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Challenges in assessing the roles of nepotism and reciprocity in cooperation networks

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Keywords: cooperation, kin discrimination, mandrills, macaques, vampire bats

14 **Abstract**

15 Nepotism and reciprocity are not mutually exclusive explanations for cooperation, because

16 helping decisions can depend on both kinship cues and past reciprocal help. The importance of

17 these two factors can therefore be difficult to disentangle using observational data. We developed

18 a resampling procedure for inferring the statistical power to detect observational evidence of

19 nepotism and reciprocity. We first applied this procedure to simulated datasets resulting from

20 perfect reciprocity, where the probability and duration of helping events from individual A to B

21 equaled that from B to A. We then assessed how the probability of detecting correlational

22 evidence of reciprocity was influenced by (1) the number of helping observations and (2) varying

23 degrees of simultaneous nepotism. Last, we applied the same analysis to empirical data on food

24 sharing in vampire bats and allogrooming in mandrills and Japanese macaques. We show that at

25 smaller sample sizes, the effect of kinship was easier to detect and the relative role of kinship was

26 overestimated compared to the effect of reciprocal help in both simulated and empirical data,

27 even with data simulating perfect reciprocity and imperfect nepotism. We explain the causes and

28 consequences of this difference in power for detecting the roles of kinship versus reciprocal help.

29 To compare the relative importance of genetic and social relationships, we therefore suggest that

30 researchers measure the relative reliability of both coefficients in the model by plotting these

31 coefficients and their detection probability as a function of sampling effort. We provide R scripts

32 to allow others to do this power analysis with their own datasets.

33

34 **Introduction**

35   A propensity for helping others is an adaptive trait when it yields a net return for the

36 actor's inclusive fitness by increasing direct fitness, indirect fitness, or both (West, Griffin, and

37 Gardner 2007a; Hamilton 1964). Indiscriminate cooperation in a well-mixed population can favor

38 'cheating' whereby less cooperative phenotypes gain the fitness benefits of receiving help from

39 cooperators without paying the same costs of being cooperative, resulting in an 'evolutionary

40 tragedy of the commons' (West, Griffin, and Gardner 2007a). Cooperation often takes the form of

41 an investment in specific individuals or types. Individuals can ensure indirect or direct fitness

42 returns on their investments by preferentially helping closer kin, *nepotism* (e.g. Griffin and West

43 2003; Cornwallis, West, and Griffin 2009) or more cooperative partners, *reciprocity* in the

44 broadest sense (Trivers 1971; e.g. Rutte and Taborsky 2008; Dolivo and Taborsky 2015; Schino

45 and Aureli 2017; Carter 2014; Taborsky, Frommen, and Riehl 2016). Crucially, these strategies

46 can coexist: helping decisions can be influenced by both kinship cues and past experience of

47 reciprocal help. These factors can also interact; for instance, reciprocity can be stronger or weaker

48 among kin than among nonkin (Van Cleve and Akçay 2014; Trivers 1971; Axelrod and Hamilton

49 1981). Evidence for nepotism and reciprocity can therefore be difficult to disentangle, especially

50 from correlational data (e.g. social networks based on cooperative behaviors such as grooming of

51 food sharing). Indeed, nepotism and reciprocity are causal mechanisms that cannot be directly

52 demonstrated with correlational data. But moreover, we will show how correlational data can lead

53 to incorrect and even opposite conclusions about the relative roles of nepotism and reciprocity

54 caused by asymmetries in the sampling effort needed to accurately estimate kinship versus

55 reciprocal helping. Nepotism can make it difficult to detect correlational evidence for reciprocity

56 even when nepotism is limited and reciprocity is perfect. We discuss the reasons for this and

57 provide a method to help assess the power to detect the effects of kinship and reciprocal help.

58   For nonhuman animals, a claim of reciprocity is far more contentious than nepotism.

59 Despite growing correlational and experimental evidence, there is still disagreement about the

60   existence and importance of reciprocity outside humans (Clutton-Brock 2009; Carter 2014;

61   Taborsky, Frommen, and Riehl 2016; Schino and Aureli 2017). One reason for this debate is that

62   authors do not agree on what the term 'reciprocity' means or should mean (West, Griffin, and

63   Gardner 2007b; Noë 2006; Carter 2014; Bshary and Bergmüller 2008; Lehmann and Keller 2006).

64   Definitions of reciprocity (also called reciprocation, reciprocal altruism, reciprocal cooperation,

65   contingent cooperation, and direct reciprocity) have varied between authors and sub-disciplines

66   (Carter 2014). The original concept of 'reciprocal altruism' (Trivers 1971) was quite broad and

67   arguably ambiguous, but subsequent and more narrow definitions of reciprocity restricted its

68   general importance to humans (Carter 2014). For example, the term 'reciprocity' has been used to

69   describe: a *broad category* of enforced mutual benefit (analogous to kin selection), a *correlation*

70   between cooperation given and received across dyads or over time (analogous to kin-biased

71   association), a conditional helping *behavior* that causes this correlation (analogous to nepotism),

72   and a specific *psychological mechanism* that might cause this conditional behavior (analogous to

73   phenotype matching) (Carter 2014). For our purposes here, we define *reciprocity* broadly as help

74   given that is influenced by rates of help received (i.e. reciprocal help), where help can involve

75   different behaviors integrated over short or long timespans.

76   Reciprocity is most evident in controlled experiments where helping rates are immediate

77   responses to past help received, and where partners lack a long-term social relationship

78   (Schweinfurth and Taborsky 2018a; Schweinfurth et al. 2017; Taborsky, Frommen, and Riehl

79   2016; Dolivo and Taborsky 2015; Rutte and Taborsky 2008). Reciprocity can be harder to test in

80   the context of an enduring social relationship, because this by definition means that the partners

81   will integrate social experiences over longer timespans, and because reciprocal help can take

82   multiple forms, such as allogrooming, food sharing, coalitionary support (Schino and Aureli

83   2017; Carter 2014; Jaeggi et al. 2013; Seyfarth and Cheney 2012). In the case of such a

84   cooperative relationship, the rates of helping measured by an observer are actually a proxy for a

85   measure of the strength of the underlying causal relationship, rather than the immediate cause of

86   observed reciprocal help. In other words, helping events from A to B should predict helping

87   events from B to A, not because the first event directly caused the second event, but because A

88   and B have a cooperative relationship that causes symmetrical bidirectional helping rates (Schino

89   and Aureli 2010a, 2009). To distinguish between causation and correlation, we use the term

90   *symmetry* for the observed correlation between rates of help given and received—the most

91   common observational evidence for reciprocity. Similarly, we use the term *kinship bias* for the

92   observed correlation between help given and kinship—the most common observational evidence

93   for nepotism.

94   Semantics aside, reciprocity is also contentious because it is difficult to test, especially in

95   the presence of nepotism. Nepotism is also expected to cause symmetry in helping because

96   kinship is symmetrical; if two sisters often help each other, the help could be pure kin altruism or

97   it could be reciprocal. Whereas kinship bias is considered sufficient evidence for nepotism,

98   symmetry is not widely considered to be sufficient evidence of reciprocity (Carter 2014). A

99   demonstration of reciprocity requires experimentally manipulating helping rates and then

100   measuring a change in reciprocal helping (Schweinfurth and Taborsky 2018a; Dolivo and

101   Taborsky 2015; Rutte and Taborsky 2008; Krams et al. 2013; Krama et al. 2012; Krams et al.

102   2008; Fruteau et al. 2009). In such tests, kinship can be excluded as a factor by testing only

103   nonkin. However, reciprocity is also expected to play a role in cooperation among kin (Jaeggi and

104   Gurven 2013; Schino and Aureli 2010c; Schweinfurth and Taborsky 2018b; Taborsky et al. 2016;

105   Wilkinson 1984; Wilkinson 1988). An experimental test of both nepotism and reciprocity

106   requires simultaneously manipulating cues to both kinship and past experience of cooperation

107   (Schweinfurth and Taborsky 2018b; Zöttl et al. 2013). The logistical difficulty of such a test

108   explains why the vast majority of evidence for both reciprocity and nepotism is correlational (e.g.

109   Carter and Wilkinson 2013; Schino and Aureli 2010c).

110   Many studies, especially with primates, have compared the relative effect sizes of

111   reciprocal help and kinship on rates of cooperative behaviors such as grooming or food sharing

112   using correlational data (Jaeggi and Gurven 2013; Schino and Aureli 2010c; Carter and

113   Wilkinson 2013; Koster 2011; Silk et al. 2013; Thomas et al. 2018; Wright et al. 2016; Jaeggi et

114   al. 2016; Engelhardt et al. 2015). A challenge with interpreting this correlational evidence is that

115   the simultaneous effects of nepotism and reciprocity are not equally detectable. Kinship estimates

116   will generally be more precise than estimates of helping rates because of inherent differences in

117   sampling effort. For example, each tissue sample can yield a huge number of genetic markers for

118   assessing dyadic genetic relatedness, but each behavioral sample of watching a group of animals

119   will typically yield only few or no helping events for assessing dyadic helping rates. As a

120   consequence, the more precise estimate of the correlation between kinship and helping can often

121   be over-estimated and detected more easily compared to the less precise estimate of the

122   correlation between help given and received. This means that the presence of nepotism can make

123   simultaneous reciprocity harder to detect.

124   To assess this idea, we developed a resampling procedure for inferring power to detect

125   both kinship bias and symmetry in mixed-kinship groups. To simulate perfect reciprocity in long-

126   term social bonds, we created data of helping events where individuals based their decisions to

127   help on an unobserved history of past reciprocal help that is perfectly symmetrical within specific

128   pairs. We then systematically changed two variables: (1) the degree of nepotism and (2) the

129   number of observed helping events. Finally, we used permutation and bootstrapping to assess

130   how these two factors interactively influenced the probability of detecting evidence for

131   reciprocity.

