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TITLE

Anxiety in Geoffroy's spider monkeys (*Ateles geoffroyi*): can scratching be used as an indicator?

SHORT RUNNING TITLE

Scratching and anxiety in *Ateles geoffroyi*

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ABSTRACT

Self-directed behavior, such as self-scratching (hereafter, scratching), occurs in several taxa across the animal kingdom, including non-human primates. There is substantial evidence that scratching is an indicator of anxiety-like emotions in a variety of non-human primate species. Despite its importance as a window into emotional states, few studies have investigated scratching in Platyrrhines. We investigated scratching patterns of 24 Geoffroy's spider monkeys (*Ateles geoffroyi*) belonging to a group living in the *Otoch Ma'ax Yetel Kooh* protected area in the Yucatàn peninsula (Mexico). We assessed whether scratching could be used as an indicator of anxiety levels in this species by testing predictions based on contexts and behaviors associated with risk and uncertainty. We found no effect of the subject's sex and age, subgroup size, male presence and the occurrence of fusions between subgroups on scratching rates. Similarly, we found no effect of infant proximity on their mother's scratching rates. Supporting our prediction, we found evidence that isolation from conspecifics affected scratching rates as individuals scratched more frequently the more time they spent isolated. Being in proximity with a partner with a relationship characterized by uncertainty affected scratching rates as individuals scratched more frequently when in proximity with a partner with whom they engaged in embraces (an indicator of uncertainty) than when in proximity with a partner with whom they did not exchange embraces. Our study provides insight into the factors affecting scratching in Geoffroy's spider monkeys, suggesting that scratching may indicate anxiety in this species at least in some contexts and thus opening a window into the emotional experience of another Platyrrhine monkey species.

KEYWORDS

Scratching, spider monkeys, anxiety, self-directed behavior, uncertainty

INTRODUCTION

Self-directed behavior, such as self-grooming and self-scratching (hereafter, scratching), occurs in several taxa across the animal kingdom, with the most common examples in birds (Delius, 1988) and mammals, including human (Troisi, 2002) and non-human primates (Aureli, 2016). Maestripieri et al. (1992) proposed that self-directed behavior could provide a window into the emotional state of animals. In addition to circumstantial evidence, etho-pharmacological studies provided evidence for a link between self-directed behavior and anxiety: rates of self-directed behavior increased after monkeys were given anxiogenic drugs and decreased after treatment with anxiolytic drugs (Schino et al. 1996, Barros et al. 2000). Anxiety-like emotions can have their roots in unpredictability and uncertainty both in human (Grupe & Nitschke, 2013) and non-human primates (Troisi & Schino, 1987; Aureli & van Schaik, 1991).

In group-living primates, the emotional state of an individual can be profoundly affected by the social context: for example, anxiety can arise after conflicts (Aureli & van Schaik, 1991), and following changes in the group dominance hierarchy (Saposlky, 1992; Engh et al., 2006) or in group composition (Tkaczynski et al., 2014). In particular, the quality of social relationships with group members is likely to be relevant to anxiety (Cheney & Seyfarth, 2009; Aureli & Fraser, 2012). Relationship quality can be described by three components (Cords & Aureli, 2000): value (i.e., what the subject gains from the relationship with a partner), security (i.e., the consistency of the partner's behavioral responses) and compatibility (i.e., the general tenor of social interactions in a dyad). In particular, higher risk of aggression is typical of less compatible relationships and unpredictability in the partner's behavior is a characteristic of insecure relationships (Cords & Aureli, 2000). Individuals are expected to perceive uncertainty when interacting with partners of low-compatibility and insecure relationships, which can be a source of anxiety and therefore linked to higher scratching rates (Maestripieri et al., 1992). Indeed, characteristics of the relationship with proximity partners affect not only heart rate (Aureli at al., 1999), but also rates of self-directed behaviors (Troisi & Schino, 1987; Kutsukake 2003, Polizzi di Sorrentino et al., 2012). For example, in long-tailed macaques (*Macaca fascicularis*) and olive baboons (*Papio anubis*) scratching rates are higher when individuals are in proximity with dominant vs. subordinate individuals, possibly because of higher risk of aggression (Troisi & Schino, 1987; Pavani et al., 1991; Castle et al., 1999). Similarly, chimpanzee (*Pan troglodytes*) females scratched more often when in proximity with less compatible partners (Kutsukake, 2003).

