The Behavioral Responses of Geoffroy's Spider Monkeys to Drone Flights

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Abstract: Drones are increasingly used for monitoring wildlife, and it is therefore necessary to evaluate their impact on animal behavior. According to the landscape of fear framework, animals assess and respond to perceived risks in their environment by adjusting their behavior and space use to avoid potential threats. Understanding how drones influence risk perception is thus crucial to avoid generating stress and altering the animal's natural behavior. Geoffroy's spider monkeys (*Ateles geoffroyi*) are endangered arboreal primates, but information on their distribution and abundance is scarce throughout their geographical distribution. Drones can aid to rapidly obtain such information, but data of their impact on the monkeys are needed to design surveys that minimize disturbance (i.e., any interference or modification of the natural behavior of the monkeys caused by the presence and operation of drones). Here, we evaluated whether drone flights influenced the following spider monkey behaviors: agonistic displays, self-scratching, whinny vocalizations, feeding, resting, social interactions, and moving. We also evaluated the effect of three flight parameters, flight height (35, 50 m above ground level), speed (2, 4 m/s), and distance to the drone ("close", "medium", and "far") on spider monkey behavior and examined whether repeated exposure to drones resulted in tolerance (i.e., lack of a behavioral response). We found that drone flights influenced only agonistic displays and resting and that the only flight parameter affecting behaviors was the distance between the monkeys and the drone. We found that spider monkeys developed a tolerance to drone flights only for agonistic displays. Based on our results, we suggest that spider monkeys do not perceive drone flights as major sources of disturbance (such as predators) in the short term, and that drone monitoring can be a viable option to study this species if adequate flight protocols are implemented.

Keywords: unoccupied aerial vehicles; flight speed; flight height; distance to drone; tolerance

1. Introduction

The increasing use of drones in recent years to monitor wildlife is mainly due to two key factors [1]. First, drone technology has become more accessible and affordable, allowing a growing number of scientists and conservation organizations to incorporate drones into their research [1–3]. Second, improvement in the resolution of aerial imagery that can be obtained with several drone models has enhanced individual species identification [4], animal behavior analyses [5], and species abundance estimations [6–8].

As the use of drones to survey animal populations becomes more common, it is important to evaluate how the exposure to this technology can influence animal behavior to minimize potential negative impacts [9–11]. Drones represent novel stimuli for wildlife that may be perceived as threats given the rapid movement, the sound produced by their rotors,

their silhouette, and their size [4,11]. According to antipredator behavior theory, animals have evolved to recognize and respond to potential threats in their environment to increase their chances of survival [12]. Drone flights can therefore generate behavioral responses similar to those generated by predators, such as freezing, escaping, vigorously displaying, and even mobbing [13–17]. Prolonged exposure to predation risk can lead to behavioral responses expected within the "landscape of fear" framework [18,19]. Although adaptive to deal with predators, such behavioral responses can impact essential activities, such as feeding, rearing, and mating, and modify movement patterns, as animals may avoid areas where they had detected predators [20]. If drone exposure produces similar antipredator responses, it may be disruptive to the animals. However, drones used to monitor wildlife do not attack species, so they pose no real threat to them. Although accidents during recreational use or due to mechanical or human failures are possible [21], they are not representative of normal drone wildlife survey operations. The likelihood of such accidents is relatively low, and, under normal conditions, drones do not pose an actual threat to the wildlife under study. Nevertheless, if individuals perceive drones as a risk, repeated exposure to drones may even cause displacement, altering the species´ distribution and habitat use [20].

Although the number of studies evaluating the effects of drone exposure on wildlife species is currently increasing [22–26], only a few studies have focused on evaluating the behavioral response of primates to drones (green monkeys: *Chlorocebus sabaeus* [27]; golden-crowned sifakas: *Propithecus tattersalli* [28]; Javan langurs: *Trachypithecus auratus*; Javan gibbons: *Hylobates moloch* and *Javan surili*: *Presbytis comata* [29]). These studies reported responses to drone flights such as an increase in vigilance and escape [29]. These evaluations also show that a wide range of behaviors should be assessed to obtain a reliable understanding of how species modify their behavior in response to drones [30].

To understand the impact of drone flights on wildlife, it is important to evaluate which flight parameters influence the behavioral responses of each species. Among the most important flight parameters that may influence animal behavior are flight height, flight speed, approach distance, and flight frequency [2,3,31]. Drones flying at lower heights may elicit behavioral responses (e.g., vigilance, alarm vocalization, and escape) more frequently than flights performed higher off the ground [4,24,29]. Drone flight speed also influences species' responses [26,32], as rapidly moving drones can trigger more intense responses owing to their sudden approach, while slower speeds allow for more gradual and less intense responses [26]. Similarly, the faster the flight speed, the louder the sound generated by the drone, leading to more intense behavioral responses [33]. The approach distance (generally assessed as the horizontal distance) is the shortest distance at which drones can approach before a species detects its presence [34,35]. However, when surveying species that spend the majority of their time in the tree canopy, the height at which they are found in the canopy should be considered when evaluating the approach distance. In such cases, the diagonal distance between the individuals and the drone should be considered as an approximation of the approach distance. Evaluating the ability of animals to detect and respond to drones at different distances is vital to avoid excessive alarm responses [26]. For example, several species of African mammals increased vigilance when the drone was less than 100 m away [34]. Flight frequency (i.e., how often drone flights are performed in a study area over a certain period) impacts species' tolerance (i.e., the intensity of disturbance that an individual tolerates without responding in a defined way; [36]) to drones [37,38]. Repeated drone flights may increase tolerance among animals, potentially habituating them to the drone presence over time [39], which may affect population surveys differently depending on species and habitat characteristics. For instance, drone tolerance may cause animals living in open areas to show reduced responses, aiding in species identification and counting, whereas reduced responses can complicate detectability of arboreal species, as they are often detected through drone-induced movements in the canopy [26,40]. Consideration of the different flight parameters is therefore not only fundamental to ensure the success of wildlife monitoring programs,

but especially important to minimize disturbance and guarantee the welfare of the species being studied.

Geoffroy´s spider monkeys (*Ateles geoffroyi*) are diurnal, arboreal, fast-moving primates with a high degree of fission–fusion dynamics (i.e., the group divides into subgroups that change in size and composition throughout the day [41]), which are currently listed as Endangered on the IUCN Red List of Threatened Species mainly due to habitat loss [42]. Frequent population monitoring is needed to identify population changes over time and create timely and targeted conservation programs [43]. Due to this need and the difficulty of monitoring their populations with traditional methods (given their ecological traits mentioned above that allow them to move rapidly among the trees and change the composition of its subgroups throughout the day, which complicates their detection and accurate counting in the field [40,44,45]), drones may offer feasible alternatives [40,45,46]. However, there is a need to evaluate the impact of this technology on their populations. Some studies have reported responses to drone flights, including spider monkeys moving away from their original position during drone flights [45] and the emission of alarm calls in 41% of flights [40]. These two behaviors have also been reported for spider monkeys during predation events [47–49] and may therefore be expected to occur in the presence of an unknown object such as a drone. Although previous drone studies represent a first step toward understanding the impact of drone surveys on wild spider monkey populations, systematic studies assessing the potential impact of drone flights on their behavioral responses in more detail are lacking.