132   To demonstrate the application of our approach to empirical data, we then applied the

133   same permutation and bootstrapping procedures to three datasets where both kinship and

134   reciprocity are suspected to co-exist: allogrooming in female mandrills (*Mandrillus sphinx*),

135   allogrooming in female Japanese macaques (*Macaca fuscata*), and food sharing in female

136   common vampire bats (*Desmodus rotundus*). Mandrills appear to form large groups structured by

137   matriline (Bret et al. 2013; Abernethy, White, and Wickings 2002), and show evidence for

138   reciprocal allogrooming (Schino and Pellegrini 2009) and kin discrimination (Levréro et al. 2015;

139   Charpentier et al. 2007). Japanese macaques are nepotistic, have a despotic social network with a

140   steep dominance hierarchy based largely on maternal kinship, and direct allogrooming to

141   dominant individuals and to consistently preferred partners (Balasubramaniam et al. 2018).

142   Regurgitated food sharing in vampire bats has been a classic example of the possible co-

143   occurrence of reciprocity and nepotism (Wilkinson 1988; Wilkinson 1984).

144   To test if and how nepotism prevents the detection of evidence for reciprocity, we

145   inferred the power to detect both kinship bias and symmetry in simulated and real datasets of

146   various sizes. To generate slopes and their significance (p-values), we used a permutation test

147   designed to deal with collinearity and non-independence (Dekker, Krackhardt, and Snijders 2007).

148   We plotted the slopes and detection rates for kinship bias and symmetry as a function of sampling

149   effort (sample sizes of observed helping events). These plots show whether the relative roles of

150   kinship and reciprocal help are either remaining ambiguous or becoming clearer with more data.

151   R scripts are available online (Carter et al. 2018) so that others can apply or adapt them to their

152   own kinship and cooperation network data.

153

154   **Methods**

155   *Inferring power and precision of symmetry and kinship bias*

156   To infer power, we estimated how estimates of kinship bias (the correlation between

157   kinship and helping given) and symmetry (the correlation between help given and help received)

158   vary with an increasing number of observations (N; note that N is the number of observed helping

159   events, not the number of individuals). To create about 20 equally-spaced values of N, we started

160   at N = 20 and added 5% of the total sample of observed interactions with each next step. For

161   example, a dataset of 500 observations would mean 20 sample size values (N = 20, 45, 70, 95,

162   120 .… 500 measured events). At each step, we randomly sampled N observations from the total

163   dataset. We sampled with replacement (bootstrapping) to avoid confounding smaller variances at

164   larger samples sizes with smaller variances in our samples. We bootstrapped the datasets 1000

165   times at each sample size. For instance, at the first step we randomly sampled 20 observations

166   with replacement 1000 times. To analyze the simulated data (described below), we created a

167   different dataset of size N observations by sampling from the given probability distributions 1000

168   times, rather than bootstrapping a single dataset 1000 times as we did with the empirical data.

169   For each observed dataset, we extracted the observed coefficients of kinship and

170   reciprocal help from a matrix permutation test: multiple regression quadratic assignment

171   procedure with double semi-partialling (MRQAP-DSP, (Dekker, Krackhardt, and Snijders 2007)).

172   We defined the response variable 'help' for individual A to B as the total of duration of help from

173   A to B, divided by the total duration of help received by B for all times where A could have

174   helped B. This measure controls for differences in sampling time, and current situational factors

175   such as need (Farine 2015). 'Reciprocal help' for A to B is defined as help from B to A. We

176   applied a log transformation to the empirical allogrooming and food sharing durations because

177   they were lognormal. We z-transformed all variables to obtain standardized beta coefficients, so

178   that an observed coefficient of X for kinship indicates that a one standard deviation increase in

179   kinship predicts an increase of X standard deviations in help.

180   To calculate p-values for the observed coefficients, we used network-level permutations

181   (Farine 2017) randomizing each input variable independently using the standard approach from

182   the MRQAP-DSP function in the R package 'asnipe' (Farine 2013). We used this procedure to

183   generate one null coefficient from a randomized network for each observed coefficient, resulting

184   in 1000 observed and 1000 paired null coefficient values for the two predictors, kinship and for

185   reciprocal help, at each sample size step. At each sample size, we then calculated (1) the mean

186   and 95% confidence interval (CI) for the observed coefficients, which are the observed symmetry

187   and kinship bias estimates, (2) the mean and 95% CI for the null coefficients, which are the

188   symmetry and kinship bias estimates expected under the null hypothesis, (3) the proportion of

189   samples where the observed coefficient was greater than the paired null coefficient, which

190   indicates if the effect is real using all the samples, and (4) the proportion of observed coefficients

191   that were greater than 95% of the expected null coefficients, which indicates the power to detect

192   an effect with one sample of a given size.

193

194   *Simulating data with perfect symmetry and 0-100% nepotism*

195   We simulated 500 observations of help among 20 individuals. To simulate correlational

196   outcomes expected from perfect reciprocity, we generated a weighted directed network of

197   symmetrical social bonds, such that the helping rate from A to B was always equal to helping rate

198   of B to A. This symmetrical probability of helping, or social bond strength, could be imagined as

199   representing a history of past unobserved helping interactions in which both individuals helped

200   each other in both directions many times, in which case individuals that did not reciprocate

201   therefore no longer have a strong social bond. To create an event, we then randomly sampled one

202   individual as the actor and selected a remaining individual as the recipient with a probability that

203   was proportional to the social bond strength. The duration of help was also equal to the social

204   bond strength. All observed helping was therefore determined by a symmetrical social bond.

205   To simulate nepotism as an additional factor, the social bond strength must also correlate

206   with kinship to varying degrees. Nepotism determines the degree to which kinship predicts past

207   reciprocal helping, so we calculated social bond strength (b), as a combination of a random

208   kinship value (r) and a random non-kinship value (c), weighted by a 'nepotism coefficient' (n),

209   which ranges from 0 to 1:

210    $b = nr + (1-n)c$

211   The nepotism coefficient therefore represents the degree to which the social bond

212   strength (and hence the probability of helping) correlates with kinship. For simplicity, we

213   sampled r and c from uniform distributions, but we obtained similar results from other

214   distributions. Increasing nepotism will increase the observed kinship bias, and we created

215   populations where nepotism equaled either 0, 0.25, 0.5, 0.75, or 1 (Table S1). Finally, we added a

216   step to ensure that all individuals were observed helping at least one other individual.

217   In sum, these simulations generated an observed set of helping events where individuals

218   could have based their actual helping decisions entirely on the experience of past reciprocal help.

219   However, this reciprocity co-existed across a spectrum of nepotism from 0% nepotism, where

220   helping rates were symmetrical and kinship played no role, to 100% nepotism, where helping

221   rates were symmetrical but social bonds only ever formed among kin, such that the relative causal

222   roles of reciprocal help and kinship are therefore unclear without experimental evidence. There

223   are of course many possible causes of symmetrical helping besides reciprocity. The point of this

224   simulation is to ask: If perfect reciprocity did exist among individuals that were also somewhat

225   nepotistic, how likely are we to detect the evidence for reciprocity or to overestimate the evidence

226   for kinship bias?

227

228   *Real datasets*

229   We applied this resampling procedure as a power analysis for three real datasets. Each

230   dataset including a list of cooperative interactions (either grooming or regurgitated food sharing),

231   the duration of the trial (sampling period) during which each occurred, the individuals present

232   during the trial (possible actors and receivers), the actor, the receiver, and the interaction duration.

233   The first two studies were conducted on mandrills and Japanese macaques housed at the Rome

234   Zoo (Bioparco) in Italy. In both studies, kinship was based on maternal pedigrees, all subjects

235   were available as potential grooming partners during the study, and an observer recorded the

236   duration of all female-female grooming episodes involving a focal subject as actor or recipient.

237   The first dataset contained 1703 observations of mandrill allogrooming collected between July

238   2014 and June 2015 from 10 sexually mature female mandrills in a group that also included two

239   mature males. A past study of six female mandrills from the same captive population found that

240   allogrooming A to B predicted allogrooming B to A, when controlling for kinship (Schino and

241   Aureli 2010c), or when controlling for kinship and rank and excluding recent reciprocal grooming

242   (Schino and Pellegrini 2009).

243   The second dataset contained 737 observations of macaque allogrooming collected

244   between April and November 1996 from 22 sexually mature female Japanese macaques in a

245   group of 71 that also included mature males and juveniles. Similar to the mandrills, analyses of

246   allogrooming in the same captive population of Japanese macaques found symmetry in female

247   allogrooming, and also found that allogrooming predicted support in social conflicts when

248   controlling for kinship, rank, or time spent in proximity (Schino et al. 2007), and allogrooming

249   was better predicted by kinship than by grooming received (Schino and Aureli 2010c).

250   The third dataset included 408 regurgitated food-sharing donations among 15 female

251   common vampire bats from previous studies where food sharing was induced by fasting a subject

252   (for details, see Carter and Wilkinson 2015, 2013). Each donation size was estimated by the total

253   seconds that the unfed subject licked the mouth of a fed groupmate. Kinship was estimated using

254   a maternal pedigree and maximum likelihood estimates applied to genotypes of 19 polymorphic

255   microsatellite markers (for details see Carter and Wilkinson 2015). Past analyses of these same

256   data found that food sharing was better predicted by reciprocal sharing than by kinship, when

257   controlling for grooming and donor sex (Carter and Wilkinson 2013a; Carter and Wilkinson

258   2013b), and this conclusion was supported by later experiments showing that the bats were

259   attracted to the calls of nonkin donors more than nondonor kin (Carter and Wilkinson 2016), and

260   that females that previously fed more nonkin were less affected by the removal of a donor from

261   their food-sharing network (Carter et al. 2017).

262

263   *Code availability*

264   Data and R code, including functions to apply the same procedure to other datasets, is

265   available online at the *figshare* data repository (Carter, Schino, and Farine 2018b; Carter, Schino,

266   and Farine 2018a).