The absence of nearby group members can also be perceived as anxiety-producing because of an increased risk of predation (Treves, 1999; Barros & Tomaz, 2002). Predation risk is one of the main factors affecting survival in wild animals, and anti-predatory benefits are considered one of the driving factors behind the evolution of group living (van Schaik, 1983; Roberts, 1996). Predators are likely to be spotted more quickly in large groups (van Schaik et al., 1983; Krause et al., 2002; Stankowich & Blumstein, 2005), and animals spend less time vigilant in larger groups (van Schaik & van Hooff, 1983; Roberts, 1996; Beauchamp, 2019). In addition, individuals in close proximity can have a large impact on vigilance. Monkeys with no partners nearby were found to be more vigilant than those with at least one nearby conspecific (*Procolobus badius*, *Cercopithecus ascanius*, Treves, 1999; *Ateles geoffroyi*, Busia et al., 2016). As anti-predatory vigilance is shared with group members in relatively close proximity (i.e., within 5 meters) in *A. geoffroyi* (Busia et al., 2016), having no conspecific nearby could increase the predation risk perceived by an individual. Additionally, having no conspecific nearby can be perceived as a lack of social support from other group members (e.g., lack of potential coalition partners, Castles et al., 1999). Both types of perception could result in anxiety-like emotions. Indeed, there is evidence that monkeys perform higher rates of self-directed behaviors when distant from conspecifics, reflecting the anxiety experienced in such situations (Castles et al., 1999; Polizzi di Sorrentino et al., 2012).

In mothers, another source of anxiety-like emotions could be represented by their own infants. Primate mothers are protective toward their offspring (Maestripieri, 1994) and regulate other individuals' access to the infant (Schino et al., 2003). Infants who are not in close proximity with their mothers are more likely to be victims of conspecific harassment and may more easily be preyed upon (especially when the mother is engaging in social interactions; Maestripieri, 1993b), suggesting that being at a distance from her infant may be a source of anxiety for a mother. Supporting this view, mother's scratching rate increases when their infants move away from them (*Macaca mulatta*, Maestripieri, 1993a).

Based on the circumstantial and etho-pharmacological evidence accumulated in many non-human primate species, self-directed behavior is a well-accepted non-invasive indicator of anxiety (Aureli & Fraser, 2012). However, only a few studies using such an indicator have been carried out in either captive (*Saimiri sp*., Biben & Champoux ,1999*; Cebus apella*, Daniel et al., 2009) or wild populations of Platyrrhine monkeys (*Cebus capucinus*, Manson & Perry, 2000; *Cebus apella*, Polizzi di Sorrentino et al., 2012). In addition, a validation of self-directed behavior as an anxiety indicator is lacking for most Platyrrhine monkey species apart from marmosets and squirrel monkeys (*Callithrix penicillata*, Barros et al., 2000; *Saimiri* sp*., Callithrix jaccus*, Barros & Tomaz, 2002).

In this study, we investigated whether scratching can be used as an indicator of anxiety in wild Geoffroy's spider monkeys (*Ateles geoffroyi*), a Platyrrhine monkey. Spider monkeys live in large groups characterized by a high degree of fission-fusion dynamics (Aureli et al., 2008), in which individuals separate in subgroups of variable size and composition multiple times during the same day to reduce competition over resources (Kummer, 1971). Individuals who share more valuable, secure and compatible relationships (Cords & Aureli, 2000) tend to fission together (Busia et al., 2017), thus spending more time together in the same subgroup. The outcome of such a high degree of fission-fusion dynamics is a lower likelihood of aggressive interactions (Asensio et al., 2008) and reduced relevance of dominance relationships (Aureli & Schaffner, 2008; Chapman et al., 1995). As a result, we could not rely on post-aggression situations and dominance-related interactions (the two most common contexts in which researchers have documented evidence for scratching as an anxiety indicator; Aureli, 2016) as anxiety-eliciting contexts in spider monkeys. There are however other factors that may affect uncertainty and unpredictability and thus generate anxiety in spider monkeys. Although aggression is rare, its likelihood can be used to identify anxiety-eliciting situations. For example, sex and age of the individuals involved predicts the direction of aggression. Females are usually the recipient of aggression from adult and subadult males (Fedigan and Baxter, 1984; Aureli and Schaffner, 2008). Although male-male aggression is rare (Slater et al., 2009), adult males are the main initiators and the outcome may even be lethal for subadult males (Campbell, 2006; Valero et al., 2006; Vick, 2008). Also, during fusion of subgroups there is a higher risk of aggression (Aureli & Schaffner, 2007). Additionally, spider monkeys use embraces to reassure partners and reduce the likelihood of aggression. For example, other females embrace mothers with young infants before infant handling (Slater et al., 2007), and the exchange of embraces between members of different subgroups reduces post-fusion aggression (Aureli & Schaffner, 2007). Furthermore, embraces are exchanged more often between individuals who are more aggressive with each other (Rebecchini et al., 2011), and young males embrace older males, who are valuable but potentially dangerous partners (Schaffner et al., 2012). Thus, embraces indicate the perception of risk and uncertainty in spider monkeys (Saldaña Sánchez et al., 2020).