The aim of our study was to assess the behavioral responses of Geoffroy´s spider monkeys to repeated drone flights using different flight parameters. We had three objectives. First, we evaluated whether the monkeys change their behavior when exposed to drone flights. We predicted that spider monkeys engage in agonistic displays, self-scratching (hereafter scratching; a marker of anxiety in the context of uncertainty in this species: [50–52]), and whinny vocalizations (hereafter whinnies, their typical contact call: [53]) more frequently during flights than before and after flights, and more frequently after than before flights. We also predicted that spider monkeys spend less time feeding, resting, and engaging in social interactions during flights than before and after flights, and less after than before flights, whereas they spend more time moving and performing alarm calls during flights than before and after flights, and more after than before the flights.

Second, we evaluated whether three flight parameters; flight speed (2 and 4 m/s), flight height (35 and 50 m above ground), and distance between the monkey and the drone ("close", "medium", and "far") affected spider monkey behavior. We predicted that spider monkeys perform agonistic displays, run away, scratching, vigilance, and whinnies more frequently when the drone is flown at a lower height, faster speed, and when the distance to the drone is shorter compared to when the drone is higher, slower, and at greater distances. We also predicted that spider monkeys spend more time feeding, resting, and engaging in social interactions when the drone is higher, slower, and at greater distances, whereas we predicted the opposite for moving and alarm calls.

Third, we evaluated whether spider monkeys develop tolerance to repeated drone flights. We predicted that spider monkeys perform agonistic displays, run away, scratching, vigilance, and whinnies more frequently during initial flights compared to later flights. We also predicted that for short-duration, wildlife-survey flights where the drone only flies over the monkeys for a few seconds up to a few minutes, spider monkeys spend less time feeding, resting, and engaging in social interactions during initial flights than during later flights, whereas we predicted the opposite for moving and alarm calls.

2. Materials and Methods

2.1. Study Site

We evaluated the behavioral responses of spider monkeys to drone flights through direct observations at a site in the "Uxuxubi al Natural" reserve (20°27′29.10″ N, 87°23′34.42″ W), which consists of a relatively flat terrain (i.e., not mountainous), like the rest of the Yucatan

Peninsula of Mexico. The reserve has an approximate size of 10,000 ha and was created in 2007 through the initiative of more than 150 local small landowners interested in the conservation of the region's natural resources. We performed all drone flights on a site of approximately 15 ha (Figure 1). This site is mainly composed of regenerating forest in late stages of succession (>30 years old) and mature forest (>50 years old), with a high density of important spider monkey feeding tree species such as *Brosimum alicastrum*, *Manilkara zapota*, *Metopium brownei*, and *Ficus* spp. Maximum canopy height at the site is between 20 and 25 m. We selected this site because local landowners mentioned that it contains several spider monkey sleeping trees (i.e., a sleeping site), increasing the probability of frequently finding the monkeys. Given that spider monkeys have high site fidelity over time [54], the same group can be found repeatedly at the same sleeping site. Due to tourist activities in the reserve, spider monkeys are habituated to human presence and the noise of car and motorcycle engines. We therefore expected that the presence of researchers would not influence the behavior of the spider monkeys. Another critical reason for selecting this site was that according to the local landowners of the association in charge of managing the reserve, the local spider monkey population had never been exposed to drone flights.
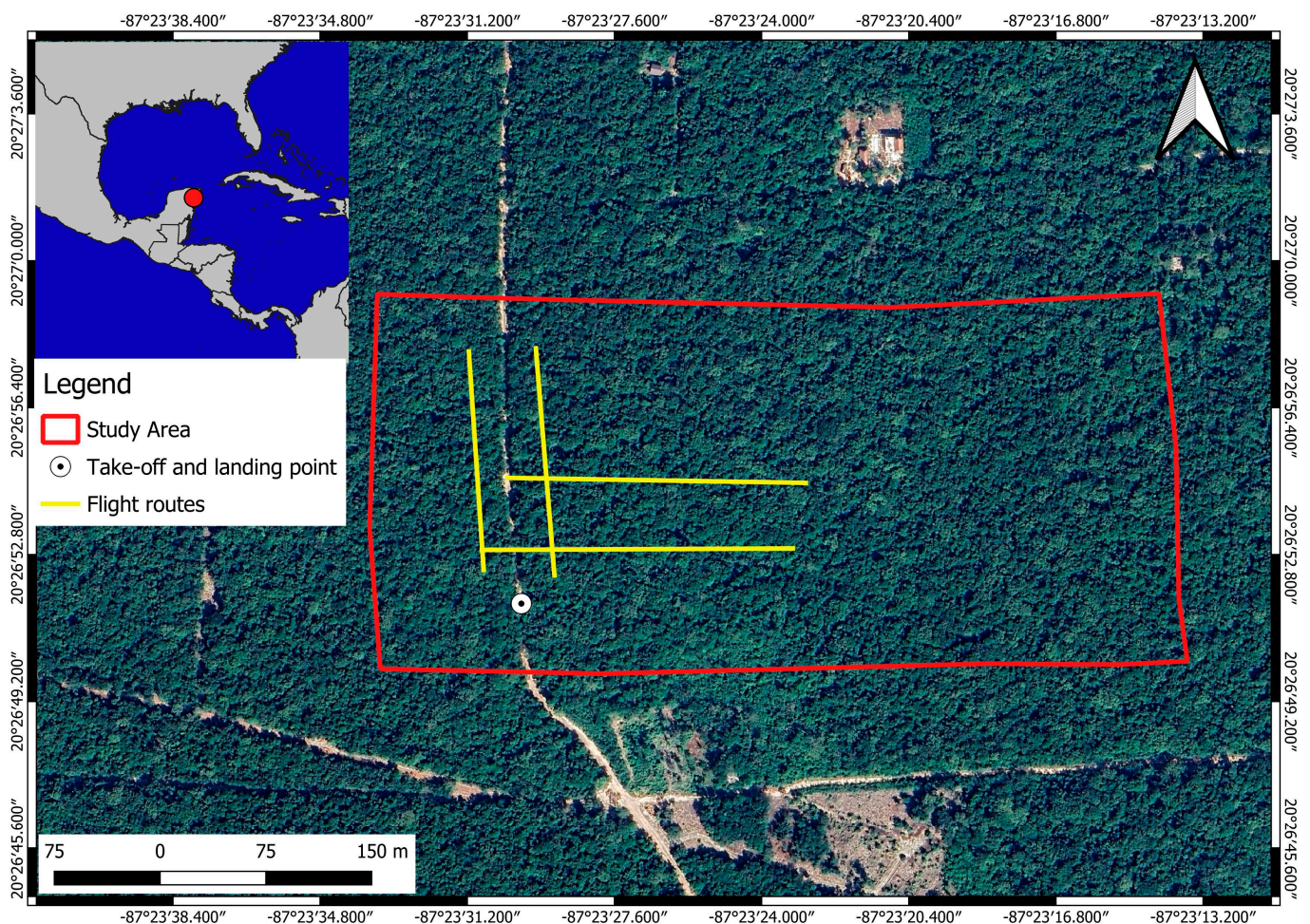

Figure 1. Study area located in the "Uxuxubi al natural" reserve, Yucatan Peninsula, Mexico where drone flights were performed to evaluate the behavioral response of the spider monkeys. The flight routes shown on the map are just a few examples of those used during the study.

