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Homosexual Behavior Between Male Spider Monkeys (*Ateles geoffroyi*)

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22 Abstract

23 Homosexual behavior is defined as genital contact or genital manipulation between same-sex
24 individuals. In nonhuman primates it may regulate social relationships by serving as a means
25 of reconciliation, tension alleviation, or alliance formation. Grappling is a rare and complex
26 behavior, which most frequently occurs between same-sex individuals of the genus *Ateles*
27 and can include mutual manipulation of the genitalia. Here we report three cases of penile-
28 anal intromission during grappling between wild male spider monkeys living in the natural
29 protected area of Otoch Ma'ax Yetel Kooh, Mexico. In all the observed cases the same adult
30 male was the actor. To our knowledge, this is the first report of penile-anal intromission
31 between males in any New World primate species.

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33 **Key words:** *Ateles*, homosexual behavior, mounting, grappling

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47 **Introduction**

48 Homosexual behavior, defined as genital contact or genital manipulation between same-sex
49 individuals, has been described in mammals, birds, reptiles, amphibians, fishes, insects, and
50 other invertebrates (Bagemihl, 1999; Sommer & Vasey, 2006). Homosexual behavior has
51 also been documented in many primate species (Vasey, 2017). It has been interpreted as
52 facilitating alliance formation (e.g., Clay & de Waal, 2015), reconciliation (e.g., Hohmann &
53 Fruth, 2000), dominance signaling (e.g., Vasey & Sommer, 2006) and tension regulation
54 (e.g., Clay & de Waal, 2015).

55 Spider monkeys are New World primate species for which homosexual behavior has
56 not been previously reported. Like chimpanzees (*Pan troglodytes*) and bonobos (*Pan*
57 *paniscus*), spider monkeys live in multi-male, multi-female communities characterized by a
58 high degree of fission-fusion dynamics (Aureli et al., 2008). Thus, individuals are almost
59 always in subgroups comprised of only a subset of community members, and subgroups
60 change composition frequently throughout the day due to fissions and fusions with other
61 community members. This characteristic of their social system creates opportunities for
62 individuals to isolate themselves from other community members.

63 Grappling is a complex and relatively rare social interaction of spider monkeys that
64 usually occurs out of view of other community members and may involve face greeting, face
65 touching, prolonged mutual embrace, prehensile tail intertwining and mutual or unidirectional
66 manipulation of genitalia with mouth, hands or feet (Eisenberg & Kuehn, 1966; Schaffner,
67 Slater, & Aureli, 2012). Participating individuals typically make an ook-ook vocalization
68 (Eisenberg & Kuehn, 1966). Grappling can occur in male-male, female-female and male-
69 female dyads, but it is most frequently observed between males (Eisenberg & Kuehn, 1966).
70 To date, grappling has been reported between males of different age classes (Schaffner et al.,
71 2012). Even though grappling was not initially described as homosexual behavior by

72 Eisenberg and Kuehn (1966), it meets the criteria for homosexual behavior when genital
73 manipulation occurs between same-sex partners. Here we report three cases of anal-genital
74 contact with intromission by one adult male spider monkey (TU) with three different adult
75 male partners (JN, BO, EG) during grappling.

76

77 **Method**

78 **Study Site and Subjects**

79 The observations reported here were made in the natural protected area of Otoch Ma'ax Yetel
80 Kooh, Yucatan Peninsula, Mexico (20°38' N, 87°38' W), adjacent to the village of Punta
81 Laguna. The natural protected area measures 5367 ha and includes a mosaic of old-growth,
82 semi-evergreen medium forest, with trees up to 25 m in height, and 30–50 year-old
83 successional forest (Ramos-Fernandez & Ayala-Orozco, 2003).

84 Subjects were members of a well-habituated, individually recognized community of
85 spider monkeys (*Ateles geoffroyi*), which has been studied continuously since 1997. During
86 the study period, the community consisted of 37-41 individuals, including 18 adults (12
87 females and 6 males), 4-6 subadults (3-5 females and 1 male), 5 juveniles (3 females and 2
88 males), and 10-12 infants (5 females, 5-7 males). Before 2014, 3 of the 6 adult males were
89 seen in the community range only rarely, whereas during 2014 they were regularly present
90 within the community range. We therefore considered two male cohorts: the peripheral
91 cohort, which included BO and the other 2 adult males rarely seen before 2014, and the long-
92 term resident cohort, composed of the 3 other adult males (TU, JN and EG).