In this study, we first explored whether individual features, such as age and sex, affect scratching in wild Geoffroy's spider monkeys. We also explored whether subgroup size and the presence of males in the subgroup have an effect on scratching rates. Following the hypothesis that scratching can be used as an indicator of anxiety, we formulated predictions based on spider monkeys' behavioral patterns and the findings on other species in potentially anxiety-eliciting circumstances. We carried out the following exploratory analyses and tested the following predictions:

- Exploratory analysis 1 (E-1). Are scratching rates affected by individual features, such as age and sex?
- Exploratory analysis 2 (E-2). Are scratching rates affected by subgroup features such as subgroup size (i.e., the number of individuals present in the subgroup) and the presence of (other) males in the subgroup?
- Prediction 1 (P-1). Scratching rates are higher when an individual is isolated than when it is in proximity with at least one subgroup member, because of the higher perceived predation risk or perceived lack of social support when other group members are not around.
- Prediction 2 (P-2). Scratching rates are higher after fusions between subgroups compared to when no fusion occurs, because fusions are likely to trigger aggressive interactions between group members from joining subgroups.
- Prediction 3 (P-3). Individuals scratch more often when they are in close proximity with individuals with whom they have relationships characterized by low compatibility and security. Therefore, we expect:
    - Prediction 3a (P-3a). Higher scratching rates when in close proximity with unrelated vs. related individuals, as compatibility correlates with kinship (Rebecchini et al., 2011).

  - Prediction 3b (P-3b). Higher scratching rates when in close proximity with potentially aggressive individuals (i.e., adult males for subadult males; adult and subadult males for females) vs. those who are unlikely to be aggressive.
  - Prediction 3c (P-3c). Higher scratching rates when in close proximity with individuals with whom they do vs. do not exchange embraces, because embraces are more likely to occur between partners with relationships characterized by risk and uncertainty.
  - Prediction 3d (P-3d). Higher scratching rates when in close proximity with individuals with whom they spend less vs. more time in the same subgroup, because spending time together in the same subgroup is an indicator of compatibility.
- Prediction 4 (P-4). Mothers exhibit higher scratching rates when their infant is not in close proximity (i.e., 1 meter) vs. when it is nearby.

METHODS

Study site and subjects

The study was carried out in the *Otoch Ma'ax Yetel Kooh* protected area near the village of Punta Laguna, located in the north-east of the Yucatan peninsula (Mexico; lat. 20°38' N, long. 87°38' W). The protected area measures 5367 ha and comprises a mixture of old-growth, semi-evergreen medium forest and 30–50-year-old successional forest, with trees up to 25 m tall (Ramos-Fernandez & Ayala-Orozco, 2003). Study subjects were the adult and subadult members of a group of Geoffroy's spider monkeys. All monkeys were accustomed to human presence and could be identified individually by body and facial features. Group size and composition varied during the study period because of immigrations, emigrations, births and natural aging. The group consisted of 44-54 individuals: 6-8 adult males, 2-4 subadult males, 13-16 adult females, 4 subadult females, 8-16 juveniles and 11 infants (see Shimooka et al., 2008 for definitions of age classes). Maternal kinship was established using demographic records collected during the 25 years of observations of the study group (i.e., the identity of the mother was always recorded for every newborn) and was known for all group members except for immigrants who were considered not being maternally related to any group member apart from their own offspring. The study was carried out with permission of the CONANP (Comision Naciònal de Areas Naturales Protegidas) and SEMARNAT (Secretarìa de Medio Ambiente y Recursos Naturales). Our research complied with the American Society of Primatologists Ethical Principles for the Treatment of Non-Human Primates and followed the Code of Best Practices for Field Primatology published by the American Society of Primatologists (2014).

Data collection

Data collection started in January 2019 and lasted until May 2020, during which 727 focal samples were collected by FD. Data were collected 4 days a week during an average of 7.5 hrs per day of field work by means of 10-minute focal animal samples using continuous sampling (Altmann, 1974) of adult and subadult individuals of both sexes. We collected every instance of scratching (i.e. the individual repetitively rubs its own skin with the fingertips; we recorded a new scratching event after a 5-second break), embracing (i.e. the individual has one or both arms wrapped around the neck or back of another individual, while the two individuals are facing each other), pectoral sniffing (i.e. the individual orients its face toward or touches with its nose the pectoral gland or arm pit of another individual, without embracing) and kissing (i.e. the individual puts its cheek and/or mouth close to another individual's face, without embracing). We collapsed embracing, pectoral sniffing, and kissing together into same the behavioral category of "embrace", given their relatively low frequency and similar function (Schaffner & Aureli, 2005). We also recorded all occurrences of approaches within 1 meter and leaves during focal samples. The identity of every group member (including juveniles) within 1 meter and within 5 meters from the focal subject were recorded every 2 minutes during the focal sample, in addition to the focal subject's activity. Four activity categories were distinguished: foraging (the individual is either manipulating, consuming or looking for food, or drinking water), resting (the individual is sitting or lying on a branch, not displaying any of the other activities), travelling (the individual is moving, without displaying any social behavior) and socializing (the individual is involved in social behavior with a partner, e.g., grooming, playing). The subject of a focal sample was selected following a priority list based on a random order, prioritizing individuals for whom we had collected fewer focal samples. The minimum period between two focal samples on the same individual was 1 hour (mean number of focal samples collected on the same individual during the same day = 1.17, min = 1, max = 4). Focal samples were recorded using a portable digital audio recorder to avoid losing sight of the focal animal, and later decoded into worksheet files. In order to evaluate the consequences of fusions, post-fusion focal samples were carried out just after the fusion between subgroups following the same methodology (i.e., post-fusion focal samples started as soon as we identified a fusion event).