2.2. Study Design

Between May and July 2023, we conducted a total of 32 roundtrip drone flights. We performed eight repetitions for each combination of flight height and speed: 35 m height and 2 m/s speed, 35 m height and 4 m/s speed, 50 m height and 2 m/s speed and, 50 m

height and 4 m/s speed. We decided to perform 8 replicates per combination in our study as we wanted to focus on capturing the initial and acute responses of the spider monkeys to the drone flights. During the flights we never manipulated the distance between the drone and the focal individual (see Section 2.4, Data Analysis). The flights were performed by alternating the flight parameter combinations to avoid performing flights with the same parameter combinations consecutively. We performed drone flights from 6:00 to 9:00 and from 15:00 to 19:00 because spider monkeys were frequently sighted at the study site at these times of day (Pinel-Ramos, personal observation). Data collected during flights were used in all analyses.

We used a Mavic 2 Enterprise Advanced, which is a commercial off-the-shelf rotary-wing drone. It features a compact design with dimensions of 214 × 91 × 84 mm (folded) and weighs 909 g (DJI Technology Co., Shenzhen, China). The drone is grey and equipped with four rotors, allowing for stable flight and precise maneuverability. It is powered by a high-capacity LiPo 4S battery with a capacity of 3850 mAh and has a maximum flight endurance of 31 min, depending on flight parameters and weather conditions. This model has a maximum operating distance of 10 km and a OcuSync 2.0 video transmission system. This drone houses both a high-resolution visual spectrum (Red-Green-Blue; RGB camera) and a thermal camera. We selected this drone as this and similar models have been used in other spider monkey studies [40,55] and is easy to fly.

Before starting data collection, we located a spider monkey subgroup and recorded its location using a handheld GNSS device (model Garmin GPSMAP 64) to program the drone´s flight path to fly directly over the monkeys' location. To record the GPS point, the observer stood underneath the center of the spider monkey subgroup. Drone take-off and landing took place at least 100 m from the monkeys' location. We performed take-off and landing manually but the flight path was preprogrammed and executed automatically using the DJI pilot application (version 2.1.0). We raised the drone to the pre-selected height (see Section Flight Parameters) and flew it along a 200 m straight-line transect (400 m roundtrip) passing over the spider monkey subgroup (Figure 2).

Flight Parameters

We evaluated the behavioral responses of spider monkeys to the drone at two heights: 35 and 50 m above the ground (Figure 2). We selected the flight height of 50 m above ground level (approximately 25 m above canopy level) because it is the maximum height at which spider monkeys can be differentiated from other species living in the area in thermal footage, which appears to be the best way to survey spider monkeys with drones [45,55]. Therefore, we would expect spider monkey monitoring flights on flat terrain to be conducted at a maximum height of 50 m above the ground. We considered the height of 35 m above the ground (10 m above the canopy) to be the minimum safe height at which to fly the drone without running the risk of flying into trees. We also evaluated the behavioral responses of spider monkeys to drone flights at two flight speeds (2 and 4 m/s: Figure 2). We selected the speed of 2 m/s because previous spider monkey drone surveys were performed at this speed [32,40] and 4 m/s because it is the maximum flight speed at which spider monkey monitoring is feasible, as detecting individuals in videos recorded with RGB cameras at faster speeds is very difficult (Pinel-Ramos, personal observation).

2.3. Data Collection

To evaluate the effect of drone flights on spider monkey behavior we performed observations from the ground using focal animal sampling [56]. Data were collected by speaking into a voice recorder so that the observer could maintain sight of the focal monkey for the entire observation. Because the area around the study site is mainly composed of late regenerating and mature forests, the canopy is highly homogenous and visibility of the spider monkeys from the ground was high (i.e., sparse understory vegetation did not interfere with visibility). The same observer collected all behavioral sampling. As spider monkeys may change their behavior for a few minutes upon encountering humans (even

when they are habituated to human presence), we started data collection once the spider monkeys became familiar with the observer's presence and engaged again in their previous activities (between 10 to 15 min).
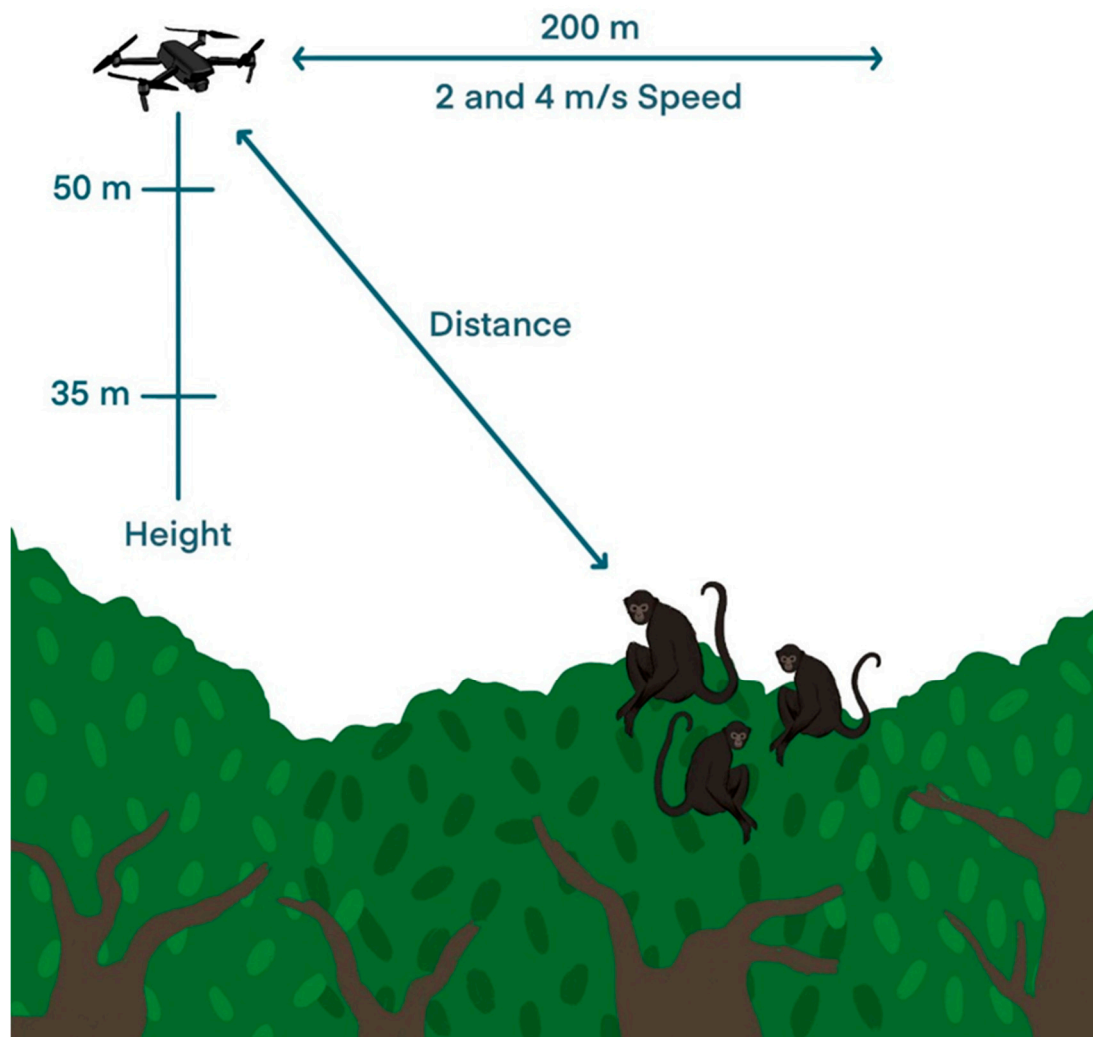

Figure 2. The 200 m straight-line flight transect along which we flew the drone over the spider monkey subgroup featuring the two heights, the two speeds, and the distance between the focal subject and the drone (illustration by Aranza María Hernández Goméz).

