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Applying Behavioral Conditioning to Identify Anticipatory Behaviors

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ABSTRACT

The ability to predict regular events can be adaptive for nonhuman animals living in an otherwise unpredictable environment. Animals may exhibit behavioral changes preceding a predictable event; such changes reflect anticipatory behavior. Anticipatory behavior is broadly defined as a goal-directed increase in activity preceding a predictable event and can be useful for assessing well being in animals in captivity. Anticipation may look different in different animals, however, necessitating methods to generate and study anticipatory behaviors across species. This article includes a proposed method for generating and describing anticipatory behavior in zoos using behavioral conditioning. The article also includes discussion of case studies of the proposed method with 2 animals at the San Francisco Zoo: a silverback gorilla (*Gorilla gorilla gorilla*) and a red panda (*Ailurus fulgens*). The study evidence supports anticipation in both animals. As behavioral conditioning can be used with many animals, the proposed method provides a practical approach for using anticipatory behavior to assess animal well being in zoos.

KEYWORDS
Animal welfare; human–animal interactions; zoo animals

A nonhuman animal's ability to anticipate the availability of resources such as food, water, or shelter can result in behavioral changes directed toward acquisition of that resource (Antle & Silver, 2009). In this way, the ability to predict and anticipate events allows animals to meet their needs and makes anticipation an adaptive response to a variable environment (Balsam, Sanchez-Castillo, Taylor, Van Volkinburg, & Ward, 2009). For an animal to anticipate an event in the future, the event must be signaled in some way (Gottlieb, Coleman, & McCowan, 2013). Signals may be driven by cues in the environment or through the animal's internal processes (Dantas-Ferreira et al., 2015; Davidson, Tataroglu, & Menaker, 2005; Mistlberger, 2009; Mistlberger & Antle, 2011).

The preponderance of neurological timing mechanisms available to organisms from insects to primates supports the importance across taxa of being able to predict and adapt to events on timescales from seconds to seasons (Antle & Silver, 2009; Mistlberger & Antle, 2011; Moore, 2001). Although animals living in controlled environments may not need to anticipate resource availability or seasonal changes in the environment, they still predict and respond to regular events with specific behavioral patterns (Jensen, Delfour, & Carter, 2013; Moe et al., 2014); these behavioral patterns are referred to as anticipatory behaviors.

Anticipatory behavior is broadly defined as a goal-directed increase in activity preceding a predictable event (Spruijt, van den Bos, & Pijlman, 2001; van der Harst, Baars, & Spruijt, 2003). Food anticipatory activity, or increased activity prior to a regular feeding, is a well-studied form of anticipatory behavior often observed in animals on a predictable feeding schedule (Bassett &

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Buchanan-Smith, 2007; Stephan, 2002). Anticipation may also occur in response to nonfood rewards, including sex, drugs, or social interactions (Anderson, Yngvesson, Boissy, Uvnas-Moberg, & Lidfors, 2015; Deak, Arakawa, Bekkedal, & Panksepp, 2009; Keith et al., 2013). Anticipatory behaviors can share similar characteristics with stereotypies in that both are repetitive, seemingly purposeless patterns of behavior (Mason, 1991), but while it is difficult to distract a stereotyping animal, anticipatory behavior usually follows transitions with cues indicating the arrival of an reward and abates once an animal acquires the reward (Ikemoto & Panksepp, 1996). Anticipatory behavior can be particularly common among animals in captivity, as daily husbandry events that animals look forward to are often scheduled or follow a set of predictable cues.

A growing body of research supports the use of anticipatory behavior as an indicator of an animal's reward sensitivity and, as such, a potential metric of captive animal welfare (Folkedal et al., 2012; Hansen & Jeppesen, 2006; van der Harst & Spruijt, 2007; Watters, 2014). This work suggests that the intensity of anticipatory behavior an animal exhibits is an indicator of how the animal perceives his/her overall welfare (Watters, 2014). For instance, animals in impoverished environments often exhibit intense anticipation of predictable positive events (Morgan & Einon, 1975; van der Harst & Spruijt, 2007), with durations of anticipatory bouts much greater than those of animals in enriched environments. When positive events are rare in an animal's day, the animal may become intensely focused on the few opportunities he/she does have, thereby supporting intense anticipatory behavior as an indicator of negative welfare (Bassett & Buchanan-Smith, 2007; van der Harst et al., 2003).

