

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.

42

43 **Key words:** nonhuman primates, female defence polygyny, resource defence polygyny, contest
44 competition, rate of agonism, directional consistency

45

46

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 defensible 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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389

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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