TITLE

Environmental factors affect the social behavior of captive spider monkeys (*Ateles geoffroyi*)

SHORT TITLE

Captive Environment and Spider Monkeys

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ABSTRACT

KEYWORDS

Spider monkeys, behavior, fission-fusion dynamics, housing, welfare, rehabilitation

RESEARCH HIGHLIGHTS

1. Highlight #1
2. Highlight #2
3. Highlight #3

INTRODUCTION

To ensure good animal welfare, captive institutions are challenged to provide environments that meet the cognitive, emotional, social, and physical needs of the individuals under their care (Mason 2010). Of all species commonly kept in captive facilities, nonhuman primates are among the most cognitively and behaviorally complex and therefore can be difficult to house in adequate conditions (Hosey 2005). In recent years, the paradigm is shifting towards providing captive primates with environments that are functionally appropriate for their social behavior, not just superficially naturalistic, to ensure that the physical and emotional needs of each individual are adequately provided for at each stage in their life (Schapiro 2017).

For primates with complex social dynamics, such as bonobos and chimpanzees (genus *Pan*) and spider monkeys (genus *Ateles*), captive environments may induce stress by restricting individual movements and social interactions (Hosey 2005). In the wild, these species typically live in large communities that exhibit fluid fission-fusion dynamics (Aureli et al. 2008). Each community is composed of smaller subgroups of individuals which vary in membership, size and composition over time, thereby adjusting to fluctuating ecological conditions (various sources). In these systems, each individual chooses their associates in each context, with the emergent structure being that of a highly complex and fluid society (Aureli and Schaffner 2008, Ramos-Fernandez et al. 2010, Smith-Aguilar et al. 2018). In each of these social systems, group cohesion is low; subgroups of individuals must be able to fission from one another at will to avoid unnecessary conflict (cite Hartel? Aureli and Schaffner?), reduce competition for resources (Symington, Asensio, etc.), and pursue mating opportunities (cite Gibson 2010). In captive settings, individuals of these species cannot be permitted to roam freely or choose their own social groupings and are therefore susceptible to poor welfare (find a review?).

Housing captive primates in large, complex enclosure spaces may lessen the detrimental effects of captivity. For example, an analysis of chimpanzee social networks at the Edinburgh Zoo indicated that the spacious layout of the enclosure allowed for individuals to express patterns of social preferences like those exhibited by wild chimpanzees (Clark 2011). The relationship between available space and welfare is not linear, however, since primates like chimpanzees are able to temporarily adopt behavioral strategies that mitigate the potential risks associated with being housed at higher densities (de Waal 1989). Under a *tension reduction* strategy, individuals utilize prosocial behaviors to maintain group stability (cite). The alternative approach, *conflict avoidance*, requires that individuals refrain from risky social behaviors that may start or escalate aggression (cite). Chimpanzees may utilize these strategies interchangeably depending on social context (Caws and Aureli 2003, Videan and Fritz 2007, Duncan et al. 2013), although there is evidence that such strategies are insufficient if the amount of available space is below a certain threshold (Webb et al. 2018). In one study, chimpanzees housed at the Lincoln Park Zoo exhibited more aggression within their holding areas than in the spacious exhibit areas (Ross and Lukas 2010). Avoiding conflict may also have physiological or emotional costs for chimpanzees which may demonstrate their emotional state through increased self-directed displacement behaviors (i.e., rough scratching: Baker and Aureli 1997, Duncan et al. 2013). Therefore, assessments of enclosure suitability must consider factors other than the total amount of space.

Some studies of captive primates indicate that the structural complexity of an individual’s environment, often described as the number of accessible areas, may be more important to its welfare than the total amount of available space (Herrelko et al. 2013, Webb et al. 2018). Partitioned environments are well-suited for high fission-fusion species since visual and auditory barriers enable individuals to exercise more choice over their social partners (Ross citation, Clark 2011). Even when individuals choose to be in one area of their enclosure, simply having the choice to access additional spaces can help individuals to cope with social tension (Herrelko et al. 2013) and to freely engage in preferred activities (Kurtycz et al. 2011), mitigating the potential costs of space restriction (Caws and Aureli 2003, Duncan et al. 2013). The addition of vertical structures to existing enclosures can also increase functionality by providing further escape opportunities (Caws et al. 2008) and allowing arboreal primates to spend more time above the ground (Jensvold et al. 2008, Ross and Lukas 2010). Although numerous attempts have been made to compare the potential effects of enclosure choice and size on social primates, confounding variables such as novelty, social groupings, seasonality, and management styles have made these effects difficult to study in isolation (de Waal 1989, Caws and Aureli 2003, Kurtycz et al., Webb et al. 2018).

