1 **VARIATION IN GROUPING PATTERNS, MATING SYSTEMS, AND SOCIAL**

2 **STRUCTURE: WHAT SOCIO-ECOLOGICAL MODELS ATTEMPT TO EXPLAIN**

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27 **ABSTRACT**

28 Socio-ecological models aim to predict the variation in social systems based on a limited number

29 of ecological parameters. Since the 1960's, the original model has taken two paths: one relating

30 to grouping patterns and mating systems and one relating to grouping patterns and female social

31 structure. Here we review the basic ideas specifically with regard to nonhuman primates, present

32 new results, and point to open questions. While most primates live in permanent groups and

33 exhibit female defence polygyny, recent studies indicate more flexibility with cooperative male

34 resource defence occurring repeatedly in all radiations. In contrast to other animals, the potential

35 link between ecology and these mating systems remains, however, largely unexplored. The

36 model of the ecology of female social structure has often been deemed successful, but has

37 recently been criticized. We show that the predicted association of agonistic rates and despotism

38 (directional consistency of relationships) was not supported in a comparative test. The overall

39 variation in despotism is likely due to phylogenetic grade shifts. At the same time, it varies

40 within clades more or less in the direction predicted by the model. This suggests that the model's

41 utility may lie in predicting social variation within but not across clades.

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47 **1. INTRODUCTION**

48 For many animals, particularly humans and other primates, social organisation (i.e. group size,

49 composition, and cohesion), social structure (i.e. patterns of social interactions and relationships

50 among individuals), and mating systems vary widely across species, within species, and even

51 within populations [1,2] with profound consequences for reproductive skew [3,4] and genetic

52 population structure [5,6]. Examining the factors affecting this variation in social systems has

53 been a major focus of ecological research since the 1960's [1,7].

54   Although these ideas have been central to research on nonhuman primates over the past

55 decades, the initial spark goes back to John Crook's early works on birds [7], and was

56 subsequently applied to nonhuman primates in his 1966 work with John Gartlan [1]. This so-

57 called "socio-ecological model" assumed that a limited number of environmental factors affect

58 population characteristics, leading to predictable differences in social systems. The flexibility in

59 primate social systems was, therefore, considered a consequence of the variation in ecology. In

60 the following years, this concept led to a host of tests of relationships between ecology,

61 morphology, and behaviour [8-14]. Although the original idea was intended to explain primate

62 social systems using a single comprehensive (verbal) model, two different paths were

63 subsequently pursued (Figure 1): (i) models that relate to grouping patterns and mating systems

64 [8-11,15] and (ii) models that relate to grouping patterns and female social structure [12-14].

65 Despite occasional calls for considering male and female strategies together, little progress has

66 been made towards such a unified model [16,17]. Therefore, at present it seems justified to speak

67 of at least two models, which are connected through the grouping pattern (Figure 1), but have

68 become essentially independent in their attempt to explain two basic but distinct aspects of social

69 systems. The use of the term "socio-ecological model" to simultaneously refer to both models

70   has led to considerable confusion, however. Therefore, in the following, we will separately

71   describe some core ideas of each model, review historical trends in the results and criticisms,

72   present new results, and point to some open questions. We will focus primarily on ecological

73   factors, although phylogenetic, demographic, and social ones shape social systems as well [18-

74   21].

75

76   **2. ECOLOGY, SOCIAL ORGANISATION, AND MATING SYSTEMS**

77   **(a)** *Basic ideas and tests with nonhuman primates*

78   The ecological model of social organisation and mating systems (henceforth EMSOMS)

79   suggests that resources (e.g. food, nest sites) and risks (e.g. predation, disease, infanticide)

80   determine the spatiotemporal distribution of receptive females, which in turn affects the

81   strategies available to males [8-10,15,22,23]. If resources are spatially dispersed, females may,

82   depending on risks, live spatially isolated from other females. For males this opens the options

83   either for scramble competition polygyny, spatial polygyny, or monogamy. Which strategy males

84   pursue should depend on the economic defensibility of females and the requirements of infant

85   care [10,15,22,24]. In contrast, if females form groups either temporarily or permanently, males

86   may attempt to monopolize one or more clusters of females. Here, the monopolisation potential

87   will depend not only on the number of females, but also on the degree of spatial cohesion and/or

88   temporal overlap in their receptive periods ([15,25]; for more details see [10,22]).

