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2 Monitoring of group mates in relation to their activity in

3 mandrills

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5 **Short title:** Social monitoring in mandrills

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17

18 ABSTRACT

19 Primates are known to have considerable knowledge about the social
20 relationships that link their group mates, and are likely to derive this
21 information from observing the social interactions that occur in their social
22 group. They may therefore be hypothesized to pay particular attention to the
23 social interactions involving group mates. In this study, we evaluated how the
24 attention captive mandrills (*Mandrillus sphinx*) devote to their group mates was
25 modulated by the behavior of the latter. Mandrills looked most frequently at
26 foraging individuals and least frequently at sleeping individuals. Mandrills also
27 looked at grooming individuals more than at individuals that were simply sitting
28 in contact. Grooming dyads were looked at regardless of the social rank and
29 kinship of the individuals involved. These results contribute to our
30 understanding of how primates obtain their social knowledge.

31

32 **Key Words:** Social cognition; Grooming, Attention; *Mandrillus sphinx*

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35 INTRODUCTION

36 In order to survive, primates need in-depth and updated knowledge
37 about their environment. Such knowledge can be acquired either individually or
38 socially, by observing how group companions interact with potential sources of
39 food or danger (Cook & Mineka, 1990; Rapaport & Brown, 2008). In order to
40 compete successfully, primates also need updated knowledge about the social
41 relationships that link their group mates. Indeed, research conducted in the last
42 40 years has shown that primates have considerable social knowledge. Not
43 only are they aware of relatively stable characteristics of third-party social
44 relationships such as dominance and friendships (reviews in Seyfarth &
45 Cheney, 2012, 2015), but they also appear to keep updated information on
46 more transient phenomena such as sexual consortships, take-overs of one-
47 male units, and postconflict reconciliation (Crockford et al., 2007; Judge &
48 Bachmann, 2013; le Roux & Bergman, 2012).

49 Given that the verbal exchange of social information is obviously
50 precluded to nonhuman primates, they must necessarily obtain their social
51 information individually and observationally. We know very little, however,
52 about what aspects of the social life of their group mates they attend to. In one
53 of the few studies that addressed this issue, Tiddi et al. (2017) showed that
54 Japanese macaques (*Macaca fuscata*) did not obtain information about the
55 kinship relationships of their group mates by remembering early mother-infant
56 interactions, but seemed to keep an updated record of affiliative interactions
57 occurring among group mates. They apparently relied on a rule of thumb that

58 considered as related all dyads that exchanged frequent affiliation, and were
59 thus unable to distinguish the kin from the "friends" of their group mates.

60 If primates keep some sort of record of the interactions that occur
61 among their group companions, we may hypothesize that they must pay
62 particular attention to such interactions. The available information about how
63 the attention primates pay to group mates is modulated by their behavior is
64 scanty. A few studies showed primates (and non-primates) are interested in
65 observing others engaged in ecologically relevant activities such as food
66 manipulation or extraction (Ottoni et al., 2005; Range & Huber, 2007; Scheid et
67 al., 2007). Barbary macaques (*M. sylvanus*) have been shown to attend to
68 scratching in others, possibly as a way to monitor their emotional state
69 (Whitehouse et al., 2016). Bonobos (*Pan paniscus*), showed an attentional bias
70 towards images of sexual or grooming behavior (Kret et al., 2016). Overall, it is
71 clear that this is a subject that requires further investigation.

72 In this study, we first replicated previous analyses of the effects of
73 dominance rank and kinship on attention paid to group mates (Schino &
74 Sciarretta, 2016). Then we evaluated how the attention paid by captive
75 mandrills to their group mates is modulated by their activity. Given the obvious
76 ecological relevance of finding food, we expected attention directed to
77 foraging individuals to be high (although finding food may be less relevant in
78 captivity). We hypothesized that mandrills would pay particular attention to the
79 social interactions of group mates as a consequence of the need to monitor
80 the state of their social relationships. We thus compared the attention paid to

81 grooming individuals to that paid to individuals that are simply sitting in
82 contact, as well as the attention paid to individuals that are in proximity to a
83 group mate to that paid to lone individuals (see the Methods for details and
84 justification). We also expected that active individuals would attract more
85 attention. We thus compared the attention paid to sleeping and awake group
86 mates. Exploratory analyses tested whether the effects of dominance rank and
87 kinship was modulated by the activity of the target, and whether the attention
88 paid to grooming was modulated by individual characteristics. Here, we
89 hypothesized that rare grooming events should attract more attention than
90 common grooming events.