267

268 **Results**

269 *Simulated data*

270   Nepotism reduced the ability to detect perfect reciprocity in helping. We constructed the

271 simulations such that a perfectly symmetrical social bond determined helping rates at every level

272 of nepotism. At 100% nepotism, symmetry and kinship bias are completely confounded and the

273 relative roles of reciprocal help and kinship cannot be disentangled. At 25% or 50% nepotism, the

274 kinship bias is clearly not as important as the social bond strength. Yet as nepotism increased

275 above zero, the p-values were more likely to incorrectly infer that nepotism was supported by the

276 data while reciprocity was not (Figure 1). The reasons for this can be seen in the plots of the size

277 and precision of the observed and null coefficient estimates with increasing sampling effort

278 (Figure S1-S5). Nepotism increases the correlation between the two predictors: kinship and

279 reciprocal help (Figure S6), but estimates of kinship bias were less variable than the estimates of

280 reciprocal help. At 50% nepotism, kinship biases were often estimated to be larger than reciprocal

281 help, even though the generative probabilities and the actual durations of helping were always

282 perfectly symmetrical (Figure 1). In these scenarios, where we know the real contribution of both

283 kinship and reciprocal help as drivers of helping, we see that kinship bias was consistently

284 overestimated relative to symmetry. Moreover, even with zero nepotism, estimates of symmetry

285 were still underpowered at 500 observations (Figure 1, see also Figure S7).
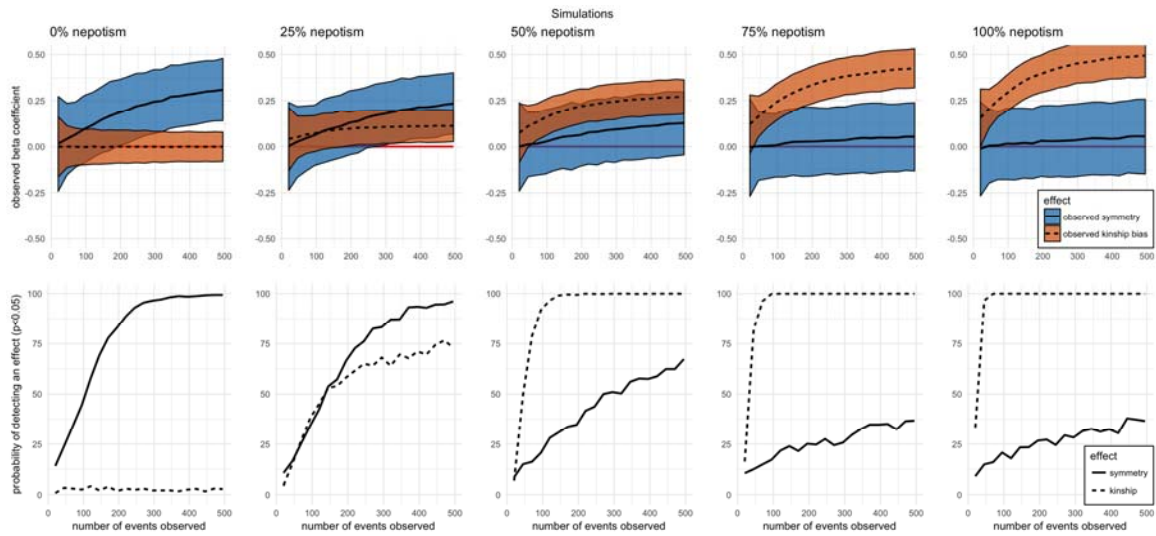
286

287 **Figure 1. Simulated data: Kinship bias masks perfect symmetry in cooperation networks.** The

288 probability and durations of help and reciprocal help are perfectly symmetrical within all dyads, and the

289 degree of simultaneous nepotism increases from left to right. Top panels show the mean and 95%

290 confidence interval of the standardized slope estimates for the effects of helping rate A to B (solid line,

291 purple shading) and kinship between A and B (dotted line, yellow shading) as predictors of helping rate B to

292 A. Bottom panels show the percentage of observed coefficients that were greater than 95% of the

293 coefficients expected based on network permutations. Supplementary Figures S1-S5 in the appendix show

294 plots for the null coefficients and for the probability of the observed coefficients being greater than expected

295 coefficients.

296

297 *Real data*

298   Results with empirical data are consistent with expectations from the simulations. For

299 female mandrill allogrooming, symmetry was eventually detected to be significantly greater than

300 kinship bias but this required more than 1250 observations (Figure 2A, 2B). The ability to detect

301 either effect was similar across sampling efforts (Figure 2C, 2D). A sample of 1703 observations

302 provided adequate power to detect both effects, but the relative effect size estimates of symmetry
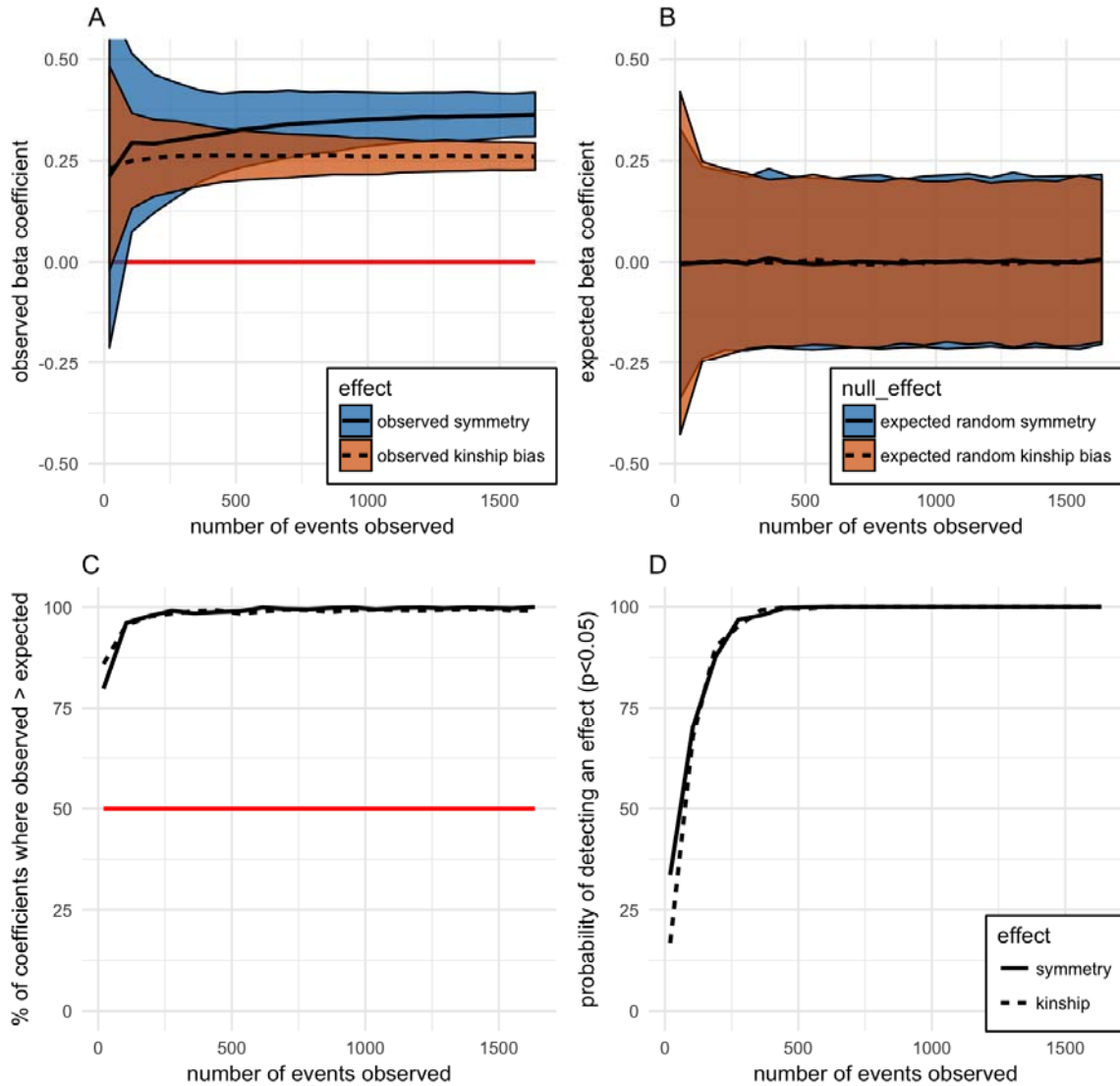
303 and kinship appear to still be diverging with more observations (Figure 2A), suggesting that the

304 relative contribution of nepotism may still be over-estimated despite this large sample size of

305 helping events.

Figure 2. Female mandrills: observed and expected symmetry and kinship bias in allogrooming networks with increased sampling effort. Panel A shows the mean and 95% confidence interval of the standardized slope estimates for the effects of helping rate A to B (solid line, purple shading) and kinship between A and B (dotted line, yellow shading) as predictors of helping rate B to A. Panel B shows the same for the expected null coefficients generated by permutation. Panel C shows the percentage of observed coefficients that are greater than the paired null coefficient generated from the same subsample. If effects are real, then these values should be higher than 50% (red line). Panel D shows the percentage of observed coefficients that are greater than 95% of expected null coefficients for that sample size.

316   For female macaque allogrooming, where nepotism is quite strong, a sample size of about

317 60 observations provided enough power to reliably detect a positive kinship bias, but the full set

318 of 737 observations did not provide enough power to reliably detect positive symmetry (i.e.