89   In contrast to other mammals [8,9,26], in which ecological factors have been linked to

90   grouping patterns and mating systems, studies of nonhuman primates have focussed less on the

91   environmental factors that underpin variation in mating systems (but see [27,28]). Rather they

92   have examined the emergence of fission-fusion sociality [29,30] or constraints of group size,

93   generally focusing on how predation avoidance and scramble competition for food set adaptive

94   limits for minimum and maximum group size, respectively [31-35].

95   More recently, it has been argued that social organisation in primates evolved from a

96   solitary, nocturnal ancestor, but that – following a switch to a diurnal lifestyle – predation

97   avoidance favoured individuals in loose, diurnal aggregations of multiple males and females

98   [36]. These loose aggregates are suggested to have then led to cohesive multimale-multifemale

99   groups, which in turn led to unimale groups and pairs in some taxa. These overarching trends

100   were posited as evidence against the adaptive approach of the "socio-ecological model" and its

101   lack of accounting for phylogenetic history [36]. This criticism, however, is misplaced, as it

102   focussed only on ecological models of female social structure (see below) instead of studies of

103   group formation and mating systems, which would be of more direct relevance to the authors'

104   analysis. Furthermore, the criticism falls short as the study does not incorporate primary factors

105   such as competition for food [13,31] or social risks such as coercion and infanticide [37], even

106   though the latter has been shown to be an especially important factor favouring male-female

107   associations among prosimians [38]. At present, therefore, it remains unclear exactly how

108   resources and risks affect female grouping patterns among nonhuman primates. While predators,

109   food, and infanticide clearly play a role, the relative importance of each factor and their

110   contribution to the flexibility of grouping remain disputed [39].

111   In contrast, it seems clear that the spatiotemporal distribution of females is one of the

112   main aspects underlying variation among primate mating systems, both across populations [e.g.

113   40,41] and across species [42,43], at least among haplorrhines [44]. Additionally, strepsirrhine

114   primates have recently been found to match the general expectations [45] that as the number of

115   females and/or the overlap in sexual receptivity increases, so too does the number of males per

116   group. Overall, therefore, most primates appear to live in a female defence polygyny system,

117   which is likely the reason that little attention has been paid to potential ecological predictors of

118   mating systems in primates.

119

120   **(b) *The roads less travelled***

121   While female defence polygyny appears to be the most common mating system among

122   nonhuman primates, the prevalence of other mating systems and their ecological bases are less

123   clear. This is largely due to the paucity of comparable ecological data on a scale important to a

124   primate [46,47] and the lack of comparable data on predation and social risks.

125   As in other mammals, the occurrence of spatially-dispersed, solitary females seems to be

126   linked to either scramble competition polygyny, as in some lemuroids and possibly orangutans

127   [48,49], or spatial polygyny, as in some strepsirrhines [50,51]. Similarly, as in other mammals,

128   spatial dispersion of females [52] appears to be the best predictor for pair-living in primates, and

129   permanent association and a monogamous mating system are likely related to the necessity for

130   direct paternal care [53] or infanticide avoidance [38,54]. In these cases, the spatial dispersion of

131   females seems to be determined by either the anti-predator benefits of crypsis (as in many small-

132   bodied primates [33]), the dependence on non-divisible resources [55], or a low abundance of

133   large resources [49]. Nevertheless, a comprehensive comparative analysis of the ecological

134   factors affecting female primate distribution in space and time is lacking.