In addition to enclosure space and complexity, there are various other aspects of captive environments that can impact the welfare of nonhuman primates (Hosey 2005). In every environment, seemingly neutral stimuli and events may be perceived by captive primates in a way that induces a stress response (Morgan and Tromborg 2007). For example, territorial species like chimpanzees are susceptible to arousal and stress when housed within auditory range of rival groups (Baker and Aureli 1996). Unpredictable stimuli and management routines may also be stressful to captive primates (Basset and Buchanan-Smith 2010, Novak et al. 2013), but too much predictability can also have negative effects (e.g., Bloomsmith and Lambeth 1995). Boredom can also have cascading effects on primate behavior in captivity and often leads to the emergence of abnormal or stereotypic behaviors as coping mechanisms (Baker and Easley 1996, Pomerantz and Terkel 2012, 2013). To mitigate boredom and predictability, managers of captive primates can enrich environments in ways that allow individuals to choose from a variety of options and exercise control over their own activities (cite).

Although substantial investigations have focused on optimizing housing for captive chimpanzees (reviewed in Webb et al. 2018), few studies have attempted to do the same for spider monkeys. Studies of spider monkeys housed in zoos and rescue centers show that they typically engage in patterns of social behavior like those of wild individuals (Klein and Klein 1971, Rondinelli and Klein 1976, Anaya-Huertas and Mondragon-Ceballos 1998, Pastor-Nieto 2001). For example, spider monkeys spend more time associating and affiliating with individuals of the same sex both in the wild (cite) and in captivity (cite). In both settings, male spider monkeys direct frequent minor aggression towards adult females as a form of social control (cite: captive and wild) and may severely injure unfamiliar or rival males in territorial conflicts (cite).

Despite the general similarities between captive and wild groups, some studies have indicated that captive spider monkeys engage in aggressive behavior more frequently than wild individuals (Klein and Klein 1971, Rondinelli and Klein 1976, (Anaya-Huertas and Mondragon-Ceballos 1998, Schaffner and Aureli 2005, Davis et al. 2009). Certain housing conditions, such as overcrowding and abnormal social groupings, may contribute to social tension and negatively impact welfare (Rondinelli and Klein 1976, Davis et al. 2009).

Although spider monkeys can utilize embraces to alleviate tension in risky situations (cite) and can form social bonds with unfamiliar individuals (Anaya-Huertas and Mondragon-Ceballos 1998, Pastor-Nieto 2001), living in a confined environment may be costly to their health and welfare. Since wild spider monkeys use fission-fusion dynamics to reduce competition and avoid conflict (Aureli and Schaffner 2007), researchers have suggested housing spider monkeys in spacious environments that permit individuals to fission from group members, thereby alleviating some negative aspects of life in captivity (Davis et al. 2009). Although some studies have examined the effect of environmental variables on captive spider monkey physiology (e.g., cite Davis et al. and cortisol/testosterone study, Rodrigues 2015), it remains unclear whether captive spider monkeys adjust their social behavior to cope with changes to the physical environment.

We observed three groups of black-handed spider monkeys (*Ateles geoffroyi*) housed at a rescue center in northern Belize to investigate how aspects of the captive environment affect patterns of individual space use, activity budgets, and measures of social proximity. Our overall objective was to assess whether the certain conditions allowed for the monkeys to exercise a greater degree of choice and experience better welfare. Although we primarily focused on the proposed effects of variable enclosure access, we also considered food availability and individual characteristics as factors. Primarily, we hypothesized that having access to the expansive Center enclosure would provide a more functional environment for spider monkeys by giving individuals a choice to separate from each other in three-dimensional space. Furthermore, under such variable conditions, we predicted that spider monkeys would employ a *tension-reduction* strategy to cope with situations that may be associated with greater social tension (e.g., temporary restriction to the smaller enclosure). Having the ability to regulate their own social relationships could mitigate injury risk and stress, thus improving their immediate welfare, and allow them to cope with environmental flux during subsequent stages of rehabilitation and reintroduction.

