

1 ***Title: Social complexity and kinship in animal societies***

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26

27 **Abstract**

28

29 Studies of eusocial invertebrates regard complex societies as those where there is a
30 clear division of labour and extensive cooperation between breeders and helpers, while
31 studies of social behaviour in mammals regard complex societies as those where
32 individual differences in dominance rank and coalitionary support determine access to
33 resources and reproductive opportunities. We show here that traits associated with the
34 complexity of social organisation among females occur in social mammals that live in
35 groups composed of close relatives while traits associated with the complexity of social
36 relationships occur where average kinship between female group members is low.
37 These differences in the form of social complexity appear associated with variation in
38 brain size and may reflect contrasts in the extent of conflicts of interest between group
39 members. Our results emphasize the limitations of any unitary concept of social
40 complexity and highlight that variation in kinship has far-reaching consequences for
41 social behaviour.

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46 **Introduction**

47

48 Although the emergence of complex societies has been identified as one of the major
49 transitions in evolutionary biology (Maynard Smith & Szathmary 1997), what is meant
50 by social complexity is frequently unclear and concepts of complexity vary. Studies of
51 eusocial insects and cooperative vertebrates have mostly followed Wilson (1971) in
52 characterising complex societies as those where there is reproductive suppression of
53 females, extensive alloparental care and a division of labour among females which is
54 often combined with functional divergence in development between breeders and non-
55 breeding workers or between different categories of workers (Bourke & Franks 1995;
56 Anderson & McShea 2001; Abbot & Chapman 2017; Korb & Thorne 2017). In contrast,
57 studies of social mammals (and of the higher primates and cetaceans in particular)
58 regard the presence of frequent competitive interactions, linear dominance hierarchies,
59 reciprocal cooperation, differentiated social relationships, and coalitions and alliances
60 between group members as indicators of social complexity (Byrne & Whitn 1988;
61 Freeberg et al. 2012; Bergman & Beehner 2015; Silk & Kappeler 2017).

62

63 There are theoretical grounds for expecting that reproductive suppression, extensive
64 alloparental care by non-breeding females and a division of labour between breeders
65 and non-breeders (which we refer to as 'organisational complexity') are likely to be
66 most highly developed where kinship between group members is high, indirect fitness
67 benefits are substantial and conflicts of interest between group members are reduced
68 (Hamilton 1971; Silk 2002; Boomsma 2009) and comparative studies of insects
69 (Hughes et al. 2008) and birds (Cornwallis et al. 2010) have shown that this is the case.
70 In contrast, conflicts of interest between group members and social traits associated
71 with them, including frequent aggression between group members, well defined

72 dominance hierarchies and behavioural tactics used to maintain social status (which
73 we refer to as ‘relational complexity’), might be expected to be most highly developed
74 in species where most group members are not closely related (Seyfath & Cheney
75 2012) and conflicts of interest between group members are common. Such differences
76 in the complexity of the social environment may have implications for the development
77 of cognitive abilities and brain structure. Where traits associated with organisational
78 complexity are well developed and there is a clear division of labour between group
79 members that is associated with contrasts in development, social relationships
80 between individuals seldom appear to be as relationships as differentiated or as
81 variable as in species where *relational* complexity is high and individuals frequently
82 need to make decisions that are cognitively demanding (Anderson & McShea 2001).

83

84 Social mammals provide an unusual opportunity to explore the relationship between
85 contrasts in the occurrence of these two forms of social complexity and variation in
86 kinship between group members across species since they include both litter-bearing
87 monogamous species, like the social mole rats and some social mongooses, where
88 average coefficients of kinship between female group members are usually between
89 0.25 and 0.5) as well as species with polygynous or polygynandrous mating systems
90 that bear single offspring, like the smaller cetaceans and all three African apes, where
91 average kinship among female group members seldom exceeds 0.05 (see
92 *Supplementary Table 1*). Moreover, the social behaviour of a relatively high proportion
93 of mammals has been studied in some detail (Clutton-Brock 2016). Here, we use
94 information on variation in social behaviour and kinship structures among mammals to
95 investigate how particular components of *structural* and *relational* complexity are
96 associated with variation in kinship.

97

98 **Materials and Methods**

99

100 The objective of our study is to assess whether traits associated with organizational
101 complexity more frequently occur in in social mammals in which average levels of
102 kinship among female group members are high, whereas traits associated with
103 relational social complexity are more likely to be present when average levels of
104 kinship among female group members are low. We extracted information from the
105 published literature and used a phylogenetic comparative approach to assess the
106 association between average levels of kinship observed within social groups and the
107 various behavioural traits. We provide extended details on the methods and definitions
108 of the variables in the Supplementary Materials at the end of this file. All data, and the
109 references we used to obtain them, are provided in Supplementary Table 1.

110

111 *Average kinship among female group members in mammals*

112 We searched for all populations of social mammals for which average kinship among
113 a group of all adult female individuals had been calculated based on similarity at
114 genetic markers. We started with species included in relevant reviews (Lukas et al.
115 2005; Briga et al. 2012) and references citing these, and searched for additional
116 studies on Google Scholar (up until August 2017) using the key terms (i)
117 “microsatellite”, (ii) “relatedness” or “kinship”, and (iii) “mammal*”. Studies were
118 included if they provided data on average levels of kinship among all adult female
119 group members based on genetic methods that could be used to estimate the extent
120 of allele sharing at microsatellite loci. We only included species in which females lived
121 in groups where the same individuals repeatedly interact with each other across
122 extended periods: these include cooperative breeders, like meerkats or wolves, in
123 which non-breeding subordinates live with dominant breeders; species where

124 individuals live in stable groups including multiple breeding females, like many of the
125 social primates; and species where adult females form regular associations by also
126 aggregate in larger, less stable groups, as in red deer or elephants.

127

128 *Social parameters in mammals*

129 For all the mammalian species for which we were able to find data on average kinship
130 among all adult female group members, we searched the primary literature for
131 information on the occurrence of asymmetrical allomaternal provisioning, infanticide by
132 females, reproductive suppression of subordinate females, division of labour between
133 breeders and nonbreeders, linear dominance hierarchies among group females, and
134 coalition formation in conflicts among females. In addition, we searched for data on
135 rates of aggression between group females and symmetry in grooming interactions.
136 For details see the Supplementary Materials.

