



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

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Abstract

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

Keywords *Ateles* · Homosexual behavior · Mounting · Grappling

Introduction

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

Spider monkeys are New World primate species for which homosexual behavior has not been previously reported. Like chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*),

spider monkeys live in multi-male, multi-female communities characterized by a high degree of fission–fusion dynamics (Aureli et al., 2008). Thus, individuals are almost always in subgroups comprised of only a subset of community members, and subgroups change composition frequently throughout the day due to fissions and fusions with other community members. This characteristic of their social system creates opportunities for individuals to isolate themselves from other community members.

Grappling is a complex and relatively rare social interaction of spider monkeys that usually occurs out of view of other community members and may involve face greeting, face touching, prolonged mutual embrace, prehensile tail intertwining, and mutual or unidirectional manipulation of genitalia with mouth, hands, or feet (Eisenberg & Kuehn, 1966; Schaffner, Slater, & Aureli, 2012). Participating individuals typically make an ook–ook vocalization (Eisenberg & Kuehn, 1966). Grappling can occur in male–male, female–female, and male–female dyads, but it is most frequently observed between males (Eisenberg & Kuehn, 1966). To date, grappling has been reported between males of different age classes (Schaffner et al., 2012). Even though grappling was not initially described as homosexual behavior by Eisenberg and Kuehn (1966), it meets the criterion for homosexual behavior when genital manipulation occurs between same-sex partners. Here we report three cases of anal–genital contact with intromission by one adult male spider monkey (TU) with three different adult male partners (JN, BO, and EG) during grappling.

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Method

Subjects

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

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

Procedure

Each day we recorded the identity of every member of the subgroup we initially encountered and all changes in

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

Social interactions such as grappling, copulations, sexual solicitations, pectoral sniff, embrace, arm wrapping, grooming, and grooming solicitations (see Table 1 for descriptions) were recorded ad libitum (Altmann, 1974) by the first and the second authors as a part of a study involving 1800 h of fieldwork spread across 300 days between October 16, 2012, and December 11, 2014 (high interobserver reliability: Pearson coefficient > 0.9). Observations were made from no closer than 10 m with 8 × 40 binoculars. We recorded the observations with a digital audio recorder and later transcribed the details into computer files.

Results

Case 1

On April 15, 2014, just before 07:00 h, the first and the second authors and two local field assistants were following a subgroup consisting of an adult female with a dependent male infant of approximately 2 years of age. At 07:25 two of the long-term resident adult males, TU and JN, joined the female. JN fissioned after approximately 13 min. TU

Table 1 Behavior and vocalization descriptions

Behavior and vocalization	Definition
Arm wrapping	The wrapping of one or both arms around another individual's body while facing away from each other and jointly threatening a third individual. It is considered a coalitionary behavior
Copulation	Sexual intromission of the penis into the female's vagina, typically accompanied by thrusting movements by the male
Embrace	Wrapping one or two arms around the shoulders or torso of another individual while facing each other; it can be mutual if both individuals put one or two arms around the body of the other simultaneously; it can be accompanied by a pectoral sniff and a guttural vocalization. Embraces have multiple functions related to reassurance (e.g., conflict reduction), and the guttural vocalization appears to have an appeasement function
Grooming	Manipulation of another individual's fur with the mouth and/or hands
Pectoral sniff	The placement of the face close to or in contact with the pectoral or armpit region of another individual; it was recorded only when it did not occur as a part of an embrace
Solicit copulation	The presentation of the anogenital region to another individual
Solicit grooming	Presentation of a body region—with the exclusion of the anogenital region—to another individual; most frequently accompanied by a single raised arm
Whinny	Contact call that could be heard at a maximum distance of 300 m
Growl	Vocalization associated with aggressive behavior
Loud call	Contact call that could be heard at a maximum distance of 800 m
Ook–ook vocalization	Vocalization associated with grappling

Definitions are based on Van Roosmalen and Klein (1988), Eisenberg and Kuehn (1966), and our own observations and expertise on spider monkeys

and the female remained together as they foraged and rested from 07:50 until 08:43. During this period, the adult female approached and solicited copulation from TU by presenting her anogenital region to him, four times, as a type of proceptive behavior. After the first solicitation, TU displayed a fully erect penis and started to copulate with the female. After several thrusts and about 10–15 s of intromission, TU separated from the female and left her proximity. No evidence of ejaculation was observed. Each of the female's subsequent solicitations resulted in TU leaving her proximity, without an observable penile erection and without attempting further intromission. At 08:43, TU and the female with her infant began to travel in the same direction.