For each drone flight, the observer collected three 10 min focal animal samples on the same individual, one before, one during, and one after the drone flight. We selected 10 min because this was the approximate duration of the flights. During each focal animal sample, the observer used all-occurrence sampling for event-type behaviors and instantaneous scan sampling every minute for state-type behaviors (Table 1). We recorded the sex and age class (juvenile or adult; [57]) of the focal individual. As it was not possible to individually recognize the monkeys, if the focal individual went out of sight and could not be found again, we chose another individual from the same subgroup of the same sex and age class as the focal individual to complete sampling. If 30 min after the end of the drone flight another spider monkey subgroup arrived at the sampling site, we started a focal sample on an individual of the new subgroup and performed a drone flight with a different height and speed combination. The team in charge of flying the drone was in constant communication with the observer via telecommunication radios to coordinate the flight starting time and ensure that the observer had the focal individual in sight before beginning the flight.

Table 1. Event and state type behaviors recorded during focal samples.

Type	Behavior	Description
State	Resting	Lying down, sitting, or dangling in the same place
State	Feeding	Manipulating or ingesting plant parts (fruits, leaves, flowers) or some other element of the environment (e.g., water, insects, bark)
State	Alarm calling	Emitting alarm vocalizations (they are emitted in long sequences)
State	Moving	Any movement beyond 0.5 m from the current position in any direction independent of the drone's location
State	Social	Two individuals perform any of the following interactions: chasing, lunging, grooming, embracing, playing
Event *	Whinny	Emitting a whinny vocalization (they are usually emitted discretely, not in sequence)
Event *	Agonistic display	Vigorously moving the branches or leaves
Event *	Scratching	Self-scratching using the fingers on any own body part
Event *[#]	Vigilance	Being alert, with the head oriented upwards, while paying attention to the surroundings.
Event *[#]	Escape	Rapidly moving from their original location away from the drone's location (recorded only the first occurrence).

Based on [50,53,58–60]. * We scored a new event 5 s after the end of the previous event. [#] As these behaviors are directly related to the drone's presence, they were only recorded during the flights to be analyzed for objectives 2 and 3.

We recorded the time at which the focal monkey performed each behavior listed in Table 1. We also took a GPS track for the duration of the focal sample to obtain the location of the focal individual so that we could extract the location where each behavior was performed in relation to the drone´s location. We calculated the height of the 10 trees where the focal monkeys spent the majority of the observation time of all the focal samples with the help of a Suunto PM-5 clinometer. We used these data to calculate the distance between the drone and the focal individual (see Section 2.4. Data Analysis).

2.4. Data Analysis

The analyses were performed in R version 4.3.0 [61], running all models using the glmer function of the "lme4" package [62]. For Objective 1, to evaluate the effect of drone flights on event-type behaviors (scratching, whinny and agonistic displays), we ran GLMMs with a Poisson error distribution. The response variable in each model was the frequency of the behavior, including the sampling time as an offset given that drone flights differed in duration (mean ± SD = 6.1 min ± 1.05 min). In all models, the predictor variable was the observation period (before, during and after the flight), with the flight number as a random factor to control for pseudoreplication [63].

To evaluate the effect of drone flights on state-type behaviors (resting, moving, feeding, and social), we calculated the number of one-minute instantaneous scans in which the focal animal engaged in each behavior. We ran GLMMs with a binomial error distribution. The response variable was the number of scans in which the focal individual engaged in one of the four state-type behaviors (e.g., resting) relative to the number of scans in which it did not (e.g., engaged in traveling, feeding or social), using cbind. In these models it was not necessary to use an offset because the way the response variable was entered into the models took potential differences in the number of one-minute scans between focal samples into account.

For objectives 2 and 3, we only used data collected during flights and evaluated the effects of flight parameters and repeated flights on spider monkey behaviors that were found to be influenced by drone flights in the GLMMs for objective 1, in addition to vigilance and escape that were sampled only in focal samples conducted during drone flights. For objective 2, we evaluated the influence of flight parameters using two subsets

of models, one for both flight height (35 and 50 m) and speed (2 and 4 m/s) and another for distance, given that the distance between the drone and the focal individual was calculated for each behavior performed. For event-type behaviors, we used GLMs with the frequency of each behavior as the response variable and sampling time (i.e., flight duration) as an offset variable. As we found overdispersion when modelling agonistic displays and vigilance with a Poisson error distribution in the first subset, we ran GLMs with a negative binomial distribution using the glm.nb function of the "mass" package [64]. For resting (the only state-type behavior that was affected by drone flights), we ran a GLMM with a binomial distribution using the glmer function of the "lme4" package [62] with the response variable being the number of scans in which the focal individual engaged in resting relative to the number of scans in which it did not, using cbind. In this model, we included an observation-level random effect (OLRE) to account for overdispersion [65]. We evaluated potential collinearity between the two categorical predictor variables [66] with Cramer's V coefficient using the assocstats function of the "vcd" package [67]. Cramer's V values range from 0 to 1, where 0 refers to a weak or lack of association and 1 refers to a strong association between variables [68]. All comparisons between predictor variables had Cramer's V values of <0.01, and therefore the two variables (flight height and speed) were included in each GLM and GLMM. Additionally, to evaluate whether increasing the sample size would allow us to find differences in the behavioral response of the spider monkeys, we analyzed the data by grouping them by flight height only. For both event-type and state-type behaviors, the structure of the models was the same as mentioned above, except that in this case, flight height was the only predictor variable.

The other model subset included only the distance from the drone to the focal individual as the predictor variable. To calculate this distance for each behavior, we extracted the coordinates of the drone location from the flight log file each time the focal individual performed a behavior. We used the location of the drone, the location of the focal individual (obtained from the gps tracks), the height of the drone and the mean height of the monkeys calculated from the estimated heights of the 10 trees where the spider monkeys spent most of the observation time during the 32 drone flights to calculate the distance between the drone and the focal individual for all behaviors performed by the focal animal (Figure 2) using the distVincentySphere function of the "geosphere" package in R [69]. We then grouped all distances into 3 categories, each of which included 33% of the data: close distance (0–66 m), medium distance (67–133 m), and far distance (>134 m). The predictor variable "distance" was therefore categorical with three levels: "close", "medium", and "far". For event-type behaviors, we ran GLMMs with a Poisson distribution, with the frequency of each behavior as the response variable and flight duration as an offset variable. For resting, we ran a GLMM with a binomial distribution in which the response variable was the number of scans in which the focal individual engaged in resting relative to the number of scans in which it did not, using cbind. In all models of this subset, we included flight number as a random factor to control for pseudoreplication given that the datasets included multiple data points from the same flight, corresponding to each behavior recorded during the same flight and the associated distance between the drone and the focal individual.