137

138 *Brain and body size*

139 Data on body, brain, and neocortex size were extracted from the published literature
140 (Shultz & Dunbar 2010; Barton & Capellini 2011; Isler & van Schaik 2012). When
141 information was present in several datasets, we calculated median values for species
142 and manually checked for outliers. Since it is still debated exactly how brain size
143 evolves, we relied on four different approaches: first, we used absolute brain size as a
144 response variable in a regression with relational complexity and in a regression with
145 average levels of kinship; second, we used absolute brain size as a response variable
146 in a regression with relational complexity/average kinship while controlling for body
147 size; third, we additionally included longevity, diet, and seasonal variation as predictor
148 variables, ecological parameters which have been indicated to influence brain size
149 variation in mammals; and fourth, we used the size of the neocortex as a response

150 variable in a regression with relational complexity and in a regression with average
151 levels of kinship. We used comparative databases to extract information on diet
152 category and activity strata (de Magalhaes & Costa 2009; Jones et al. 2009; Price et
153 al. 2012; Botero et al. 2014; Wilman et al. 2014).

154

155 Statistical approaches

156 Regressions to assess the relationship across mammals between specific forms of
157 behaviour and average levels of kinship were performed while accounting for
158 phylogenetic relatedness among species using MCMCglmm (Hadfield & Nakagawa
159 2010). We relied on the updated mammalian supertree (Fritz et al. 2009) to estimate
160 phylogenetic relatedness between species. The tree was truncated to match our
161 sample using functions of the package ‘ape’ (Paradis et al. 2004) in the statistical
162 software R (R Development Core Team 2010). We included the phylogenetic
163 relationship between species as covariance matrix, used a broad prior, 1,000,000
164 iterations, a burn-in of 200,000, and a thinning interval of 10. The analysis was
165 repeated three times, and visually inspected for convergence. Terms were considered
166 statistically significant when the calculated pMCMC values were less than 0.05.

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170 **Results**

171

172 As among insects (Hughes et al. 2008) and birds (Cornwallis et al. 2010), traits
173 associated with organisational complexity (including the presence of non-breeding
174 female helpers, extensive provisioning of juveniles by females other than the mother
175 and a clear division of labour between breeders and non-breeders) are more
176 commonly found in social mammals where average levels of kinship between females
177 living in the same group are high than where they are low (Fig 1, a-d: effect of average
178 kinship on presence of: *allomaternal provisioning* 117.32 (95% CI 16.2, 227.7),
179 $p < 0.001$, $n = 41$ species; *female infanticide* 139.4 (95%CI -4.4, 409.2), $p = 0.03$, $n = 31$
180 species; *reproductive suppression* 276.9 (95%CI 57.7, 441.3), $p < 0.001$, $n = 42$ species;
181 *division of labour* 216.2 (95% CI 41.3, 325.5), $p < 0.001$; all $n = 42$ species). In some
182 species where average kinship between group members is high and traits associated
183 with organisational complexity are present (including naked mole-rats and Kalahari
184 meerkats), there are also obvious morphological differences between breeding and
185 non-breeding females which resemble those between queens and workers in eusocial
186 insects, though they are less pronounced (Bennett & Faulkes 2000; Clutton-Brock
187 2016; Zöttl et al. 2016). While helpers are usually closely related to the young they are
188 raising in these species, individual differences in contributions to alloparental care are
189 seldom closely associated with variation in relatedness between helpers and the
190 individuals that they are assisting (Griffin & West 2003; Clutton-Brock 2006).

191

202 In contrast, high rates of aggression between females, well defined linear dominance
203 hierarchies and differentiated social relationships between individuals involving
204 coalitions and alliances are typically found in species where average kinship between
205 group members is low. The frequency of aggressive interactions between female group
206 members increases as average kinship between resident females falls (Fig 2a: effect
207 of average kinship on *rate of aggression per female per hour* -4.0 (95%CI -7.5, -0.6),
208 $p=0.03$; $n=22$ species) and average kinship between females is a better predictor of
209 rates of aggression between individuals than the number of adult group members
210 (effect of average kinship on *rate of aggression per female per hour* -2.5 (95% CI -
211 5.31, -1.62), $p=0.01$, effect of number of adult females per group 0.03 (95% CI -0.02,
212 0.08), $p=0.32$; $n=22$ species). Contrary to some predictions (Isbell 1991; Sterck et al.
213 1997), interspecific differences in rates of aggression among females do not appear to
214 be closely associated with major species differences in diet, habitat use or longevity
215 among the species in our data set (*Supplementary Table 2*). Well defined dominance
216 hierarchies that include all resident females are also more commonly found where
217 average kinship between group members is low than where they are high (Fig 2b:
218 effect of average kinship on *presence of linear dominance hierarchy* -198.9 (95%CI -
219 429.8, -17.6), $p<0.01$; $n=42$ species) although there is commonly a clear difference in
220 dominance between breeding females and non-breeding helpers in groups where both
221 are present. Supportive coalitions between female group members (which are often
222 used in competition for resources or breeding partners) are also more frequent in
223 species where average kinship between group members is low (Fig 2c: effect of
224 average kinship on *presence of coalitionary behaviour* -261.1 (95% CI -445.2, -57.1),
225 $p<0.001$; $n=42$ species) and are usually rare or absent in species where average
226 kinship between group members is high and groups include nonbreeding helpers.
227 Several other behavioural traits, including the redirection of aggression, reconciliation

228 and consolation between female group members (Byrne & Whiten 1988; Marino et al.
229 2007; Jaeggi & Gurven 2013) also appear to be restricted to species living in groups
230 where kinship between group members is low, although the available data do not yet
231 allow quantitative comparisons.

