Observer effects in a remote population of large-headed capuchins, *Sapajus macrocephalus*

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Abstract

Human observers often are present when researchers record animal behavior, which can create observer effects. These effects are rarely explicitly investigated, often due to the assumption that the study animal is habituated to or unaffected by a human's presence. We investigated the effect of human pressure gradients on a remote population of large-headed capuchins, *Sapajus macrocephalus*, looking specifically at the effects of number of observers, distance to observers, and distance to the research base. We conducted this study over 4 months in the Pacaya-Samiria Nature Reserve, Peru, and collected 199 two-minute focal samples of capuchin behavior. We found that capuchin monkeys fed less when human observers were closer to the focal individual, when more observers were present, and when capuchins were closer to the research base. We found no other consistent differences in capuchin monkey behavior across the measured human pressure gradients, although capuchins directed a high proportion of their vigilance toward humans (29% in adults and 47% in infants). Our results support the hypothesis that human pressure gradients influence animal behavior. Given the proportion of human directed vigilance, we recommend that all studies that use human observers to record animal behavior consider human-directed vigilance, record the number of observers, as well as the observer-focal animal distance, to check for these effects.

Keywords Animal behavior · Human influence · Vigilance · Peruvian Amazon

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Introduction

Observer effects occur when the behavior of studied organisms changes in response to researcher presence (McDougall, 2012). Some researchers mitigate these changes by habituating study animals before data collection takes place (Crofoot et al., 2010; Williamson & Feistner, 2011). However, even if study animals are habituated, some behaviors, such as vigilance, can change over a behavioral study (Jack et al., 2008). For example, habituated groups of white-faced capuchins, *Cebus capucinus*, increase their observer-directed behavior, including vigilance and alarm calls, and become more agitated when exposed repeatedly to humans, whereas nonhabituated groups show fewer displays of agitation as behavioral studies progress (Jack et al., 2008). Samango monkeys, *Cercopithecus mitis erythrarcus*, decrease their vigilance and eat more food from ground-level feeding sites in the presence of humans, suggesting that they perceive less threat from terrestrial predators when humans are present (Nowak et al., 2014; Nowak et al., 2016). In habituated groups, different individuals have different tolerances to human presence and therefore different flight initiation distances (Allan et al., 2020). These examples show how human presence can change animal risk perception and animal behavior. These effects could mean that deductions from research using human observers to collect data may not hold true for individuals that are less exposed to humans, for example, in very remote populations.

We can test for observer effects in the presence and absence of humans. For example, wild white-faced capuchins, *Cebus capucinus*, which researchers had fitted with remote sensors on radio collars to collect movement and location data, showed that spatial capuchin behavior did not change in the presence of humans (Crofoot et al., 2010). However, understanding observer effects requires information on other behaviors (such as feeding and vigilance) that researchers cannot so easily measure remotely. One alternative method to understand how observers can affect behavior is to explore how animal behavior changes with changes in human presence gradients. Previous research has used the term “human pressure gradient” to investigate spatiotemporal changes in land-use along a gradient of population density (Biasi et al., 2017); we extend the term to include any spatial or temporal changes in diverse measures of human encounters with animals, for example, the frequency of encounters, number of observers, or distances between observers and animals.

Previous studies that have looked at observer effects with differing human pressure gradients have found evidence of behavioral change across a range of taxa (Baker & McGuffin, 2007; LaBarge et al., 2020; Pereira et al., 2016). Fur seals, *Arctocephalus australis*, usually react to human approaches of less than 10 m by moving away, although sometimes they threaten the observer by orienting their head toward them (Cassini, 2001). As many animals move away with decreasing human distance, researchers have used flight initiation distance as a proxy for fearfulness across species (Stankowich & Blumstein, 2005). Animals also change their behavior in areas and at times when they encounter more humans (Geffroy et al., 2015; Mikula et al., 2018; Riley et al., 2016). Brown bears, *Ursus arctos*,

make beds in areas of denser foliage during the day (when human activity is greater) than they do at night, and rest further from towns and villages during the hunting season (Ordiz et al., 2011). A review of the effects of tourists on animal behavior showed various species exhibit greater behavioral change when more tourists are present (Geffroy et al., 2017).