91

92 METHODS

93 **Ethical Note**

94 This was a purely observational study conducted in a zoo setting. It
95 complied with the Italian law, which requires no authorization for such studies,
96 and with the American Society of Primatologists' principles for the ethical
97 treatment of non-human primates.

98

99 **Subjects and Housing**

100 The subjects of this study belonged to a captive group of mandrills living
101 in the Rome zoo (Bioparco). Initially, the group included two males and 10
102 females, but one male and one female died shortly after the beginning of data

103 collection, and the few data that had been collected on them were discarded.

104 Details on the group composition can be found in Table 1.

105 The group lived in a 240 m² outdoor enclosure connected with indoor
106 rooms. The enclosure was enriched with ropes, trunks and perches. Mandrills
107 were fed twice a day with vegetables, fruits, seeds and monkey chow. Seeds
108 were often dispersed in the substrate, and mandrills spent a considerable
109 amount of time searching for food. Water was available ad libitum.

110 Information on maternal kinship was derived by demographic records.
111 Animals were arranged in a linear dominance hierarchy on the basis of
112 unidirectional dyadic aggressions using the I&SI method as implemented in
113 DomiCalc (de Silva et al., 2017; Schmid & de Vries, 2013). Further information
114 on the subjects of this study can be found in Table 1.

115

116 **Data Collection**

117 Data on glances were collected during "focal dyad" observations lasting
118 three minutes. Each observation session had a subject and a target. The
119 observer recorded all glances directed by the subject to the target. We
120 collected data on a single target for two reasons: first, we felt it would increase
121 the reliability of data collection (focusing on a single target is easier than having
122 to take into account all possible targets); second, our stringent criteria about
123 the visibility and activity of the target (see below) were impossible to be
124 monitored continuously on all possible targets.

125 Glances were defined as "orienting the head towards the target". Note
126 that since data were not collected when the subject was engaged in any social
127 interaction (see below), this definition excludes the sustained looking
128 associated with grooming or threatening. Since in primates staring directly at a
129 target is often interpreted as a threat, glances directed at group mates are
130 generally very brief. This is the reason most previous studies on social
131 attention measured rates rather than durations. We followed this tradition.
132 Furthermore, being glances very brief, measuring their duration would be
133 nearly impossible under the observational conditions of this study. Actual gaze
134 direction (as revealed by eye movement) helped identify glances but was not
135 always recognizable by the observer. Recording actual gaze direction in freely
136 interacting animals is extremely difficult. That is why most previous studies
137 resorted to definitions that included head orientation (see the Supporting
138 Information in Allan & Hill 2017). It is reasonable to assume that measuring
139 head orientation as an estimate of gaze direction introduces noise but not bias
140 in the data.

141 Observation sessions were not initiated if an aggression (involving any
142 member of the social group) had occurred in the previous 10 minutes. At the
143 beginning of the observation session, the subject had to be awake and not
144 engaged in any social interaction. The target had to be visible by the subject,
145 involved in one of the activities described in Table 2, and had to be at least 1 m
146 away from the subject.

147 Observation sessions were interrupted if: the subject or the target were
148 not any more visible to the observer; the target was not any more visible to the
149 subject; the subject was involved in any social interaction; an aggression
150 occurred in the group; the target changed its activity, including a change in the
151 direction of grooming; the distance between the subject and the target
152 decreased to less than 1 m. Observation sessions lasting less than 30 s were
153 discarded. We were interested in (and analyzed) the effects of characteristics
154 of the grooming dyad such as the difference in dominance rank between
155 groomer and groomee. That is why we interrupted the observation session if
156 the direction of grooming changed. Note also that: i) observation sessions
157 were rather short (3 minutes) so that this sort of interruption occurred rarely; ii)
158 there is no reason to suppose that interrupting observation sessions
159 introduced any bias in the data.

