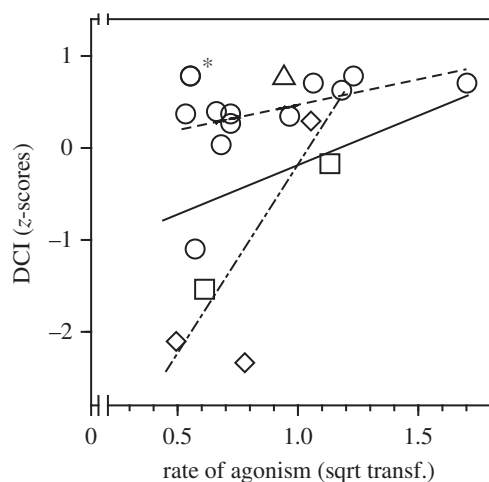


Figure 5. Rates of agonism among female non-human primates in relation to directional consistency (DCI) for phylogenetic tests with one value per population using a consensus tree (19 populations, 16 species): squares, platyrrhines; circles, cercopithecines; diamonds, colobines; triangles, hominoids. Note that one circle (*) represents two cercopithecine populations. Regressions lines are added for demonstration purpose only and represent all populations (solid line: $y = -1.27 + 1.08 \times x$), cercopithecines (dashed line: $y = -0.08 + 0.55 \times x$) and non-cercopithecines (mixed-dashed line: $y = -4.27 + 4.10 \times x$).

relationship between rate of agonism and directional consistency was positive (see regression lines in figure 5), but the slope of the relationship was significantly shallower among cercopithecines, whereas it was much steeper for all other primates combined. Whether the latter is a real effect cannot be addressed at the moment, owing to the scarcity of data for non-cercopithecine primates, which prohibits phylogenetic analysis. Nevertheless, we conducted two standard least-square regressions for cercopithecines and other primates and found that in both cases the effect of rate of agonism on DCI was marginally significant (cercopithecines: $R^2 = 0.223$, $\beta = 0.71$, $t = 1.86$, $p = 0.087$, $n = 14$; all other primates: $R^2 = 0.477$, $\beta = 2.61$, $t = 2.34$, $p = 0.058$, $n = 8$; see also figure 5).

Pending further data becoming available to permit thorough phylogenetic testing, these results may indicate that the overall variation of directional consistency is linked to phylogenetic grade shifts [119]. Within these grades, there is low variation in directional consistency within cercopithecines and rather high variation in other primates. The degree to which this variation is linked to flexibility in rates of agonism is unknown, and may or may not be in support of the predictions of the EMFSR. In either case, the different relationships between agonism and DCI seem to mandate not only the use of phylogenetic methods, but also that the predictions need to be tested within and not across clades as suggested earlier [85].

4. Summary and conclusions

From this overview and our current analyses, three main conclusions emerge.

First, past primate behaviour studies of grouping and mating systems (EMSOMS) focused on how social organization varies with the number of females and receptivity overlap [42,43,45] as well as the effects of food availability, predation and infanticide on group size and cohesion [31,35,38]. In contrast to studies in other animals, the

association of ecological parameters with group formation and mating systems in primates has received little attention (but see [27,28]). Moreover, non-human primates also exhibit more variable mating systems than just female defence polygyny. In all primate radiations, males may singly or cooperatively defend resources, in addition to females [59,62,65, 68,71,72]. Thus, primate grouping and mating systems are more flexible than some past analyses suggest. Whether this flexibility truly relates to ecological factors and whether the EMSOMS provides the right framework remains to be seen. In any case, studies clarifying the possible relationships of ecology and primate grouping and mating systems would be immensely important for our understanding of the existing variation and potential constraints.

Secondly, the EMFSR has been (rightly) criticized for implicitly assuming an independence of trait variation from phylogeny [18,21,36,39]. So far, however, we are not aware of any studies, other than our own, which have used datasets spanning most major primate radiations using wild, unprovisioned populations. In the absence of such studies, calls for abandoning the model would essentially throw out the baby with the bathwater. Before final conclusions can be drawn, better ecological measures are needed [46,47,108]. To our knowledge, Lloyd's extended index [109] currently seems to be the only measure that might capture the ecological components necessary to test the model's prediction. Progress in this area will depend on more researchers adopting this measure.

Lastly, we found no evidence for a link between rates of agonism and directional consistency. It is, however, premature to use this result to refute one of the core assumptions of the model. Our analysis clearly showed a complex picture with a strong phylogenetic signal and strong phylogenetic differences across primate clades, while within clades agonism and DCI seem to vary more or less in the predicted direction. This may indicate that, because of phylogenetic grade shifts, the EMFSR has limited utility in explaining the overall variation in female social relationships across the primate order or other animals. Clarifying what drives these potential differences across clades seems an important task for the future. At the same time, the model's utility may lie in predicting the variation in social relationships within clades [85]. Only additional data will allow testing of this suggestion.

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