Researchers have assumed that animals change their behavior as they are disturbed by increasing human pressure gradients. For example, animals scratch more after stressful events (Palagi and Norscia, 2011). Thus, as Barbary macaques, *Macaca sylvana*, scratch more when there are larger groups of human observers (Maréchal et al., 2011), this suggests that they find larger groups of human observers stressful. Wild animals also feed less when humans are closer (Parsons et al., 2016) and increase their vigilance when repeatedly exposed to humans (Jack et al., 2008). Nevertheless, although we have some understanding of how human pressure gradients affect animal behavior, there is still more that can be learnt, particularly for poorly studied animals in remote locations.

Animal behavior is affected by many variables in addition to human pressure gradients. For example, denser habitats provide more opportunities for terrestrial predators to hide and, thus, increase prey vigilance (Coleman & Hill, 2014; Makin et al., 2012), and higher numbers of fruiting trees can increase competition between primates, also causing increases in vigilance (Stevenson et al., 2000).

We investigated the effect of human pressure gradients and habitat on animal behavior in a remote population of primates. Using large-headed capuchins, *Sapajus macrocephalus*, as a study species, we also address the lack of behavioral studies on wild Amazonian *Sapajus* species (Lynch Alfaro et al., 2014) and provide information on the possible impact of observer effects in future studies. Primates are quick to adapt to new situations (Jack et al., 2008; Kalbitzer & Chapman, 2018), so they are anticipated to adapt to varying levels of human pressure gradients at a scale that can be investigated in a short-term behavioral study.

The purpose of this study is to determine whether human pressure gradients and habitat affect the behavior of a remote population of capuchins. We explore behavioral differences with (1) decreasing distance between an observer and their subject; (2) decreasing distance between a research base and the subject; (3) increasing numbers of observers; and (4) habitat variables, including density and number of fruiting trees. If capuchins perceive humans as a threat, we predict that human-directed vigilance, scratching, and time out of view will increase, whereas feeding will decrease, with increasing human pressure gradients. If capuchins perceive dense habitats as high-risk areas from predators and their conspecifics as competitors for food, then we predict that vigilance also will increase as the habitat becomes denser and the number of fruiting trees increases.

Methods

Study site

Our research took place in Pacaya Samiria Nature Reserve, Peru, at the remote “Puesto de Vigilancia 2” (PV2) – Tacshacocha. This area has low hunting pressure

due to its distance from the major town of Nauta and city of Iquitos (Bodmer & Lozano, 2001). The research base (S0571327, W9460683) has the greatest density of humans in the immediate area, with living quarters for researchers and a park guard hut. Operation Wallacea expeditions conducted primate behavioral studies at the site for a minimum of 6–8 weeks per year from 2010–2018 (Bodmer et al., 2018). For more than 35 years, researchers have repeatedly visited the larger region of the research site to collect data on wildlife and environmental variables (Puertas et al., 1995; Bodmer et al., 2009; Bodmer et al., 2018). However, the capuchins at PV2 are only occasionally exposed to humans, as there is little human pressure and no hunting.

Large-headed capuchins are medium sized primates with a semi-prehensile tail that live at high densities in a range of forest habitats (Lynch Alfaro et al., 2012). They have a black cap on their forehead that researchers can use to identify individuals due to its distinctive form, together with other facial markings (Pokorny & Waal, 2009). There are aerial and terrestrial predators of capuchins in the reserve, with a diversity of raptors (Knight, 2010), the jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), and puma (*Puma concolor*) (Pittet & Bennett, 2014) present.

We conducted this study from 22 April to 3 August 2018. Data collection occurred daily from 07.00–12.00 and 14.00–17.30. We paused data collection at midday for scheduled lunch breaks for research assistants—a feature of this field site. For the purpose of this study, we used ten transects of approximately 3-km each, established near the research base in 2010 for long-term monitoring of many taxa (Bodmer et al. 2018). The distance between transects varies. We were unable to sample all transects equally due to external circumstances, such as temporary flooding of some transects (Bodmer et al. 2018). Furthermore, the primary goals of the long-term research project at this site took precedence over the needs of this study. Therefore, we could only use transects when sampling was not taking place for the long-term research project (Fund Amazonia, 2021). We did not sample transects in the afternoon that had been visited by other researchers in the morning, because many of the protocols (e.g., for habitat sampling) for the long-term project did not restrict noise and included placement of research materials, such as mist nets and cameras traps.

Within these constraints, we chose one of ten transects at random for morning data collection and a different transect for afternoon data collection. We walked the transect until we found a group of large-headed capuchins. We randomly selected one of the visible individuals in this group as the subject of a 2-minute focal sample (Altmann, 1974), and we recorded the behavior and habitat variables detailed below.

