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1 **Behavioral and hormonal changes following social instability in young rhesus macaques**

2 ***(Macaca mulatta)***

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12
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24

25 **Abstract**

26 Social instability (SI) occurs when there is competition over social status. Reduced
27 certainty of social status can lead to heightened aggression, which can increase physiological
28 stress responses, as individuals prepare to fight for their social status. However, adults can take
29 proactive coping mechanisms to reduce the physiological stress induced by SI, such as increasing
30 affiliation. Very little is known, however, about the behavioral and hormonal effects of SI early
31 in development. Filling these gaps in knowledge would add to the fields of primatology and
32 developmental and comparative psychology. We conducted an opportunistic study of a peer
33 group of 18 rhesus macaque (*Macaca mulatta*) yearlings before and during SI. We used social
34 network analysis to measure individuals' dominance certainty (DC, in their aggressive and
35 submissive network) and their position in affiliative networks (grooming and play) and analyzed
36 hair cortisol concentrations (HCCs). **As predicted, during SI, we observed a decrease in DC,**
37 **indicating that individuals had less stable dominance positions.** As well, during SI, we observed
38 increased rates of social grooming and decreased rates of social play, reflecting potential coping
39 mechanisms. **More socially connected individuals in social grooming and social play networks**
40 **received higher levels of coalitionary support.** Contrary to predictions, DC did not predict HCCs;
41 rather individuals that were more connected in the social play network exhibited smaller
42 increases in HCCs during SI, revealing a potential buffering effect of social play. Our results
43 underscore the need for further research on the effects of SI during ontogeny.

44 **Keywords:** instability, social network, hair cortisol, eigenvector centrality, play

45

46

47 **Introduction**

48 Across a wide range of animal species, including humans, dominance hierarchies
49 structure the organization of social groups (Grosenick et al., 2007; Hawley & Little, 1999;
50 Williamson et al., 2016). When a new social group is formed, individuals may use a variety of
51 strategies to establish dominance ranks, including sensory cues (e.g., auditory, olfactory, or
52 visual), in addition to aggression. When utilizing aggression, “a pecking order” can often be
53 established relatively quickly, even within minutes (Issa et al., 1999; Meese & Ewbank, 1973;
54 Wooddell et al., 2017). The presence of a social hierarchy is beneficial to prevent prolonged and
55 intense fighting, as the establishment of a social relationship can govern future interactions,
56 including approach and retreat behaviors (Casey et al., 2015).

57 Although dominance relationships can remain stable for an extended amount of time,
58 they are not completely static. They may be maintained via bouts of fighting or periods of
59 conflict that can result in temporary social instability (SI), during which dominance ranks may be
60 fluctuating and unstable. Accordingly, SI is commonly assessed by measuring changes in
61 dominance ranks or the proportion of bidirectional interactions (e.g., Neumann et al., 2011). In
62 free-ranging animal populations, SI commonly occurs when immigrant males attempt to enter
63 into a new group and challenge the resident males, which may lead to excessive violence,
64 including infanticide (Beehner & Berman, 2008; Hrdy, 1974; Pusey & Packer, 1994). Thus, in
65 captivity, paradigms to induce SI (in order to study its physiological effects) are introductions of

66 novel males or revolving group memberships (e.g., Almeida et al., 2014; Capitanio & Cole,
67 2015; Guibert et al., 2010; Manuck et al., 1983) and group formations (e.g., Dise & Goldina,
68 2017; Linden et al., 2019). However, SI is not just limited to new individuals entering groups, as
69 rank changes can occur even in established social groups (both captive and free-ranging) with
70 long-term dominance relationships (e.g., Ehardt & Bernstein, 1986; Beisner et al., 2015; Higham
71 & Maestripieri, 2010; Kaburu et al., 2013; Meese & Ewbank, 1972; Perry, 1998; Setchell &
72 Dixson, 2001).

73 During SI, individuals are at risk for severe traumas, infanticide and other reproductive
74 failures, and even death (e.g., Dettmer et al., 2015), and decades of research have examined the
75 effects that SI has on animals' physiological regulation, with a particular focus on the link
76 between SI and glucocorticoid (GC) levels (Bartoš et al., 2010; Haller et al., 1999; Van Meter et
77 al., 2009). GCs (i.e., cortisol and corticosterone) are steroid hormones that help animals mobilize
78 energy reserves whenever their body needs it, such as during a stress response. Since GCs are
79 part of the "fight or flight" response, they are expected to be elevated during periods of
80 potentially intense fighting seen with contested dominance ranks because these metabolic
81 demands require immediate energy expenditure (Muller & Wrangham, 2004). Accordingly,
82 several studies have found that GC levels (measured by blood, urine, fecal, or hair) are elevated
83 during periods of SI (Engh et al., 2006; Haller et al., 1999; Higham et al., 2013; Mendonça-
84 Furtado, et al., 2014; Sapolsky, 2005; Vandeleest et al., 2019; Wooddell et al., 2016; but see
85 Milich et al., 2018). The heightened GCs are particularly salient for vulnerable individuals, for
86 example, lactating mothers at risk of losing their infants to infanticide during male takeovers
87 (Crockford et al., 2008; Engh et al., 2006; Wittig et al., 2008) and high-ranking individuals at
88 risk of losing their social standing (Higham et al., 2013; Sapolsky 2005; Wooddell et al., 2016).