232

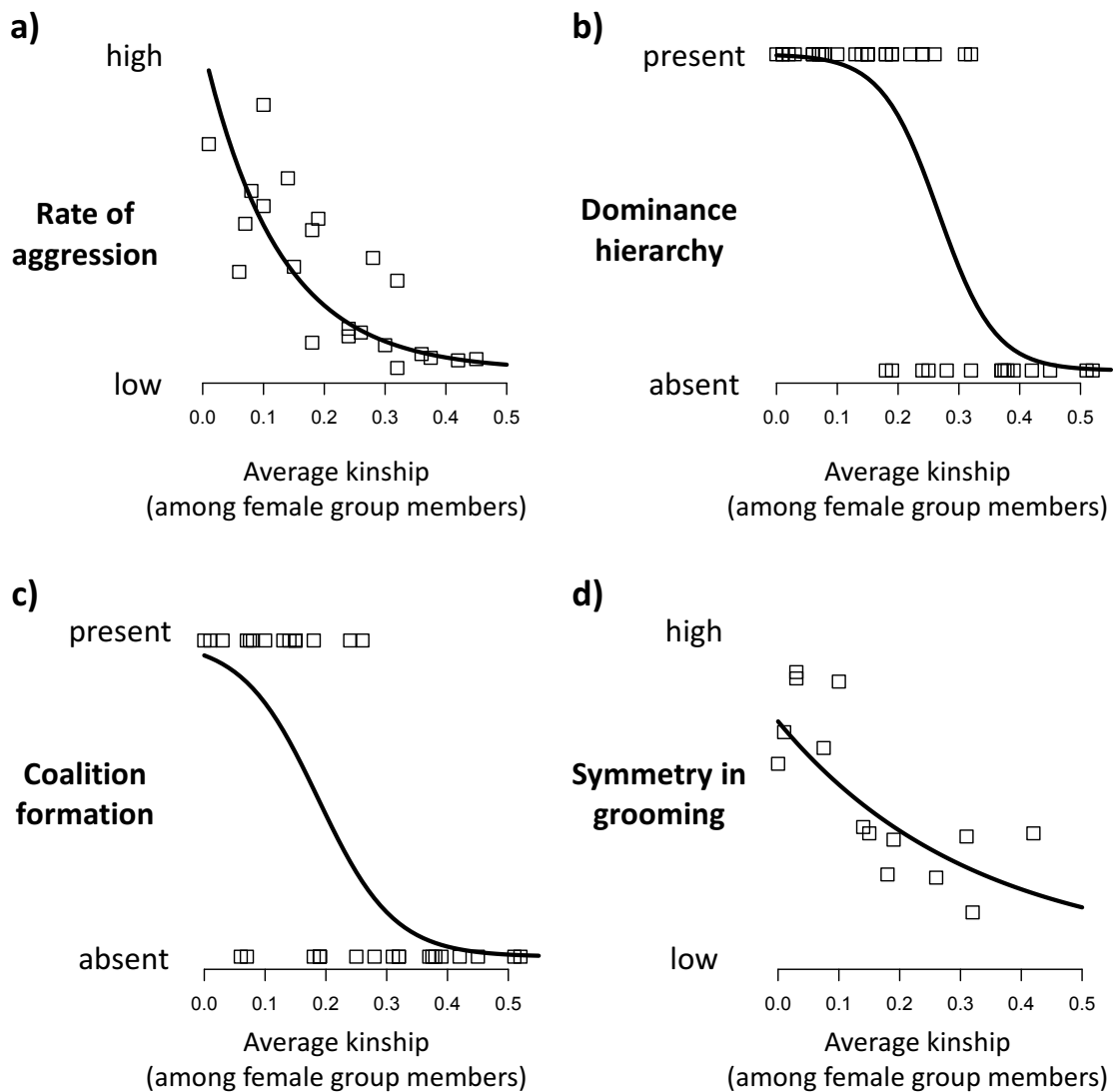
233 Contrasts in average kinship between group members may also affect the distribution
234 of cooperative behaviour between interacting individuals: in species where few group
235 members are close relatives, individuals commonly direct asymmetrical forms of
236 assistance at the relatively small number of individuals to which they are closely related
237 (Silk 2002) whereas, in species where most group members are close relatives, there
238 is usually little evidence that closer kin are preferentially targeted (Griffin & West 2003,
239 Clutton-Brock 2006). Mutualistic forms of cooperation, like social grooming, can occur
240 whether group members are closely related or not but, since individuals are unlikely to
241 gain substantial indirect fitness benefits where levels of kinship between group
242 members are low, interactions should be more symmetrical in species where
243 cooperating partners are not closely related (Lehmann & Keller 2006). In line with this
244 prediction, allogrooming relationships appear to be more symmetrical in species where
245 average kinship between group members is low than where it is high (Fig 2d: effect of
246 average kinship on *reciprocity in pairwise grooming interactions* -1.4 (95%CI -2.36, -
247 0.43), $p < 0.01$; $n = 13$ species).

248

249

250 **Fig 2. Average levels of kinship among female group members and occurrence**
 251 **of traits associated with relational complexity across social mammals**

252 Traits associated with high *relational* complexity – (a) frequent aggressive interactions
 253 among group members (rate of aggression between female group members), (b) well-
 254 defined linear dominance hierarchies, (c) coalition formation in fights among group
 255 members, and (d) symmetry in cooperative interactions (reciprocity in grooming
 256 interactions among female group members) – are all more likely to be present in
 257 species with low average levels of kinship between group members than in those
 258 where average kinship between group members is high.



259
 260

261 It has been suggested that complex, social relationships between group members may
262 have favoured the evolution of improved cognitive abilities and increases in brain
263 development (Dunbar & Shultz 2007), though the extent to which gross differences in
264 relative brain size reflect contrasts in cognitive abilities has been questioned (Logan
265 et al. 2017) and the relative effects of social versus ecological parameters on brain
266 development are widely debated (Clutton-Brock & Harvey 1980; Isler & van Schaik
267 2014; deCasien et al. 2017). Previous studies have shown that eusocial insects (Farris
268 2016) and cooperatively breeding birds (Iwaniuk & Arnold 2004) frequently have brain
269 sizes smaller than related non-cooperative taxa while, in mammals, several
270 cooperative breeders show little evidence of advanced cognitive abilities (Thornton &
271 McAuliffe 2015). In contrast, many of the mammals that are thought to possess the
272 most advanced cognitive abilities have relatively large brains (like the higher primates,
273 the social hyenas and the smaller cetaceans) and live in groups where average kinship
274 between group members is low and social relationships between individuals are
275 complex and unstable (Marino et al. 2007; Clutton-Brock 2016). Across the mammals
276 in our sample, indices of both absolute and relative brain size are positively associated
277 with the expression of traits associated with *relational* complexity (effect of presence
278 of traits associated with relational complexity on log-transformed *brain mass* 1.84 (95%
279 CI 0.7, 2.9), $p = 0.001$, $n = 36$ species) and negatively with estimates of average kinship
280 between female group members (effect of average kinship among females on log-
281 transformed *brain mass* -6.1 (95% CI -9.79, -2.75), $p < 0.01$, $n = 36$ species). Both these
282 associations are present after accounting for the effects of body size, diet, and
283 arboreality on variation in brain size and persist when estimates of relative brain size
284 are replaced by other estimates of brain development, including the size of the
285 neocortex (*Supplementary Table 3*).