Subgroup composition was updated continuously with the help of trained field assistants, taking into account the occurrence of fission and fusion events. Any individual less than 30 meters from a subgroup member was considered as part of the followed subgroup, following a chain rule developed for the study group (Ramos-Fernandez, 2005; cf. Croft et al., 2008). Fusion occurred when one or more individuals from a different subgroup came within 30 meters from any member of the followed subgroup and merged to form a single subgroup, whereas fission occurred when individuals from the followed subgroup were not seen within 30 meters from a subgroup member for at least 30 minutes (Rebecchini et al., 2011).

Data analysis

Statistical analyses included data from 26 focal subjects: 8 adult males, 4 subadult males and 14 adult females (see Table S1 in the Supplementary Materials). No focal samples on subadult females were included, because they emigrated from the group 2 months after the data collection period started. Two additional females were not included in the analysis because they immigrated into the group 2 months before the end of the data collection period, which made their sightings rare and their identification unreliable. We used Generalized Linear Mixed Models (GLMMs; Baayen et al., 2008), using the RStudio software (version 1.3.1093, RStudio Team, 2020) in the R environment (version 4.0.3, R Core Team, 2020). We used the *lme4* package to run our models in R (version 1.1–17; Bates et al., 2014). We entered random intercepts for the ID of the focal subject and the day of observation (numbered progressively from the first day of fieldwork) in all models to avoid pseudoreplication (West et al., 2006). We also added individual random slopes for all predictor and control factors in all models (Barr et al., 2013), except in the model testing the predictions of Hypothesis 3 (see below). The random effect structure did not include correlations between random intercepts and random slopes to allow model convergence. We used the DHARMa package (Hartig, 2021) to determine the best distribution fit for each GLMM, which was the Poisson distribution for all models. In all models but one (see below), each focal sample constituted a data point, and scratching count during the focal sample was the dependent variable, with the duration in seconds of the focal sample entered as an offset term (i.e., an exposure variable with a known value; the offset term was log-transformed before being included in the model; Lindsey 2000; Hutchinson & Holtman, 2005) because not all focal samples had the planned 10-minute duration (N = 179, i.e., 24.6% of the total focal samples). Time of day (i.e., the hour block in which the focal sample started: e.g., 09.00-10.00) and the focal subject's activity were added as fixed control factors in all models. Focal subject's activity was based on the data collected every 2 minutes during the focal sample. If the focal subject engaged in the same activity for more than 50% of the 2-minute scans, such activity was selected for the focal sample (i.e., if the monkey foraged in more than 50% of the scans, the focal sample activity was categorized as foraging). In case no activity was performed for more than 50% of the 2-minute scans, the focal sample activity was categorized as mixed. We used variance inflation factors (VIF; Field, 2005) to examine collinearity across predictor and control factors: no factors showed a VIF value higher than 3 and therefore none was removed from the models (Field, 2005). We assessed model dispersion via the *DHARMa* package (Hartig, 2021); when a GLMM was overdispersed, we added an observation-level random factor to the model to account for the model dispersion (Harrison, 2014): such was the case for models related to E-1 and E-2 (original model dispersion = 1.46; final model dispersion = 1.08), P-1 (original model dispersion = 1.48; final model dispersion=1.08) and P-3 (original model dispersion = 1.31; final model dispersion = 0.93). Numeric variables were z-transformed to improve model convergence. Additionally, categorical variables were transformed into dummy variables and z-transformed when involved in interactions in a model in order to allow interpretation of main effects (Schielzeth, 2010). No model was overfit (i.e., each dataset was comprised of a minimum of 15 data-points per factor included in the model; Babyak, 2004). We compared each model with the corresponding null model containing only control fixed factors and/or random factors via a likelihood ratio test (Dobson et al., 2001). If a model significantly differed from the corresponding null model, we conducted a likelihood ratio test using the "*drop1*" function (Barr et al., 2013). Detailed results are presented only when the model differed significantly from the corresponding null model. Plots were created using the *ggplot2* package (Wickham, 2016).