93

94 **Procedure**

95 Each day we recorded the identity of every member of the subgroup we initially
96 encountered and all changes in subgroup membership due to fission and fusion events. An

97 individual was considered part of the followed subgroup if it was <30 m from another
98 subgroup member (Ramos-Fernandez, 2005). We recorded fission events when one or more
99 individuals were not seen within 30 m of a subgroup member for 30 min. We recorded fusion
100 events when one or more individuals came within 30 m from any member of the followed
101 subgroup (Rebecchini, Schaffner, & Aureli, 2011).

102 Social interactions such as grappling, copulations, sexual solicitations, pectoral sniff,
103 embrace, arm-wrapping, grooming, and grooming solicitations (see Table 1 for descriptions)
104 were recorded ad libitum (Altmann, 1974) by the first and the second authors as part of a
105 study involving 1800 hours of fieldwork spread across 300 days between October 16, 2012
106 and December 11, 2014 (high interobserver reliability: Pearson coefficient >0.9).

107 Observations were made from no closer than 10 m with 8x40 binoculars. We recorded the
108 observations with a digital audio recorder and later transcribed the details into computer files.

109

110 **Results**

111 **Case 1**

112 On April 15, 2014 just before 07:00 hrs, the first and the second authors and two local field
113 assistants were following a subgroup consisting of an adult female with a dependent male
114 infant of approximately 2 years of age. At 07:25 two of the long-term resident adult males,
115 TU and JN, joined the female. JN fissioned after approximately 13 min. TU and the female
116 remained together as they foraged and rested from 07:50 until 08:43. During this period, the
117 adult female approached and solicited copulation from TU by presenting her anogenital
118 region to him, four times, as a type of proceptive behavior. After the first solicitation, TU
119 displayed a fully erect penis and started to copulate with the female. After several thrusts and
120 about 10-15 s of intromission, TU separated from the female and left her proximity. No
121 evidence of ejaculation was observed. Each of the female's subsequent solicitations resulted

122 in TU leaving her proximity, without an observable penile erection and without attempting
123 further intromission. At 08:43, TU and the female with her infant began to travel in the same
124 direction.

125 Several minutes after the female's "whinny" greeting vocalization and TU's loud call,
126 JN re-joined the subgroup. For about 30 min JN, TU, and the female foraged for fruit and
127 rested, then they started traveling. At 09:25, the two males fissioned when they moved in a
128 different direction from the female, who did not follow them but emitted frequent contact
129 calls and scanned the surrounding forest. At 09:40, TU approached JN and gave him a
130 pectoral sniff. They stayed in contact with each other and did not respond to the contact calls
131 of the female (followed by the second author), who was now about 120 m away. At 09:43,
132 TU put his cheek and mouth close to JN's face and they remained sitting in contact. At 09:54,
133 JN successfully solicited grooming from TU and at 09:56 grappling behavior started. TU had
134 a penile erection from the beginning, while touching JN's anogenital region with his tail. At
135 10:07, TU inserted his erect penis into JN's anus twice, with thrusting movement. The two
136 intromissions were short and occurred one after the other. During both intromissions, the two
137 males were sitting in a ventroventral position while TU clutched JN's tail with his hands. JN
138 made high-pitched vocalizations and twisted a few times in a possible attempt to separate
139 from TU, but TU maintained a firm grip on JN's hindquarters and tail. Eventually, JN
140 separated from TU and pressed his anogenital region against a branch while TU tried to
141 gently put him back into the previous position. After several minutes, JN shifted his position
142 and TU resumed thrusting while pressed against JN. Although the first author's view of TU
143 and JN's genital regions was slightly obscured, thrusting and TU and JN's ventroventral
144 position were still in clear view and intromission likely re-occurred. In both intromission
145 occurrences, no evidence of ejaculation was observed. At 10:30 the males ceased grappling
146 behavior and began to travel together.