160 A total of 4358 observation sessions were available for analysis (details
161 in Tables 1 and 2). We were especially interested in the monitoring of the social
162 interactions of group mates, and biased data collection accordingly (Table 2).
163 Our ability to obtain data was however constrained by the relative frequencies
164 of the different behaviors so that, for example, sitting in contact was
165 underrepresented in our sample.

166 We also conducted group scans every 15 minutes (for a total of 2196
167 scans) recording all dyads engaged in grooming. Finally, we recorded
168 aggressive events (threats, chases and physical assaults) ad libitum.
169

170 **Data analysis**

171 All our analyses were within-subject (fixed effect) conditional Poisson
172 regressions with bootstrap standard errors. Within-subject regressions allow
173 the use of multiple data points per subject while avoiding pseudoreplication. In
174 within-subject regressions, each individual is compared only with itself
175 (similarly to a paired sample t test), so as to exclude the effects of unknown
176 and unmeasured variables and avoid the confusion between within-subject
177 and between-subject effects (Allison, 2009; van de Pol and Wright, 2009).

178 The dependent variable of all analyses was the count of glances
179 recorded in each observation session (i.e., each observation session
180 contributed one data point). The duration of the observation sessions was
181 entered as an exposure variable. Independent variables included the rank of
182 the target, the degree of maternal kinship between the subject and the target,
183 and the activity of the target. The latter was entered as a dummy variable (i.e.,
184 as a set of six indicator variables each corresponding to one of the activities)
185 and we assessed its significance using a Wald test that tested the null
186 hypothesis that the effects of all the indicator variables were jointly zero.

187 Pairwise comparisons of the effects of the different activities of the
188 target applied the Šidák correction in order to control for repeated testing.
189 Beside presenting all possible pairwise comparisons, we focused on specific
190 pairs of activities comparing target behaviors that differed, as much as
191 possible, in a single key aspect. In particular, we felt it important to compare
192 behaviors that were comparable in terms of general activity level, as more

193 active animals may simply be more conspicuous (see also below for a
194 comparison focusing directly on activity level). "Foraging" was compared both
195 with "Awake alone" and with "Proximity" (since our definition of Foraging did
196 not specify whether the target should be alone or not). We compared
197 "Grooming" with "Sitting in contact", since both these contexts implied that
198 two animals were stationary and very close to each other. We compared
199 "Awake alone" with "Proximity" since for both contexts our definition did not
200 specify whether the animals were sitting or standing and the only difference
201 was the presence (within 1 m) of a group mate. Finally, we compared
202 "Sleeping" with "Awake alone" since in both contexts no group mate was
203 present nearby.

204 A separate analysis (again, a within-subject conditional Poisson
205 regressions with bootstrap standard errors) focused on grooming (i.e., was
206 limited to those observation sessions in which the target was involved in
207 grooming). It tested the effects of characteristics of the grooming dyad such as
208 their kinship, rank distance, and baseline frequency of grooming on glance
209 rate.

210 All statistical analyses were run on Stata 14.2 (StataCorp, 2015).

211

212 RESULTS

213 Both target rank and subject-target kinship affected the rate of glances
214 directed by the subject to the target: mandrills directed more glances at high-
215 ranking and at unrelated individuals (coeff.=-0.036, z=-8.22, N=4358, P<0.001

216 and coeff. $=-0.262$, $z=-3.05$, $N=4358$, $P=0.002$, respectively). Controlling for
217 rank and kinship, the behavior of target affected potentially the glance rate of the
218 subject (Wald test: $\chi^2=363.57$, $df=5$, $P<0.001$; Fig. 1).

219 Pairwise comparisons between target behaviors showed several
220 significant differences (Table 3). Foraging was the target behavior most looked
221 at by mandrills; specifically, it was looked at more than both "Awake alone"
222 and "Proximity". Confirming our predictions, animals engaged in grooming
223 were looked at more than animals that were simply sitting in contact to each
224 other. Similarly, animals that were in proximity to a group mate were looked at
225 more frequently than lone animals (compare "Proximity" with "Awake alone").
226 Finally, awake individuals were looked at more than sleeping individuals
227 (compare "Awake alone" with "Sleeping alone").