To test E-1 and E-2, which investigate the effects of individual features, such as age and sex, and subgroup features, such as subgroup size and the presence of males in the subgroup, on scratching rates, we ran a GLMM, with age class (adult or subadult) and sex of the focal subject, subgroup size (i.e., the number of individuals in the subgroup, including juveniles and infants) and the presence of at least one male in the subgroup (i.e., a male other than the focal subject) as predictor. We did not include an interaction term between age and sex because no data on subadult females were available.

To test P-1, which predicts the effect of being isolated from conspecifics on scratching rates, we ran a GLMM using the proportion of time spent isolated in a 5-meters radius during the focal sample (calculated as the proportion of 2-minute scans in which the focal individual did not have any other monkey, except infants, within 5 meters) as predictor. We tested P-2, which investigated the effect of fusion on scratching rates, by running a GLMM using the occurrence of a fusion just before the focal sample as a binomial predictor (present or absent).

We tested P-3a, P-3b, P-3c and P-3d by examining the effect on scratching rates of features of the relationship the focal subject had with the proximity partner, such as their degree of relatedness, the degree of risk, the degree of uncertainty, and the degree of compatibility. Based on the occurrences of approach and leave collected during focal samples, we created a dyadic database, in which every row represented a subject-partner dyad considering only the parts of the subject’s focal samples in which the partner was the only individual in 1-meter proximity with the subject (to remove the influence of bystanders). Each subject-partner dyad constituted a data point (N = 93; proximity mean ± SE = 509 ± 49 seconds) in the dataset, which was used to test all four predictions in the same GLMM. We ran a GLMM using the scratching count displayed by the subject as dependent variable and the amount of time in which the dyad partner was the only individual within 1 meter of the subject as the offset term. We used the following predictors: maternal kinship between the subject and the proximity partner (binomial: kin or non-kin; kin being mother-offspring, full siblings and maternal half-siblings), the degree of risk from the proximity partner (binomial: yes or no; adult and subadult males were considered as potentially aggressive partners for females; adult males as potentially aggressive partners for adult males and subadult males), the degree of uncertainty in the relationship with the proximity partner (binomial: high uncertainty or low uncertain, based on the occurrence of at least one embrace by the subject to the partner during the data collection period; embrace is an indicator of uncertainty with a partner, Saldaña Sánchez et al., 2020), the degree of compatibility with the proximity partner based on the proportion of time the subject and the partner spent in the same subgroup, calculated as follow:

Proportion of time spent together = time (A+B) / [time (A) + time (B) – time (A+B)]

where time (A+B) is the time individuals A and B were observed together in the same subgroup, and time (A) and time (B) are the total observation time of individuals A and B, respectively. The ID of the focal subject and ID of the proximity partner were added as random factors. We did not include a random slope for the degree of uncertainty because it did not fulfill the criteria proposed by Barr et al. (2013).

To test P-4, which investigated the effect of the infant's proximity to the mother on the mother's scratching rates, we created a database using all focal samples for females who had an infant older than 3 months (because infants younger than 3 months are in proximity with the mother most of the time; Vick, 2008) and younger than 12 months (as individuals older than 12 months are more independent, Shimooka et al., 2018). The dataset was based on 102 focal samples from 7 females (Table S2). In each focal sample we considered separately the segments when the infant was or was not within 1 meter of the mother, based on approaches and leaves recorded continuously during the focal samples. The dataset therefore comprised 136 data points. We ran a GLMM with presence of the infant within 1 meter from the mother (present within 1 m or not) and its interaction with infant age (expressed in months) as predictors.

RESULTS

Analyses E-1 and E-2 showed that there was no evidence that scratching rates related to the subject's age class and sex, subgroup size and presence of males in the subgroup, as the model including these predictor variables did not differ statistically from the corresponding null model ($\chi^2 = 4.710$, df = 4, p = 0.318).

There was evidence that scratching rates related to being isolated from conspecifics (P-1), as individuals scratched more often the more time they spent isolated ($\beta = 0.262$, SE = 0.114, $\chi^2 = 4.614$, df = 1, p = 0.031; Figure 1, Table S3). There was no evidence that scratching rates related to fusion between subgroups (P-2), as the model including this predictor variable was not different from the corresponding null model ($\chi^2 = 0.013$, df = 1, p = 0.910).