286

287 **Discussion**

288

289 Our analysis emphasises the limitations of any unitary concept of social complexity:
290 traits associated with a clear division of reproduction and labour between group
291 members are seldom highly developed in species where traits associated with
292 relational complexity are highly developed and vice versa. Moreover, there are other
293 forms of social complexity, including variation in the stability of groups and the
294 frequency with which members of different groups associate with each other (Kummer
295 1968; Moss & Lee 2011).

296

297 Our analyses support Hamilton's (1971) suggestion that variation in kinship is likely to
298 have far-reaching consequences for social behaviour and social relationships among
299 vertebrates as well as among invertebrates (Bourke 1999, Silk 2002). One reason why
300 the association between complex, differentiated social relationships and low average
301 levels of kinship between group members has not been widely recognised may be the
302 assumption that average levels of kinship are high in social animals where females
303 commonly breed in the group where they are born so that most female group members
304 are related to each other. However, even where most females remain in their natal
305 groups throughout their lives, average kinship between resident females is usually low
306 if groups include multiple breeding females, including individuals from successive
307 generations, mating systems are polygynous or polygynandrous, and the breeding
308 tenure of males is short (Lukas et al. 2005). As a result, conflicts of interest between
309 group members are likely to be common and may promote the evolution of traits used
310 in competitive encounters, including competitive coalitions and alliances and complex
311 forms of manipulation (Byrne & Whiten 1988).

312

313 Comparisons between species also suggest that cognitive capacities and brain size
314 may be more highly developed in animals social where average kinship between group
315 members is low and social relationships are complex and competitive than in those
316 where average kinship is high and reproductive suppression and cooperation are
317 highly developed as the 'social brain' hypothesis suggests. However, previous studies
318 have shown that the relationship between gross differences in brain size and cognitive
319 abilities is inconsistent and the effects of variation in social behaviour on brain
320 development are disputed (Clutton-Brock & Harvey 1980; Isler & van Schaik 2014;
321 deCasien et al. 2017; Dunbar & Shultz 2017).

322

323 The association between average kinship between group members and the two
324 contrasting forms of social complexity may also have implications for our
325 understanding of the evolution of human societies. Most of the higher primates and all
326 three African apes live in social groups where average coefficients of relatedness
327 between group members are low and reproductive suppression of adult females,
328 alloparental provisioning and a division of labour between group members are rare
329 (Lukas & Clutton-Brock 2012). Since hominins presumably developed from ancestors
330 that lived in groups where average kinship between group members was also low
331 (Chapais 2009; Hill et al. 2011), this suggests that the presence of extensive
332 alloparental care and a pronounced division of labour between group members in
333 human and non-human societies is likely to have evolved by different evolutionary
334 pathways.

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346 **Statement of authorship:** DL and TCB designed the study; DL collected the data

347 and carried out statistical analyses; DL and TCB wrote the manuscript; and DL and

348 TCB gave final approval for publication.

349

350

351 **Data accessibility:**

352 All data are included as supplement and are deposited at the Knowledge Network for

353 Biocomplexity (doi:10.5063/F1FB513K).

354

355

356 **Keywords:** sociality; evolution; social complexity; eusociality; behaviour;

357 cooperation; competition; kinship; relatedness

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501

502 **Supplementary Material for pre-peer-reviewed version of:**

503

504 ***Social complexity and kinship in mammal societies***

505

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508

509 **Supplementary text:** Extended methods and definitions of the variables

510 **Table S1:** All data used in the analyses with references

511 **Table S2:** Output of the statistical model assessing the association between rates of
512 aggression among females and ecological parameters

513 **Table S3:** Output of the statistical models assessing the association between
514 measures of brain size and relational complexity and average levels of kinship

515

516

517 **Supplementary text: Extended methods and definitions of variables**

518

519 *In the following, we provide more information on the definition of the variables and our*
520 *data collection procedures. This additional information is included here as the article*
521 *was submitted to a journal with word limits but without copyright transfer of the*
522 *supplementary material.*

523

524

525 **Average kinship among female group members in mammals**

526 We searched for all populations of social mammals for which average kinship among
527 a group of all adult female individuals had been calculated based on similarity at
528 genetic markers. We started with species included in relevant reviews (Lukas et al.
529 2005; Briga et al. 2012) and references citing these and searched for additional studies
530 on Google Scholar (up until August 2017) using the key terms (i) “microsatellite”, (ii)
531 “relatedness” or “kinship”, and (iii) “mammal*”. Studies were included if they provided
532 data on average levels of kinship among all adult female group members based on
533 genetic methods that could be used to estimate the extent of allele sharing at
534 microsatellite loci. We only included species in which females lived in groups where
535 the same individuals repeatedly interact with each other across extended periods.
536 These include cooperative breeders, like meerkats [*Suricatta suricata*, Schreber 1776]
537 or wolves [*Canis lupus*, Linnaeus 1758], in which non-breeding subordinates live with
538 dominant breeders; species where individuals live in stable groups including multiple
539 breeding females, like many of the social primates; and species where adult females
540 form regular associations but also aggregate in larger, less stable groups, as in red
541 deer [*Cervus elaphus*, Linnaeus 1758] or elephants [*Loxodonta Africana*, Blumenbach

542 1797]. Some studies reported levels of kinship among dyads based on the degree of
543 microsatellite allele sharing, relative to the average sharing in the population. Here,
544 estimates were taken directly from the publications based on calculations by the
545 original authors. Average kinship based on these estimates approximates to 0.5 for
546 parent-offspring and full-sibling relations, 0.25 for half-siblings, and 0.00 for individuals
547 distantly or un-related, and can even be negative if individuals share fewer alleles than
548 expected (for example, if individuals are immigrants into the local population). Where
549 average kinship among females was negative, we set this value to 0.00 to match data
550 derived from pedigrees (see next), indicating that individuals are unrelated. For some
551 species, multi-generational pedigrees and data on maternity and genetically-
552 determined paternity were available for all adult individuals, and here, we derived
553 kinship levels for adult females from the pedigree for all same-sex dyads, setting
554 relatedness to 0.5 for parent-offspring or full-siblings, 0.25 for half-siblings (populations
555 did not contain any adults whose grandparents were still alive), and 0.00 for all
556 remaining less closely related pairs. For the species in which we have information both
557 on average relatedness and pedigree relationships, the values from the two methods
558 correlate closely ($n=7$ species, $r^2=0.85$, $p<0.01$), so we treated data from both
559 measures equally. In instances in which multiple estimates of average kinship among
560 females were present (either from multiple social groups within the same study or from
561 different studies), we calculated the average across reported values to generate a
562 single value per species.