228 In order to evaluate whether the effects of target rank and of subject-
229 target kinship were modulated by the behavior of the target, we repeated the
230 first analysis presented above adding the interactions between target rank and
231 target behavior and between subject-target kinship and target behavior. The
232 interaction between target rank and target behavior was significant (Wald test:
233 $\chi^2=60.38$, $df=5$, $P<0.001$), while that between subject-target kinship and target
234 behavior was not ((Wald test: $\chi^2=6.85$, $df=5$, $P=0.232$). Analyses of the effect of
235 target rank split by target behavior revealed that glance rate increased with
236 increasing target rank for all behaviors examined but for grooming and sitting
237 in contact (Fig. 2). Note that while the nonsignificant effect obtained for targets
238 engaged in sitting in contact may be explained by the relatively small sample

239 size, this is not a likely explanation for grooming, that had by far the largest
240 sample size of all the activities we considered (Table 1).

241 Focusing on grooming, we analyzed the effects of the characteristics of
242 the grooming dyad on the glances the subject directed to it. Neither the rank
243 difference between groomer and groomee (coeff.=0.010, $z=0.75$, $N=1520$,
244 $P=0.451$), nor their degree of kinship (coeff.=0.206, $z=0.97$, $N=1520$, $P=0.330$),
245 nor their baseline frequency of grooming (coeff.=-0.156, $z=-0.11$, $N=1520$,
246 $P=0.916$) affected the glances they received from the subject.

247

248 DISCUSSION

249 The results of this study show that the behavior of group mates is a
250 potent modulator of the attention mandrills pay to them. Mandrills looked most
251 often at foraging individuals and showed particular interest for individuals
252 involved in social interactions. Mandrills also differentiated sleeping from
253 awake individuals, showing that they were sensitive to rather subtle differences
254 in the behavior of their group mates.

255 A previous study showed mandrills devoted particular attention at
256 individuals that had recently been involved in a fight (individuals that are also
257 known to be particularly likely to redirect aggression to bystanders; Schino &
258 Marini, 2012; Schino & Sciarretta, 2016). In the same vein, in this study more
259 glances were directed at high-ranking and at unrelated individuals (see also
260 Emory, 1976; Pitcairns, 1976), and very little glances were directed at sleeping
261 individuals (that presumably present very little danger). These observations are

262 coherent with field studies reporting a greater attention devoted to potentially
263 dangerous individuals and social contexts (e.g., Gaynor & Cords, 2012; Watts,
264 1998). Generally speaking, one of the functions of monitoring group mates
265 seems to be the detection and possibly the anticipation of the risk of
266 aggression, although in the field vigilance against predators often makes the
267 identification of social monitoring more difficult (Allan & Hill, 2017; Treves,
268 2000).

269 It should be noted that our observation that mandrills looked at
270 unrelated individuals more than at their kin stands in direct contrast with the
271 results of a previous study on the same social group (Schino & Sciarretta,
272 2016). While it is difficult to find an explanation for this discrepancy, it should
273 be noted that the two studies differed somewhat in the group composition (in
274 the previous study several subadult, natal males were present), in the data
275 collection procedure (in the previous study observation sessions had two
276 targets instead of one, and the target activity was not controlled) and in the
277 data analysis (in the previous study averages per dyad, rather than individual
278 observation sessions, were the unit of analysis). None of these differences
279 stands as an obvious candidate for explaining the different results obtained
280 about the effect of kinship on glance rate. At any rate, the differences between
281 the results of these two studies highlight that patterns of social attention may
282 in some cases be sensitive to methodological details that appear of minor
283 importance (see also Allan & Hill 2017). It should however also be noted that
284 other patterns of social attention seem in contrast to be extremely robust even

285 in the face of interspecific and methodological differences. In fact, our
286 observation that mandrills looked at high-ranking individuals more than at low-
287 ranking individuals is consistent with several previous studies conducted both
288 by us and by others (Emory, 1976; Keverne et al., 1978; Pitcairns, 1976; Schino
289 & Sciarretta, 2016).

290 Both primates and non-primates have been shown to be particularly
291 attentive to foraging individuals (Ottoni et al., 2005; Range & Huber, 2007;
292 Scheid et al., 2007). Our observation that mandrills paid particular attention to
293 foraging individuals suggests that, even in a captive environment, group mates
294 may constitute an important source of ecologically relevant information.