We found evidence that partially supported our predictions about the effects of features of the relationship between subject and the proximity partner on scratching rates. We found no evidence to support P-3a, P-3b and P-3d as there was no significant effect of kinship ($\beta = 0.210$, SE = 0.515, $\chi^2 = 0.172$, p = 0.678), degree of risk ($\beta = -0.4469$, SE = 0.5800, df =

1, $\chi^2 = 0.589$, $p = 0.443$), and degree of compatibility ($\beta = 2.203$, SE = 1.471, df = 1, $\chi^2 = 1.954$, $p = 0.162$) on scratching rates. However, the degree of uncertainty had a significant effect on scratching rates (P-3c), with subjects scratching more often when in proximity with a partner to whom they directed at least one embrace than when in proximity with a partner to whom they did not direct any embrace ($\beta = 1.353$, SE = 0.460, df = 1, $\chi^2 = 10.966$, $p = 0.001$; Figure 2, Table S4; see Table S5 for results of an alternative model in which the degree of uncertainty was the number of embraces given to the partner).

There was no evidence that infant proximity and infant age were related to the mother's scratching rates, as the model including these predictor variables was not different from the corresponding null model ($\chi^2 = 6.030$, df = 1, $p = 0.110$).

DISCUSSION

This study provides evidence that may justify the use of scratching as an indicator of anxiety in Geoffroy's spider monkeys, at least in some contexts. Overall, our results suggest that variation in scratching rates is related to being isolated from conspecifics and uncertainty in the relationship between individuals, but not to several of the other factors that we investigated.

Despite evidence that likely recipients of aggression have higher scratching rates in other species (*Macaca sylvanus*, Kaburu et al., 2012), we did not find such a pattern in wild Geoffroy's spider monkeys, in which females and subadult males are typical recipients of aggression (Fedigan & Baxter, 1984; Vick, 2008), possibly reflecting the overall low frequency of aggression.

Subgroup size and the presence of at least one male in the subgroup also were not associated with scratching rates. Subgroup members can be at a substantial distance from one another (Aureli et al., 2012). Thus, the sheer presence of potentially dangerous adult and subadult males in the subgroup may not pose a significant threat, while the simple presence of more subgroup members may not provide a significant increase in protection from predators (or, at least, not one that the subjects can detect).

Prediction P-1 was supported by our findings: being isolated from conspecifics seems to increase scratching rates in spider monkeys, possibly highlighting the antipredator function of group living. Indeed, there is evidence that the spider monkeys at the study site can fall prey to terrestrial predators (i.e., puma, *Puma concolor*, Busia et al., 2018). Anti-predatory vigilance can be shared most effectively with close-by individuals, so that having no group member within 5 meters could result in a higher perception of predation risk and thus in higher scratching rates. This result is in accordance with studies on other primate species (e.g., Castles et al., 1999; Polizzi di Sorrentino et al., 2012; but see Manson and Perry, 2000). Nonetheless, not being surrounded by conspecifics does not relate only to predation risk but can also be perceived as a lack of social support (e.g., lack of potential coalition partners, Castles et al., 1999). It is also important to note that the effect on scratching rates was relatively small (Figure 1). Therefore, further studies on the relation between scratching and isolation from group members are needed to shed light on the causes eliciting anxiety-like emotions under these circumstances.

Prediction P-2 was not supported by our results: despite being a potentially risky event, in which aggression is more likely to occur (Aureli & Schaffner, 2007), there was no evidence that fusion between subgroups influenced scratching rates. This result may be explained by spider monkeys exchanging embraces after fusions, which reduce the likelihood of aggression (Aureli & Schaffner, 2007). The possibility to cope actively with the increased aggression risk may have prevented an increase in anxiety. Rats (*Rattus norvegicus domestica*), who could actively cope with the occurrence of a stressor, showed lower stress levels than individual who were unable to actively cope (Helmreich et al., 1999). It is possible that a similar effect underlies our finding.

We found mixed evidence for Prediction P-3, for which we expected individuals to scratch more often depending on the characteristics of the relationship with the proximity partner. Contrary to P-3a, we did not find an effect of being in close proximity with kin or non-kin on scratching rates. This finding is in contrast with what was found in tufted capuchin monkeys (*Cebus apella*), who scratched more often when in proximity with non-kin than when in proximity with kin (Polizzi di Sorrentino et al. 2012). Prediction P-3b was also not supported by our findings as close proximity with categories of potentially aggressive individuals (i.e., adult males for subadult males; adult and subadult males for females) did not affect scratching rates, despite the documented pattern of aggression found in the study species (Aureli & Schaffner, 2008). This result contrasts with findings on tufted capuchin monkeys, in which scratching occurred more often when individuals were in close proximity to potentially aggressive conspecifics (Polizzi di Sorrentino et al., 2012). Our results could be due to variables such as age and sex not accurately capturing subtle differences across partners in spider monkeys. For example, even if adult males are generally aggressive to females, being in proximity with a less aggressive adult male may elicit less anxiety compared to being in proximity with a more aggressive adult male.