89 However, given GCs' role in suppressing the immune system and inflammatory response,
90 chronic high levels of GCs can result in immune suppression, infertility, and cardiovascular
91 impairments (Sapolsky, 2005), and individuals can take proactive coping strategies to limit this
92 GC surge, such as narrowing their social networks to focus on a few preferred social partners
93 (Crockford et al., 2008; Engh et al., 2006; Wittig et al., 2008) or enhancing grooming rates in
94 general (Wooddell et al., 2016). In these studies of adult primates, social affiliation seemed to
95 buffer individuals during periods of social unrest.

96 Importantly for group-living primates, adults are not the only individuals witnessing or
97 experiencing SI. Many wild and captive troops contain multi-generational members, including
98 immatures (i.e., infants and juveniles). However, it still remains unclear how SI affects both
99 behavioral and hormonal profiles in juveniles and whether coping mechanisms against chronic
100 stress emerge early in life, which would be an adaptive strategy for preparing for stressful events
101 in adulthood.

102 To examine how SI influences both behavioral and hormonal coping mechanisms, we
103 conducted an opportunistic study of a peer group of rhesus macaques (all approximately 1-year
104 old) after social group formation and relocation. We have previously studied this group
105 extensively to examine the predictors of rank acquisition (Wooddell et al., 2017) and the
106 development of social networks (Wooddell et al., 2019). However, until now we did not have the
107 capability to study their hormonal regulation and potential coping mechanisms during SI, which
108 was the aim of the present study. This period of SI provides an excellent opportunity to examine
109 how young primates adapt to SI both behaviorally and hormonally, especially in the absence of
110 kin support. Given that mothers and kin can be a significant social buffer for developing primates
111 (Hennessy et al., 2009; Kikusui et al., 2006; Sanchez et al., 2015), studying a peer group allows

112 us to examine individual-level coping mechanisms, which could provide a relevant monkey
113 model for the study of human development in the absence of kin support (e.g., foster children,
114 orphans, institutionalized children) or in settings where peer interactions predominate (e.g.,
115 school settings: Kim et al., 2006; 2009; Tschann et al., 1996). We used dominance interactions
116 to calculate dominance hierarchies and certainty (DC) and relied on social grooming and social
117 play data to construct social networks. For the present study, we also analyzed hair samples to
118 measure hair cortisol concentrations (HCCs), a measure of chronic GC production (Davenport et
119 al., 2006; Meyer & Novak, 2012) that reflects aggregate HPA axis activity over the preceding
120 months. We predicted that 1) DC would decrease during SI, reflecting the presence of or an
121 increase in unstable dominance relationships. However, if young monkeys can utilize affiliative
122 social relationships to modify their DC, we then predicted that 2a) individuals more central in
123 affiliative social networks (grooming and play) would have greater DC, as 2b) individuals with
124 more social connections may benefit from a larger network of coalitionary support. Given that
125 weaker DC is associated with unstable dominance relationships, which may equate to more
126 intense fighting, we also predicted that 3) individuals with less DC should have higher HCCs,
127 particularly during SI. However, if immatures can use affiliation as a coping strategy, we would
128 predict that 4) lower HCCs during SI should be associated with a higher centrality in social
129 grooming and social play networks.

130 **Methods**

131 *Subjects and housing*

132 Subjects were 14 male and 4 female rhesus macaques (*Macaca mulatta*, N=18) born
133 between March and May 2015 at the Laboratory of Comparative Ethology at the NIH Animal
134 Care Center in Poolesville, Maryland. Monkeys were reared at this facility through August 2016,

135 when they were approximately 1.5 years old (see Wooddell et al., 2017; 2019, for detailed
136 methodology). All procedures described adhered to the NIH Guide for the Care and Use of
137 Laboratory Animals and were approved by the National Institute of Child Health and Human
138 Development Animal Care and Use Committee.

139 Nine of the subjects (eight males and one female) were reared in a 2.0 ha naturalistic
140 outdoor, open-air enclosure (field station), which has previously been described in detail (e.g.,
141 see Dettmer et al., 2014; Wooddell et al., 2016; 2017). The troop consisted of approximately 80
142 mixed-sex semi-free ranging rhesus macaques (age range: 0-18 years) from three different
143 matrilineal kinship lines (Wooddell et al., 2016; 2017). Offspring acquired their mothers'
144 dominance ranks in infancy, as dominance ranks among peers were settled even before 8 months
145 of age (Wooddell et al., 2016; 2017; 2019). Families contained infants/siblings, mothers, aunts,
146 grandmothers, and even great-grandmothers, reflecting the naturalistic multigenerational (MG)
147 social structure. Following our previous approach (Wooddell et al., 2017; 2019), these subjects
148 were referred to as MG subjects, reflecting this type of early social experience.