319 power < 80%, Figure 3). This highlights the combined impacts of greater nepotism and fewer
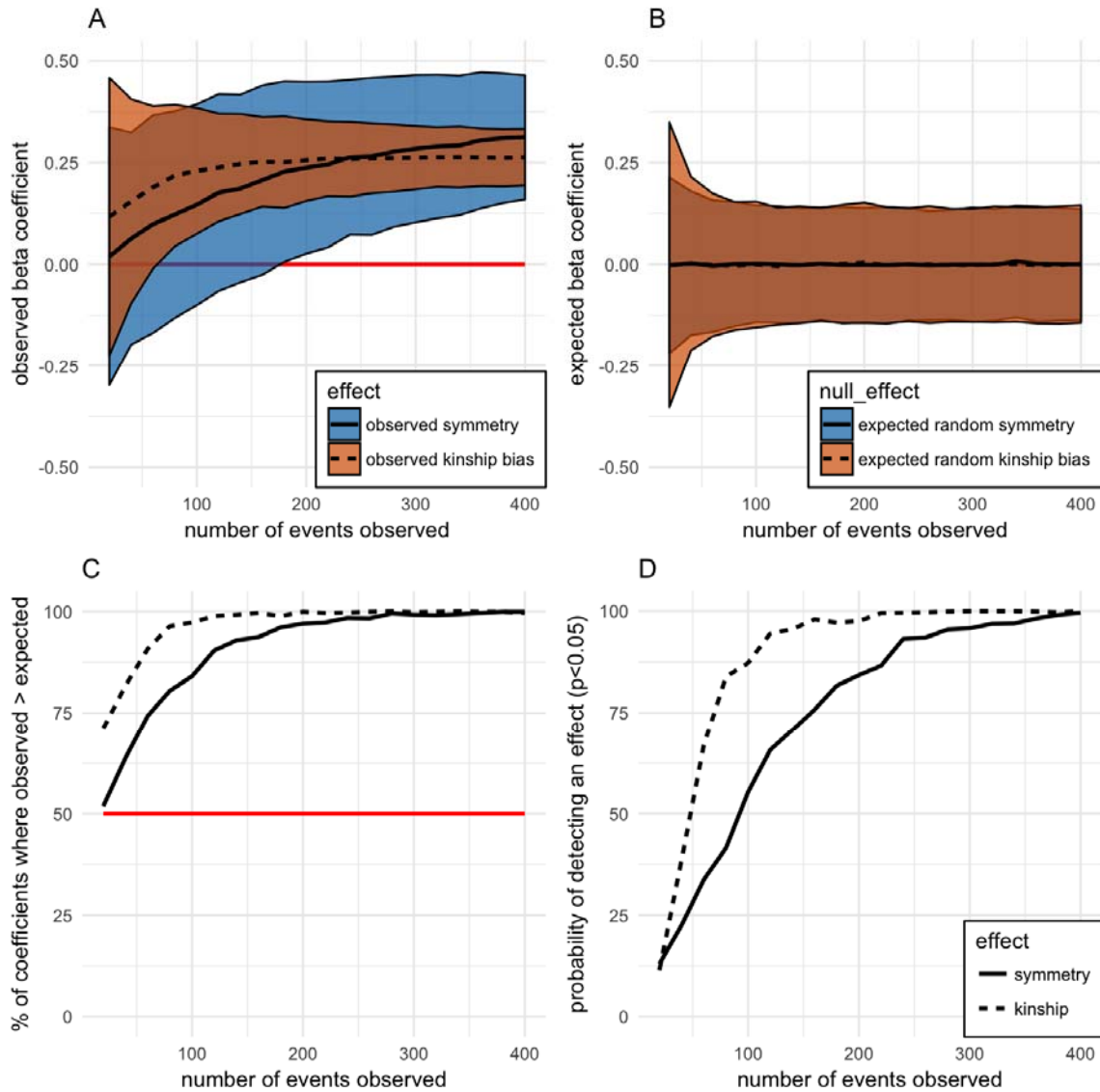
320 helping events per dyad.

321
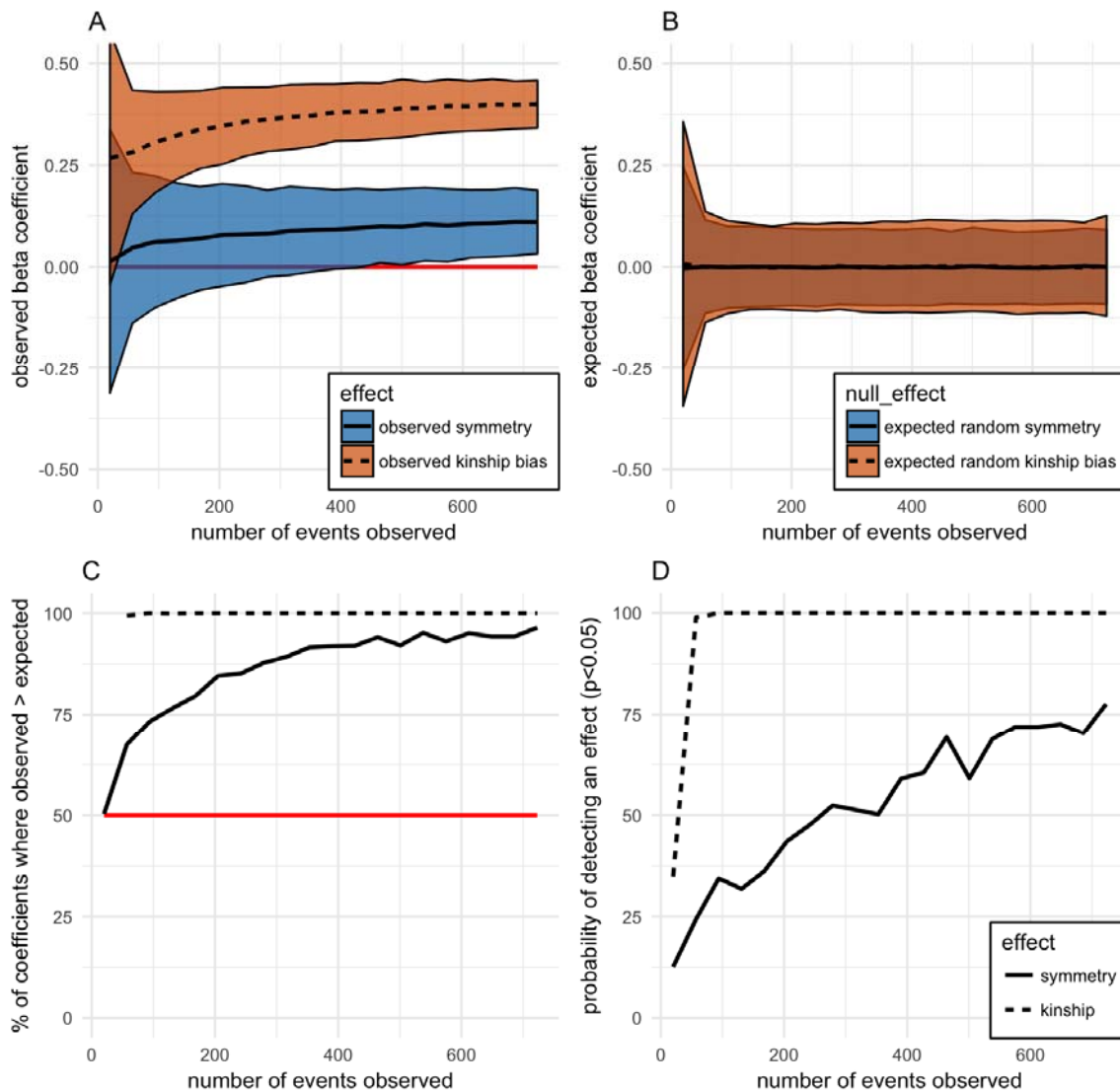
323 **Figure 3. Female Japanese macaques: observed and expected symmetry and kinship bias in food-**

324 **sharing networks with increased sampling effort.** See Figure 2 for explanation of plots.

325

326   For food sharing in female vampire bats, kinship bias is detected more reliably than

327   symmetry at all sample sizes (Figure 4). The estimate of kinship bias is relatively stable at about

328   200 observations, but at 400 observations the estimate of symmetry is still increasing with

329   additional sampling. There is enough power to detect positive kinship bias and symmetry, but

330   power is lacking to reliably estimate the amount of symmetry (Figure 4). Together the plots from

331   our simulations combined with those from the empirical datasets illustrate how and why detecting

332   kinship bias and symmetry requires much less sampling effort than identifying their relative

333   importance.

334

Figure 4. Female vampire bats: observed and expected symmetry and kinship bias in food-sharing networks with increased sampling effort. See Figure 2 for explanation of plots.

Discussion

Nepotism can make evidence for reciprocity harder to detect

If kinship and long-term reciprocal help are simultaneous predictors of helping events, then nepotism will often be easier to detect and its role will often be overestimated relative to long-term reciprocal help (or social bond strength). Looking at the simulation results of Figure 1,

345   consider a scenario of 100 helping observations, where individuals are performing perfect

346   reciprocity. At zero nepotism, symmetry (the correlation between help given and received) will

347   be detected ('statistically significant') with a 50% probability, and nepotism will have a low rate

348   of false positives. At 25% nepotism, however, a researcher is now equally likely to detect

349   symmetry versus a kinship bias. At 50% nepotism, kinship bias further masks symmetry and the

350   probability of correctly detecting symmetry drops to less than 25% and kinship bias is detected

351   about 90% of the time. At 75% and 100% nepotism, kinship bias is always detected while

352   symmetry is usually not.

353   Even if both effects are detected, the relative coefficient sizes would give the clear but

354   misleading appearance that helping decisions must be influenced more by kinship than by social

355   experience. In the 100% nepotism scenario, where the symmetry and kinship bias are exactly

356   equal, kinship bias is always detected. By comparison, the same sampling effort in the 0%

357   nepotism scenario gives us only 50% power to detect evidence of reciprocity.