135   Furthermore, in recent years it has become clear that, across the primate order, certain

136   populations or species living in multimale-multifemale groups may not fit the pattern observed in

137   female defence polygyny [56]. Some non-phylogenetic comparative studies suggest that risk of

138   predation and/or infanticide may be associated with the number of males per group [37,57]. In

139   addition, although heavily disputed and long considered absent among primates [58], some

140   multimale primate societies may indeed exhibit mating systems that can be characterized as

141   resource defence (or territorial) polygyny [10,15,26]. In contrast to Emlen and Oring's [15]

142   original idea of solitary females being attracted to individual males that defend territories or

143   resources, however, in nonhuman primates multiple males jointly defend a group's territory, and

144   this may occur both with female dispersal or philopatry [27,59].

145   At present, such a cooperative male resource defence polygyny seems to be the best

146   characterization of the mating system for common chimpanzees, in which males patrol and

147   defend an area [59]. The lethal aggression and intercommunity killings that have been observed

148   at multiple sites [60,61] may ultimately help to expand a group's area [61], which can benefit

149   female reproductive performance [59]. Similarly, cooperative male resource defence polygyny

150   appears to be the mating system of Phayre's leaf monkeys, a mid-sized Asian colobine we

151   studied in Thailand [56,62]. Although it remains unclear whether males benefit reproductively

152   from the size or quality of an area, males jointly defended territories with little overlap between

153   neighbouring groups [56,62]. While home range size generally increased with group size, the

154   multimale group was able to defend and maintain a larger territory than the similarly-sized and

155   even the larger one-male group (Figure 2).

156   More generally, cooperative male resource defence polygyny can be found in platyrrhines

157   (lion tamarins and some tamarins [63,64]; capuchin monkeys [27,65-68]; spider monkeys

158   [69,70]), cercopithecines (mangabeys, guenons [71]), colobines (colobus monkeys [72]; Phayre's

159   leaf monkeys, see above) and hominoids (polyandrous gibbons [73]; chimpanzees, see above).

160   Additional cases in point are male resource defence polygyny in one-male groups of platyrrhines

161   (saki monkeys [74]), monogamous/ polygynous strepsirrhines (bamboo lemurs [75]), and

162   resource defence monogamy in hylobatids ([76], but see [77]). Thus, although less common than

163   female defence polygyny, male resource defence occurs in all major radiations of primates.

164   Among these species, the nature of between-group encounters seems to relate to

165   ecological variables (e.g. the availability of certain foods [78]), although the occurrence and

166   outcome of aggression between groups may be mediated by the numerical asymmetry in male

167   group size or encounter location [78,79]. As in other cases in which individuals benefit through

168   group augmentation [80], multimale groups might be beneficial in these systems if they increase

169   the group's competitive ability. Although some of these additional males are likely to defect

170   during collective aggression against other groups [81], given the indirect nature of the benefits to

171   male reproductive success [17,82]. Moreover, the presence of additional males could increase the

172   frequency or effectiveness of paternal care (including infant protection) and the options for male

173   protectors, decreasing predation and infanticide risk and increasing female mate choice options

174   (discussion in [23]). Thus, while the costs to males of shared reproduction will increase with the

175   presence of additional competitors, both males and females might ultimately benefit from males

176   defending resources. To date, however, the conditions – ecological, demographic, or social – that

177   have led to the evolution of male resource defence among nonhuman primates remain unknown,

178   as are the factors that help overcome the potential collective action problems [82].

179   In sum, the past primary focus on female defence polygyny among nonhuman primates

180   has painted a picture of a rather impoverished and inflexible mating system across the primate

181   order. This has been further exaggerated by the use of simplistic categories when attempting to

182   reconstruct the evolution of primate sociality [36]. In contrast, the more recent results

183   summarized above indicate that primate mating systems are more flexible than has been

184   acknowledged. The EMSOMS provides one framework that, in addition to phylogenetic,

185 demographic, and social factors [18-21], allows for the examination of this flexibility and its

186 underlying ecological factors.