149 The other nine subjects (six males, three females) were born and reared into one of three
150 social groups, each of which consisted of 10-12 same aged females, one adult male, and several
151 same-aged infants (detailed in Wooddell et al., 2017; 2019). Infants born into these groups were
152 paternal half-siblings. Contrary to the MG subjects, these groups exhibited very little age
153 diversity, with only maternal and infant generations, and were thus classified as unigenerational
154 (UG) subjects (Wooddell et al., 2017; 2019). It is important to note, however, that MG and UG
155 subjects not only differed in the complexity of rearing in terms of generations, but also in group
156 size: MG subjects were reared in a much larger group size than UG subjects.

157 *Peer group formation and social instability (SI)*

158 In January 2016, the nine MG immatures and their mothers were removed from the field
159 station due to a rare overthrow of the social hierarchy in the field station (Wooddell et al., 2017).
160 These nine subjects (all approximately 8-months old) were the infants of females who suffered
161 severe aggression and trauma but did not receive trauma themselves. They were all from the
162 same matriline. The other nine subjects, UG immatures, were removed from their mothers at
163 approximately 8-months of age to adhere to standardized laboratory procedures to place them
164 into a group with same-aged peers (see Dettmer et al., 2012).

165 All 18 subjects (nine MG and nine UG) were placed together in a new social group, as
166 previously described in detail (Wooddell et al., 2017; 2019), and then relocated in May 2016
167 (when all subjects were approximately 1-yr of age), due to management decisions unrelated to
168 the research objectives. The relocation resulted in a turnover of the peer group's relatively new
169 social hierarchy (Wooddell et al., 2017; 2019). The group remained there until it was disbanded
170 in August 2016 (when all subjects were approximately 17-months old), again due to management
171 decisions. Thus, the total duration of the study was eight months (Figure 1), with approximately
172 18 weeks of pre-SI and 10 weeks of SI.

173 *Behavioral data collection: aggression, dominance ranks, and dominance certainty*

174 Detailed methodologies for dominance data collection in this group have previously been
175 reported (see Wooddell et al., 2017; 2019). In addition to direct aggressive interactions,
176 coalitionary support was also recorded, indicating which individual they supported in the
177 aggressive interaction (see Wooddell et al., 2017). Coalitionary support was totaled for each
178 dyad, in counts across each study period for initiating coalitionary support to another partner and
179 counts for receiving coalitionary support from another partner. Elo-rating, a method commonly
180 used to track rank changes over time (Neumann et al., 2011) was used to establish dominance

181 ranks, which has previously been documented in detail for this group (Wooddell et al., 2017;
182 2019).

183 Contrary to dominance rank, DC is a relatively new method that utilizes both direct and
184 indirect information via social network analysis to gauge the overall “fit” of an individual’s
185 position in the dominance network (Fushing et al., 2011; Linden et al., 2019; Schrock et al.,
186 2019; Vandeleest et al., 2016; 2019). DC was calculated from dominance interactions (threats,
187 chases, attacks, displacements, **silent-bared teeth displays**) using the percolation and conductance
188 method implemented via the Perc package (Fujii et al., 2015; Vandeleest et al., 2016) in R
189 software (v 3.3.3) **This is a network-based method that handles missing data better than other**
190 **ranking methods by measuring both direct and indirect pathways and transitivity in the**
191 **dominance networks. In other words, the Perc package computes dominance information from**
192 **all network pathways, even for those pairs that were never recorded interacting, measuring the**
193 **probability of each individual outranking another. Therefore, individuals high in DC indicate that**
194 **individuals are more certain of their rank position compared to individuals with low DC.** Values
195 typically range from 0.5 (uncertain position; an individual has an equal probability of ranking
196 higher or lower than another individual) to 1 (certain position; an individual has a 100%
197 probability of ranking higher than another individual). Previous studies in have reported an
198 inverted-U function of DC, where both low- and high-ranking individuals have the greatest DC
199 (i.e., the most consistent or stable dominance position), with the most uncertainty (i.e., the
200 greatest inconsistency or unstable dominance position) typically exhibited by mid-ranking
201 individuals (e.g., Schrock et al., 2019; Vandeleest et al., 2016).

202 *Behavioral data: affiliation and social networks*

203 Detailed methodologies for affiliative social behavior collection in this group have
204 previously been reported (see Wooddell et al., 2017; 2019). For the purposes of this study, we
205 only focused on social grooming and social play, as these are common affiliative behaviors in
206 juvenile macaques (Kulik et al., 2015).