Alternatively, animals in enriched environments may have several positive opportunities daily and show a high frequency of subtle or relatively blasé bouts of the behavior. Which behaviors are expressed can also provide insight into how an animal regards an upcoming event. If the animal is attentive and moving toward a stimulus, he/she is likely expecting a positive outcome (Bloomsmith & Lambeth, 1995), whereas if the animal moves away or begins engaging in self-injurious behaviors, he/she is likely anticipating a negative event (Bassett & Buchanan-Smith, 2007). Thus, anticipatory behavior can be useful in determining whether animals themselves perceive specific events to be pleasurable or disagreeable. An animal's location can also indicate anticipation of an event particularly if the event typically occurs in the same part of the animal's enclosure (Jensen et al., 2013). Observing the type of behaviors as well as behavior frequency, duration, and location during bouts of anticipatory activity can be useful for assessing an animal's overall and moment-to-moment welfare (Watters, 2014).

Anticipatory behaviors vary among species and may depend on species-specific or learned reward acquisition behaviors (van den Bos, Meijer, van Renselaar, van der Harst, & Spruijt, 2003). Nonetheless, some general patterns have been described. Increased activity levels prior to regular feeding have been described in rodents, birds, fish, and some primates; however, studies of chimpanzees (*Pan troglodytes*), dolphins (*Tursiops truncatus*), and cats (*Felis silvestris catus*) have shown decreased activity levels prior to anticipated events (Bloomsmith & Lambeth, 1995; Jensen et al., 2013; Mistlberger, 2009). The presentation of anticipatory behavior may also differ among individuals of the same species due to differences in environment, management, or learning (Mistlberger, 1994; Vinke, Houx, van den Bos, & Spruijt, 2006). Thus, methods for generating and describing anticipatory behavior in different species and under varying management conditions are necessary to make the best use of the welfare applications of anticipatory behaviors in captive animals.

Here we describe a method for generating and describing anticipatory behavior. We present findings from the use of this method in two species, Western lowland gorillas (*Gorilla gorilla gorilla*) and the red panda (*Ailurus fulgens)*, in a zoo setting. Our goal for this study was to assess whether a positive human–animal interaction was sufficient to generate anticipatory behavior in the focal animals and, if so, to describe the resulting anticipatory behaviors. We recognize that not all animals might find the opportunity to interact with humans as positive. The method described here could be used to assess an animal's anticipation of feeding or other positive event in an animal's day.

Materials and methods

General method for generating anticipatory behavior

We tested a method for generating and describing anticipatory behavior in two species at the San Francisco Zoo. We selected animals for the study based on the behavioral ecology of their species as well as individual temperament. Gorillas are highly social primates and can benefit from positive social interactions with human caretakers while in captivity (Chelluri, Ross, & Wagner, 2013). We focused on the silverback gorilla in the troop because of the potential for the dominant male to exclude other gorillas from engaging in the indoor experimental sessions (Stoinski, Lukas, Kuhar, & Maple, 2004; Stokes, 2004). Based on information provided by keepers, we selected the focal red panda because he was highly interactive with his caretakers at the time of the study. Based on his temperament toward interacting with humans, we had reason to expect an additional social interaction with a human could be a positive event for him.

At each focal exhibit, we set up a digital video camera to record the animal's behavior. We began recording and then sounded a buzzer. Four minutes after the buzzer sounded, a member of the animal management staff approached the enclosure to engage in a "positive" interaction with the animal for 15 min. Positive interactions included being present with a nonthreatening posture and talking to the animal with a gentle voice. For both focal species, the person approaching was an individual with no involvement in the animal's day-to-day care and did not provide any stimulus besides social interaction. To provide an additional level of predictability for the animals, we conducted experimental sessions at the same time of day throughout the experiment. We expected that over time, the focal animals would demonstrate interest, disinterest, or indifference to taking part in the interaction, with changes or a lack of changes in their behavioral repertoire during the 4 min prior to the arrival of the person.

The resulting videos were placed in random order with the date and time removed for data collection. Observers watched the videos and created an ethogram for each species to describe the behaviors in the videos (Table 1 and Table 2). As observers recorded data on all individuals present in the videos, we prioritized entrances and exits of individuals to help keep track of individuals present in view. We also prioritized several behaviors based on species-specific and individual behaviors. For example, the bilabial trill is a vocalization the silverback makes when agitated, so it was of particular interest to assess how the silverback responded to the staff member. The rumble vocalization was prioritized because it is a generally accepted indicator of contentment or positive social interactions in gorillas (Fossey, 1972). Looking behaviors took priority over other behaviors because we assumed the direction of a look indicated an object or individual of interest to the animal.