358   Why does this happen? Estimating a correlation or slope coefficient requires having

359   accurate data on the predictor as well as the response variables. Cases with two highly correlated

360   predictors can lead to imprecise estimates of both coefficients, making each effect harder to

361   detect. More critically, the most precisely estimated predictor, in this case kinship, will often

362   appear to have a relatively larger coefficient and to be more important, regardless of its true

363   causal role. The precision of kinship estimates is independent of the number of helping events

364   observed, whereas symmetry uses the number of helping events to estimate rates of help both

365   given and received.

366   Genetic relatedness is becoming increasingly easy to measure compared to the history of

367   helping interactions. Pedigrees can be supplemented or replaced by genetic or genomic data,

368   which is becoming cheaper and easier to collect (Städele and Vigilant 2016). The precision of

369   marker-based relatedness estimates is also often estimated by resampling methods. In contrast,

370   the history of cooperation between any two individuals is often unknown and this lack of

371   precision is not always noticed, because there is often confusion about whether each helping

372   event from A to B is just a data point for estimating an underlying cooperative relationship or the

373   direct cause for the next helping event in the other direction (Carter 2014; Schino and Aureli 2017,

374   2010b; Schino and Aureli 2009; de Waal and Brosnan 2006; Seyfarth and Cheney 2012). In most

375   cases where both reciprocity and nepotism are expected to co-exist (as in the primates and

376   vampire bats examined here), reciprocity is thought to occur in the context of a long-term

377   cooperative relationship. The existence and strength of an underlying cooperative relationship

378   must be estimated by sampling many helping events given and received (e.g. allogrooming, food

379   sharing, or coalitionary support) to calculate dyadic helping rates. When such cooperative

380   interactions are rare or difficult to observe, these dyadic helping rates will be imprecise measures

381   of the true cooperative relationship between the individuals. For example, we might have

382   observed A helping B, but never B helping A, despite the fact that B has helped A in the past, or

383   may do so in the future.

384   Imprecision in the estimate of helping symmetry will have twice the effect on the ability

385   to find support for reciprocity because it will affect both the predictor (how much B helps A) and

386   the response (how much A helps B), whereas it affects nepotism estimates only once through the

387   response variable (how much A helps B). The sample size of helping observations does not affect

388   the estimates of kinship, but it does determine the accuracy of the dyadic rates of help given and

389   received, so fewer helping observations will directly and greatly impact estimates of symmetry,

390   but not kinship. Even if we observe only one helping event for each dyad, those data could be

391   sufficient to detect and estimate an existing kinship bias, but we could never use the same data to

392   detect evidence for reciprocity. If a cooperative relationship exists, then kinship estimates will

393   generally be more precise than estimates of helping rates (the cooperative relationship).

394   This asymmetry in precision is compounded in larger study populations. The number of

395   possible dyadic helping rates is almost the square of the number of individuals, n*(n-1).

396   Observing enough dyadic helping interactions to accurately estimate a cooperation network

397 (Farine and Strandburg-Peshkin 2015) is a far greater challenge than estimating pairwise kinship

398 among the same number of individuals. The former requires many unique behavioral samples per

399 individual, whereas the latter might require applying the same panel of genetic markers to one

400 genetic sample per individual. As population size increases, so too does the inequality between

401 the effort required to estimate helping rates versus pairwise kinship across all dyads. As a result,

402 the power to detect helping symmetry relative to kinship bias will almost always decrease with

403 more individuals.

404   Even when kinship plays a less important role than reciprocal help in determining

405 cooperation, nepotism can essentially overshadow some or all of the evidence of reciprocity,

406 especially with a smaller sample of events. This is important because observations of costly

407 helping events, such as food sharing, are often quite rare. For example, more than 400 hours of

408 focal sampling of wild vampire bats over 26 months of fieldwork yielded 110 observations of

409 regurgitated food sharing and only 21 observations of non-maternal sharing between adults with

410 known association and relatedness (Wilkinson 1984). Researchers studying meat sharing in

411 chimpanzees observed an average of only 1.3 sharing episodes between adult male chimpanzees

412 per successful hunt (Mitani and Watts 2001). When captive capuchin monkeys were separated by

413 mesh barrier and given opportunities to share food, observations of 9896 interactions over food

414 yielded only 18 instances of apparent food sharing and 4 unambiguous cases of one monkey

415 directly giving food to the other (de Waal 1997a). More frequent interactions such as grooming

416 are therefore useful for providing a window into cooperative relationships that may drive more

417 costly helping decisions, but effect sizes based on these most frequent interactions can still be

418 underpowered despite a surprisingly large numbers of helping events (Figure 1).

419

420 *How to infer power to detect symmetry and kinship bias*

421   The relative precision of the estimates of kinship bias and symmetry are unclear in a

422 single statistical test. However, as we have shown, one can estimate the relative precision of

423   helping symmetry and kinship bias through resampling methods. Researchers often use

424   resampling to assess the reliability of genetic marker-based estimates of relatedness (Kalinowski

425   et al. 2006; Queller and Goodnight 1989; Wang 2011). Similar methods can be used to create

426   confidence estimates for social relationships (Farine and Strandburg-Peshkin 2015;

427   Sánchez-Tójar et al. 2018).

428   Our resampling procedure allows one to determine how symmetry and kinship bias

429   respond to increased sampling. For each effect (kinship and reciprocal help), we used

430   subsampling and bootstrapping to generate confidence intervals and trajectories with increasing

431   sampling. By inspecting the resulting plots, one can infer if more power is needed to test a

432   hypothesis about symmetry or kinship bias. For instance, if the coefficients are on a crossing

433   trajectory, then more data are required before drawing any conclusions. If the trajectories are

434   diverging, then more reliable conclusions can be drawn about which predictor is more important,

435   but not by how much. If the trajectories are stable, this suggests that the precision of the estimate

436   would probably not be improved with more sampling.

437

438   *Other reasons why reciprocity is hard to detect*

439   We've shown that symmetrical helping rates in a nepotistic population can be hard to

440   detect for purely statistical reasons. Several biological factors can also make observational

441   evidence for reciprocity difficult to detect. First, symmetry is more difficult to detect in the

442   timespan of a short-term study because stable relationships are also expected to have a longer

443   timescale for reciprocation (Seyfarth and Cheney 2012; Gomes and Boesch 2011; Gomes and

444   Boesch 2009; Gomes, Mundry, and Boesch 2008; de Waal 1997; Carter and Wilkinson 2013;

445   Jaeggi et al. 2013; Sabbatini et al. 2012; Schino and Aureli 2017). Strongly bonded individuals

446   show dyadic helping rates that are more predicted by a foundation of past events and less

447   predicted by recent events, compared to weakly bonded individuals (de Waal 1997; Seyfarth and

448   Cheney 2012, 1984; Schino and Aureli 2009; Jaeggi et al. 2013). If individuals invest in

449   relationships for long-term benefits, then a strong social bond might only show symmetry over a

450   year but not a month or week. Hence, greater social stability makes it harder to detect helping

451   symmetry over short time periods, whereas lower social stability makes it harder to detect

452   symmetry over long time periods. The relative importance of recent events versus longer-term

453   past experience in driving decisions to cooperate is an open question for most behaviors and

454   species.

455   Second, relationships are not completely stable and can change during the course of a

456   study. This is generally true for any measure of a social relationship such as dominance or

457   association rate. Social decisions are also influenced by immediate costs and benefits (Newton-

458   Fisher & Kaburu, 2017). For instance, one study reported that an alpha male chimpanzee was

459   attacked and killed by his most strongly affiliated and most frequent grooming partner, that many

460   observers might label as a 'friend' (Kaburu, Inoue, & Newton-Fisher, 2013). Social relationships

461   can not only change suddenly, but often asynchronously across dyads.

462   Third, in addition to the helping rate, the relative importance of reciprocity and nepotism

463   for determining the helping rate can change over time. For example, the care invested by a mother

464   in her two daughters when they are young might be 100% nepotistic and 0% reciprocal, with

465   equal helping allocated to each daughter. However, when her daughters become adults, the

466   mother's investment might also be influenced by each daughter's reciprocal investment in her,

467   and she may have a stronger relationship with one daughter over another.

468   Fourth, reciprocity can be more difficult to detect than nepotism because cooperative

469   returns can take different forms (Fruteau et al. 2009; de Waal and Berger 2000; de Waal 1997;

470   Gomes and Boesch 2011; Gomes and Boesch 2009; Seyfarth and Cheney 1984; Borgeaud and

471   Bshary 2015). If each decision to help is based on a weighted sum of different forms of past help,

472   then any one form of help might not show much symmetry even if the relationship is balanced

473   when all forms of help are considered. The notion of reciprocity by 'emotional book-keeping'

474   (Schino and Aureli 2009), implies that 'grooming on Tuesday can create an emotional bond that

475   causes meat sharing on Saturday afternoon' (p. 167, Seyfarth and Cheney 2012). Asymmetries in

476   any one service are expected if subordinates groom more dominant individuals in exchange for

477   tolerance (Borgeaud and Bshary 2015; Tiddi et al. 2011; Port, Clough, and Kappeler 2009;

478   Ventura et al. 2006), or if individuals adjust their grooming rates based on the ability of partners

479   to provide food relative to others (Fruteau et al. 2009). Such asymmetries play a key role in

480   biological market theory (Noë and Hammerstein 1995, 1994) but pose a problem for simple 'tit-

481   for-tat' models of reciprocity.

482   Finally, reciprocity and nepotism might interact: the degree of contingency in a reciprocal

483   relationship may be more or less strict among kin. A negative interaction between contingency

484   and kinship was observed in cooperatively breeding cichlids where dominants share their nests

485   with subordinate helpers that must 'pay-to-stay', but subordinates nonkin help more than kin

486   because dominants tolerate subordinate kin regardless of their degree of alloparental care (Zöttl et

487   al. 2013). Such differences in reciprocity between kin and nonkin may also exist in primate long-

488   term cooperative relationships, but they can only be detected through repeated manipulations of

489   helping among both kin and nonkin.