207 Two separate social networks were constructed: one for social grooming and one for
208 social play, both after group formation and after relocation/SI (thus totaling four separate
209 networks). To construct social networks, we totaled the number of intervals in which each
210 subject engaged in either social grooming or social play with each social partner. We then used
211 weighted and undirected information to create social networks using the “Statnet” and “SNA”
212 (Handcock et al., 2006) packages in R software (R Core Team, 2020; v 3.3.3). We used the
213 *evcent* function to calculate weighted eigenvector centrality (EC) for each individual, for both
214 social grooming and social play. EC measures the strength of an individual’s direct connections,
215 but also the strength of its indirect connections (i.e., how socially integrated an individual’s
216 social partners are; Bonacich, 2007; Farine & Whitehead, 2015), and higher EC indicates that
217 individuals are more socially connected within the group. EC has been found to be associated
218 with several measures of fitness, such as female fertility (e.g., Brent et al., 2013), offspring
219 survival (e.g., Cheney et al., 2016), biomarkers of inflammation (e.g., Wooddell et al., 2019), and
220 survival (e.g., Stanton & Mann, 2012).

221 *Hair cortisol concentrations (HCCs)*

222 Owing to the longitudinal nature of this study, we utilized HCCs in the present study.
223 Short-term samples such as blood and saliva are influenced by circadian rhythm and even the
224 sampling procedure itself, whereas HCCs are not (Davenport et al., 2006; Meyer & Novak, 2012;
225 Meyer et al., 2014). Similarly, cortisol concentrations in urine and feces only reflect HPA axis

226 activity up to 24 hours, which would require numerous samplings over the course of the study,
227 whereas HCCs are a cumulative measure over several weeks/months (Davenport et al., 2006;
228 Meyer & Novak, 2012; Meyer et al., 2014). Hair samples were collected longitudinally at
229 routine quarterly health exams for all subjects from birth onwards following a shave, re-shave
230 procedure. For the purposes of this study, the baseline shave occurred one day before group
231 formation on January 18, 2016 (when subjects were approximately 8 months old). The re-shaves
232 occurred three months after peer group formation on April 25, 2016 (when subjects were
233 approximately 13 months old), and again on July 11, 2016 (when subjects were approximately
234 15 months old). These re-shave samples thus reflect the formation of the hierarchy and social
235 networks (April 2016; see Figure 1), as well as SI that occurred after the relocation to a new
236 housing environment on May 30, 2016 (the July 2016 samples; see Figure 1). For the purposes of
237 this study, we report on April and July samples (or a change between those two samples).
238 Samples were collected by shaving the back of the animals' necks with commercial pet
239 grooming clippers and were stored in an aluminum pouch at -80°C until further processing.
240 Samples were assayed according to previously established procedures (Davenport et al., 2006;
241 Meyer & Novak, 2012; Meyer et al., 2014). In short, samples were washed twice with 5 mL
242 isopropanol alcohol and dried under a fume hood for 5-7 days until being ground to a fine
243 powder with a ball-mill grinder (MM200; Retsch, Newton, PA). Samples were then rotated in
244 methanol for 24 hours and aliquots of the methanol extract were dried down and reconstituted
245 with assay buffer, then analyzed with an enzyme immunoassay using a salivary cortisol kit (#1-
246 3002; Salimetrics, Carlsbad, PA). Resulting values ($\mu\text{g}/\text{dL}$) were converted to pg/mg for
247 analysis. Inter-assay and intra-assay coefficients of variation were $<9.0\%$. One subject's hair
248 sample for April 2016 was spilled during processing and is thus missing from analysis.

249 *Statistical Analysis*

250 We used the R function *glmmTMB* to run generalized linear mixed model (GLMM)
251 analysis to test our predictions. However, before running the GLMM analysis, we first conducted
252 an exploratory analysis to assess the presence of outliers and collinearity between predictors
253 using the R package “HighstatLib V8.R” provided by Zuur et al. (2013). Outlier presence was
254 assessed using the function *Mydotplot* while collinearity was tested using the functions *Mypairs*
255 and *Mybwplot*. While this exploratory analysis did not reveal any outlier, we did find some
256 predictors that were correlated: (1) social grooming and social play eigenvector values were
257 negatively correlated ($r(16) = -0.63, p < 0.001$); (2) both social grooming and social play
258 eigenvector values varied with early social experience condition, with MG infants having higher
259 social grooming EC and lower social play EC than UG infants (social grooming: $t(16) = 5.2, p <$
260 0.001 ; social play: $t(16) = -3.35, p = 0.002$); and (3) DC varied with relocation, with mean DC
261 values being significantly higher before relocation than after ($t(16) = -2.84, p = 0.008$).
262 Following this exploratory analysis, we tested the effect of social grooming and social play on
263 the outcome variable in separate models, and we excluded early social experience conditions in
264 models that included either social grooming or social play as predictors. Similarly, we excluded
265 relocation condition when DC was included as predictor.