We found evidence to support Prediction P-3c, as individuals showed higher scratching rates when in close proximity with group members with whom they engaged in embraces than when in close proximity with group members with whom they did not engage in embraces. As spider monkeys give embraces to reassure partners and reduce aggression (Aureli & Schaffner, 2007; Slater et al., 2007; Schaffner et al., 2012), our result suggests spider monkeys experience anxiety when close to conspecifics with whom they have relationships characterized by risk and uncertainty. Our result also indicates that self-directed behavior, such as scratching, could be used to identify the asymmetry related to how a relationship is perceived by each partner (Schino et al., 2007) if further studies focus on the scratching rates of both the individual giving and the partner receiving embraces.

Finally, Prediction P-3d was not supported by our findings as there was no evidence that time spent together in the same subgroup with a proximity partner affected scratching rates. This is in contrast with what was reported in chimpanzees who scratched more often when in proximity with partners with whom they spent less time in proximity (Kutsukake, 2003). We expected a similar result for spider monkeys as they fission preferentially in subgroups with group members with whom they have more compatible and secure relationships (Busia et al., 2017). The difference in the results of the two studies could reflect the use of different variables: time spent together in the same subgroup in our study and time spent in proximity in Kutsukake (2003). Further research is needed to shed light over the reason of this difference.

We did not find support for P-4 as infant proximity was not associated with the mother's scratching rates. When the infant is not in close proximity to its mother, it may face an increased risk of harassment (Maestripieri, 1993b) or predation (e.g., by *Coragyps atratus*, F. Dell'Anna, personal observation). The mother may experience increased anxiety because of her diminished ability to protect her infant, but we did not find an increase in scratching rates when the mother was not in close proximity to her infant. Our findings are in accord with a study on wild chimpanzees, in which there was no effect of the infant proximity on the mother's scratching rate (Kutsukake et al., 2003).

In sum, we found evidence that scratching can be used as an indicator of anxiety in Geoffroy's spider monkeys given that they scratched more often when they were isolated from conspecifics (P-1) or faced higher uncertainty in the relationship with proximity partners (P-3c). Nevertheless, scratching did not increase in other social contexts that can be considered as anxiety eliciting. Although additional research is needed to further investigate individual and social factors affecting self-directed behavior in a variety of non-human primate species, especially the under-studied Platyrrhines, our study provides insight into the factors affecting scratching in Geoffroy's spider monkeys. Most importantly, we found evidence that, in some contexts, scratching can be used as an indicator of anxiety in this species, opening a window into the emotional experience of another Platyrrhine monkey species.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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RESEARCH HIGHLIGHTS

- Individuals showed higher scratching rates the more time they spent alone, possibly due to perception of increased predation risk.
- Spider monkeys scratched more frequently when in proximity with a group member with whom they had a relationship characterized by uncertainty (indicated by the engagement in embraces) than when in close proximity with other group members.

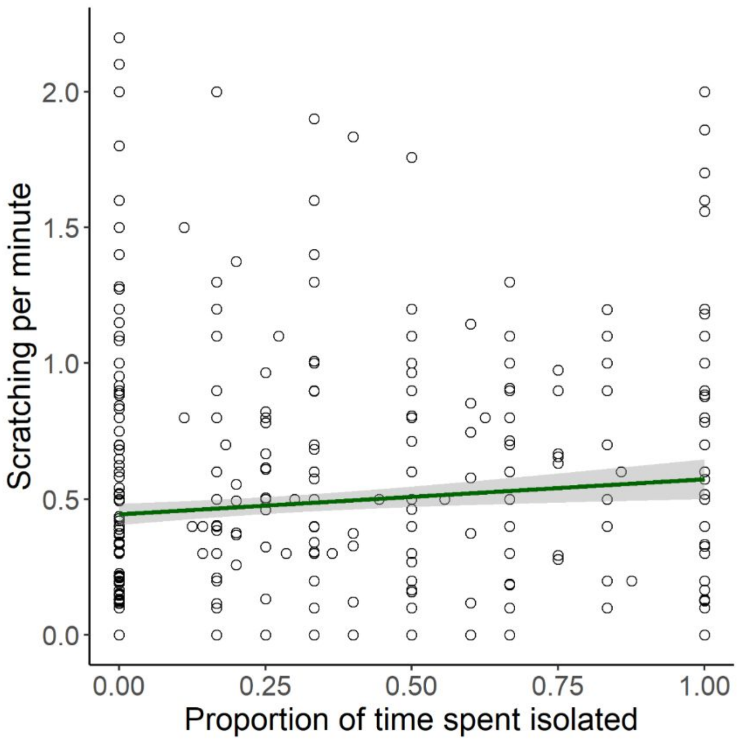

Figure 1. The relation between scratching rates per minute and the proportion of time spent isolated from conspecifics in a 5-meters radius. Data points (hollow dots), estimated regression slope (blue line) and 95% confidence interval of the estimated slope (grey area) are shown.