295 Clearly, in captivity the degree to which foraging group mates attract attention
296 is likely to depend on the details of the routine of food administration. When
297 food is dispersed in the enclosure, group mates can more easily provide useful
298 information than when food is clumped in a single pile or always put in the
299 same place.

300 Mandrills seemed to be interested in the social interactions among their
301 group mates. Very little comparable information is available in the literature, a
302 notable exception being a study by Kret et al. (2016) that showed bonobos
303 biased their attention towards pictures of grooming and sexual behavior.

304 Whether this is a general primate pattern remains to be ascertained.

305 Intriguingly, in mandrills grooming individuals were looked at irrespective of
306 their dominance rank. While for most of the target's behaviors that we
307 examined high-ranking individuals were looked at more than low-ranking

308 individuals, grooming low-ranking individuals were looked at as much as
309 grooming high-ranking individuals. Also, grooming was looked at irrespective
310 of the rank difference between groomer and groomee, of their kinship, and
311 (contrary to our expectations) of their baseline frequency of grooming (that is,
312 rare grooming events were not looked at more than common events).
313 Grooming seemed to be always equally interesting.

314 The general attention paid to grooming cannot be explained in terms of
315 the need to monitor potentially dangerous situations, as grooming individuals
316 do not constitute an impending threat. In contrast, the interest shown towards
317 grooming individuals is likely to derive from the need to monitor and update the
318 information about social relationships among group mates. Primates may need
319 an unbiased estimate of the grooming interactions occurring among group
320 mates and, accordingly, mandrills did not bias their attention towards any
321 particular class of grooming dyads. It is also interesting to note that mandrills
322 differentiated between grooming and sitting in contact. Although human
323 observers often conflate grooming and passive contact as indicators of general
324 affiliation (e.g., Silk et al., 2013), these two behaviors imply different costs and
325 benefits and seem to be regarded by monkeys themselves as differentially
326 worth of attention.

327 Visual monitoring has been shown to have a specific genetic basis
328 (Watson et al., 2015) and is likely to have adaptive consequences by allowing
329 the acquisition of valuable social and ecological knowledge. Primates are
330 known to use in agonistic contexts the social knowledge they derive from

331 monitoring group mates (Perry et al., 2004; Schino et al., 2006), although we
332 still have very little evidence that this social knowledge actually has positive
333 functional consequences (Tiddi et al., 2017). Elucidating the fitness
334 consequences of variation in social knowledge seems thus to be an important
335 research priority for future studies.

336

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341

342 DATA AVAILABILITY STATEMENT

343 Data available on request from the authors.

344

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444

Table 1. Subjects of the study.

Name	Sex	Rank	Matriline	Observation sessions as subject	Observation sessions as target
Bart	m	1	b	302	374
Beta	f	10	b	442	262
Blanca	f	2	b	407	564
Bunni	f	3	b	463	403
Genni	f	7	g	508	552
Giorgia	f	8	g	499	485
Giulia	f	5	g	410	468
Greta	f	6	g	445	321
Irene	f	4	g	481	593
Malinka	f	9	m	401	336

Table 2. Behaviors of target considered in this study.

Behavior	Definition	N° of observation sessions
Awake alone	Sitting or standing with eyes open; no other individual is within 2 m	508
Foraging	Eating or searching in the substrate	683
Grooming	Careful picking and/or slow brushing of another monkey's fur using the hands and/or the mouth; if interrupted for more than 15 s it is considered terminated; both grooming given and grooming received are included	1525
Proximity	Being within 1 m of another individual (but not in contact)	1101
Sleeping alone	Sitting or lying with eyes closed; no other individual is within 2 m	416
Sitting in contact	Sitting in physical contact with another individual who is also sitting	125

Table 3. Glances directed at the target in relation to its behavior: pairwise comparisons.