266 To test prediction 1, we ran a GLMM analysis in which we set DC as the outcome
267 variable with beta distribution (since DC values can only range between 0 and 1) while
268 dominance rank (Elo-rating), relocation (before vs after), and early social experience (UG vs
269 MG) were included as predictors (see Table 1). Similarly, we ran two separate GLMM models to
270 address prediction 2a. While both models included DC values as outcome variables, the models
271 had different predictors, with one model including, as an explanatory variable, social grooming

272 EC and relocation, whereas a second model included social play EC and relocation (see Table 1).
273 Additionally, in order to assess whether EC was associated to the number of coalitionary
274 supports individuals were involved in (prediction 2b), we ran six negative binomial GLMM
275 models. These models included either the number of coalitionary support given, the number of
276 coalitionary support received, or total number of coalitionary supports as outcome variables with
277 a negative binomial error structure because the Poisson models were too overdispersed
278 (Dispersion values > 2). We then set relocation and either social grooming EC or social play EC
279 as predictors (see Table 1). To assess the effect of DC (prediction 3), as well as social network
280 position (prediction 4) on HCCs, we ran linear mixed model analysis (LMM) with Gaussian
281 distribution using the *lmer* function. In all three LMM models HCCs were included as an
282 outcome variable, while each model had a different set of predictors: 1) DC and early social
283 experience in one model; 2) relocation and social grooming EC in a second model; and 3)
284 relocation and social play EC in a third model (see Table 1). All the mixed model analyses
285 included subjects' IDs as random factors in order to control for pseudoreplication since the same
286 individuals were sampled twice (both before and after relocation). For all the analyses, we ran
287 each model three times: one as a null model (i.e., with only the random factors but with no
288 predictors); one with predictors entered as main effects, and one with predictors entered as
289 interaction. We then, for each analysis, compared Akaike's information criterion (AIC) values
290 between the three models in order to find the model with the best fit (i.e., with the lowest AIC
291 value). Furthermore, we used the *check_model* function from the "performance" package to
292 verify that all (G)LMM models met the necessary assumptions of model validity (i.e.,
293 distribution of residuals, residuals plotted against fitted values). Finally, we used regression
294 analysis to assess whether social grooming and social play EC during SI significantly predicted

295 changes in HCCs after relocation compared to before relocation. To this end, we calculated, for
296 each individual, the percentage of changes in HCCs between the two time points (i.e., after group
297 formation and after group relocation) by dividing the difference in HCCs between the two time
298 points by the HCCs values after group formation and multiplying the ratio by 100. This
299 percentage was included as the outcome variable in two regression models. In each model, we
300 included either social grooming or social play EC during SI along with the early social
301 experience (UG or MG) as a control variable. Each of these regression models were run twice,
302 both with and without (i.e., null model) the main predictors. AIC values between the two models
303 were compared in order to find the model with the best fit. In all models, we z-transformed
304 continuous predictors in order to better compare effect sizes of variables that are on different
305 scales.

306 **Results**

307 *Prediction 1: Dominance certainty should decrease during social instability*

308 Our GLMM analysis showed that the model that included the three-way interaction
309 between Elo-rating, relocation (before vs after), and early social experience (MG vs UG) had a
310 better fit compared to both the model in which the three predictors were set as main effects and
311 the null model (Table 2 and S1). This analysis revealed that the three-way interaction
312 significantly predicted DC (estimate= -1.60, SE=0.32, z-value=-4.97, $p < 0.001$, Table 2). In
313 particular, before relocation, for both MG and UG, higher-ranking subjects had greater DC than
314 lower-ranking subjects, but this effect was much stronger for MG than for UG subjects (Figure
315 2a). In contrast, after relocation, the situation was reversed for MG, with higher-ranking MG
316 subjects displaying less DC than lower-ranking MG subjects, while higher-ranking UG subjects

317 had greater DC than lower-ranking UG subjects (Figure 2b). These results (partially) support
318 prediction 1.

319 *Prediction 2: Individuals with greater centrality in social grooming and social play networks*
320 *should have greater dominance certainty*

321 Our GLMM analysis to test prediction 2 revealed that the models that included the
322 predictors as main effects had a better fit compared to the null model as well as the models with
323 the interaction term (Tables S2 & S3). This analysis showed that, while social grooming EC did
324 not predict variation in DC, there was a negative relationship between social play EC and DC,
325 (Tables 3 & 4), indicating that individuals who were more peripheral in the play network had
326 somewhat higher DC. Overall, these results fail to support prediction 2a.

327 In the GLMM models we ran to assess whether the position in the social grooming
328 network significantly predicted the number of coalitionary supports, we found that models with
329 the interaction between network position and relocation had a better fit compared to the null
330 model and the model with predictors set as main effects (Tables S4-S6 & Table 5). This analysis
331 shows a positive relationship between social grooming EC and coalitionary support before
332 relocation, but a negative relationship *after* relocation (i.e., after the onset of SI; Figures 3a-c). In
333 contrast, we found that social play EC significantly predicted only the number of coalitionary
334 supports received (vs. coalitionary support given and total coalitionary support; Tables S7-S9
335 and Table 6). This model revealed a negative relationship between social play EC and
336 coalitionary support received before relocation and a positive (albeit weak) relationship after
337 relocation (Figure 4). Collectively we found some support for prediction 2b, with coalitionary
338 support positively correlated with social grooming EC only before relocation and with social
339 play EC only after relocation.