147

148 **Case 2**

149 On July 14, 2014, the first and the second authors, and two local field assistants were
150 following a subgroup consisting of four adult females and their dependent offspring. At 14:51
151 a subgroup fusion took place with an aggressive interaction between two or more previously
152 unseen individuals and at least one of the four adult females in the followed subgroup. The
153 long-term resident adult males TU, EG, the long-term resident subadult male MS, and the
154 peripheral adult male BO had all joined the followed subgroup. Following the conflict, BO
155 moved to within sight of TU, who made high-pitched vocalizations, which increased in
156 volume as EG passed by. At 15:03, BO approached TU and the two embraced. TU stopped
157 vocalizing and began to forage. At 15:08, while sitting in proximity to TU, BO vocalized
158 sharply and bared his teeth at the second author. BO and TU then exchanged another
159 embrace. At 15:20, BO and TU exchanged another embrace, and then started to move out of
160 sight of the other members of the subgroup. At 15:21, BO softly vocalized and then
161 approached TU; the two males exchanged a very long embrace with their prehensile tails
162 intertwined. Suddenly, BO turned and presented his hindquarters and anogenital region to
163 TU. TU wrapped his legs around BO's hips and began to thrust. Although their genitalia were
164 out of the researchers' view, TU's genitals were likely in contact with BO's anal region given
165 their relative position. TU thrust his hips forward repeatedly for several seconds. During
166 the likely intromission, BO did not vocalize and looked in the direction of the researchers,
167 away from TU. When they separated, less than 30 sec after the first thrust, TU had a penile
168 erection while BO did not. No evidence of ejaculation was observed. As they separated, TU
169 made a high-pitched vocalization and both males stared in the direction of the adult male EG
170 whom had just moved into the researchers' field of view seconds earlier. BO growled and
171 stared at EG, whereas TU moved away and down from EG while making high-pitched

172 vocalizations. No physical interaction was seen between BO and EG, and no further contact
173 between TU and BO was observed. By 15:25, all subgroup members resumed foraging and
174 TU fissioned from the subgroup around 16:00.

175

176 **Case 3**

177 On December 01, 2014, at 12:14, high-pitched vocalizations were heard from the forest just
178 behind the field house. When encountered, EG and TU were hanging in contact with each
179 other and started to stare nervously at the observers. No other monkeys were within view. EG
180 was in front of TU with TU's arm on his back. TU stopped staring at the observers and began
181 to touch and sniff EG's hindquarters and anogenital region. At 12:15 EG and TU moved to a
182 wide branch and began to grapple. At 12:16 TU touched the base of EG's tail with his foot,
183 first on the dorsal side and then underneath near EG's genitals. EG and TU lay on their sides,
184 face-to-face, and each put one arm around the other's shoulders. TU then slightly shifted and
185 inserted its erect penis into EG's anus, while in a ventroventral position. TU thrust his hips
186 forward several times, and both males continued making the same high-pitched vocalizations
187 with increasing intensity. The duration of the intromission was approximately 15 seconds. No
188 evidence of ejaculation was observed. The behavior was suddenly interrupted when EG
189 looked further into the forest, made a sharp and harsh vocalization, and separated from TU.
190 Soon afterwards, males MS and JN moved rapidly toward TU and EG. JN joined with TU
191 and together they arm-wrapped and growled while looking at EG. EG made high-pitched
192 vocalizations and stared back at JN and TU from across a gap in the canopy. At 12:21, all the
193 males stopped vocalizing, sat and vigorously scratched themselves, which is a behavior
194 indicative of anxiety in several primate species (Coleman & Pierre, 2014). No further
195 interaction was observed.

196

197 **Discussion**

198 Our observations reveal that homosexual penile-anal intromission occurs among wild male
199 spider monkeys, a finding that to our knowledge has not been reported in any New World
200 primate. Although the small number of observed cases ($N = 3$) does not allow for an in-depth
201 analysis, our observations might be elucidated in light of two of the sociosexual explanations
202 of animal homosexual behavior: strengthening social relationships (Bagemihl, 1999) and
203 tension regulation (Clay & de Waal, 2015).