187

188 **3. ECOLOGY, COMPETITION, AND FEMALE SOCIAL RELATIONSHIPS**

189 **(a)** *Basic ideas and critique of the model*

190 With the ecological model of female social relationships (henceforth EMFSR) a new dimension

191 was introduced to the socio-ecological model [1]. R. W. Wrangham [14] reasoned that food

192 availability and distribution should have major effects not only on the grouping and dispersal

193 patterns of females, but also on their agonistic and affiliative relationships within and between

194 groups. This idea was extended by van Schaik and colleagues to include predation risk as an

195 ecological factor [13] and later infanticide as a social factor favouring grouping [17,38,83]. In

196 the following, we restrict the discussion of the EMFSR to suggestions specifically incorporating

197 cost-benefit approaches, while not considering more qualitative approaches and those based on

198 behavioural indicators of competition [12,84].

199   The EMFSR suggests that ultimately females may form groups due to predation pressure,

200 a defendable distribution of high quality resources, and/or social benefits via infanticide

201 avoidance [13,14,83]. Among group-living females, the availability of high-quality patches that

202 can be monopolised (or usurped) by a subset of residents will affect social relationships. Because

203 these resources may promote within-group contest competition, females may form either

204 despotic-nepotistic or despotic-nepotistic-tolerant relationships to maximize access and inclusive

205 fitness benefits, with tolerance being predicted when between-group competition is strong [83].

206 In case such resources are rare or absent, females should either form egalitarian relationships and

207   disperse or remain philopatric, if strong between-group competition favours kin-based coalitions

208   to defend group-controlled resources [83].

209   Over the past years this verbal model has been criticized for a variety of reasons

210   [18,21,39]. Some critiques have related to re-evaluations of hypotheses and predictions [72,85],

211   incorporating formal (mathematical) modeling [86], incorporating phylogenetic relationships to

212   capture phylogenetic similarity and constraints [87,88], excluding dispersal patterns [18,85], or

213   extending the model to incorporate cooperative actions [89,90]. Others criticized the

214   overemphasis of competition and underemphasis of affiliation and cooperation [91]. Importantly,

215   mismatches between predictions and results have been pointed out [92,93] and the lack of

216   phylogenetic methods and the presence of correlations among social variables [94,95] have

217   resulted in calls to abandon the model altogether [21] or to investigate different components

218   separately [18].

219   The importance of the mismatches is currently difficult to judge because large-scale,

220   cross-species comparisons of wild, unprovisioned primates are lacking [85]. Instead,

221   comparative approaches have used primarily captive or provisioned populations [87,88] or

222   included only a few wild, unprovisioned populations or species [96-98]. To date, only two

223   broader comparisons have been conducted with wild, unprovisioned primates [91,99], and both

224   studies were restricted to agonistic behaviour. Unfortunately, one of these analyses has serious

225   conceptual and analytical flaws [100], and neither directly tested predictions of the model or

226   controlled for phylogeny. As noted previously, the assumption of independence of species'

227   responses to local ecological conditions, which is implicit in the model, is a serious problem that

228   should be incorporated in comparative studies [85]. Nevertheless, given the paucity of data for

229   certain aspects of the model [85], it is clear that a general test is currently unfeasible. It therefore

230   seems that investigating individual aspects of the model is indeed the most viable route [18].

231

232   **(b)** *Testing links between agonism and social structure*

233   Central to the EMFSR is the idea that there is a link between 1) the abundance,

234   distribution, size, and quality of resources; 2) the frequency and form of agonistic behaviour and

235   its energetic consequences; and 3) characteristics of the dominance relationships of females

236   (Figure 3). Specifically, if contestable resources predominate, females should exhibit high rates

237   of agonism over food and energy gain should positively correlate with aggression rate in a given

238   patch (i.e. short-term consequence) and be skewed by dominance rank overall (i.e. long-term

239   consequence) [13,83]. If this so-called within-group contest competition prevails, females are

240   expected to form despotic dominance relationships characterised by stable and unidirectional

241   (i.e. consistent) relationships that are strong (i.e. high steepness) and arranged in a transitive

242   pattern (i.e. linear hierarchies). In addition to despotism, the rank order should exhibit a

243   nepotistic pattern (i.e. matrilineal hierarchies [13,83]; see Figure 3).