340 *Prediction 3: Individuals with less dominance certainty should have higher hair cortisol*
341 *concentrations*

342 HCCs ranged from 49.84 pg/mg to 160 pg/mg in April 2016 before relocation, to
343 between 58.58 pg/mg and 113.17 pg/mg after relocation in July 2016 (before: M= 92.82, SD =
344 23.80; after: M = 85.92, SD = 15.07). The change in HCCs ranged from -81.01 to 34.22 pg/mg
345 (M= -8.07, SD = 28.13)

346 GLMM analysis revealed that the model that included the interaction between DC and
347 early social experience (MG/UG) had a better fit compared to the null model and the model in
348 which predictors were set as main effects (Table S10). However, we did not find any significant
349 effect of either DC or early social experience on HCC values (Table 7). Overall, we found no
350 support for prediction 3.

351 *Prediction 4: Individuals more central in social grooming and social play networks should have*
352 *lower HCCs*

353 We have previously reported that rates of social grooming significantly increased
354 following relocation and SI, whereas rates of social play significantly decreased (Wooddell et al.,
355 2017). We also previously reported that there was no significant change in social grooming EC
356 values during SI (Wooddell et al., 2019; i.e., individuals did not change in their social
357 connectedness during SI). Rather, social grooming EC values before and after SI were highly
358 correlated ($r(16) = 0.87, p < 0.0001$), similar to social play EC values ($r(16) = 0.63, p = 0.005$),
359 indicating that individuals had similar social network positions before and during SI.

360 Data from the current study partially supported prediction 4. The GLMM models that
361 included the interaction between affiliative EC (social grooming and social play) and relocation

362 (before/after) had the best fit (Tables S11 & S12), but neither social grooming nor social play EC
363 values individually (nor their interactions with relocation) significantly predicted HCCs (Tables
364 8 & 9), failing to support prediction 4. However, after the relocation, young monkeys' EC in the
365 social play network negatively predicted the percentage of change in HCCs from April 2016 to
366 July 2016. This relationship approached significance and explained ~ 20% of the variation in the
367 difference in HCC values between before and after relocation (estimate= -14.0, SE=6.8, $t(16)=-$
368 2.05, $p=0.060$, $R^2= 0.22$; Figure 5). In other words, juveniles that were more central in the social
369 play network (i.e., had more direct and/or indirect connections) exhibited smaller increases in
370 HCCs levels during SI. Monkey's EC in the social grooming network did not predict changes in
371 HCCs (Table S13). Collectively, these data partially support prediction 4.

372 **Discussion**

373 In our study of behavioral and hormonal changes during SI in young macaques, we found
374 that DC decreased during a period of social instability. Individuals that were socially peripheral
375 in the social play network had increased DC. Before SI, individuals more central in social
376 grooming networks received more frequent coalitionary support, although this relationship was
377 opposite during SI. Individuals more central in social play networks received less frequent
378 coalitionary support prior to SI, but more frequent coalitionary support during SI. DC did not
379 predict HCCs, rather affiliation in social networks seemed to buffer individuals during SI.
380 Yearlings who were more central in their social play network appeared to exhibit smaller
381 increases in chronic cortisol production during a period of SI. We interpret this finding to mean
382 that juveniles with more direct and/or indirect connections (i.e., more "friends") may be buffered
383 against the physiological stress of social instability. We now discuss the relevance and possible
384 explanations of these findings.

385 As predicted, DC decreased following a period of SI. Therefore, as the subordinate (UG)
386 peers challenged the dominant (MG) peers, there was generally an overall increase in the
387 presence of ambiguous relationships. This is particularly evident, as prior to SI, higher-ranking
388 MG subjects had greater DC than lower-ranking MG subjects. However, during SI, higher-
389 ranking MG subjects and lower-ranking UG had lower DC than lower-ranking MG subjects and
390 higher-ranking UG subjects, respectively. This is likely because higher-ranking MG subjects and
391 lower-ranking UG subjects were now the middle-ranking animals, and ranks were unsettled
392 among the highest-ranking MG subjects and the lowest-ranking UG subjects, as they were
393 challenging each other, whereas ranks among the MG subjects remained perfectly stable
394 (Wooddell et al., 2017). This is consistent with other literature indicating mid-ranking animals
395 typically have the lowest DC (Schrock et al., 2019; Vandeleest et al., 2016).