We recorded the age class of the individual as infant, juvenile, subadult, or adult—identifiable by body size and proportions. The characteristics that we used to distinguish between age class included:

- Infants—small body size and carried by others with no independent locomotion;
- Juveniles—smaller than adults and larger heads relative to body size with fuzzier pelage; can move around by themselves but less confident in their locomotion than adults;

- Subadults—not fully grown but resembled adults in pelage and locomotor ability;
- Adults—fully grown individuals that were sexually mature.

Where possible, we also recorded the group and individual identity (using facial characteristics and group composition to identify groups). When we could not identify a group, it was assigned a unique identification number. Once we had recorded data on this individual, another visible individual in the group was chosen at random and another focal sample was taken. We repeated this until all individuals in the group had been used for the data collection or until we could no longer follow the group. To prevent pseudo-replication, if we could not identify an individual that was distinct from the previous samples for that day, we left the primate group and we began searching for a new group. We recorded the location of groups, and if we recognised the group or it was likely to be the same group already sampled on that day (based on group structure, individual facial features, and the time and location of the previous sighting), then we would not sample the group again. We only recorded multiple capuchin groups on the same transect on the same day 19 times. We located three groups on the same transect on only 3 days, whereas the other 16 cases featured only two groups, demonstrating the low likelihood of unknowingly sampling the same group twice in a day.

Measuring behavior

One observer recorded all behavioral data by observing the focal individual through binoculars (vector 8 x 42 waterproof binoculars) during a 2-minute focal sample and described the behaviors observed. A second observer entered the data into “Behavioral Observation Research Interactive Software” (BORIS) (Friard & Gamba, 2016), installed on a Lenovo HLA2-U8P(10) tablet. There was always a minimum of two observers to comply with field safety regulations (range 2-6). BORIS recorded the duration of the behavioral states feeding, locomotion, resting, and when the focal individual was out of view in seconds using time stamps (Table I). We also recorded scratching and vigilance (Table I) as point event behaviors.

Human influence

We measured the distance between the base and the location of the individual at the end of the focal sample (measured using an etrex 10 Garmin GPS) in metres. We recorded the number of people present during data collection and horizontal distance between the observer and the focal individual at the end of the 2-minute sample, which varied from 1-60 m. We measured the distance using a Silverline MT40 50 m fiberglass surveyors tape or a Track life 60-m laser distance meter.

Table 1 Ethogram of behaviors recorded in BORIS during a 2-minute focal sample on large-headed capuchins

	Behavior	Description
Vigilance behavior	Look human	Focal individual looks at the human observer.
	Look up	Focal individual looks up. This may be a movement of gaze direction only, or a movement of the head where the chin is lifted. May be a single movement or may continue to move head (e.g., side to side) whilst maintaining an upwards gaze.
	Look down	Focal individual looks down. This may be a movement of gaze direction only, or a movement of the head where the chin is lowered. May be a single movement or may continue to move head (e.g., side to side) whilst maintaining a downwards gaze.
	Look other	Focal individual looks at another item. This may be another individual, food, or any other item apart from a human.
Behavioral state	Look around	Focal individual looks around them in a sweeping motion of the head or eyes.
	Feeding (s)	The grasping of edible material, which the focal individual moves towards their mouth to consume.
	Locomotion (s)	Focal individual moves either arboreally, terrestrially or by leaping.
	Resting (s)	Minimal movement of focal individual while sitting, standing, or laying on the ground, branch, or other substrate.
Other behaviors	Out of view (s)	Behaviors of the focal individual cannot be recorded as obstacles lie in the visual path of the observer.
	Scratching	When the focal individual uses one of its limbs to scratch itself. For analysis, we converted this to a binomial result within a 2-minute sample—"scratch" or "did not scratch."

We recorded feeding, locomotion, resting, and out of view as behavioral states in seconds. We also recorded vigilance and scratching as events. For analysis, we classified focal samples as either including or not including scratching due to its relatively low occurrence. We collected data between 22 April and 3 August 2018 at Puesto de Vigilancia 2 (PV2), Tacshacocha, Pacaya Samiria Nature Reserve, Peru

Measuring habitat

We also recorded variables that can impact behavior, including habitat characteristics, group size, and age class (infant, juvenile, subadult or adult, identifiable by body size and proportions) of the focal individuals. We measured three habitat variables at the location of an individual at the end of the 2-minute focal sample: type of habitat (liana, levee, or other), and the number of fruiting trees and tree crowns within 5 m (Table II). We also calculated the height of the focal individual using the distance from the observer to immediately below the location of the individual (using a Silverline MT40 50-m fiberglass surveyors tape or a Track life 60-m laser distance meter), the angle of observation (measured with a BM-5/360PC Suunto 360° clinometer), and the eye height of the observer.