490

491   *Experimental evidence for simultaneous nepotism and reciprocity*

492   To test the causal roles of reciprocity and nepotism, experiments must manipulate both

493   the helping history and kinship cues that influence decisions to help. To our knowledge, this has

494   only been accomplished once using an experimental paradigm where rats are trained to

495   understand how to pull a bar to deliver a food reward to a partner rat. In a series of experiments,

496   reciprocity was evident because decisions to pull for a partner were influenced by factors such as

497   past food received or allogrooming received from the partner (Rutte and Taborsky 2008;

498   Schweinfurth and Taborsky 2018a). To test for a simultaneous kinship effect, outbred wild-type

499   male rats were separated from littermates, housed with non-kin, tested for an ability to recognize

500   kin, and then tested in the same food-pulling task with partners that varied in both their past

501   reciprocal help and kinship (Schweinfurth and Taborsky 2018b). The rats demonstrated kin

502   discrimination by preferring to associate with unfamiliar kin over unfamiliar nonkin, but they did

503   not show nepotism in the food pulling task; kinship did not increase food pulling nor did it

504   change the symmetry of reciprocal pulling rates (Schweinfurth and Taborsky 2018b).

505

506   *When is nepotism harder to detect than symmetry?*

507   There are also several conditions under which nepotism is unlikely to be detected relative

508   to reciprocity, such as when kinship estimates are inaccurate or when there is insufficient

509   variation in kinship among dyads (Csilléry et al. 2006). Although genetic and genomic data is

510   becoming cheaper, easier, and more available (Städele and Vigilant 2016), kinship estimates

511   based on genetic data can still be quite imprecise (Csilléry et al. 2006; Pemberton 2008; van Horn,

512   Altmann, and Alberts 2008). Second, relatedness estimates become severely biased using allele

513   frequencies calculated from only a few animals (Wang 2017). If genetic samples are used to score

514   relatedness in a small subset of individuals, it is crucial to calculate the baseline population allele

515   frequencies from a much larger sample. In studies using pedigrees based on births, 'kinship' is

516   actually maternal kinship. These estimates may be ecologically valid if the animals themselves

517   cannot recognize paternal kin, but increasing evidence suggests that some primates for instance

518   can recognize unfamiliar paternal kin (Levréro et al. 2015; Charpentier et al. 2007).

519   Although helping rates are less precise than kinship estimates, association rates might

520   often be more precise than kinship estimates if dyadic association rates are based on automated

521   methods that can involve many thousands of observations (Aplin et al. 2015; Alarcón‐Nieto et

522   al. 2018). In such cases, the social networks could be described more accurately than the genetic

523   relationships, and association will be easier to detect than kinship as a predictor of cooperation.

524

525   *Quantifying if and how nepotism contributes to symmetrical helping in network data*

526   If both reciprocity and nepotism exist, decomposing the inclusive fitness benefits of a

527 cooperative trait into the relative fitness and indirect fitness components is implausible using

528 empirical observational data. On the other hand, both controlled experiments and some

529 observational analyses can help to identify the relative roles of different proximate mechanisms.

530 Experiments can directly identify the relative importance of different conflicting cues used to

531 make helping decisions (Schweinfurth and Taborsky 2018b). Observational studies can also play

532 an important role in looking at what proximate factors best predict cooperation in nature by

533 investigating how cooperation network structures arise. For example, consider two hypotheses. In

534 the first, kinship determines proximity, which then determines symmetrical grooming. In the

535 second, individuals associate in space independent of kinship, but they preferentially groom their

536 kin. Recent developments in social network analysis (Farine and Whitehead 2015) and null

537 models (Farine 2017) can provide potentially useful tools for distinguishing between such

538 scenarios by constructing different mechanistic networks (VanderWaal et al. 2014; Ilany and

539 Akçay 2016) or by constructing different null models that allow different aspects of associations

540 to vary (Farine et al. 2015). Linking these models to tests of symmetry and kinship bias could

541 yield greater insights into whether kinship or past experience shape patterns of helping directly or

542 via more simple processes (Puga-Gonzalez, Hoscheid, and Hemelrijk 2015).

543   Ultimately, patterns generated by reciprocal helping should have a temporal signature in

544 that helping given should reflect some degree of helping received in the past. However, as we

545 noted above, a major challenge is determining over what timeframe reciprocity takes place in a

546 stable cooperative relationship. Few studies to date are likely to have a sufficiently complete

547 dataset of helping behaviors to use temporal analyses. However, once such data are available,

548 temporal social network analysis (Pinter-Wollman et al. 2013; Blonder et al. 2012; Farine 2018)

549 could provide useful tools for investigating these topics.

550

551 *Practical recommendations*

552   When testing simultaneously for evidence of nepotism and reciprocity in cooperation

553 networks, researchers should be aware of the necessity to estimate the reliability of estimates of

554 both kinship and helping rates (the network edge weights) before comparing their relative

555 importance. The most obvious way to improve inferences is to collect more interactions and to

556 estimate kinship using more pedigree or genetic data. Adding more individuals, however, cannot

557 compensate for a lack of repeated measures of the same individuals, which is what determines the

558 precision of network edge weights (Farine & Strandburg-Peshkin 2015). One way to increase

559 such repeated measures is to induce acts of cooperation. For example allogrooming can be

560 induced by applying substances to the fur (Hemelrijk 1994; Schweinfurth, Stieger, and Taborsky

561 2017), cooperative mobbing can be induced with fake predators (Krams et al. 2013; Krama et al.

562 2012; Krams et al. 2010; Krams et al. 2008), food sharing can be induced by fasting individuals

563 (Carter and Wilkinson 2013; Wilkinson 1984) or by creating opportunities to provide (Silk et al.

564 2013).

565   We used network permutations which account for the network structure and hold the total

566 help given and received by each individual constant. However, network permutations do not

567 account for biased sampling, so the helping rates (network edge weights) must take into account

568 the relative opportunity for individuals to help each other. We accomplished this by defining edge

569 weights as the proportion of help received from individual X divided by the total help received

570 from all other individuals that could have otherwise come from individual X because X was

571 present at the time. Another possibility is to define edges as the help from X over the opportunity

572 for X to help. If helping events are scored as yes/no events, then an even more rigorous approach

573 is to use pre-network permutations (Farine 2017), where the helping acts in the dataset are

574 permuted across individuals present at the time, rather than permuting the helping rates in the

575 network. Pre-network permutations allow for precise control over the null hypothesis by

576 swapping within time periods or locations, and also control for biased sampling; however, they

577 are most appropriate when the helping events are binary (0/1) and hence interchangeable. In

578   conclusion, due to differences in the ease of detecting symmetry and kinship bias, it is useful to

579   assess the reliability of each effect as a function of sampling effort. We provide R code (Carter et

580   al. 2018) to produce plots that allow one to assess the relative power for detecting evidence of

581   nepotism and reciprocity in simulated datasets or in a given dataset of helping observations in

582   humans or nonhuman animals.

583

590

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Appendix
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R code can be found here:
https://doi.org/10.6084/m9.figshare.6072272.v2

Datasets can be found here:
https://doi.org/10.6084/m9.figshare.6072254.v2

The R function "infer_power_reciprocity_kinship" uses the following arguments:
- **individuals:** a vector with unique IDs for all individuals in the study
- **observations:** a data frame with columns: actor, receiver, duration, possible.actors.list
- **possible.actors:** a matrix where each column contains a list of possible actors for each observation. The number of rows is the max number of possible actors.

- **relatedness:** a matrix of relatedness between all individuals - row and column orders must match the order of individuals
- **nreps:** number of repeated subsamples at each sample size
- **jumps:** number of observations to increment each sample size step (default = 20). First sample size is always 20.
- **simulate_data**: if set to "TRUE", the function will simulate data. If set to "FALSE" then the function will use actual data provided by arguments above.
- **nepotism** (only used with simulated data): degree of nepotism (0 to 1)
- **N** (only used with simulated data): number of simulated individuals
- **n.events** (only used with simulated data): number of simulated helping events

Note: Depending on the number of observations and replications, this function can take several hours to run.

Table S1. Mean correlation between social bond strength and kinship in simulated data. Values based on 10,000 simulations. Social bond strength is always symmetric and determines probability and duration of observed helping events.

Nepotism	Mean Pearson's correlation (0.025 – 0.975 quantiles)
0%	0 (-0.14—0.14)
25%	0.32 (0.19—0.44)
50%	0.71 (0.64—0.76)
75%	0.95 (0.94—0.96)
100%	1 (1—1)