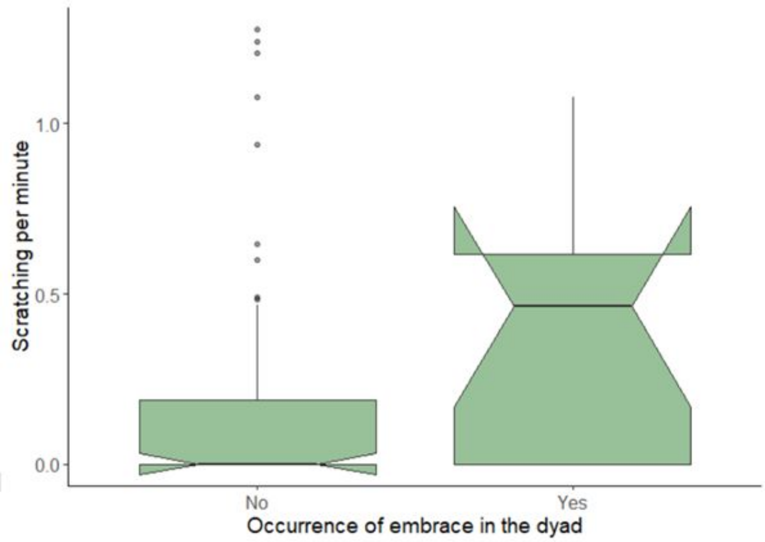

Figure 2. The subject's scratching rates per minute when in 1-meter proximity with a partner to whom the subject directed at least one embrace (Yes) and when in 1-meter proximity with a partner to whom the subject did not direct any embrace (No) during the study period. Boxplots show minimum and maximum values (lower and upper whiskers), first and third quartile (lower and upper box limits), medians (black lines) and outliers (hollow dots). Notches are used to show 95% confidence interval.

SUPPLEMENTARY MATERIALS

for “Anxiety in Geoffroy’s spider monkeys (*Ateles geoffroyi*): can scratching be used as an indicator?” by F. Dell’Anna, G. Schino and F. Aureli

Table S1 – ID, sex and age classes of the study subjects

Subject ID	Sex	Age Class
Boxhuevo	Male	Adult
Digit	Male	Adult
Eulogio	Male	Adult
Juan	Male	Adult
Korea	Male	Adult
Marcos	Male	Adult
Sancho	Male	Adult
Wiguiberto	Male	Adult
Andrés	Male	Subadult
Apolo	Male	Subadult
Daniel	Male	Subadult
Nacho	Male	Subadult
Antena	Female	Adult
China	Female	Adult
Elisa	Female	Adult
Flor	Female	Adult
Joanne	Female	Adult
Linda	Female	Adult
Lola	Female	Adult
Mandíbula	Female	Adult
Marylin	Female	Adult
Mich	Female	Adult
Pancha	Female	Adult
Rwanda	Female	Adult
Tanga	Female	Adult
Verónica	Female	Adult

Study subjects are listed with all males first, in order of age and then alphabetical order, followed by adult females in alphabetical order. No subadult females were included as study subjects, because they emigrated from the group 2 months after the data collection period started.

Table S2 - Number of focal samples per female in the dataset used to test Prediction 4.

Subject ID	Number of focal samples
Antena	2
China	23
Elisa	5
Flor	8
Joanne	25
Manidibula	13
Veronica	26

Table S3 - Results of the likelihood ratio tests for the model testing Prediction 1.

Predictor	Degrees of freedom	χ^2	p
Hour of the day	7	11.167	0.132
Subject's activity	4	23.840	<0.0001
Proportion of time spent isolated	1	4.614	0.031

The model was different from the corresponding null model ($\chi^2 = 4.614$, df=1, p = 0.003).

Table S4 - Results of the likelihood ratio tests for the model testing Prediction 3 including uncertainty as a binary variable based on the presence/absence of embraces.

Predictor	**Degrees of freedom**	χ^2	**p**
Kinship	1	0.172	0.678
Risk	1	0.589	0.443
Uncertainty	1	10.966	0.001
Compatibility	1	1.954	0.162

The model was different from the corresponding null model (χ^2 = 14.81, df=4, p = 0.005).

Table S5 - Results of the likelihood ratio tests for the model testing Prediction 3, including uncertainty as the number of embraces given.

Predictor	**Degrees of freedom**	χ^2	**p**
Kinship	1	0.216	0.642
Risk	1	0.752	0.386
Uncertainty	1	9.292	0.002
Compatibility	1	2.024	0.155

The model was different from the corresponding null model (χ^2 = 13.14, df=4, p = 0.011).