Finally, more intense forms of locomotion such as charging or trotting took priority over less-involved forms of locomotion such as walk. Observers also created diagrams of the exhibits in the videos, so each behavior observed was paired with the location where the behavior occurred. Data collection was done using JWatcher (Blumstein, Daniel, & Evans, 2010). The timestamp of each new behavior and corresponding location was recorded while watching videos in JWatcher, and recording the beginning of a new behavior indicated the end of the previous behavior. Three observers watched and recorded data from video files, with all observers recording data from the same video. We ensured interobserver reliability by calculating Fleiss's kappa (Fleiss, 1971) for each video. If the interobserver reliability for any video was less than 98%, observers watched the video and recorded data together to ensure agreement on behaviors and locations.

We calculated the duration and counted the frequency of each behavior during the 4-min trial period. We also calculated duration of time spent in and frequency of visits to each location in the animal's enclosure. As we were interested in how the animals' responses to the auditory cue changed over time, we included a variable for the number of days since the first trial in the experiment. We were interested in how the amount of time between experimental trials impacted the animals'

Table 1. Gorilla behaviors and descriptions observed during experimental videos.

Behavior	Description
Charge	The silverback moves quickly toward something in an aggressive manner.
Displace	Individual leaves sitting, resting, or standing spot when the silverback approaches. The silverback may or may not occupy the space.
Drag	The silverback moves an object, such as food, from one place to another by keeping it in his hand as he walks.
Enter	The silverback enters the viewable area.
Exit	The silverback exits the viewable area.
Grab	The silverback grasps an object, such as food or the hammock. This may or may not turn into a drag behavior.
Hit	The silverback uses one or both hands to slap an object, such as the hammock.
Lie Down	The silverback is lying down, resting, or sleeping.
Look	The silverback deliberately moves his head toward a focus that is not a visible individual or the camera.
Look - Camera	The silverback deliberately moves his head toward the camera.
Look - Individual	The silverback deliberately moves his head toward an individual.
Mesh Hold	The silverback holds onto mesh with hands and/or feet.
Out of View	The silverback is not in view.
Scoot	The silverback is already sitting and moves his body to face a new direction or to a close location without getting up and walking.
Sit	No other behavior is taking place other than sitting.
Stand	No other behavior is taking place. Standing occurs on all 4 feet.
Standup	No other behavior is taking place. Standing occurs on only back feet.
Vocalize - Bilabial Trill	Silverback purses his lips together and blows air between them. He repeats multiple times and sounds like a human's "raspberry."
Vocalize - Rumble	Silverback vocalizes a deep rumbling sound.
Walk	Silverback moves from one location to another by walking.

Note. Because we collected data on all gorillas in the videos, some behaviors took precedence over other behaviors when they occurred at the same time. Vocalizations took precedence over all other behaviors. Each of the look behaviors took precedence over all other behaviors except vocalizations. Drag and charge took precedence over walk. Enter and exit took precedence over all behaviors.

Table 2. Red panda behaviors and descriptions observed during experimental videos.

Behavior	Description
Enter	Individual enters the viewable enclosure.
Exit	Individual exits the viewable enclosure.
Trot	Individual locomotes by a fast walk or slow jog.
Look - Gate	Individual looks toward area of the gate and pathway from which the keeper approaches.
Look - Camera	Individual looks at the camera.
Look	Individual looks out and around into the open.
Bipedal stand	Individual places front paws up onto a vertical surface (such as the glass) and looks around.
Scent mark	Individual scent marks an object by rubbing his anal scent glands on an object.
Air sniff	Individual raises nose up to sniff air.
Walk	Individual locomotes by walking. No other behaviors besides walking take place simultaneously.
Rest	Individual lies down or sleeps.
Sit	Individual sits upright.
Stand	Individual stands on all 4 legs but does no other behavior.
Out of view	Individual is out of view or inside the house.

Note. Because we collected data on both red pandas in the exhibit, some behaviors took precedence over other behaviors when they occurred at the same time. Trotting took precedence over all behaviors. Looking behaviors took precedence over all other behaviors except trotting.

behaviors, so we included the number of days since the most recent previous trial as well. We excluded from further analyses any behaviors or locations accounting for less than 1% of the observed behavioral frequency or total duration. For example, the gorilla dragged an object two times out of 257 behaviors observed over 36 trials; thus, "drag" was excluded from further analyses.