METHODS

Study Site and Subjects

We collected the data for this study as part of a general examination of spider monkey welfare (Denice 2017) at the Wildtracks Primate Rehabilitation Centre (“Wildtracks”). The center is located near the village of Sarteneja in the Corozal District of northern Belize (18° 12’ 12” N, 88° 8’ 48” W). Through a partnership with the Belizean Forestry Department, Wildtracks receives, rehabilitates, and releases displaced native wildlife into suitable protected habitats in northern Belize (cite). Between June and September of 2016, Wildtracks housed twenty spider monkeys within the rescue center, eleven of which lived in the three social groups examined in this study (Table 1).

Each of the three social groups resided within its own rectangular *satellite* enclosure (244.2 m3) and only had access to the expansive *Center* enclosure (2012 m3) every third day. All enclosures were amply furnished with native plants, wooden perches, climbing ladders, ropes, and hammocks. In some places, the chain-link caging was fitted with metal roofing for cover and shade cloth for visual barriers. The space between adjacent enclosures was only a few meters, enabling all of the monkeys to maintain visual and auditory contact at will. The Center enclosure contained a living sapote tree (*Manilkara zapota*, Family: Sapotaceae) which did not bear fruit during this study. Caregivers prepared and served four meals of fresh produce and native browse each day, distributing the food around the perimeter of each satellite. Fresh drinking water was always available from plastic bottles mounted on the caging. Every morning, caregivers opened a set of manually-operated doors to permit just one group to access the Center enclosure while the other groups remained in their satellites.

Data Collection

We collected data 4-7 days per week from June 10, 2016 through September 10, 2016. Each day, the first author and a research assistant collected data simultaneously using complementary sampling methods on a fixed rotation. The rotation allowed us to collect continuous focal samples and sets of instantaneous scans on each individual and group, respectively, without overlapping or duplicating samples. Sampling began at sunrise (typically around 6:30 a.m.) and ended before dusk, once all samples were complete (typically around 4:30 p.m.).

During focal samples, the observer continuously recorded a focal individual’s behavioral state and surroundings according to the ethogram (Table 2). After completing a 20 minute sample, the focal observer moved to the next individual, according to the fixed rotation, until all individuals were represented. Meanwhile, the second observer collected instantaneous scan samples from a different group at ten-minute intervals for two-hour periods. For each scan, the observer randomly selected an individual from their focal group and recorded their location and proximity to all other individuals in the group according to the ethogram (Table 2). Both observers utilized tablets equipped with the Animal Behaviour Pro application (cite) for data collection.

We tested interobserver reliability by simultaneously recording the activity of focal individuals and comparing the observed frequencies of each activity and behavioral event (N = 25). The frequencies showed a strong positive correlation (r(25) = .995, p < .001), indicating a high level of agreement between observers. We attributed most errors to differences in focal visibility between observers. We conducted similar tests for estimating interindividual distances and height indices. For distances, the average difference between observers was negligible (m = 0.6m) and the estimations showed a strong positive correlation between observers (r(25) = .974, p < .001). Estimations differed by less than 2m 92% of the time. For classifying height indexes, observers showed complete agreement throughout the test (r(25) = 1, p < .001).

Statistical Analysis

We performed all analyses using R (cite). We used the “dplyr” package (cite) to aggregate, summarize, and explore the data. For both focal and scan samples, we created categorical variables to describe the environmental conditions and characteristics of focal individuals (identity, sex, age class, and social group). We considered each measurement of space use, activity, and social proximity as its own dependent variable, then used generalized linear mixed models (cite) to determine which factors best explained the observed patterns of each response variable. We always included focal identity as a random effect and nested it within the focal’s *social group* for all but one model. We used the methods of Zuur et al. (cite) and the R packages “lme4” (cite) and “glmmTMB” (cite) to construct mixed models and optimize model fit using Akaike’s Index Criterion (AIC) as an indicator. When necessary, we transformed data using log- or arc-sine transformations. For each response variable, we used backwards selection to remove insignificant factors and utilized the Tukey method as a post hoc comparison between levels of each significant factor in each model. We used an alpha level of

RESULTS

DISCUSSION

REFERENCES

TABLES

FIGURE LEGENDS

APPENDICES