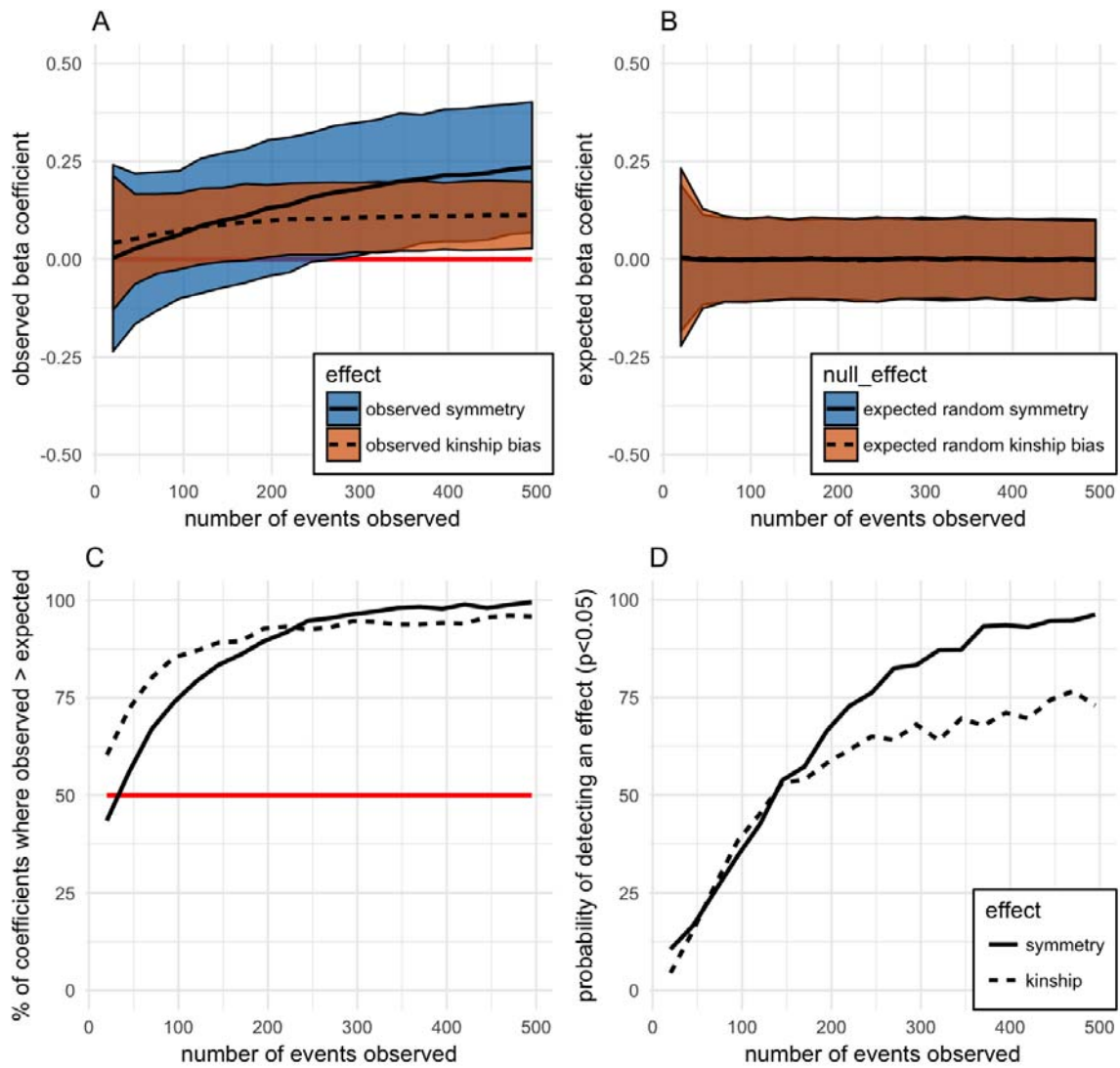859
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863 **Figure S1. Power analysis for simulation of symmetrical helping with 0% nepotism.** Panel A
864 shows the mean and 95% confidence interval of the standardized slope estimates for the effects of
865 helping rate A to B (solid line, purple shading) and kinship between A and B (dotted line, yellow
866 shading) as predictors of helping rate B to A. Panel B shows the same for the expected null
867 coefficients generated by permutation. Panel C shows the percentage of observed coefficients that
868 are greater than the paired null coefficient generated from the same subsample. If effects are real,
869 then these values should be higher than 50% (red line). Panel D shows the percentage of observed
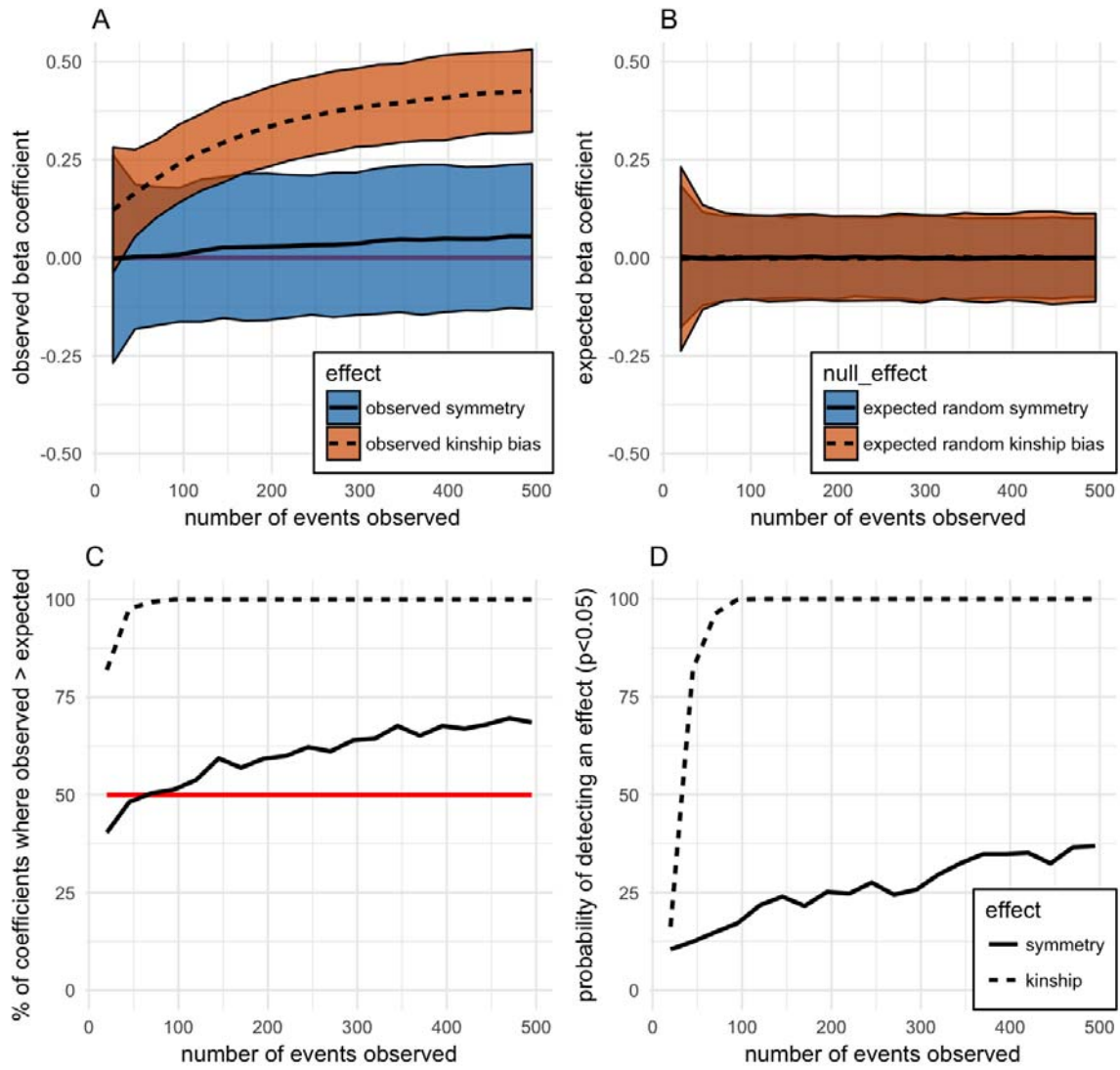870 coefficients that are greater than 95% of expected null coefficients for that sample size.