We assessed whether behaviors increased or decreased in total duration, average bout duration, and frequency during the course of the experiment. Total behavior duration was calculated as the total number of seconds each behavior occurred during the 4 min between the buzzer and when the person arrived. Average bout duration for each behavior was the average duration of each occurrence of the behavior, and frequency was calculated as the total number of times each behavior occurred. To assess the location of where animals spent their time during the 4-min trials, we used a similar method. We calculated the total time spent in each location in seconds and counted the number of times any behavior occurred in each location. We also had video observers watch and record data on videos from 4 min after the keeper arrived to socialize with the animals. We compared total duration, average bout duration, and frequency of each behavior during the 4 min before the keeper arrived and the 4 min after using paired *t* tests.

We used Poisson regression to assess changes in the animals' behaviors or where the behaviors took place during the entire course of the experiment. We included the number of days since the first trial and the number of days since the most recent previous trial as the predictor variables in models of behavior and location duration and frequency. If the variance of the frequency or duration was greater than the mean, we used a negative binomial regression to account for overdispersion in the data (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

Gorillas

We focused on the male silverback gorilla's behavioral responses to our proposed method for generating anticipatory behaviors. At the time of the experiment, the male gorilla was 33 years old and the only adult male in the troop of seven individuals. The rest of the troop consisted of four adult females (ages 16 years, 16 years, 33 years, and 34 years), one young male (6 years old), and a female infant (younger than 1 year old). Videos were recorded in the gorilla holding area out of view from the public; however, they were recorded during hours when the zoo was open to the public. The gorilla holding area consists of several mesh enclosures, but we focused our observations on one of these enclosures as well as a foyer area that leads to the animals' outside yard area.

During the day, the gorillas were allowed access to these two indoor areas. We partitioned this enclosure into four quadrants with Quadrants 1 and 2 being nearest the area adjacent to where animal care staff works. Quadrants 3 and 4 were farther back from the keeper area (Figure 1). Various items, including a hammock, blankets, and enrichment items were regularly inside the enclosure. All gorillas had full access to indoor and outdoor areas at all times while recording was taking place. The experiment ran from June 2014 through October 2014. The staff member socializing with the gorillas during the experiment arrived through a door in the animal care staff area, which was closest to Quadrant 1 and where the camera was set up.

Red pandas

To test our method for generating anticipatory behavior in red pandas, we focused on the behaviors of the young, male, red panda at the San Francisco Zoo. At the time of the experiment, he was 1.5 years old. He lived with a 9-year-old female in the same exhibit for the duration of the experiment. We recorded videos of the outdoor red panda yard from a pathway accessible only to zoo personnel; however, videos were recorded during hours when the zoo was open to visitors.

The red panda yard consists of a grass lawn with a small pool near the front of the exhibit, where there are glass walls for viewing by the public. A large Cyprus tree near the center of the exhibit has a platform built around the trunk about 10 feet off the ground. Tree branch ladders connect the platform perch to another perch in the exhibit and connect with other tree branches providing access to the ground (Figure 2). Both red pandas had access to indoor and outdoor areas at all times during the experiment. The experiment ran from June 2014 through December 2014. The person who socialized with the red panda during the experiment arrived by a walking path at the back of the red panda exhibit and proceeded through a gate, behind which the interaction occurred. The camera was set up on the walking path and faced toward the gate and the back of the red panda exhibit (Figure 2).