563

564 *Social parameters in mammals*

565 For all the mammalian species for which we were able to find data on average kinship
566 among all adult female group members, we searched the primary literature for
567 information on (i) the presence or absence of allomaternal provisioning, (ii) infanticide

568 by females, (iii) reproductive suppression of subordinate females, (iv) division of labour
569 between breeders and nonbreeders, (v) linear dominance hierarchies among group
570 females, and (vi) coalition formation in conflicts among females. In addition, we
571 searched for quantitative data on (vii) rates of aggression between group females and
572 (viii) symmetry in grooming interactions. We assigned each species a single value for
573 each behaviour. For the first six social parameters, we assumed them to be present if
574 observations had been reported and to be absent if the no reports existed despite
575 direct observations or if papers stated that the parameter is absent. For the latter two
576 social parameters, we extracted quantitative estimates either from single reports or as
577 averages across multiple values, even if values were recorded in different populations
578 or at different times than when levels of kinship had been calculated. For some
579 parameters, data are only available for a small number of species and additional data
580 may alter the relationships we describe. Our aim was to provide a framework for
581 research into social complexity and we hope that it will stimulate further analyses.

582

583 *Alloparental provisioning*

584 We considered alloparental care to be present if females contribute to the nursing or
585 feeding of offspring that are not their own. We focused on these two provisioning
586 behaviours (compared to behaviour such as group defense) as they can be easily
587 observed, are likely to carry an immediate cost, and are clearly targeted at offspring.
588 We based our classification on the review by Packer et al. (1991) and differentiated
589 between species in which all offspring receive at least some support from females that
590 are not their mothers (alloparental care present) from those in which offspring never
591 receive alloparental support or rare instances most likely represent theft (alloparental
592 care absent).

593

594 *Female infanticide*

595 We obtained data on the occurrence of female infanticide (the killing of conspecific
596 young by females) from reviews and the primary literature. We only included records
597 of female infanticide from wild populations in which the killer was unambiguously
598 identified as an adult female and females killed neonates born to others in the same
599 group that they lived in. Species recorded as not showing female infanticide were
600 restricted to those where natural observations on breeding females and juveniles were
601 available over more than three reproductive seasons and female infanticide was not
602 reported. Since in most species records of female infanticide originate during ad libitum
603 observations rather than systematic observations, we did not calculate rates of
604 offspring mortality from infanticide, but only scored whether instances of females killing
605 offspring born to other mothers had been observed (infanticide present) or not
606 (infanticide absent).

607

608 *Reproductive suppression of subordinate females*

609 Groups were classified as containing non-breeding adults if records showed that more
610 than half of all subordinate females in a group did not breed successfully in a single
611 breeding season. Levels of reproductive skew among females within social groups are
612 not continuously distributed across mammals, but clearly fall into two categories of
613 either high or low skew (Lukas & Clutton-Brock 2012, Rubenstein et al. 2016),
614 supporting a binary classification into those species in which non-breeding females are
615 present versus those in which they are absent. Non-reproductive female group
616 members do not necessarily participate in social activities and might simply be
617 tolerated by dominant breeders (see also Griesser et al. 2017).

618

619 *Reproductive division of labour between breeders and nonbreeders*

620 We followed Wilson (1971) in classifying species as having a reproductive division of
621 labour if non-breeders show contributions to the care of young born to breeders that
622 consistently differ from the maternal care shown by breeders. Activities that, in these
623 species, are only shown by non-breeders include babysitting, digging for food, carrying
624 offspring, or feeding weaned offspring. A reproductive division of labour can only occur
625 in species in which non-reproducing females and alloparental care are present (the
626 two variables defined above) but is only present in a subset of these species. We
627 decided to include these separate categories as they might facilitate comparisons with
628 other taxonomic groups. In addition, we would predict that they represent increases in
629 organisational complexity, and that the association between high levels of average
630 kinship among group members and a reproductive division of labour is particularly
631 pronounced.

632

633 *Dominance hierarchies*

634 We classified groups as having linear dominance hierarchies if studies showed that all
635 female group members could be arranged in a linear ordering based on their
636 aggressive/submissive interactions. If interactions among some individuals were too
637 rare to determine their relative status, species were classified as not having dominance
638 hierarchies, even if they contained a single individual who was clearly dominant. For
639 the subset of species in which linear dominance hierarchies were reported to be
640 present among females, we searched for data on the stability of the hierarchy as
641 measured by Vries' (1998) linearity index h' , which ranges from 0 (in situations where
642 all individuals are equally likely to win during an aggressive encounter) to 1 (in
643 situations where all dyadic relationships are fully decided and relationship among all
644 individuals are transitive).

645

646 *Within-group coalitions*

647 We based our data on the occurrence of coalitions between individuals on relevant
648 reviews (Olson & Blumstein 2009; Bissonnette et al. 2015), and checked papers
649 referenced in or citing these reviews. We recorded coalitionary support during
650 aggressive interaction as occurring if some interactions between females belonging to
651 the same social groups involved two females simultaneously threatening or attacking
652 one or more other same-sex individuals from the same group. We excluded species in
653 which individuals only formed coalitions against individuals from other groups.

654

655 *Rates of aggression*

656 We collected data on rates of aggression between female group members in wild
657 populations from relevant reviews (Fournier & Festa-Bianchet 1995; Wheeler et al.
658 2013), and we searched for primary publications reporting observations of aggression
659 in species for which we had data on average kinship. We recorded the number of any
660 form of aggressive interactions per individual per hour involving other group members
661 of the same sex. We excluded studies in which authors had only recorded high-
662 intensity aggression as well as studies of captive animals. Since rates of interactions
663 are influenced by how often dyads are in physical proximity or not, we only included
664 species in which social groups are stable and coherent, excluding species where
665 individuals form fission/fusion groups, like chimpanzees or dolphins, as well as those
666 where groups are unstable and individuals are often widely dispersed, as in many
667 ungulates and macropods.