Statistical analysis

We used five response variables to measure capuchin behavior: counts of human-directed vigilance and nonhuman vigilance (all other vigilance); number of seconds spent feeding; whether we observed scratching behavior during a focal sample; and the number of seconds the capuchin was out of view. We included capuchin age class (infant, juvenile, subadult, adult), number of nearest neighbours (number of individuals within 5 m of the focal individual), the number of human observers, the distance to the observer, the distance to the base, the height of the capuchin, the total crowns, habitat type (levee, liana, or other), and the number of fruiting trees as explanatory variables in all analyses. We used multiple generalised linear mixed models (GLMM) in RStudio version 1.1.442, R version 3.4.4 (R Core Team, 2018), with the monkey group ($N = 48$) included as a random effect and an interaction term between the number of observers and the distance to the base camp in all models. We used diagnostic plots of the predictions and residuals to check the assumptions of all models. We conducted type II ANOVAs on human directed vigilance, feeding and scratching GLMMs to test the significance of the explanatory variables, and type III ANOVAs on the nonhuman vigilance and out of view GLMMs due to the significance of the interaction. The human directed vigilance model uses a zero inflated error structure within the R package GLMM Template Model Builder (glmmTMB) (Broioks et al., 2017), and we calculated R^2 using the sjstats package (Lüdecke, 2019). We use the optimizer bobyqa to undertake the nonhuman vigilance and the feeding GLMMs and the r.squaredGLMM function from the MuMIn package (Barton, 2018) to calculate R^2 . We report the trigamma estimate for both the marginal and conditional R^2 values for all models with numerical response variables. As we analysed the time out of view, feeding and scratching models with a binomial distribution, we report the theoretical marginal and conditional R^2 . The feeding model compares the time the capuchin was in view and feeding, with when they were in view and not feeding. We conducted post-hoc Tukey tests using the ghlft function in the multcomp package (Hothorn et al., 2008) for all GLMMs except the zero inflated

Table II Habitat variables measured in a behavioral study of large-headed capuchins

Habitat Variables	Description	Predicted relationship with behavior
Total crowns	The number of tree crowns within a 5-m radius of where the capuchin was last sighted, these crowns can be at the same height, lower or higher than the focal individual.	As the area around the capuchin becomes denser, they are expected to become more vigilant (Coleman & Hill, 2014).
Habitat	Liana Intertwined liana vines dominate the area, often very dense with low to intermediate canopy height.	Liana habitat has higher foliage density that offers more opportunities for terrestrial predators to hide; higher antipredator behavior is expected closer to the canopy floor in these habitats (Makin et al., 2012).
	Levee These areas are dominated by larger trees. Due to the higher ground level there the flood line is lower than other habitats, and there is greater ground flora.	Levee habitat has taller trees and so towards the top of the canopy is more at risk from areal predation; more antipredator behavior is expected here (Makin et al., 2012).
	Other This is any habitat that does not fall into the liana and levee categories. It can include, riverine forest, open understorey, tree fall gaps and palm swamps, and occupied small parts of the study area.	
Fruiting trees	The number of fruiting trees within a 5-m radius of where the capuchin was located at the end of the focal sample.	As the number of fruiting trees increases capuchins are expected to increase vigilance, to be aware of unwanted competition (Stevenson et al., 2000).

We collected data between 22 April 3 August 2018 at Puesto de Vigilancia 2 (PV2), Taeshacocho, Pacaya Samiria Nature Reserve, Peru

human vigilance model where we used the emmeans package (Lenth, 2019). All these analyses used an alpha level of 0.05.

We made 199 observations of individuals, but the number of individuals included in analyses (N) varies 138–167 due to NAs. For all statistical analyses, we filtered the dataset to remove groups where we only sampled one capuchin, as uneven sampling of random effects can result in unstable model estimates (Harrison et al., 2018). We encountered a maximum of 92 capuchin groups on the 10 transects. For the models of nonhuman vigilance, human vigilance, feeding, and scratching behavior, these 199 observations only included capuchins that had been in view for at least 70 seconds in a 2-minute focal sample ($n = 167$).

Ethical note

The Royal Holloway University of London University Research Ethics committee approved the research prior to its commencement. We followed all applicable institutional and/or national guidelines for the care and use of animals.