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

Case 2

On July 14, 2014, the first and the second authors and two local field assistants were following a subgroup consisting of four adult females and their dependent offspring. At 14:51, a subgroup fusion took place with an aggressive interaction

between two or more previously unseen individuals and at least one of the four adult females in the followed subgroup. The long-term resident adult males TU, EG, the long-term resident subadult male MS, and the peripheral adult male BO had all joined the followed subgroup. Following the conflict, BO moved to within sight of TU, who made high-pitched vocalizations, which increased in volume as EG passed by. At 15:03, BO approached TU and the two embraced. TU stopped vocalizing and began to forage. At 15:08, while sitting in proximity to TU, BO vocalized sharply and bared his teeth at the second author. BO and TU then exchanged another embrace. At 15:20, BO and TU exchanged another embrace and then started to move out of sight of the other members of the subgroup. At 15:21, BO softly vocalized and then approached TU; the two males exchanged a very long embrace with their prehensile tails intertwined. Suddenly, BO turned and presented his hindquarters and anogenital region to TU. TU wrapped his legs around BO's hips and began to thrust. Although their genitalia were out of the researchers' view, TU's genitalia were likely in contact with BO's anal region given their relative position. TU thrust his hips forward repeatedly for several seconds. During the likely intromission, BO did not vocalize and looked in the direction of the researchers, away from TU. When they separated, less than 30 s after the first thrust, TU had a penile erection while BO did not. No evidence of ejaculation was observed. As they separated, TU made a high-pitched vocalization and both males stared in the direction of the adult male EG whom had just moved into the researchers' field of view seconds earlier. BO growled and stared at EG, whereas TU moved away and down from EG while making high-pitched vocalizations. No physical interaction was seen between BO and EG, and no further contact between TU and BO was observed. By 15:25, all subgroup members resumed foraging and TU fissioned from the subgroup around 16:00.

Case 3

On December 01, 2014, at 12:14, high-pitched vocalizations were heard from the forest just behind the field house. When encountered, EG and TU were hanging in contact with each other and started to stare nervously at the observers. No other monkeys were within view. EG was in front of TU with TU's arm on his back. TU stopped staring at the observers and began to touch and sniff EG's hindquarters and anogenital region. At 12:15, EG and TU moved to a wide branch and began to grapple. At 12:16, TU touched the base of EG's tail with his foot, first on the dorsal side and then underneath near EG's genitalia. EG and TU lay on their sides, face to face, and each put one arm around the other's shoulders. TU then slightly shifted and inserted its erect penis into EG's anus, while in a ventroventral position. TU thrust his hips forward several times, and both males continued making the

same high-pitched vocalizations with increasing intensity. The duration of the intromission was approximately 15 s. No evidence of ejaculation was observed. The behavior was suddenly interrupted when EG looked further into the forest, made a sharp and harsh vocalization, and separated from TU. Soon afterward, males MS and JN moved rapidly toward TU and EG. JN joined with TU and together they arm-wrapped and growled while looking at EG. EG made high-pitched vocalizations and stared back at JN and TU from across a gap in the canopy. At 12:21, all the males stopped vocalizing, sat and vigorously scratched themselves, which is a behavior indicative of anxiety in several primate species (Coleman & Pierre, 2014). No further interaction was observed.

Discussion

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

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

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

A peculiar finding of our study was that the males in Cases 1 and 3 assumed a ventroventral position during intromission. All descriptions of spider monkey heterosexual copulation

report dorsal–ventral positioning between participants (Gibson, 2010) as we observed in Case 2. In addition to never being reported during sexual intromissions in the genus *Ateles*, ventroventral positioning during sexual interactions has been reported only in a handful of nonhuman primate species (Japanese macaques, Leca, Gunst, & Vasey, 2014; bonobos, Kano, 1980; mountain gorillas, *Gorilla gorilla beringei*, Yamagiwa, 1987; white-handed gibbons, *Hylobates lar*, Edwards & Todd, 1991; orangutans, *Pongo pygmeus*, Schiirmann, 1982). From an evolutionary perspective, ventroventral positioning during sexual interactions is likely facilitated by the anatomical specialization of the shoulder for the suspensory patterns of brachiation (Dixson, 2009), which is one of spider monkeys' most typical locomotion patterns (Youlatos, 2008).

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

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

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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