668

669 *Grooming symmetry*

670 We extracted information on the degree of symmetry in grooming interactions between
671 females from studies in which authors reported the correlation in grooming efforts

672 (depending on how it was measured in a given study, i.e. amount time spent grooming
673 or number of bouts) between all pairs of female group members (Schino & Aureli 2008).
674 We extracted reports of the Pearson product moment correlation coefficient between
675 the pairwise matrix showing all grooming given from females to all female partners and
676 the matrix showing all grooming received. A value of -1 indicates a complete mismatch
677 among all pairs, where individuals who receive the most grooming give the least, a
678 value of 0 indicates that grooming is distributed randomly, and a value of +1 indicates
679 that in all dyads individuals perfectly match each other. High symmetry in grooming
680 likely reflects that individuals have differentiated relationships, whereas dyads might
681 show imbalances in grooming if individuals are related and might receive indirect
682 fitness benefits from their efforts. For comparative purposes, we used values reported
683 in a previous meta-analysis (Schino & Aureli 2008) even if additional primary
684 information was available, and added single values for species from analyses which
685 used an identical approach.

686

687 *Combined presence of traits associated with relational complexity*

688 In order to combine the three traits into a single measure as a proxy for the extent to
689 which traits of *relational* complexity are expressed in a given species, we transformed
690 the data on rates of aggression among females into a binary variable, classifying
691 species with rates of aggression above the median (0.745 interactions/female/hour) as
692 having frequent aggression and those with rates below the median as not. We then
693 used this classification of the presence or absence of frequent aggression, the
694 classification on the presence or absence of a dominance hierarchy, and the
695 classification on the presence or absence of coalitionary support to determine the
696 relative presence of traits associated with *relational* complexity. A species in which all
697 of these three traits for which we had data were absent was scored as 0, as 0.33 if one

698 of the three traits was present, all the way up to 1 if all of the three traits for which we
699 had data were present.

700

701 *Group size*

702 We obtained data on the number of individuals residing in social groups from papers
703 reporting levels of kinship. For the purpose of this paper, group size was the total
704 number of females of reproductive age, including both breeding and non-breeding
705 individuals. We calculated the average number of females across all social groups for
706 which levels of kinship had been calculated.

707

708 *Brain and body size*

709 Data on body, brain, and neocortex size were extracted from the published literature
710 (Shultz & Dunbar 2010; Barton & Capellini 2011; Isler & van Schaik 2012). When
711 information was present in several datasets, we calculated median values for species
712 and manually checked for outliers. Since it is still debated exactly how brain size
713 evolves, we relied on four different approaches: first, we used absolute brain size as a
714 response variable in a regression with *relational* complexity and in a regression with
715 average levels of kinship; second, we used absolute brain size as a response variable
716 in a regression with *relational* complexity/average kinship while controlling for body
717 size; third, we additionally included longevity, diet, and seasonal variation as predictor
718 variables, ecological parameters which have been indicated to influence brain size
719 variation in mammals; and fourth, we used the size of the neocortex as a response
720 variable in a regression with *relational* complexity and in a regression with average
721 levels of kinship. We used comparative databases to extract information on diet
722 category, longevity and activity strata (de Magalhaes & Costa 2009; Jones et al. 2009;
723 Price et al. 2012; Botero et al. 2014; Wilman et al. 2014).

724

725 Statistical Models

726 We built the following regression models: four models with average levels of kinship
727 as a predictor of each of the traits of *organisational* complexity (alloparental
728 provisioning, female infanticide, reproductive suppression, reproductive division of
729 labour; these traits were coded binary as presence/absence and we assumed a
730 categorical distribution for each of them); five models with average levels of kinship as
731 a predictor of each of the traits associated with *relational* complexity (rates of
732 aggression, reciprocity in grooming, strictness of dominance hierarchy: these traits
733 were coded as continuous measure, assuming a gaussian distribution for them; and
734 linear dominance hierarchy, coalitionary behaviour: these traits were coded binary as
735 presence/absence and we assumed a categorical distribution for them); models with
736 absolute brain mass as the response variable (log10 transformed, coded continuously,
737 assuming a gaussian distribution) and the combined measure of *relational* complexity
738 as predictor variable on its own, the combined measure of *relational* complexity
739 together with body mass, and together with body mass and diet/arboreality; and
740 models with absolute brain mass as the response variable (log10 transformed, coded
741 continuously, assuming a gaussian distribution) and average levels of kinship as
742 predictor variable on its own, average levels of kinship together with body mass, and
743 together with body mass and diet/arboreality.

744

745 **Supplementary Table S1:** Average levels of kinship and traits associated with organisational and with relational complexity across
 746 social mammals (references for data are listed in brackets). The table is arranged by average kinship among female group members
 747 (from high to low). For a text copy of the dataset see: <https://knb.ecoinformatics.org/#view/doi:10.5063/F1FB513K>
 748

Species	Average kinship among female group members	Number of adult females per group	Alloparental provisioning	Infanticide by females	Reproductive suppression	Reproductive division of labour	Rate of aggression among female group member (acts per female per hour)	Dominance hierarchy among female group members	Reciprocity in grooming among female group members (correlation between grooming given and received across all dyads)	Coalitions among female group members	Presence of relational complexity	Brain Mass (grams)	Neocortex Mass (grams)	Body Mass (grams)	Diet	Strata
<i>Cryptomys damarensis</i>	0.52 (1)	10 (1)	Present (1)	NA	Present (60)	Present (60)	NA	Absent (80)	NA	Absent (80)	0.00	1.80	NA	162.00	Herbivore	Ground
<i>Saguinus mystax</i>	0.51 (1)	2 (1)	Present (1)	NA	Present (60)	Present (60)	NA	Absent (99)	NA	Absent (81)	0.00	11.10	5.88	535.00	Omnivore	Arboreal
<i>Castor canadensis</i>	0.45 (1)	2 (1)	Present (1)	NA	Present (60)	Absent (60)	0.09 (61)	Absent (82)	NA	Absent (82)	0.00	45.90	NA	19286.00	Herbivore	Ground
<i>Suricata suricatta</i>	0.42 (1)	5 (1)	Present (1)	Present (34)	Present (60)	Present (60)	0.08 (62)	Absent (62)	0.39 (91)	Absent (83)	0.00	10.29	NA	776.00	Omnivore	Ground
<i>Canis simensis</i>	0.39 (1)	2 (1)	Present (1)	Present (35)	Present (60)	Absent (60)	NA	Absent (35)	NA	Absent (84)	0.00	80.67	NA	12675.00	Carnivore	Ground
<i>Sus scrofa</i>	0.38 (1)	3 (1)	Present (1)	Present (36)	Present (60)	Absent (60)	NA	Absent (85)	NA	Absent (85)	0.00	180.93	NA	111900.00	Omnivore	Ground
<i>Callithrix jacchus</i>	0.375 (1)	2 (1)	Present (1)	Present (37)	Present (60)	Absent (60)	0.1 (63)	Absent (63)	NA	Absent (81)	0.00	7.37	4.37	342.00	Omnivore	Arboreal
<i>Ctenodactylus gundi</i>	0.37 (1)	3 (1)	Present (1)	NA	Absent (60)	Absent (60)	NA	Absent (86)	NA	Absent (86)	0.00	NA	NA	289.00	Herbivore	Ground