244   Individual studies of food distribution and agonism have supported parts of these

245   predictions (overview in [86,101]), including widespread evidence that monopolisable resources

246   elicit increased rates of agonism [102-107]. Broader comparisons across a large number of

247   species have been hampered by the paucity of studies that incorporate measures of contestability

248   on a scale that is relevant to the study animals [46,47,108]. Such a "consumer-centred measure"

249   is represented by Lloyd's Extended Index, which can incorporate data on resource size, quality,

250   and abundance [109]. So far, however, it has been incorporated in only a single study, which

251   facilitated successful prediction of agonistic behaviour in one population of capuchin monkeys

252   [108]. Future progress in testing the link between food and agonism depends on more studies

253   using this method to quantify food distribution. Less direct testing using broad dietary categories

254   (e.g. frugivory or folivory) as proxies for the distribution or contestability of resources [12,13]

255   have proven unsatisfactory, because food categories do not appear to accurately capture the

256   spatiotemporal heterogeneity of food quality [47,84,98]. Nevertheless, the widespread use of

257   dietary categories to make inferences about social relationships (e.g. in a recent review [18]), and

258   the strong link between diet and various aspects of primate behaviour [110] make it important to

259   conduct a comparative study of the presumed link between diet and agonism.

260   Another crucial step in testing the model is to investigate the link between agonism, skew

261   in energy gain or fitness, and social relationships (Figure 3). Unfortunately, relatively few studies

262   have provided data on either energy gain or fitness in relation to agonism or dominance rank

263   [101]. Thus, at present, only the predicted link between rates of agonism and dominance

264   relationships (i.e. higher rates of agonism occur in association with more despotic dominance

265   relationships) can be tested. Here we present such a test using published and unpublished data for

266   22 groups from 19 populations representing 16 primate species, including 2 platyrrhines, 10

267   cercopithecines, 3 colobines, and 1 hominoid (see Figure S1 and Table S2; supplementary

268   electronic material).

269

270   (i) *Data selection and methods*

271   We selected studies that provided data on rates of agonism among adult females that were

272   collected exclusively using focal animal continuous recording [111]. Because we were unable to

273   find sufficient data for agonism over food, we used data from all contexts. We tested the

274   predicted link of these rates to one component of despotism, the directional consistency of

275   dominance relationship, quantified via the "Directional Consistency Index" *DCI* [112]. In

276   contrast to both linearity and steepness [47,113], *DCI* has not been demonstrated to be sensitive

277   to unknown relationships and currently seems to be the most accurate measure of despotism.

278   Data for dominance matrices to characterise *DCI* usually came from the same groups as the

279   agonistic rates (details see Table S2; supplementary electronic material), but were collected via

280   focal and *ad libitum* sampling [111] and included either all types of agonistic behaviours or only

281   submissive behaviours. *DCI* values calculated from dominance matrices using MatMan, Version

282   1.1 [114] or taken from the literature. Because of the effect of small group sizes on dominance

283   characteristics [47], analysis was limited to groups with at least 6 adult females.

284   To test whether rates of agonism predicted *DCI* we used standard least-square regression

285   [115] as well as phylogenetic generalized least squares (PGLS; [116]) based on the consensus of

286   1000 phylogenetic trees obtained from the 10K Trees website [117] and the maximum-likelihood

287   of the phylogenetic signal in the relationship between agonism and despotism, using the "pgls"

288   function in the caper package [118] for the R statistical environment (see Figure S1 and Table

289   S3; supplementary electronic material). As the sample size was small, we repeated the

290   comparison across the component phylogenetic trees to incorporate uncertainty in either the

291   topology or branch lengths of the consensus tree (Nunn, personal communication).