Data availability The datasets generated during the current study are not publicly available but are available from the corresponding author on reasonable request.

Results

Large-headed capuchins looked at an observer $1.6 \pm \text{SD } 2.3$ ($N = 199$) times in a 2-minute focal sample and made a mean of $2.9 \pm \text{SD } 2.9$ nonhuman vigilance scans ($N = 199$). Capuchins displayed more human-directed vigilance in liana habitats, and focal individuals showed highest human directed vigilance when they were closer to the ground (Fig. 1). No other independent variables had a significant effect on human directed vigilance by capuchin monkeys (Table III). The fixed effects explain 43% of the variance in human-directed vigilance (Poisson GLMM, marginal $R^2 = 0.43$, conditional $R^2 = 0.52$, $N = 139$).

Capuchins displayed more non-human vigilance in levee and liana habitats than in “other” habitats (Table III), but all Tukey post hoc tests were nonsignificant. Non-human vigilance was not significantly affected by any other measured independent variable (Table III). The fixed effects explain 30% of the variance in nonhuman vigilance (Poisson GLMM, marginal $R^2 = 0.30$, conditional $R^2 = 0.52$, $N = 167$).

Capuchins spent a mean of $41 \pm \text{SD } 41$ seconds of a 2 minute focal sample ($N = 199$) feeding. Individuals fed less when more observers were present (Table III; Fig. 2), although a Tukey post hoc test was nonsignificant. Capuchins increased feeding as the distance to the observer increased (Fig. 2), in larger groups, in habitats with more crowns within 5 m, when further from the research base, and when closer to the ground (Table III). Capuchins also fed more in levee than in liana habitat (Table III, post-hoc Tukey test, levee-liana $Z = 3.54$, $P = 0.001$). Capuchin feeding behavior was not associated with differences in the number of

Fig. 1 The frequency that large-headed capuchins showed human directed vigilance during a 2-minute focal sample vs. the height of the capuchin. We used the function `geom_smooth()` with method `glm` to draw the prediction and standard error from the model. We added a 0.02-cm jitter to allow overlapping points to be viewed. We collected data between 22 April and 3 August 2018 at Puesto de Vigilancia 2 (PV2), Tacshacocha, Pacaya Samiria Nature Reserve, Peru.

fruiting trees (Table III). The fixed effects explain 21% of this model (Binomial GLMM, marginal $R^2 = 0.21$, conditional $R^2 = 0.99$, $N = 139$).

Capuchins scratched in 57% of focal observations ($N = 199$). The model explained 16% of the variance during the observations (Binomial GLMM, marginal $R^2 = 0.16$, conditional $R^2 = 0.16$, $N = 138$), but this was due to group level differences in scratching and none of the fixed effects were significantly associated with scratching (Table III).

The capuchins were out of view for a mean of $15 \text{ s} \pm \text{SD } 21$ ($N = 199$) in a 2-minute sample. The number of observers had a significant effect on the time the capuchin spent out of view (Table III). A post-hoc Tukey showed the difference lay between two and three observers ($Z = 3.59$, $P = 0.002$) and three and four ($Z = -3.40$, $P = 0.004$). The higher the capuchin, and the fewer crowns within 5 m, the more time they spent out of view (Table III). Capuchins also spent more time out of view in the liana habitat than levee or other habitats (Table III, post-hoc Tukey, liana - levee $Z = 3.93$, $P < 0.001$; liana - "other" $Z = 3.62$, $P < 0.001$). None of the other fixed effects were significantly associated with the time spent out of view (Table III). Overall, the fixed effects in the model explained 43% of

Table III Estimates and standard errors (SE) of the change in five response variables describing capuchin behavior associated with various explanatory variables describing human pressure gradients and the habitat