204 Males involved in Case 1 (TU and JN) were regularly observed in the same subgroup
205 and frequently interacted affiliatively during the whole study period. This suggests that the
206 observed homosexual interaction was a means to strengthen their long-term social
207 relationship, as proposed in other species resulting in higher likelihood of alliance formation
208 (e.g., olive baboons, *Papio cynocephalus anubis*, Smuts & Watanabe, 1990; bonobos, Idani,
209 1991). Strengthening relationships among the long-term resident males was particularly
210 important during the observation period, as the three peripheral adult males associated
211 regularly with community females in a manner indistinguishable from the long-term resident
212 males. The peripheral males represented a potential threat to long-term resident males as male
213 group takeover has been documented previously in this species of spider monkey (Aureli, Di
214 Fiore, Murillo-Chacon, Kawamura, & Schaffner, 2013).

215 Case 2 (involving males TU and BO) was observed following a subgroup fusion
216 characterized by a brief intragroup aggression during which peripheral male BO and the two
217 long-term resident males TU and EG were present. Thus, the subsequent homosexual
218 behavior after the aggression event might support the tension-regulation hypothesis.
219 Similarly, homosexual contact is used by bonobos to reduce tension during or after conflicts
220 (e.g., Clay & de Waal, 2015).

221 A peculiar finding of our study was that the males in Cases 1 and 3 assumed a
222 ventroventral position during intromission. All descriptions of spider monkey heterosexual
223 copulation report dorsalventral positioning between participants (Gibson, 2010) as we
224 observed in Case 2. In addition to never being reported during sexual intromissions in the
225 genus *Ateles*, ventroventral positioning during sexual interactions has been reported only in a
226 handful of nonhuman primate species (Japanese macaques, Leca, Gunst, & Vasey, 2014;
227 bonobos, Kano, 1980; mountain gorillas, *Gorilla gorilla beringei*, Yamagiwa, 1987; white-
228 handed gibbons, *Hylobates lar*, Edwards & Todd, 1991; orangutans, *Pongo pygmeus*,
229 Schiirmann, 1982). From an evolutionary perspective, ventroventral positioning during
230 sexual interactions is likely facilitated by the anatomical specialization of the shoulder for the
231 suspensory patterns of brachiation (Dixson, 2009), which is one of spider monkeys' most
232 typical locomotion patterns (Youlatos, 2008).

233 The homosexual interactions we observed occurred in the absence of other
234 community members. This is in accordance with reports of both heterosexual copulations
235 (Gibson, 2010) and same-sex grappling (Schaffner et al., 2012), which are almost always
236 performed in secret. Indeed, in Cases 2 and 3, intromission was interrupted when the
237 participants likely perceived the arrival of conspecifics. Case 1 also had an element of
238 secrecy as neither participant responded to the contact calls of the nearby female, suggesting
239 an unwillingness to be located. Contrary to heterosexual copulation, in which most
240 intromissions last 14-17 minutes (Gibson, 2010), the observed male-male intromissions lasted
241 less than 30 seconds. The participants were of the same age class (fully-grown adults, 10-14
242 years old during the study period) and the oldest of the grappling partners (TU) seems to have
243 initiated at least two of the three observed intromissions. These observations complement
244 previous reports of younger males initiating grappling toward older males in the same

245 community (Schaffner et al., 2012) and contribute to the understanding of male-male social
246 interactions.

247 There are limitations to the conclusions we can make. These are the first observations
248 of penile-anal intromission despite continuous monitoring on this monkey population since
249 1997. Our observations highlight the benefits of conducting long-term field investigations on
250 habituated primate groups (Kappeler & Watts 2012), including the observation of rare but
251 significant events (e.g., within-community killing: Valero et al. 2006; infanticide: Alvarez et
252 al. 2014; incursions into neighboring territory: Aureli, Schaffner, Verpooten, Slater, &
253 Ramos-Fernandez, 2006) and concealed behaviors in *Ateles* (i.e. copulation, grappling:
254 Schaffner et al. 2012).

255

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