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

293   constrained and because grade shifts may occur, a single best fit model might not be appropriate

294   [119]. We, therefore, tested for differences of *DCI* across radiations using a phylogenetic

295   ANCOVA [120] with taxon as an independent variable and agonistic rates as a covariate.

296   Because the sample size was small and data were unevenly distributed across clades, we

297   compared cercopithecines ($N = 13$ populations) against all other taxa combined ($N = 6$). All

298   analyses were conducted with transformed data (agonism: square-root transformation; *DCI*: z-

299   scores [115]).

300

301   (ii) *Results and discussion*

302   In a standard least-square regression, we did not find the expected relationship between

303   rates of agonism and *DCI* ($R^2 = 0.103$, $\beta = 0.91$, $t = 1.52$, $P = 0.144$, $N = 22$; Figure 4). Similarly,

304   for phylogenetic generalized least squares analysis *DCI* was not significantly associated with rate

305   of agonism (adjusted $R^2 = 0.100$, $\beta = 1.08$, $t = 1.73$, $P = 0.101$, $\lambda = 0.650$, $N = 19$; Figure 5). The

306   high value of Pagel's lambda reaffirms the necessity to employ phylogenetic methods [21]. The

307   latter result did not change when we repeated the comparison across 1000 different phylogenetic

308   trees. Except for one tree, in which the *P* value was marginally below 0.1, all other 999 values

309   were above (see Figure S2 and Table S4; supplementary electronic material). Thus, based upon

310   the data that are currently available, the model's prediction of an association of rates of agonism

311   with despotism would appear unsupported.

312   Yet, inspection of Figure 5 indicates that directional consistency varies tremendously

313   across different primate clades, with the highest values shown by cercopithecines and the lowest

314   for platyrrhines and colobines. Moreover, the relationship between agonism and *DCI* seemed to

315   vary across clades, as well. A phylogenetic ANCOVA revealed that there is no main effect of the

316   rate of agonism (phylogenetic $P = 0.786$) on *DCI*; however, both taxon (phylogenetic $P < 0.001$)

317   and the interaction of agonism and taxon (phylogenetic $P = 0.012$; complete test values in Table

318   S5; supplementary electronic material) significantly affected *DCI*. In both cases (i.e.

319   cercopithecines and other primates), the relationship between rate of agonism and directional

320   consistency was positive (see regression lines in Figure 5), but the slope of the relationship was

321   significantly shallower among cercopithecines, whereas it was much steeper for all other

322   primates combined. Whether the latter is a real effect cannot be addressed at the moment, due to

323   the scarcity of data for non-cercopithecine primates, which prohibits phylogenetic analysis.

324   Nevertheless, we conducted two standard least-square regressions for cercopithecines and other

325   primates and found that in both cases the effect of rate of agonism on *DCI* was marginally

326   significant (cercopithecines: $R^2 = 0.223$, $\beta = 0.71$, $t = 1.86$, $P = 0.087$, $N = 14$; all other primates:

327    $R^2 = 0.477$, $\beta = 2.61$, $t = 2.34$, $P = 0.058$, $N = 8$; see also Figure 5).

328   Pending further data becoming available to permit thorough phylogenetic testing, these

329   results may indicate that the overall variation of directional consistency is linked to phylogenetic

330   grade shifts [119]. Within these grades there is low variation in directional consistency within

331   cercopithecines and rather high variation in other primates. The degree to which this variation is

332   linked to flexibility in rates of agonism is unknown, and may or may not be in support of the

333   predictions of the EMFSR. In either case, the different relationships between agonism and *DCI*

334   seem to mandate not only the use of phylogenetic methods, but also that the predictions need to

335   be tested within and not across clades as suggested earlier [85].