For objective 3, to assess whether spider monkeys develop tolerance to repeated drone flights, we compared spider monkey behavior during drone flights over time. As there was a 20-day break between the first 18 flights, and the remaining 14 flights due to logistical complications, we divided the flights into two subsets: the first 18 flights (performed over 18 days), and the last 14 flights (performed over 22 days). For event-type behaviors, we ran GLMs with negative binomial distributions to account for the overdispersion found in models with a Poisson error distribution. We included the frequency of each behavior as the response variable and flight duration as an offset variable. For resting, we ran a GLMM with a binomial distribution with the number of scans in which the focal individual engaged in resting relative to the number of scans in which it did not as the response variable (using cbind) and an observation-level random effect to account for overdispersion. In all models

we entered the flight subset (first or last subset) into the models as the predictor variable. See Supplementary Materials for examples of the different models.

We tested all model assumptions using the simulateResiduals function of the "DHARMa" package [70]. All models met the assumptions of normality and homogeneity of variance of the residuals. We compared each GLM or GLMM with the corresponding null model using a likelihood ratio test (LRT) with the lrtest function to assess the significance of the fixed predictor variable. For GLMs the null model included only the offset variable. For GLMMs the null model included the random factor and the offset variable, if applicable [71]. We performed Tukey post-hoc tests using the glht function of the "multcomp" package when predictor variables with more than two levels were significant [72]. We calculated the McFadden pseudo-R^2 for the GLMs (pR^2), using the pR2 function from the "pscl" package [73], and the marginal R^2 (R^2m; i.e., the variance explained only by the predictor variables) and conditional R^2 (R^2c; i.e., the variance explained by the predictor variables and random factors) for the GLMMs, using the r.squaredGLMM function of the package "MuMIn" [74]. In the GLMMs where the only random factor was an observation-level random effect to deal with overdispersion, we did not calculate the conditional R^2 because the value is misleading [65].

3. Results

With respect to objective 1, we found no difference between observation periods (before, during and after the drone flight) for scratching (LRT: $\chi^2 = 4.94$, df = 2, $p = 0.08$, $R^2m = 0.02$, $R^2c = 0.63$) and whinnies (LRT: $\chi^2 = 1.52$, df = 2, $p = 0.46$, $R^2m = 0.01$, $R^2c = 0.58$), whereas there was difference for agonistic displays (LRT: $\chi^2 = 14.36$, df = 2, $p < 0.001$; $R^2m = 0.08$, $R^2c = 0.78$). Spider monkeys performed agonistic displays more frequently before (Tuckey test: $p = 0.001$) and during ($p = 0.006$) compared to after drone flights, whereas there was no difference between focal samples before and during the flight ($p = 0.96$; Figure 3a). Spider monkeys performed at least one agonistic display in 28% of the focal samples before, 22% during and 19% after the drone flights (n = 32).

In the case of state-type behaviors, we found that the observation period only influenced the proportion of scans in which spider monkeys rested (LRT: $\chi^2 = 18.74$, df = 2, $p < 0.001$, $R^2m = 0.05$, $R^2c = 0.88$). Resting was performed in a higher proportion of scans during the drone flights compared to before ($p < 0.001$) and after ($p = 0.001$) flights, while there was no difference between before and after flights ($p = 0.69$; Figure 3b). There was no evidence that the observation period influenced spider monkeys engaging in feeding (LTR: $\chi^2 = 2.70$, df = 2, $p = 0.25$, $R^2m = 0.01$, $R^2c = 0.87$), moving (LTR: $\chi^2 = 1.61$, df = 2, $p = 0.44$, $R^2m = 0.02$, $R^2c = 0.66$), and social behaviors (LTR: $\chi^2 = 0.28$, df = 2, $p = 0.86$, $R^2m = 0.001$, $R^2c = 0.96$). We could not test alarm calling because the monkeys did not emit such vocalizations during data collection.

With respect to objective 2, for event-type behaviors we found no evidence that flight height and flight speed influenced the frequency of agonistic display (LRT: $\chi^2 = 1.27$, df = 2, $p = 0.53$, $pR^2 = 0.02$) and vigilance (LRT: $\chi^2 = 2.44$, df = 2, $p = 0.29$, $pR^2 = 0.02$). We obtained similar results when we analyzed the data grouped by flight height only (agonistic display, LRT: $\chi^2 = 0.69$, df = 1, $p = 0.41$, $pR^2 = 0.01$; vigilance, LRT: $\chi^2 = 2.15$, df = 1, $p = 0.14$, $pR^2 = 0.06$). However, we found that the distance between the drone and the focal individual influenced the frequency with which the spider monkeys performed vigilance (LRT: $\chi^2 = 28.56$, df = 2, $p < 0.001$, $R^2m = 0.25$, $R^2c = 0.50$), but there was no evidence for agonistic display (LRT: $\chi^2 = 2.24$, df = 2, $p = 0.33$, $R^2m = 0.02$, $R^2c = 0.77$). The spider monkeys performed vigilance during 84% of the flights. Vigilance was more frequent when the distance between the focal monkey and the drone was "close" ($p < 0.001$) and "medium" ($p < 0.001$) than when it was "far", whereas there was no difference between "close" and "medium" distances ($p = 0.42$; Figure 4a). As we recorded only 8 escape events during drone flights, we could not perform statistical analyses. Of these 8 events, 3 occurred when the flight was performed at a speed of 2 m/s and 35 m height, 2 when the flight was performed at 2/s and 50 m, and 3 when the flight was performed at 4 m/s and 35 m.
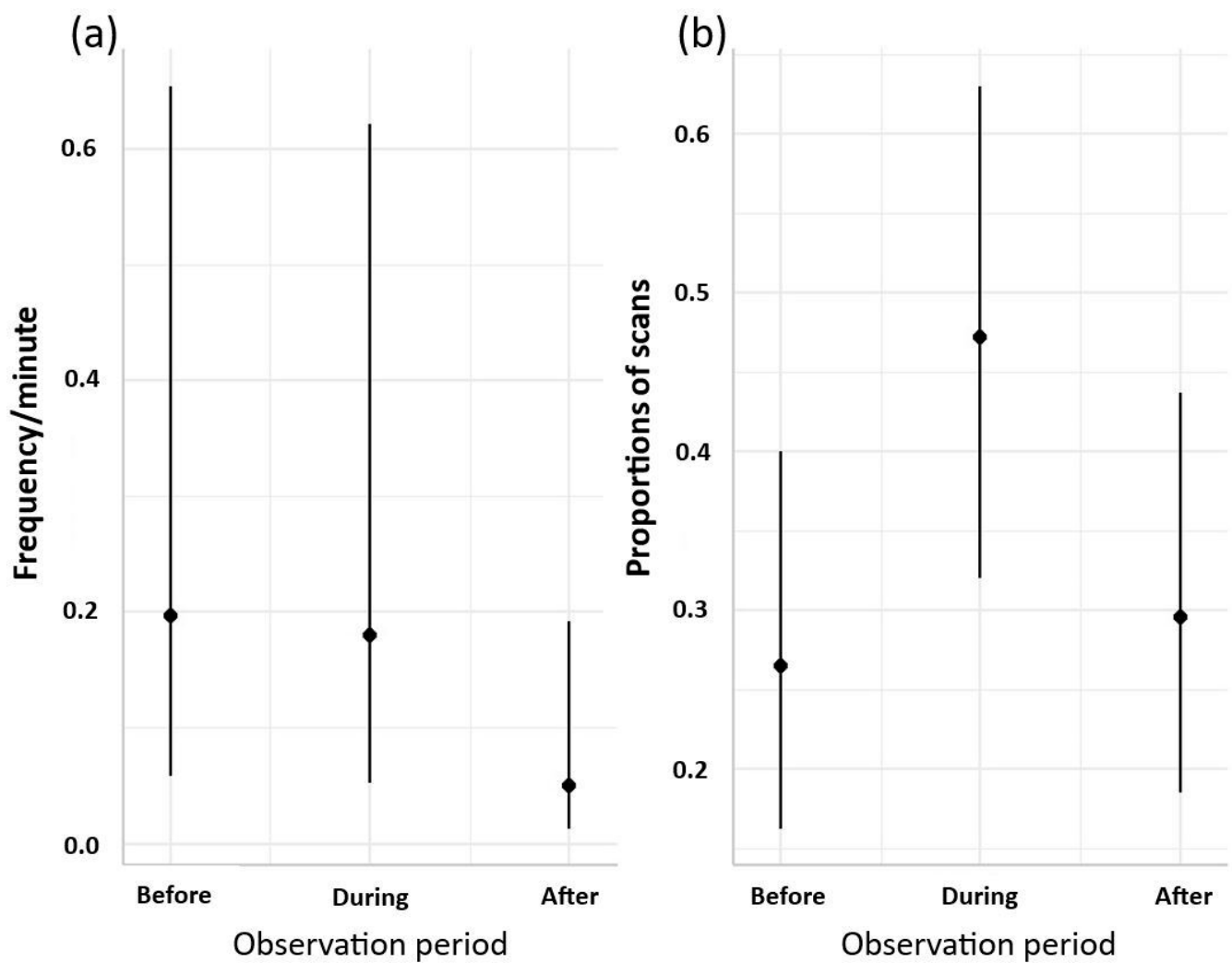
Figure 3. Predicted frequencies of agonistic display (**a**) and proportion of scans spent resting (**b**) based on the two GLMMs testing the effect of observation period. The bars represent the predicted estimates' 95% confidence intervals.