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<i>Vulpes vulpes</i>	0.37 (1)	NA	Present (1)	Present (38)	Present (60)	Absent (60)	NA	Absent (100)	NA	NA	0.00	45.21	NA	4897.00	Omnivore	Ground
<i>Helogale parvula</i>	0.36 (2)	4 (2)	NA	NA	NA	NA	0.13 (64)	NA	NA	NA	0.00	NA	NA	NA	NA	NA
<i>Alouatta seniculus</i>	0.32 (4)	3 (4)	Absent (4)	Absent (40)	Absent (60)	Absent (60)	0.02 (65)	Present (4)	NA	Absent (81)	0.33	49.90	31.66	6049.00	Herbivore	Arboreal
<i>Canis lupus</i>	0.32 (1)	2 (1)	Present (1)	Present (41)	Present (60)	Absent (60)	0.71 (66)	Absent (66)	0.14 (92)	Absent (84)	0.00	128.32	NA	30750.00	Carnivore	Ground
<i>Colobus guereza</i>	0.31 (1)	3 (1)	Absent (1)	Absent (40)	Absent (60)	Absent (60)	NA	Present (101)	0.38 (93)	Absent (81)	0.50	76.85	NA	9838.00	Herbivore	Arboreal
<i>Equus burchellii</i>	0.3 (5)	3 (5)	NA	NA	NA	NA	0.2 (67)	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Lycaon pictus</i>	0.28 (1)	4 (1)	Present (1)	Present (42)	Absent (60)	Absent (60)	0.89 (68)	Absent (68)	NA	Absent (84)	0.33	129.00	NA	26817.00	Carnivore	Ground
<i>Panthera leo</i>	0.26 (1)	6 (1)	Present (1)	Absent (43)	Absent (60)	Absent (60)	0.3 (69)	Present (69)	0.25 (94)	Present (84)	0.67	231.06	121.09	157250.00	Carnivore	Ground
<i>Octodon degus</i>	0.25 (1)	4 (1)	Present (1)	Absent (44)	Absent (60)	Absent (60)	NA	Absent (87)	NA	Absent (87)	0.00	2.10	NA	235.00	Herbivore	Ground
<i>Eulemur fulvus</i>	0.24 (6)	3 (6)	Absent (30)	Present (45)	Absent (60)	Absent (60)	0.33 (70)	Present (6)	NA	Present (81)	0.67	23.29	12.21	2788.00	Herbivore	Arboreal
<i>Oryctolagus cuniculus</i>	0.24 (1)	3 (1)	Present (1)	Present (46)	Absent (60)	Absent (60)	0.27 (71)	Absent (46)	NA	NA	0.00	10.30	NA	1653.00	Herbivore	Ground
<i>Pecari tajacu</i>	0.24 (1)	NA	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (102)	NA	NA	1.00	101.50	NA	20869.00	Omnivore	Ground
<i>Cuon alpinus</i>	0.22 (1)	NA	Present (1)	Present (47)	Absent (60)	Absent (60)	NA	Present (103)	NA	NA	1.00	94.80	NA	14255.00	Carnivore	Ground
<i>Ctenomys sociabilis</i>	0.19 (7)	2 (7)	Present (29)	NA	Absent (60)	Absent (60)	NA	Absent (88)	NA	Absent (88)	0.00	NA	NA	NA	Herbivore	Ground
<i>Papio hamadryas</i>	0.19 (8)	8 (8)	Absent (31)	Absent (40)	Absent (60)	Absent (60)	1.2 (72)	Present (72)	0.37 (95)	Absent (81)	0.67	145.11	118.78	16014.00	Omnivore	Ground

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<i>Propithecus verreauxi</i>	0.19 (9)	3 (9)	Absent (29)	Absent (48)	Absent (60)	Absent (60)	NA	Present (9)	NA	Absent (81)	0.50	26.45	12.19	4329.00	Herbivore	Arboreal
<i>Cebus capucinus</i>	0.18 (1)	7 (1)	Absent (1)	Absent (49)	Absent (60)	Absent (60)	1.11 (73)	Present (104)	0.26 (93)	Present (81)	1.00	71.28	46.43	2629.00	Omnivore	Arboreal
<i>Colobus vellerosus</i>	0.18 (10)	9 (10)	Absent (99)	Absent (50)	Absent (60)	Absent (60)	0.22 (74)	Present (112)	NA	Absent (113)	0.33	NA	NA	NA	NA	NA
<i>Lontra canadensis</i>	0.18 (11)	NA	Absent (11)	NA	Absent (60)	Absent (60)	NA	Absent (11)	NA	NA	0.00	52.31	NA	7808.00	Carnivore	Ground
<i>Cynomys ludovicianus</i>	0.15 (13)	3 (13)	Absent (29)	Present (51)	Absent (60)	Absent (60)	NA	Present (90)	NA	Present (90)	1.00	6.66	NA	958.00	Herbivore	Ground
<i>Loxodonta africana</i>	0.15 (1)	7 (1)	Absent (1)	Absent (52)	Absent (60)	Absent (60)	0.82 (75)	Present (52)	NA	Present (84)	1.00	4789.45	2460.00	4153500.00	Herbivore	Ground
<i>Macaca mulatta</i>	0.15 (14)	NA	Present (29)	NA	Absent (60)	Absent (60)	NA	Present ()	0.39 (93)	Present ()	1.00	NA	NA	NA	NA	NA
<i>Tursiops aduncus</i>	0.15 (1)	8 (1)	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (89)	NA	Present (89)	1.00	NA	NA	NA	NA	Marine
<i>Macaca fascicularis</i>	0.14 (15)	9 (15)	Absent (29)	Absent (40)	Absent (60)	Absent (60)	1.52 (73)	Present (105)	0.41 (93)	Present (81)	1.00	64.51	NA	4909.00	Carnivore	Ground
<i>Varecia variegata</i>	0.13 (16)	3 (16)	Absent (29)	Absent (48)	Absent (60)	Absent (60)	NA	Present (16)	NA	Present (81)	1.00	31.59	NA	3551.00	Herbivore	Arboreal
<i>Antilocapra americana</i>	0.1 (17)	8 (17)	NA	NA	NA	NA	2.1 (76)	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Crocuta crocuta</i>	0.1 (18)	14 (18)	Absent (29)	Present (49)	Absent (60)	Absent (60)	1.3 (77)	Present (18)	NA	Present (84)	1.00	149.17	85.20	63000.00	Carnivore	Ground
<i>Lemur catta</i>	0.1 (19)	NA	NA	NA	NA	NA	NA	NA	0.87 (93)	NA	NA	NA	NA	NA	NA	NA
<i>Papio cynocephalus</i>	0.08 (21)	19 (21)	Absent (29)	Present (50)	Absent (60)	Absent (60)	1.42 (78)	Present (106)	NA	Present (81)	1.00	156.10	116.00	NA	Carnivore	Ground
<i>Pygathrix roxellana</i>	0.075 (22)	3 (22)	Absent (32)	Absent (51)	Absent (60)	Absent (60)	NA	Present (51)	0.66 (96)	Present (81)	1.00	NA	NA	14750.00	NA	Arboreal