336

337   **4. SUMMARY AND CONCLUSIONS**

338   From this overview and our current analyses three main conclusions emerge:

339   First, past primate behaviour studies of grouping and mating systems (EMSOMS)

340   focussed on how social organisation varies with the number of females and receptivity overlap

341   [42,43,45] as well as the effects of food availability, predation, and infanticide on group size and

342   cohesion [31,35,38]. In contrast to studies in other animals, the association of ecological

343   parameters with group formation and mating systems in primates have received little attention

344   (but see [27,28]). Moreover, nonhuman primates also exhibit more variable mating systems than

345   just female defence polygyny. In all primate radiations males may singly or cooperatively defend

346   resources, in addition to females [59,62,65,68,71,72]. Thus, primate grouping and mating

347   systems are more flexible than some past analyses suggest. Whether this flexibility truly relates

348   to ecological factors and whether the EMSOMS provides the right framework remains to be

349   seen. In any case, studies clarifying the possible relationships of ecology and primate grouping

350   and mating systems would be immensely important for our understanding of the existing

351   variation and potential constraints.

352   Secondly, the EMFSR has been (rightly) criticized for implicitly assuming an

353   independence of trait variation from phylogeny [18,21,36,39]. So far, however, we are not aware

354   of any studies, other than our own, which have used data sets spanning most major primate

355   radiations using wild, unprovisioned populations. In the absence of such studies, calls for

356   abandoning the model would essentially throw out the baby with the bathwater. Before final

357   conclusions can be drawn, better ecological measures are needed [46,47,108]. To our knowledge,

358   Lloyd's extended index [109] currently seems to be the only measure that might capture the

359   ecological components necessary to test the model's prediction. Progress in this area will depend

360   on more researchers adopting this measure.

361   Lastly, we found no evidence for a link between rates of agonism and directional

362   consistency. It is, however, premature to use this result to refute one of the core assumptions of

363   the model. Our analysis clearly showed a complex picture with a strong phylogenetic signal and

364   strong phylogenetic differences across primate clades, while within clades agonism and *DCI*

365   seem to vary more or less in the predicted direction. This may indicate that, because of

366   phylogenetic grade shifts, the EMFSR has limited utility in explaining the overall variation in

367   female social relationships across the primate order or other animals. Clarifying what drives

368   these potential differences across clades seems an important task for the future. At the same time,

369   the model's utility may lie in predicting the variation in social relationships within clades [85].

370   Only additional data will allow testing of this suggestion.

371

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697

698   **FIGURE LEGENDS**

699   **Figure 1**. Flow-diagram of the two main strings of ideas both dubbed the "socio-ecological

700   model": a model relating to grouping patterns and mating systems [15] and to grouping patterns

701   and female social structure [13].

702

703   **Figure 2.** Home range size of Phayre's leaf monkeys in relation to group size and number of

704   adult males. Depicted are annual home ranges in 2004, 2005, and 2006 for three groups (two

705   one-male groups, one multimale group). Regression lines added for demonstration purpose only.

706   one-male groups: $y = 0.22 + 0.03 * x$, multimale group: $y = 0.40 + 0.03 * x$.

707

708   **Figure 3.** Ecological conditions for within-group contest competition and predictions for

709   behavioural responses and energetic consequences, as well as their social outcomes for

710   dominance relationships and hierarchies. Predictions do not consider conditions for between-

711   group competition as they concern a separate prediction for tolerance (for details of other

712   competitive regimes see [13,83,85,101]). * - variables used in the current comparative analysis.

713

714   **Figure 4.** Rates of agonism among female nonhuman primates in relation to directional

715   consistency (*DCI*) for standard least-square regression using all 22 groups representing 19

716   populations and 16 species. Note that one triangle (*) represents two cercopithecine groups.

717   Regression line added for demonstration purpose only: $y = -0.79 + 0.87 * x$.

718

719   **Figure 5.** Rates of agonism among female nonhuman primates in relation to directional

720   consistency (*DCI*) for phylogenetic tests with one value per population using a consensus tree

721   (19 populations, 16 species): squares: platyrrhines; circles: cercopithecines; diamonds: colobines;

722   triangles: hominoids. Note that one circle (*) represents two cercopithecine populations.

723   Regressions lines are added for demonstration purpose only and represent all populations (solid

724   line: $y = -1.27 + 1.08 * x$), cercopithecines (dashed line: $y = -0.08 + 0.55 * x$), and non-

725   cercopithecines (mixed-dashed line: $y = -4.27 + 4.10 * x$).

726