	Awake alone	Foraging	Grooming	Proximity	Sleeping alone	Sitting in contact
Awake alone		z=-4.77 P<0.001	z=-1.01 P=0.997	z=-3.94 P=0.001	z=7.16 P<0.001	z=4,53 P<0.001
Foraging	z=4.77 P<0.001		z=7.23 P<0.001	z=2.46 P=0.191	z=14.87 P<0.001	z=6.72 P<0.001
Grooming	z=1.01 P=0.997	z=-7.23 P<0.001		z=-8.14 P<0.001	z=9.34 P<0.001	z=5.10 p<0.001
Proximity	z=3.94 P=0.001	z=-2.46 P=0.191	z=8.14 P<0.001		z=11.05 P<0.001	z=7.71 P<0.001
Sleeping alone	z=-7.16 P<0.001	z=-14.87 P<0.001	z=-9.34 P<0.001	z=-11.05 P<0.001		z=-2.63 P=0.120
Sitting in contact	z=-4,53 P<0.001	z=-6.72 P<0.001	z=-5.10 p<0.001	z=-7.71 P<0.001	z=2.63 P=0.120	

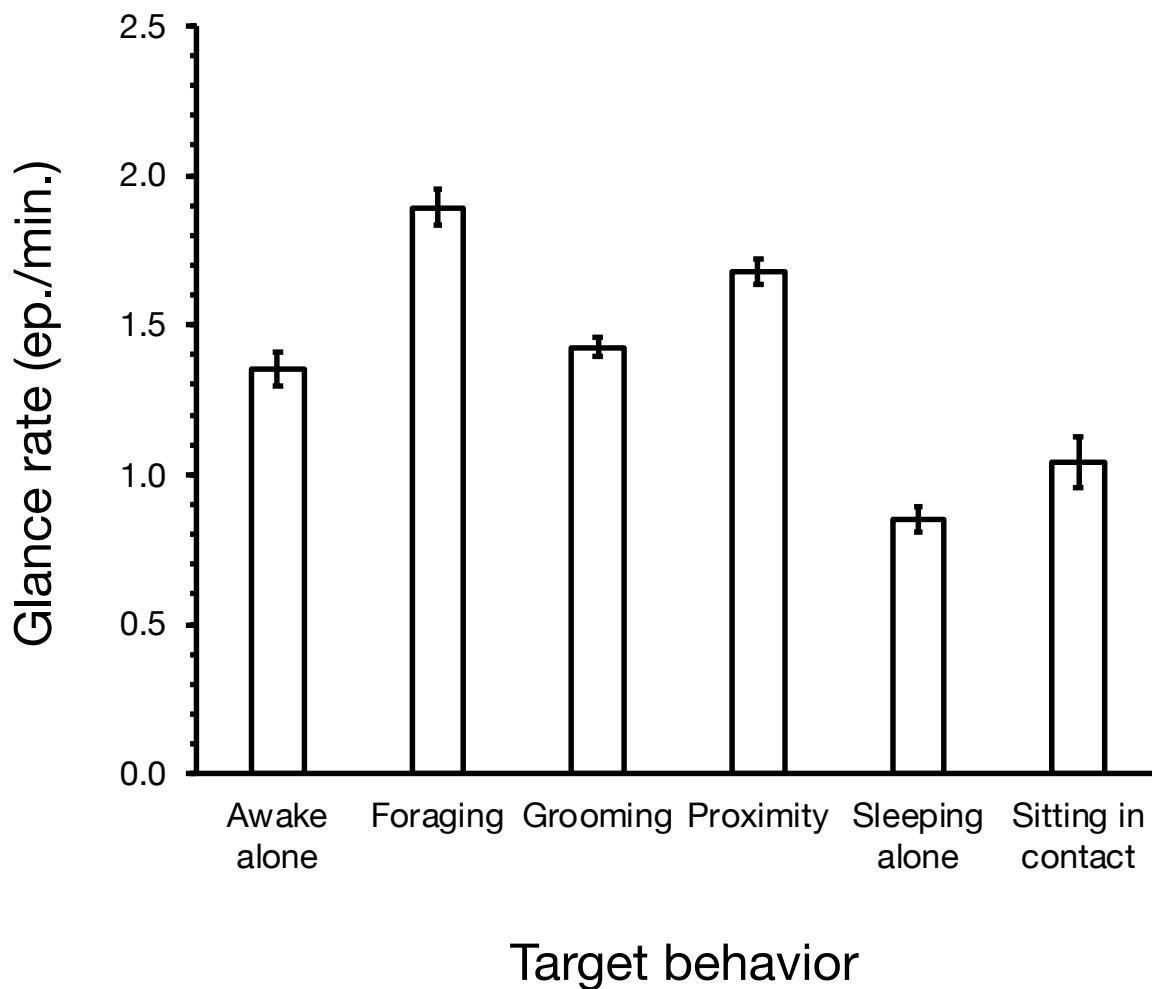


Figure 1. Effects of the target behavior on the rate of glances the subject directed to the target. Marginal means and standard errors, controlling for variation in the target dominance rank and in target-subject kinship.