Response variables	Human directed vigilance				Nonhuman vigilance				No. second capuchin fed				Whether the capuchin scratched				No. of seconds capuchin spent out of view			
	Esti- mate $\pm$ SE	χ^2	DF	P	Estimate $\pm$ SE	χ^2	DF	P	Esti- mate $\pm$ SE	χ^2	DF	P	Esti- mate $\pm$ SE	χ^2	DF	P	Esti- mate $\pm$ SE	χ^2	DF	P
Intercept	0.89 $\pm$ 0.50				0.73 $\pm$ 0.40				-4.37 $\pm$ 0.55				0.21 $\pm$ 1.26				-0.34 $\pm$ 0.15			
Observers: 3	-0.07 $\pm$ 0.37	2.76	3	0.431	-0.06 $\pm$ 0.29	3.34	3	0.342	-0.79 $\pm$ 0.43	58.34	3	<0.001	0.22 $\pm$ 0.71	1.10	3	0.777	0.46 $\pm$ 0.13	22.27	3	<0.001
Observers: 4	-0.45 $\pm$ 0.58				-0.03 $\pm$ 0.43				-0.93 $\pm$ 1.13				-0.78 $\pm$ 1.19				-0.22 $\pm$ 0.22			
Observers: 5+	-0.66 $\pm$ 1.00				-1.08 $\pm$ 0.64				-1.14 $\pm$ 1.17				-0.47 $\pm$ 1.43				0.43 $\pm$ 0.26			
Distance to capuchin	0.05 $\pm$ 0.10	0.20	1	0.653	0.10 $\pm$ 0.07	2.24	1	0.134	0.19 $\pm$ 0.03	36.20	1	<0.001	0.12 $\pm$ 0.22	0.30	1	0.583	-0.03 $\pm$ 0.02	3.44	1	0.063
Distance to base	-0.20 $\pm$ 0.45	0.00	1	0.982	-0.38 $\pm$ 0.35	1.18	1	0.278	0.41 $\pm$ 0.61	102.43	1	<0.001	0.82 $\pm$ 0.92	1.34	1	0.248	0.33 $\pm$ 0.19	3.06	1	0.080
Capuchin height	-0.22 $\pm$ 0.10	4.60	1	0.032	-0.10 $\pm$ 0.08	1.75	1	0.186	-0.39 $\pm$ 0.03	133.68	1	<0.001	-0.30 $\pm$ 0.23	1.74	1	0.187	0.07 $\pm$ 0.02	14.62	1	<0.001
Group density	-0.03 $\pm$ 0.04	0.41	1	0.521	0.04 $\pm$ 0.04	0.99	1	0.319	0.39 $\pm$ 0.02	364.86	1	<0.001	-0.02 $\pm$ 0.11	0.05	1	0.818	-0.01 $\pm$ 0.01	0.59	1	0.442
Total crowns	-0.01 $\pm$ 0.04	0.06	1	0.803	-0.01 $\pm$ 0.04	0.08	1	0.774	0.08 $\pm$ 0.02	21.40	1	<0.001	-0.05 $\pm$ 0.10	0.20	1	0.654	-0.05 $\pm$ 0.01	40.31	1	<0.001
Habitat: levee	-0.04 $\pm$ 0.22	6.91	2	0.032	0.41 $\pm$ 0.19	7.78	2	0.020	0.14 $\pm$ 0.08	12.67	2	0.002	-0.60 $\pm$ 0.56	1.63	2	0.443	-0.05 $\pm$ 0.05	18.63	2	<0.001
Habitat: liana	0.45 $\pm$ 0.19				0.41 $\pm$ 0.17				-0.17 $\pm$ 0.07				0.13 $\pm$ 0.45				0.15 $\pm$ 0.04			
Number of fruiting trees	0.04 $\pm$ 0.11	0.15	1	0.702	-0.04 $\pm$ 0.08	0.24	1	0.623	-0.02 $\pm$ 0.04	0.04	1	0.508	0.15 $\pm$ 0.27	0.34	1	0.562	0.02 $\pm$ 0.02	0.69	1	0.407

Table III (continued)