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872
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874 **Figure S2. Power analysis for simulation of symmetrical helping with 25% nepotism.** See
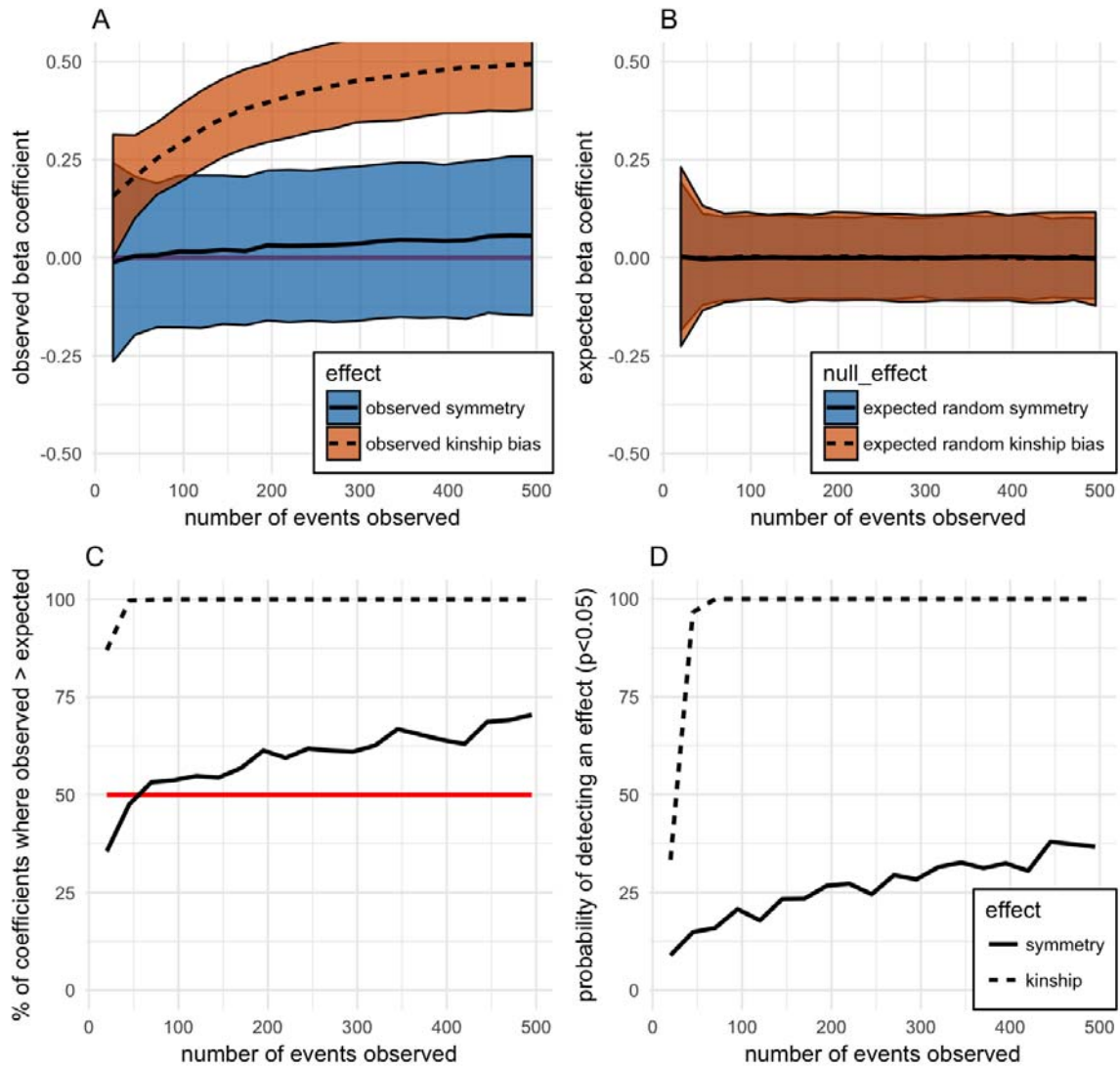875 plot Figure S2 for explanation.
876
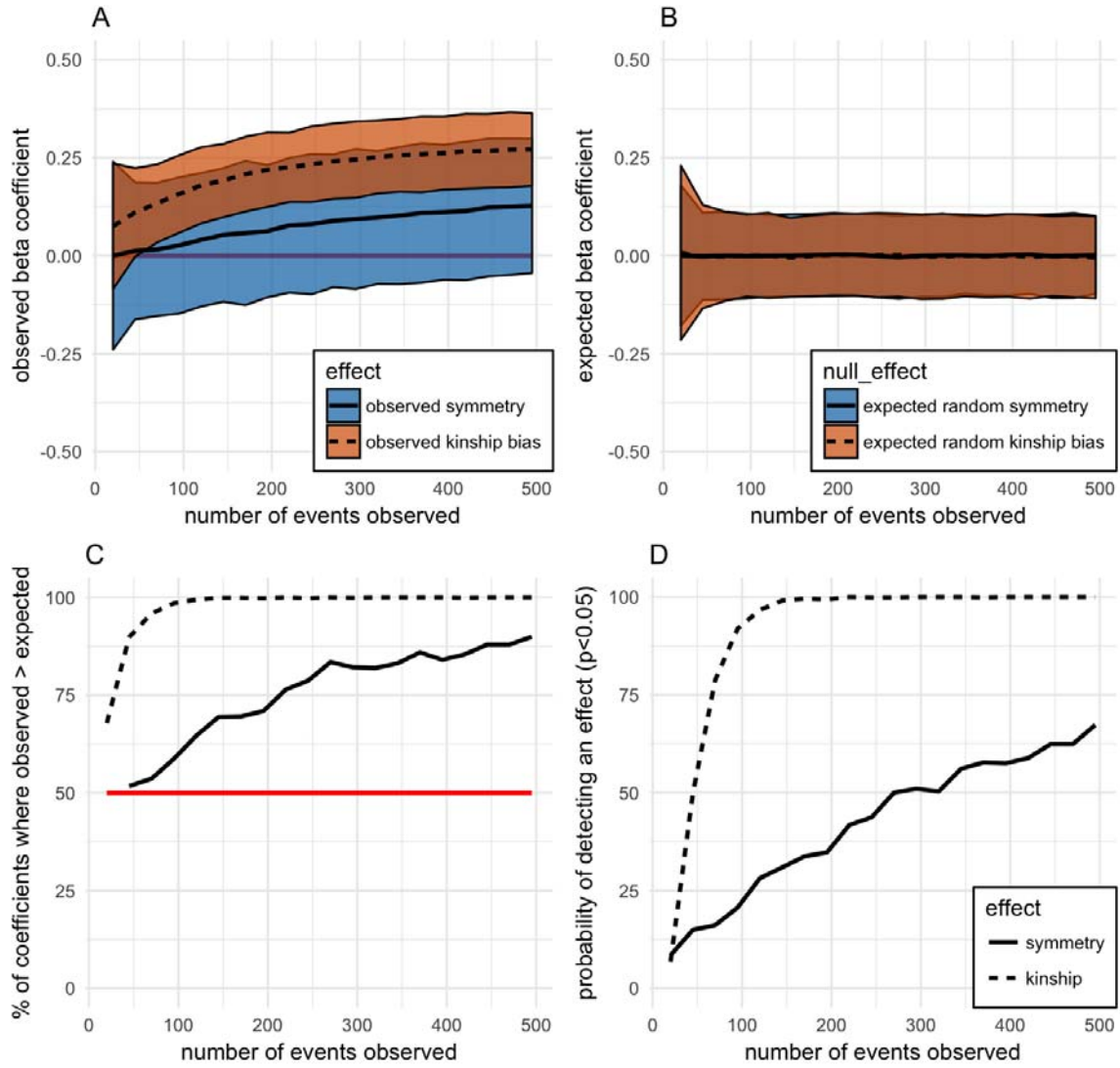
Figure S3. Power analysis for simulation of symmetrical helping with 50% nepotism. See plot Figure S3 for explanation.

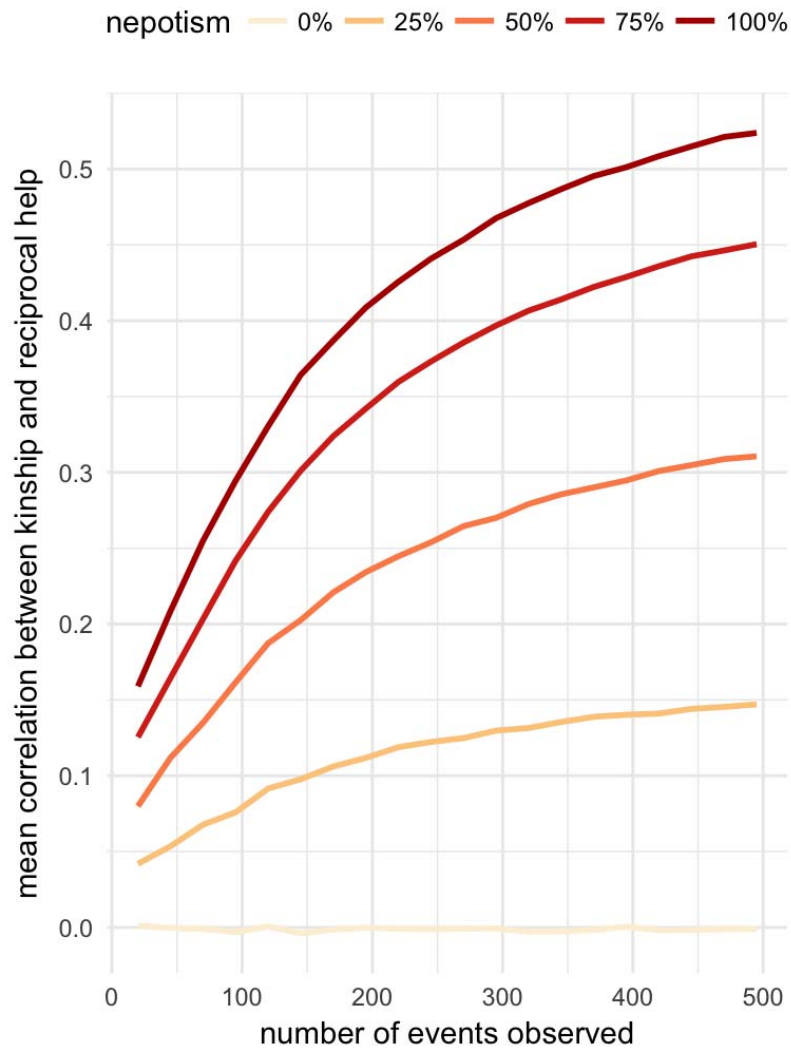**Figure S4. Power analysis for simulation of symmetrical helping with 75% nepotism.** See plot Figure S4 for explanation.

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887
888 **Figure S5. Power analysis for simulation of symmetrical helping with 100% nepotism.** See
889 plot Figure S5 for explanation.
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Figure S6. Collinearity. Mean Pearson's R correlation between the predictors kinship and reciprocal help for each degree of nepotism with increased sampling effort.
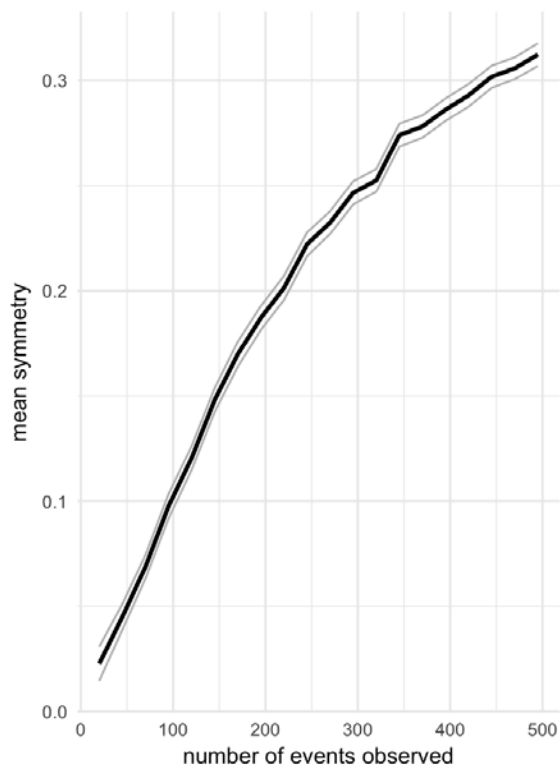
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898   **Figure S7. Symmetry with increased sampling effort expected with perfect reciprocity and**
899   **zero nepotism**. Plot shows mean (black) and 95% confidence interval (grey) of Pearson's
900   correlation between help given and received.
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902