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<i>Elephas maximus</i>	0.07 (1)	7 (1)	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (107)	NA	Present (84)	1.00	5084.35	NA	3178000.00	Herbivore	Ground
<i>Gorilla beringei</i>	0.07 (1)	4 (1)	Absent (114)	Absent (40)	Absent (60)	Absent (60)	1.16 (73)	Present (115)	NA	Absent (115)	0.67	NA	NA	NA	NA	NA
<i>Cervus elaphus</i>	0.06 (24)	4 (24)	Absent (29)	Absent (52)	Absent (60)	Absent (60)	0.78 (79)	Present (52)	NA	NA	1.00	335.90	218.78	165111.00	Herbivore	Ground
<i>Gorilla gorilla</i>	0.06 (1)	4 (1)	Absent (1)	Absent (53)	Absent (60)	Absent (60)	NA	Present (53)	NA	Absent (81)	0.50	470.26	341.44	120614.00	Herbivore	Ground
<i>Aepyceros melampus</i>	0.03 (26)	NA	NA	NA	NA	NA	NA	NA	0.88 (98)	NA	NA	NA	NA	NA	NA	NA
<i>Equus caballus</i>	0.03 (25)	3 (25)	Absent (33)	Absent (48)	Absent (60)	Absent (60)	NA	Present (97)	0.9 (97)	Present (84)	1.00	642.74	NA	246073.00	NA	Ground
<i>Vicugna vicugna</i>	0.02 (1)	NA	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (108)	NA	NA	1.00	199.90	NA	50000.00	Herbivore	Ground
<i>Ateles belzebuth</i>	0.01 (1)	NA	Absent (1)	Absent (57)	Absent (60)	Absent (60)	NA	Present (117)	NA	NA	1.00	112.70	48.88	6467.00	Herbivore	Arboreal
<i>Oreamnos americanus</i>	0.01 (28)	6 (28)	NA	NA	NA	NA	1.79 (79)	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Pan troglodytes</i>	0.01 (1)	12 (1)	Absent (1)	Present (58)	Absent (60)	Absent (60)	NA	Present (109)	0.71 (93)	Present (81)	1.00	375.98	291.59	41301.00	Herbivore	Ground
<i>Pan paniscus</i>	0 (1)	9 (1)	Absent (1)	Absent (59)	Absent (60)	Absent (60)	NA	Present (110)	0.61 (93)	Present (81)	1.00	328.00	242.36	36329.00	Herbivore	Ground

750 **Supporting References**

751

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1069 **Supplementary Table S2:** Results from regressions of ecological parameters on the
1070 rate of aggression among female group members

1071

1072 Herbivore vs Carnivore vs Omnivore: n=22 species, all $p > 0.63$

1073

1074 Lifespan: n=13 species, $p = 0.94$

1075

1076 Environmental Harshness: n=13 species, $p = 0.98$

1077

1078 Arboreal vs Ground: n=22 species, all $p > 0.84$

1079

1080 Seasonal breeding: n=17 species, $p = 0.79$

1081

1082 **Supplementary Table S3:** Results from regressions of brain mass on the expression
 1083 of traits associated with relational complexity. All analyses include the phylogenetic
 1084 relatedness among the 43 species (26 species in the analysis including rainfall
 1085 seasonality and diet) as a covariate.

1086

1087 **BrainMass_g ~ RelationalComplexity**

	post.mean	l-95% CI	u-95% CI	pMCMC
1088 (Intercept)	3.348	2.522	4.197	< 8e-05 ***
1089 RelationalComplexity	1.842	0.698	2.904	0.00078 ***

1091

1092 **BrainMass_g ~ BodyMass_g + RelationalComplexity**

	post.mean	l-95% CI	u-95% CI	pMCMC
1093 (Intercept)	-2.3542	-2.9905	-1.7260	< 8e-05 ***
1094 RelationalComplexity	0.4560	0.1105	0.7921	0.00961 **
1095 BodyMass_g	0.6811	0.6107	0.7509	< 8e-05 ***

1097

1098 **BrainMass_g ~ BodyMass_g + RelationalComplexity + Diet**

	post.mean	l-95% CI	u-95% CI	pMCMC
1099 (Intercept)	-2.57177	-3.32084	-1.82613	< 8e-05 ***
1100 RelationalComplexity	0.52710	0.17328	0.86694	0.00472 **
1101 BodyMass_g	0.69429	0.62212	0.76397	< 8e-05 ***
1102 DietHerbivore	-0.03875	-0.42158	0.34620	0.83260
1103 DietOmnivore	0.33121	-0.08629	0.76995	0.12079

1105

1106

1107

1108

1109 **BrainMass_g ~ BodyMass_g + RelationalComplexity + Arboreality**

	post.mean	l-95% CI	u-95% CI	pMCMC
1110				
1111 (Intercept)	-2.32499	-2.91525	-1.69945	<8e-05 ***
1112 RelationalComplexity	0.40730	0.06860	0.74700	0.0203 *
1113 BodyMass_g	0.70539	0.63161	0.78137	<8e-05 ***
1114 StrataGround	-0.31431	-0.69025	0.07247	0.100

1115

1116

1117 **NeocortexMass_g ~ RelationalComplexity**

	post.mean	l-95% CI	u-95% CI	pMCMC
1118				
1119 (Intercept)	2.223	0.621	3.801	0.0117 *
1120 RelationalComplexity	2.957	1.062	5.076	0.0052 **

1121

1122