We found no evidence that flight height and speed influence the proportion of scans in which the monkeys rested (LTR: $\chi^2 = 1.86$, df = 2, $p = 0.39$, $R^2m = 0.07$). We obtained similar results when we analyzed the data grouped by flight height only (LTR: $\chi^2 = 1.86$, df = 1, $p = 0.17$, $R^2m = 0.07$). However, the distance between the drone and the focal animal did influence resting (LRT: $\chi^2 = 22.01$, df = 2, $p < 0.001$, $R^2m = 0.24$, $R^2c = 0.68$). The proportion of scans in which spider monkeys engaged in resting was lower when the distance to the drone was "close" compared to when it was "medium" ($p < 0.001$) and "far" ($p < 0.001$), whereas we found no difference between "medium" and "far" ($p = 0.96$; Figure 4b).
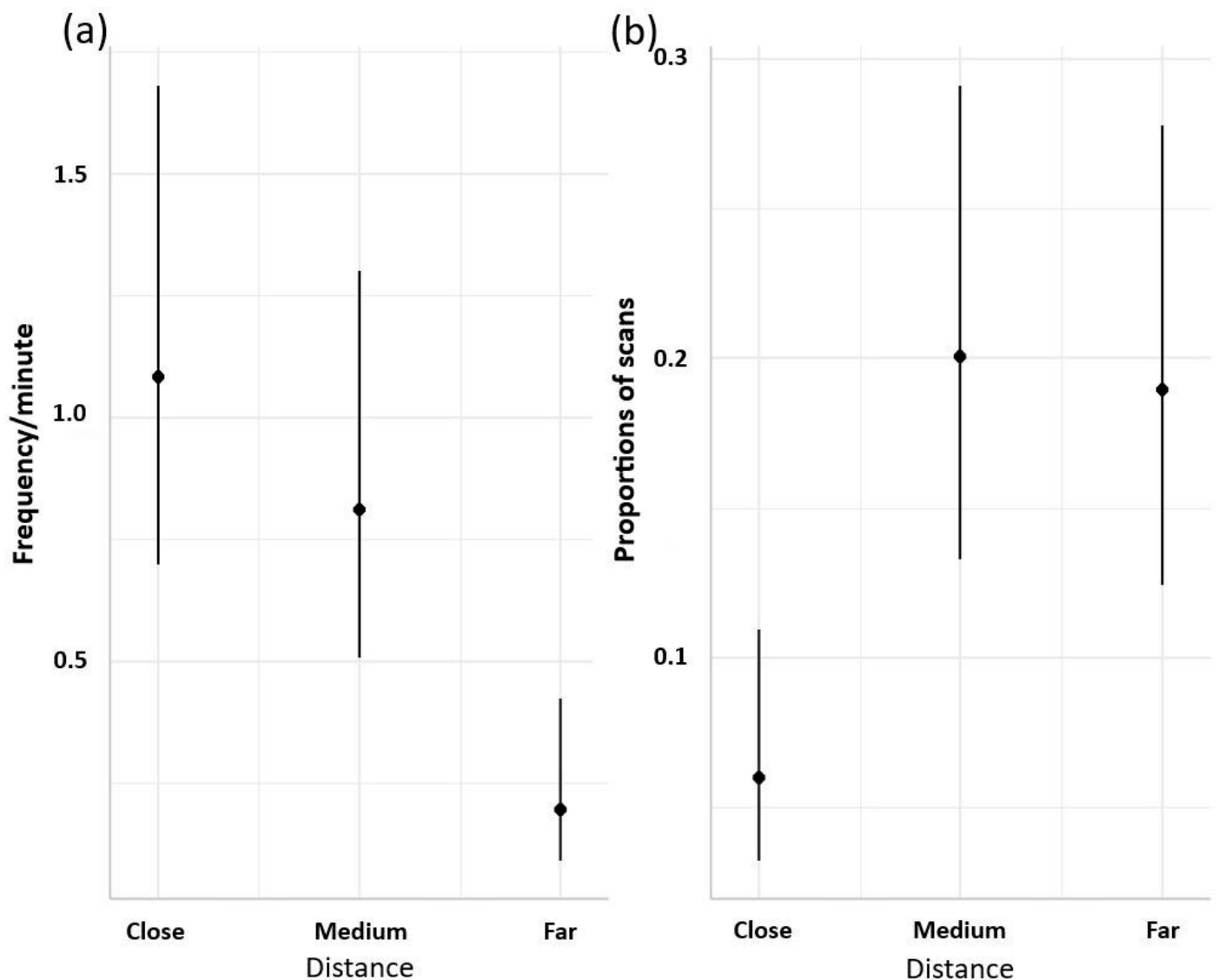
Figure 4. Predicted frequencies for vigilance (**a**) and proportion of scans spent resting (**b**) based on the two GLMMs testing the effects of the three distance categories. The bars represent the predicted estimates' 95% confidence intervals.