396 Surprisingly, individuals more peripheral in social play networks had increased DC, as
397 these individuals may have been high- or low-ranking to begin with, which often have certain
398 dominance positions (Schrock et al., 2019; Vandeleest et al., 2016). In addition, given that play
399 fighting can quickly escalate to real fighting (Paquette, 1994), social play may have been too
400 risky, as dominance ranks were being established. Therefore, individuals less connected in social
401 play networks may have been more certain of their dominance ranks, because they did not
402 engage in risky play behavior, as social play can also be used as a way to assess competitors
403 (Cordoni et al., 2021), which would be useful information to have in case of a rank challenge. In
404 addition, we had predicted that individuals with more social connections might have benefitted
405 from a larger network of coalitionary support, making their rank position more certain (i.e.,
406 higher DC). Prior to SI, yearlings more central in social grooming networks received more
407 frequent coalitionary support. Similarly, a broad range of studies has shown that grooming is

408 traded for agonistic support in several primate species (Carne et al., 2011; Hemelrijk, 1994,
409 Kaburu and Newton-Fisher, 2015; Schino et al., 2007; Seyfarth and Cheney, 1984; Silk, 1992),
410 but our work provides preliminary evidence that such exchange might emerge early in life,
411 which is an exciting avenue for continued research. During SI, however, individuals more central
412 in social grooming networks received less frequent coalitionary support. There are several
413 possible explanations, all which require follow-up study. First, during SI, it is possible that social
414 relationships and “trust” may have been broken down, and they must be re-established, which
415 may have been done through grooming (e.g., Kaburu & Newton-Fisher, 2013), which is a
416 common way to solidify social bonds (McFarland, 2018). Similarly, it is possible that during SI,
417 individuals focused more on social grooming as a way to indicate social support, rather than
418 providing energetic and costly coalitionary support. Given that social grooming can lower heart
419 rates and reduce tension, the increased rates of social grooming during SI (Wooddell et al., 2017)
420 may have been a needed mechanism to help reduce tension and reduce distress during SI (Aureli
421 & Yates, 2010). Finally, it is possible that individuals connected in the social grooming network
422 may not have needed coalitionary support, as they were not as engaged in the fighting.

423 We did, however, find that coalitionary support was negatively related to social play EC
424 before and during SI, which is the opposite of the finding on social grooming. This may be
425 because the two social networks were negatively correlated with each other. Given the
426 dissociation between the two networks, this might indicate that although both of these behaviors
427 are considered “pro-social”, they may have different underlying functions, similar to how social
428 grooming can have several different functions depending on context (e.g., parasite reduction,
429 thermoregulatory, tolerance/exchange for other commodities, maintain social cohesion:
430 McFarland, 2018), whereas social play can refine motor skills (Palagi, 2018), maintain social

431 relationships (Shimada & Sueur, 2018), and assess the strength of opponents (Cordoni et al.,
432 2021). While play bouts are often short and require an equal investment between the individuals
433 involved, grooming often requires a substantial investment in time and effort and is mainly
434 disproportionately performed by only one member of the pair. Animals may make economic
435 decisions by exchanging cooperative behaviors on the basis of how much they are willing to
436 invest in a relationship (Noe et al., 2001), and grooming might offer a more honest signal than
437 play, which might explain why grooming, rather than play, was exchanged for coalitionary
438 support during the group formation, which was reversed during SI. Furthermore, if social play
439 can be a way to “test competitors,” (Cordoni et al., 2021) more socially connected individuals in
440 the social play network could be receiving more frequent coalitionary support, as individuals are
441 providing support to strong competitors. By forming alliances with strong competitors, this could
442 result in a cooperative exchange of coalitionary support.

443 Contrary to our predictions, we did not find that lower DC predicted higher HCCs, as
444 there were no significant main effects or interactions with DC on HCCs. First, there was high
445 variability in HCCs across the study period, which is partially due to the small sample size. This
446 high variability thus indicates that other factors, still unknown to us, predicted HCCs. Second,
447 although we found little overt behavioral evidence of SI following the formation of the social
448 group, as the hierarchy was formed in less than 30-minutes (Wooddell et al., 2017), the
449 formation of a novel social group is most certainly a stressor (see Dettmer et al., 2012). For all
450 the subjects in this study, this group formation was compounded by the effects of the overthrow
451 (MG subjects) and/or removal of caregivers (all subjects). Thus, the group formation itself may
452 have contributed to the variable HCCs in the period before SI. Given that cortisol is a metabolic

453 hormone that regulates energy, HCCs may be elevated in general due to higher activity budgets
454 in a group formation process.

455 SI did result in changes in social behavior. Similar to adults, rates of social grooming in
456 the peer group significantly increased (i.e., the frequency tripled) during SI, potentially as a
457 coping mechanism (Engh et al., 2005; Schino et al., 1988; Wooddell et al., 2016), whereas rates
458 of social play significantly decreased (e.g., the frequency nearly halved), possibly due in part to
459 the risky nature of social play interactions (e.g., Paquette, 1994), which may be further escalated
460 during a new group formation. However, individuals' social network positions (measured via
461 EC) were rather stable across the study. This finding indicates that juveniles did not expand their
462 social network during SI. Therefore, it is likely that peers did not change their social connections
463 (for an example, see Testard et al., 2021), but instead strengthened (via enhanced rates of
464 grooming) their connections with their preferred social partners, which requires follow-up study.
465 This may have been advantageous, as previous research has indicated that strong social bonds
466 with a few social partners have consequences for both GC production (Wittig et al., 2008) and
467 longevity (Silk et al., 2009; 2010).