Response variables	Human directed vigilance				Nonhuman vigilance				No. second capuchin fed				Whether the capuchin scratched				No. of seconds capuchin spent out of view			
	Esti- mate $\pm$ SE	χ^2	DF	P	Estimate $\pm$ SE	χ^2	DF	P	Esti- mate $\pm$ SE	χ^2	DF	P	Esti- mate $\pm$ SE	χ^2	DF	P	Esti- mate $\pm$ SE	χ^2	DF	P
Age class: subadult	0.03 $\pm$ 0.38	9.65	3	0.022	0.01 $\pm$ 0.23	9.92	3	0.019	2.28 $\pm$ 0.10	621.94	3	<0.001	-0.08 $\pm$ 0.66	2.75	3	0.432	-0.11 $\pm$ 0.06	15.29	3	0.002
Age class: juvenile	0.20 $\pm$ 0.18				-0.34 $\pm$ 0.14				2.58 $\pm$ 0.14				-1.12 $\pm$ 0.95				-0.12 $\pm$ 0.03			
Age class: infant	0.70 $\pm$ 0.23				-0.16 $\pm$ 0.18				2.40 $\pm$ 0.10				-0.57 $\pm$ 0.64				-0.03 $\pm$ 0.04			
Int: distance to base and 3 observ- ers	0.21 $\pm$ 0.45	2.00	3	0.573	0.59 $\pm$ 0.35	8.05	3	0.045	-0.88 $\pm$ 0.61	2.34	3	0.506	-0.52 $\pm$ 0.92	1.90	3	0.592	0.37 $\pm$ 0.19	33.06	3	<0.001
Int: distance to base and 4 observ- ers	0.09 $\pm$ 0.55				0.48 $\pm$ 0.41				-1.18 $\pm$ 1.11				-1.31 $\pm$ 1.23				0.83 $\pm$ 0.25			
Int: distance to base and 5+ observ- ers	-1.31 $\pm$ 1.29				-1.32 $\pm$ 0.87				-1.21 $\pm$ 1.21				-1.85 $\pm$ 1.79				-0.53 $\pm$ 0.27			
Overall model results		308.10	20	<0.001		73.72	18	<0.001		3945.40	18	<0.001		44.68	18	<0.001		779.59	18	<0.001

Estimates are logged and we have included interaction terms (Int). Alpha levels below 0.05 are in bold. We collected data between 22 April and 3 August 2018 at Puesto de Vigilancia 2 (PV2), Taqshacocha, Pacaya Samiria Nature Reserve, Peru

Fig. 2 Focal individual feeding behavior plotted against the distance from large-headed capuchins to the observers (measured in seconds over a 2-minute focal sample). We added a 0.02-cm jitter to allow overlapping points to be viewed. We collected data between 22 April and 3 August 2018 at Puesto de Vigilancia 2 (PV2), Tacshacocha, Pacaya Samiria Nature Reserve, Peru.

the variation in the number of seconds a focal capuchin was out of view (Binomial GLMM, marginal $R^2 = 0.43$, conditional $R^2 = 0.96$, $N = 165$).

Discussion

We found that human pressure gradients are associated with behavioral changes in large-headed capuchins, in a remote location in the Pacaya-Samiria Nature Reserve, Peru. First, capuchins spent more time feeding when fewer observers were present, and when they were further away from the observers and research base. This supports the hypothesis that capuchins perceive an increase in human pressure as a threat (Makin et al., 2012; Nowak et al., 2016). Reduced feeding in areas of high perceived threat is an antipredator strategy: vervet monkeys, *Chlorocebus aethiops*, reduce feeding at the base of trees and the tops of the canopy in response to terrestrial and aerial predation, respectively (Makin et al., 2012), and samango monkeys, *Cercopithecus albogularis schwarzi*, reduce feeding when exposed repeatedly to live trapping (Nowak et al., 2016). Other taxa show similar responses: white tailed deer, *Odocoileus virginianus*, eastern grey squirrel, *Sciurus carolinensis*, and northern raccoon, *Procyon lotor*, perceive humans as a greater threat than their natural predator, the coyote, *Canis latrans*.

– feeding less when humans were closer, and even less so when humans are accompanied by a domestic dog, *Canis familiaris* (Parsons et al., 2016).

Although we did not find an association between capuchin vigilance and increases in human presence, studied individuals directed a non-trivial proportion of vigilance behavior at humans (>25% on average across all age classes). Future studies could compare vigilance behavior in the presence and absence of observers to understand if individuals are increasing their overall vigilance, or reducing vigilance directed elsewhere. Researchers usually measure vigilance behavior as a single variable (Busia et al., 2016) or separated into antipredator and social vigilance (Hirsch, 2002), but human directed vigilance often is not distinguished or recorded. Due to variability in definitions of vigilance behavior, it is difficult to compare vigilance between primate studies (Allan & Hill, 2018). As our understanding of predation risk increases, it becomes increasingly important to separate and carefully define different types of vigilance. This is especially true as responses to anthropogenic disturbance stimuli, such as loud noises and objects that approach at a rapid speed, are likened to predation risk (Frid & Dill, 2002).

Displacement activities, such as scratching, indicate stress (Schino et al., 1991; Troisi, 2002). Increased scratching is associated with larger groups of human observers (Maréchal et al., 2011). Although capuchins did not show changes in scratching with the human pressure gradients measured in our study, the method of data collection may have influenced this outcome as we did not use scratching duration. Researchers usually record scratching as episodes per hour (Maréchal et al., 2011; Palagi & Norscia, 2011; Schino et al., 1991) but we used presence and absence of scratching due to the short duration of focal samples.