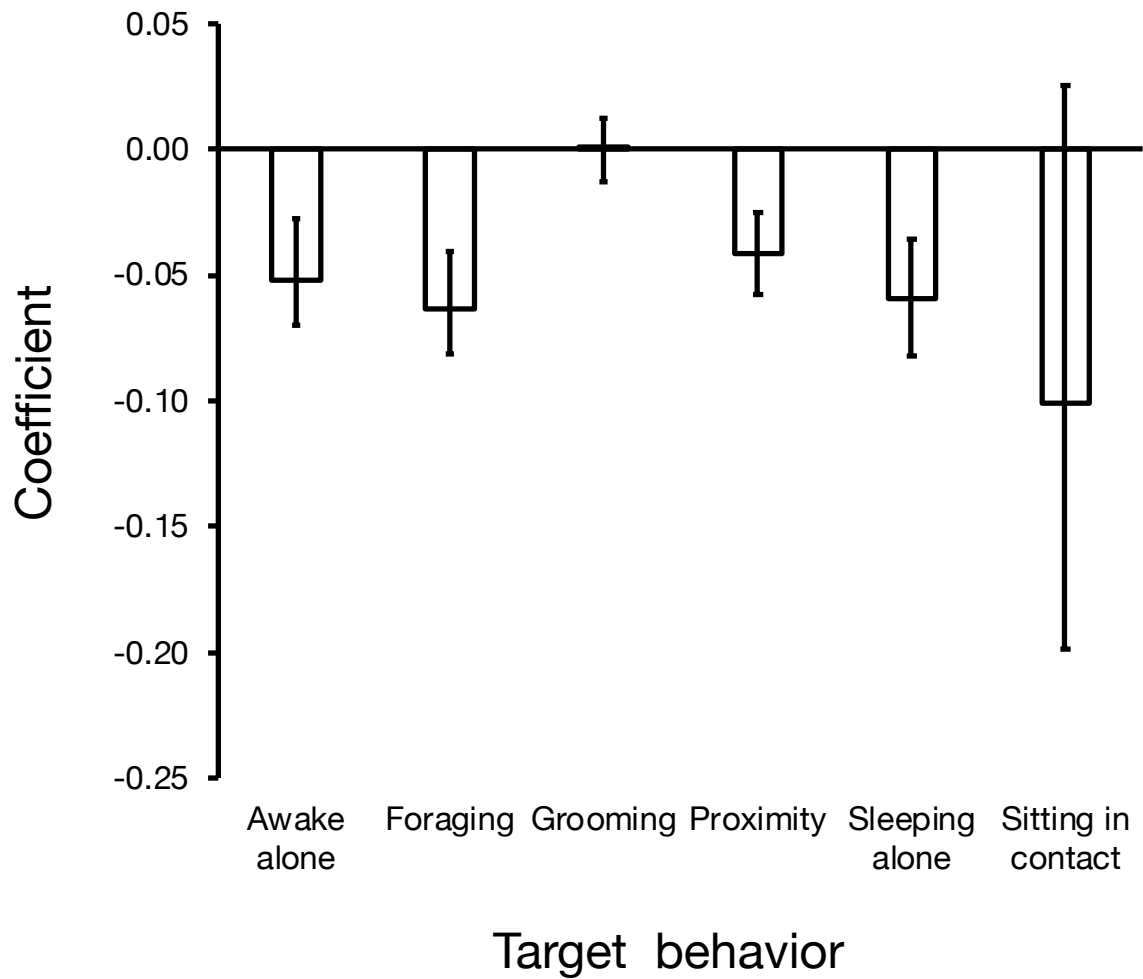


Figure 2. Effects of the target behavior on the relation between target rank and subject's glance rate. Coefficients of the separate Poisson regressions (and 95% confidence intervals), controlling for target-subject kinship.