468 A novel finding of this study is the potential buffering effect of social play during SI.
469 Although neither social grooming nor social play eigenvector values predicted HCCs at either
470 time point separately (although they were the best fit models), the social play values during SI
471 predicted a *smaller increase* in HCCs during SI. This finding indicates that although social play
472 was potentially costly and occurred at a lower frequency during SI, social play was still
473 important and individuals that were well connected and could "afford" to engage in social play
474 may have realized some benefits. In addition to the social benefits of receiving more frequent
475 coalitionary support during SI, the benefits of social play may have also been physiological. For

476 example, social play is highly rewarding, modulated by the nucleus accumbens and
477 dopaminergic transmission (Manduca et al., 2016), which can alter dendritic morphology and
478 susceptibility to social stress (Burlinson et al., 2016). Our findings are consistent with previous
479 work showing that social play is associated with decreased cortisol and stress behaviors (Biben
480 & Champoux, 1999; Norscia & Palagi, 2011; Wooddell et al., 2017), even when individuals
481 were experimentally exposed to social stressors (e.g., exposure to an unfamiliar human subject:
482 Schöberl et al., 2016), or social separations (e.g., Mustoe et al., 2014). Thus, there may be a
483 negative feedback loop, whereby stress limits but does not extinguish social play, and social play
484 also limits stress. For young mammals, in which social play is a predominant behavior, social
485 play can be particularly important in the regulation of the HPA axis. Thus social instability itself
486 may not be particularly stressful for young primates, but rather how they *behaviorally adapt* may
487 be the more important factor. Given that juvenile macaques engage in social play frequently
488 (Kulik et al., 2015) which decreases as they transition into adulthood, social play may be an
489 important regulator of the HPA axis in juvenility, which may then switch to social grooming in
490 adulthood (e.g., of social grooming on HCCs: Wooddell et al., 2016; 2017). Of course, future
491 research should corroborate our preliminary findings.

492 Our study is not without its limitations. The most obvious limitation is this study's
493 sample size. Studies that focus on SI are often opportunistic and are thus retrospective, limiting
494 our ability to have large sample sizes and multiple variables to test and control for. Replication is
495 therefore needed in larger cohorts and colonies where other variables (e.g., sex) can be explored
496 and experimentally controlled. Another limitation is this study was not conducted in a
497 naturalistic group in which there are multiple sources of kin (and nonkin). Given that kin
498 (especially mothers) can influence offspring social networks (e.g., Timme, 1995; Wooddell et al.,

499 2019), young primates can respond to SI either by direct influences of the mother and other kin
500 or indirectly by mimicking the actions of close family. Also, mothers can act as social buffers by
501 providing a meaningful form of social support that can mitigate the stress response (Sanchez et
502 al., 2015). SI in a naturalistic group also contains multiple individuals and families fighting each
503 other, which would likely be much more salient than group formation for peer group of ~1 year-
504 olds, which could explain the lack of effects of SI and DC on HCCs. Therefore, future research
505 should seek to examine social SI in a naturalistic group.

506 However, our study is advantageous in beginning to examine how juveniles respond to SI
507 in the absence of the influence of other adult kin. These findings provide a preliminary analysis
508 for future studies about how personality, genetics, and early social experiences can lead to
509 coping strategies, all of which can provide important translational research for humans. Another
510 limitation is that, given the opportunistic nature of this study, our sex ratio was heavily skewed
511 towards males (14 males, 4 females), thus not allowing us to draw conclusions about potential
512 sex differences in behavioral and hormonal adaptation to SI. Given that juvenile females direct
513 their social interactions to adult kin, particularly grooming, whereas males are more involved in
514 play interactions, particularly with peers (Kulik et al., 2015), the sexes may employ different
515 behavioral strategies in handling SI, although we were unable to study sex differences due to this
516 skewed sex ratio. Future research should include sex as an effect when examining how juveniles
517 respond to SI. Moreover, a larger observation time would have been ideal, but unexpected
518 managerial decisions precluded this. Finally, given that we studied a yearling group immediately
519 after group formation, although the behavioral data indicated the group was stable (especially
520 compared to after relocation), an ideal comparison would have been studying a long-term social
521 group during stability and instability. Given that group formations are often used as captive

522 studies of SI, this brings into question whether all types of group formations really are forms of
523 SI. Future work will be able to address these questions.

524 **Conclusion**

525 SI may occur rather frequently in the social lives of adult primates (particularly males),
526 although considerably less is known about how SI influences behavioral and hormonal
527 development in juveniles. We found that yearling rhesus macaques respond to SI with changes in
528 social behavior, and that social play may have acted as a potential social buffer in regulating the
529 HPA-axis. This research adds to the growing body of literature of the importance of social play
530 in the lives of developing primates and highlights the need for continued research.

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