The amount of time a capuchin was out of view was associated with the number of observers. However, contrary to our predictions, capuchins did not consistently spend more time out of view as the number of observers increased. This result may be due to other factors, which systematically differed between groups with different numbers of human observers but were not measured here. One possibility is that capuchin behavior differs with male and female observers, although we did not record these data. Monkey species, such as the woolly monkey, *Lagothrix poeppigii*, can distinguish between hunters, researchers, and forest gathers (Papworth et al., 2013). Because 95% of hunters are male in Peru (Francesconi et al., 2018), monkeys may perceive male observers as hunters and therefore a threat. Other unmeasured observer variables also may have affected behavior; for example, although observers were as quiet as possible in this study, the noise emitted by the human observers may have differed. Captive orangutans, *Pongo pygmaeus*, hide more when noise increases (Birke, 2002), and louder conversations reduce visibility of wild pygmy marmosets, *Cebuella pygmaea* (Sheehan and Papworth, 2019). The behavior and appearance of observers is an area of research that may therefore benefit from further consideration.

Habitat

Individuals lower in the canopy showed more human directed vigilance, even though we found no relationship between human directed vigilance and horizontal distance to observers. A capuchin monkey 20-m off the ground, but almost directly above a

human, may be able to correctly assess that the human is less able to approach than if the capuchin is 1-m off the ground but 20-m away, although the actual distance between them is identical. This suggests that capuchins, and possibly other arboreal animals, may use a vertical axis of fear to assess the risk posed by humans (Makin et al., 2012; Nowak et al., 2014). We expected nonhuman vigilance to change with the habitat, as is the case in other capuchin species (Campos & Fedigan, 2014), and as we predicted, it was higher in both liana and levee habitats.

In addition to changing behavior, using human observers can bias data collection. Because humans are restricted to the ground, their view of study animals is more likely to be obscured when the focal individual is higher in the canopy and when foliage is denser. This is supported by our results, as capuchins were out of view for longer when they were higher in the canopy and when there were more tree crowns within 5 m. Studies have tried to overcome this, using methods, such as radio collars (Crofoot et al., 2010) and accelerometers (Sellers & Crompton, 2004), but behaviors, such as vigilance and feeding cannot be measured using these methods.

Capuchins fed most in levees, which are habitats with a wide variety of flora (Jong, 2001) and thus potential sources of food for this opportunistic omnivore (Addressi, 2008). However, the number of fruiting trees did not affect any of the behaviors measured. This result was unexpected, especially as other platyrrhines, such as the squirrel monkey (*Saimiri sciureus*), decrease their fruit intake during the dry season when there are fewer fruiting trees (Stone, 2007). Other researchers have used feeding as an indicator of levels of risk (Makin et al., 2012). In this study, individuals fed less when higher in the canopy and more in areas of greater crown density. This could be an example of predator sensitive foraging (White et al., 2003), although we found no relationship between non-human directed vigilance and height or crown density, which would have further supported this hypothesis. Habitat density can influence behavior; the blue monkey, *Cercopithecus mitis*, increases its vigilance in low foliage density (Gaynor & Cords, 2012), and bats in Honduras fly in straighter lines to cross clearings surrounded by denser foliage than those bordered by more open foliage (Caras & Korine, 2009).

Conclusions

We found evidence that the behavior of large-headed capuchin monkeys at a remote location within Pacaya Samiria Nature Reserve differ with various measures of a human pressure gradient. Feeding behavior and the time that an individual spends out of view were associated with the number of human observers. Feeding behavior increased as the distance between the individual, the research base, and observer increased.

Our findings have implications for the collection of behavioral data by human observers. Although we did not find evidence that human pressure gradients are associated with capuchin monkey human-directed vigilance, we nevertheless recommend that human-directed vigilance is distinguished as a separate category in all future animal behavior studies on vigilance. This is due to the high levels of human-directed vigilance observed in this study. The effects of humans on animal behavior

are not necessarily predictable across sites or species, but with the growing evidence for observer effects, we suggest such measures should be incorporated in all studies of animal behavior to test for and control these effects. The measures we included in this study (human-directed vigilance, observer-subject distance, and observer group size) are relatively simple to include in any animal behavior study and can control for possible observer effects. If researchers record these variables and human-directed vigilance in all animal behavior studies where humans are present, this would allow them to check for behavioral biases, which might be introduced by human observers.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest. **ESM1** (PDF 100 KB)

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