Regarding objective 3, there was no evidence for changes in the behavioral response of spider monkeys to drone flights over time for vigilance (LTR: $\chi^2 = 0.0001$, df = 1, $p = 0.99$, $pR^2 = 0.0009$) and resting (LRT: $\chi^2 = 1.20$, df = 1, $p = 0.27$; $R^2m = 0.04$). However, we found evidence for spider monkeys developing tolerance to drone flights over time for agonistic displays (LTR: $\chi^2 = 4.65$, df = 1, $p = 0.03$, $pR^2 = 0.08$) as they performed agonistic displays more frequently during the first flight subset than during the second flight subset (Figure 5). Spider monkeys performed agonistic displays in six of the 18 flights of the first subset and in only one of the 14 flights of the second subset.
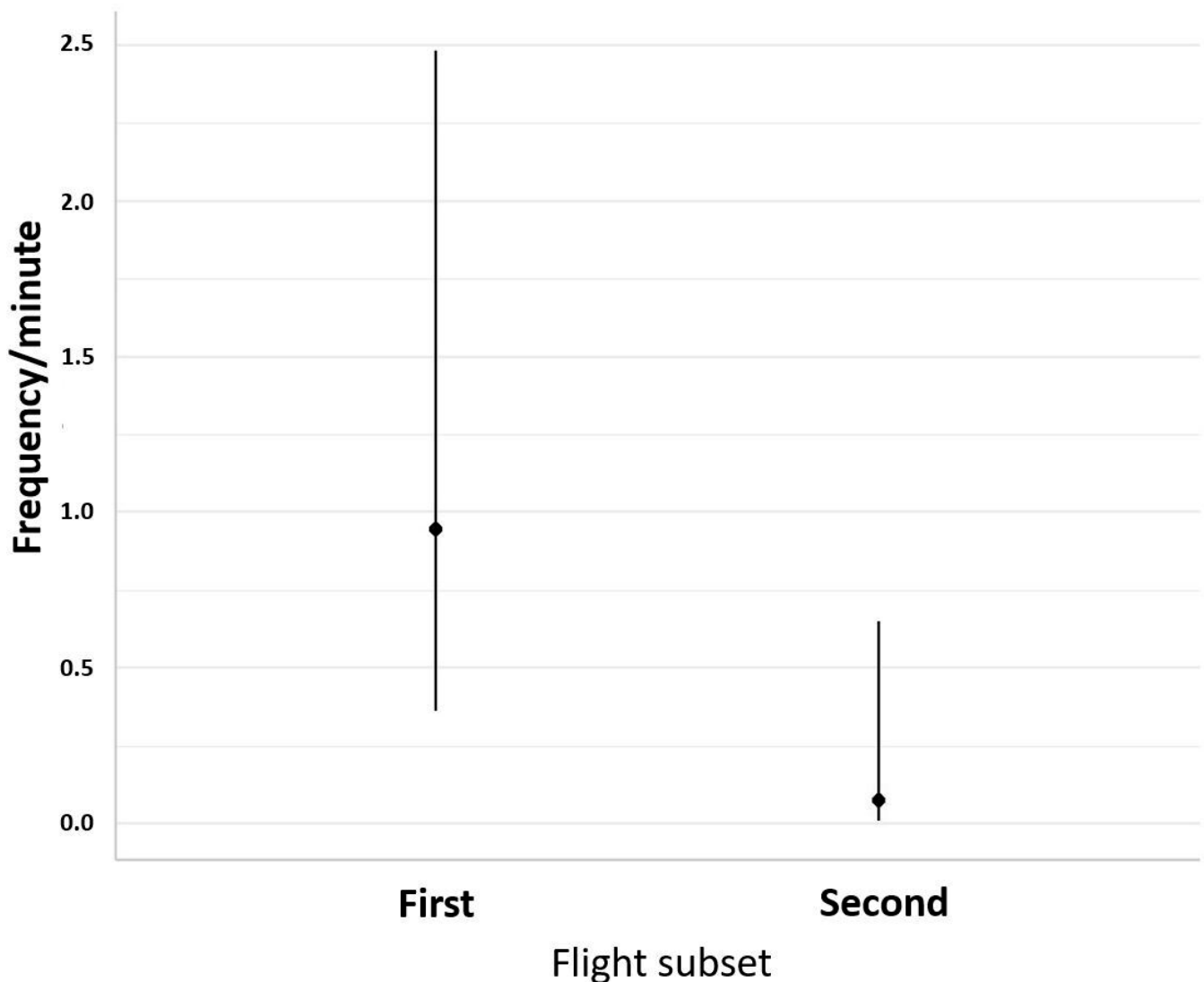
Figure 5. Predicted frequencies of agonistic display based on the GLM testing the effect of flight subset. The bars represent the predicted estimates' 95% confidence intervals.

4. Discussion

In this study, we evaluated the influence of drone flights on spider monkey behavior. We found that drones influenced the frequency of agonistic displays but not of scratching or whinnies. Of all the state-type behaviors investigated, drone flights only influenced resting, and contrary to our prediction the monkeys engaged more in resting during than before and after flights. In contrast, we found no evidence that drone flights influenced spider monkeys engaging in feeding, traveling and social interactions. The distance between the drone and the focal animal was the only flight parameter that influenced spider monkey behavior. We found no evidence that spider monkeys adjusted their behavioral responses to drone flights over time for vigilance and resting. However, in agreement with our prediction about the development of tolerance of behavioral responses to drone flights, we found that spider monkeys reduced agonistic displays in the second subset of flights relative to the first subset of flights.

Although drone flights influenced the frequency with which spider monkeys performed agonistic displays, the proportion of variance explained by the observation period was very low. Agonistic displays were more frequent during than after drone flights but, contrary to our prediction, they were also more frequent before than after drone flights and there was no difference between before and during drone flights. The higher frequency

of agonistic displays during drone flights is consistent with that observed in other species in response to novel or intrusive stimuli [75] as well as to drone flights [76,77]. For example, the number of light-mantled sooty albatross (*Phoebetria palpebrata*) and sub-Antarctic skua (*Stercorarious antarcticus*) individuals performing agonistic behaviors increases during drone flights [77]. Agonistic displays are performed to protect against a perceived potential threat [78], such as an unknown object like a drone. Although spider monkeys performed agonistic displays during 7 of the 32 flights (22%), we also observed agonistic displays before (28%) and after flights (19%). Of the total number of flights in which spider monkeys performed agonistic displays, 46% of them were performed both during the flight and in one of the other two observation periods. This pattern, along with the fact that we found no evidence for agonistic displays being more frequent during than before drone flights, suggests that there may be other stimuli in the area affecting agonistic displays. One could argue that the frequency with which spider monkeys performed agonistic displays may be high before drone flights because of the presence of the observer. Upon us encountering them (before starting data collection), the monkeys often performed agonistic displays and moved away from the observer. We therefore waited 10–15 min before collecting behavioral data to avoid introducing bias. Although spider monkeys at the Uxuxubi al Natural reserve are habituated to the presence of people, they are not used to having an observer following them closely and it is possible that agonistic displays directed at the observer continued after the 10–15 min waiting period prior the start of the before-flight focal samples.

Among the state-type behaviors, we found that only resting was influenced by drone flights, although the proportion of variance explained by the observation period was low. Contrary to our prediction, the proportion of scans in which spider monkeys rested was greater during compared to before and after flights. Staying still during drone flights may be a way to avoid being detected by potential predators and is common in other mammals [79]. By remaining still, spider monkeys may also assess the drone from a safe position, waiting to overtly respond only if a real threat is confirmed. When resting, individuals can also better engage in vigilance of the drone. Supporting this possibility, spider monkeys engaged in vigilance during 84% of the drone flights. This would also explain the reduction in resting after flights, as spider monkeys no longer need to remain still and be vigilant in the absence of the drone, and thus they can return to other activities such as moving and feeding. The relative high engagement in resting during flights also suggests that spider monkeys may not perceive the drone as a direct threat. In fact, during 69% of the flights, spider monkeys were resting before the flight and continued to rest during the flight.

As there is evidence that scratching is an indicator of anxiety and uncertainty in spider monkeys [50], it is a crucial behavior to understand the effect of different anthropogenic activities (such as drone flights) on spider monkey well-being. We found no effect of drone flights on scratching. Similarly, no alarm calling was heard during drone flights, which is the typical vocalization emitted by spider monkeys when a potential predator is perceived [47–49]. The result of scratching and the absence of alarm vocalization during flights, along with the lack of an effect of drone flights on feeding, moving, and social behavior, indicate a low level of disturbance of drone flights on spider monkeys, suggesting that spider monkeys may not perceive drones as a direct threat.

Of the flight parameters we evaluated, only the distance between the drone and the focal individual influenced spider monkey behavior, whereas we found no evidence for flight height and flight speed effects. These results are in contrast with those found for other species in which drone flight height was one of the main factors influencing behavioral responses [24,29,34,80]. This contrast may be due to the difference between the two heights evaluated in our study (35 and 50 m a.g.l.) being relatively small compared to that of other studies (e.g., from 10 to 120 m; [29]). However, we did not evaluate heights below 35 m a.g.l. because it could put the physical integrity of the monkeys, the people, and the drone at risk. In the case of the upper height limit, when flying at heights above 50 m it was almost impossible to differentiate the species of interest with certainty, since the quality of the

image and the size of the silhouette of the sighted individual diminish considerably [55], so we consider that flying drones at higher heights for monitoring spider monkeys in areas characterized by flat terrain is not effective, at least at the moment. Another possibility could be that the sample size we used was too small to detect effects if they existed. We addressed this possibility by grouping flights only by height. However, flight height continued to have no effect on spider monkey behavioral responses.

Our results indicate that distance to the drone is an important factor in how spider monkeys perceive and respond to drone flights. For example, most vigilance events occurred when the drone was at a "close" and "medium" distance compared to when the drone was "far". Although we did not run statistical analyses, we observed a similar pattern for escape where all 8 events occurred when the drone was at "close" and "medium" distances from the monkeys. These results are in line with observations of several terrestrial mammals, that increase their behavioral responses as distance to drones decreases [34]. This increased response to the drone as it approaches may be due to a combination of factors such as the increased visibility and noise of the drone when it is closer, and therefore being perceived as a greater threat. This interpretation is supported by the results for resting, as spider monkeys rested in a greater proportion of scans when the drone was at "medium" and "far" distances compared to when the drone was close. Although spider monkeys increased resting during flights compared to before and after flights (see above), individuals were likely calmer when the drone was farther away compared to when it was closer by. However, this effect of distance may not have major implications in practical terms. This is because when conducting drone surveys of wild populations, the time that the drone is within visual and/or auditory range of the spider monkeys is relatively short (ranging from a few seconds to a maximum of a few minutes per flight). This implies that individuals can return to their activities a few minutes after the flight and thus drones possibly have minimal negative effects on their well-being.

We could not individually identify the spider monkeys over which we performed the flights. However, due to spider monkeys' high site fidelity [54], it is very likely that the flights were performed over the same group. As such our evaluation of the development of tolerance was at the group level and not at the subgroup or individual level. We found no evidence for differences in spider monkey responses to drone flights across the duration of the study for vigilance and resting, but we did find evidence for a reduction in the rate of agonistic display over time. In addition, spider monkeys performed agonistic displays in six of the 18 flights of the first subset and only in one of the 14 flights of the second subset. This change in agonistic displays may indicate that spider monkeys develop some level of tolerance to drone flights. Similar results have been reported for other species in response to drone flights. For example, black bears' (*Ursus americanus*) heart rate was higher than baseline during initial drone flights but decreased from the 25th flight until reaching baseline levels during the last flights [38]. Likewise, the probability of response of African ungulates decreased by approximately 20% with each subsequent drone flight [39]. We did not find a similar pattern for vigilance and resting, but it is important to consider that our study period was relatively short, and that long-term monitoring may reveal changes in vigilance and resting over time. Another possibility is that the observed temporal changes in agonistic displays, but not in vigilance and resting, were due to the development of tolerance to the observer, given that spider monkeys increased the performance of agonistic displays before, as well as during drone flights (see above).

There are some other factors that may affect our results. For example, group size may influence the response of individuals to a potential threat [26], with larger groups showing a higher probability of response and longer flight distances than smaller groups [26]. It is therefore possible that subgroup size influences spider monkey behavioral responses to drone flights. In larger subgroups, the dilution effect may reduce individual threat perception, as the probability of being attacked decreases as the group gets larger, which could lead to a reduced flight response. However, larger subgroups may have more individuals looking out for potential threats, which could result in faster drone detection

and a more coordinated response. We could not include subgroup size into our analyses as it was difficult to estimate without individually identifying the study monkeys. Studies on individually identified groups could help to elucidate the effect of subgroup size on behavioral responses to drone flights. Another factor that may influence spider monkey behavioral responses to drone flights is the duration and type of flight (i.e., grid flights, transect flights, hover flights). For example, hover flights generate a greater behavioral response from the spider monkeys than preprogrammed grid flights [45]. This may be due to the overall time that the drone flies over the monkeys. In hover flights the drone is directly over the monkeys for a greater amount of time than in preprogrammed grid or transect flights.

In addition to behavioral responses, there are other important factors to be considered in future studies using drones. One of these factors is to evaluate the physiological responses (e.g., changes in heart rate or glucocorticoid concentrations), whenever feasible, as they can complement the information obtained from behavioral responses. For example, studies on koalas (*Phascolarctos cinereus*), black bears, and common eider ducks (*Somateria mollissima*) suggest that drone surveys using adequate flight protocols do not have detrimental effects on wildlife physiology [25,38,81]. However, to the best of our knowledge, this type of study has not yet been conducted on wild primates. Another factor to consider is the impact drone flights can have on the monitored species in comparison to that of other monitoring methods. Up to now, the few studies that compared the behavioral responses to drone flights and to ground counts found less intense responses to drone flights [29,82,83], indicating that drones provide effective opportunities for large-scale, non-invasive surveys of wildlife when using adequate flight protocols.

Overall, the results of our study suggest that the use of drones for monitoring spider monkeys may be less disruptive than expected [84], making drones a viable tool for research and monitoring their populations. Our study contributes to the assessment of the potential impact of drone flights on the behavior of Geoffroy´s spider monkeys, which is an essential first step to use this technology to monitor their populations throughout their range. Although we did not find evidence for strong responses to drone flights, we believe that continued monitoring of the long-term effects of drone flights is essential, as it could reveal cumulative effects or subtle changes in spider monkey behavior. As each species responds differently to drone flights, we recommend conducting comparative studies across species in the same and different habitats to develop specific guidelines for drone use in various research and conservation settings.

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