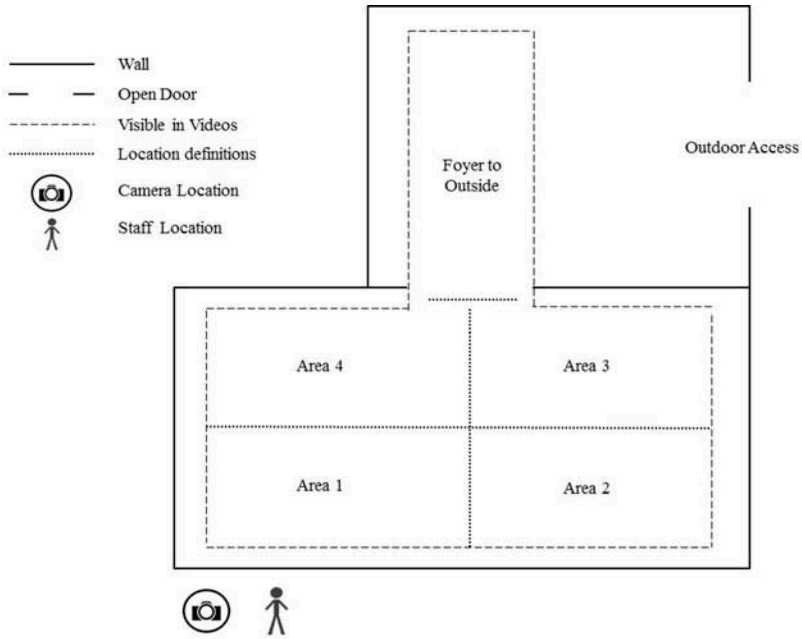

Figure 1. Diagram of the gorilla holding area. Gorillas had outdoor access at all times during the study. Dashed lines indicate areas visible in videos. Dotted lines delineate how locations were recorded during data collection.

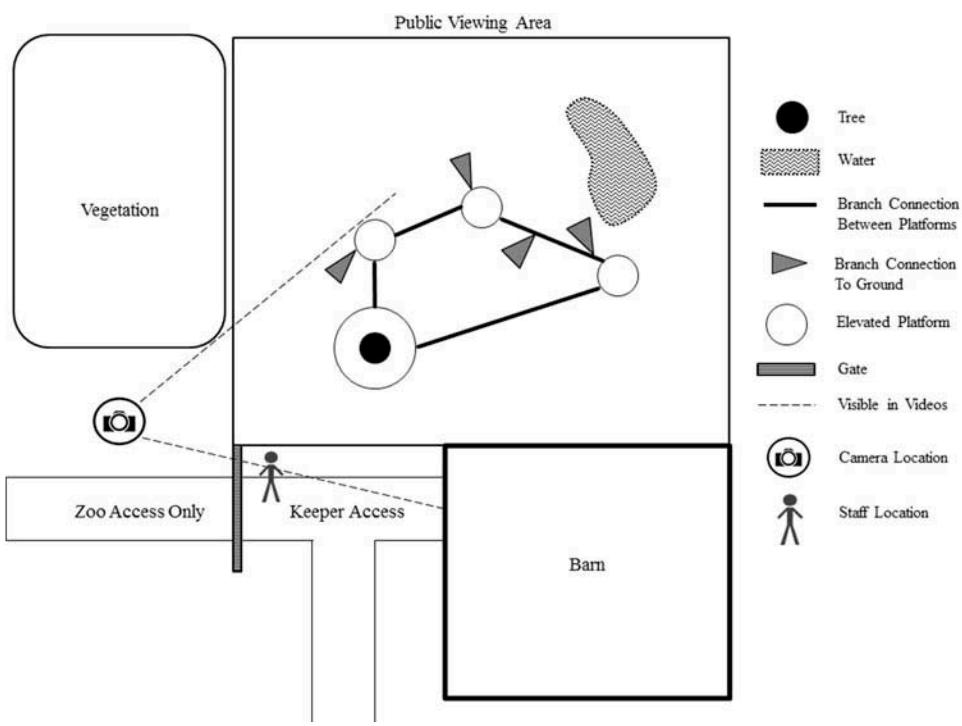

Figure 2. Diagram of the red panda yard. Red pandas had access to all parts of the yard during the study.

The trial for the red panda experiment followed the same protocol as the gorilla experiment, with some small differences. First, the person socializing with the animal was different for the red panda study but remained the same throughout the experiment. Also, the social interaction between the person and red panda occurred through the glass windows of the enclosure instead of mesh as for the gorillas.

Observers collected data using JWatcher as described earlier, and we analyzed the data using Poisson regression of days since the first trial and days since the most recent previous trial on behavioral frequency and duration.

Results

Gorillas

We recorded 36 experimental trials with the gorillas during the course of 119 days. The average time between trials was 3.4 days (± 2.2 days). The behaviors with the longest total duration across all trials were sitting, standing, and walking (Table 3). The most frequently occurring behaviors across all trials were walking, sitting, and looking at the camera (Table 3). Most behaviors occurred in Area 1, as determined by duration and frequency (Table 4 and Table 5; $X^2 = 138.2$, $df = 36$, $p < .001$).

The frequency and the total duration of mesh holding by the male gorilla before the staff member arrived increased during the course of the experiment ($p = .03$ and $p < .001$, respectively; Table 6, Figures 3 and 4). The average bout duration of looking around before the staff member entered the room increased during the course of the experiment ($p < .001$; Table 6, Figure 5). Looking at other gorillas decreased in both average length of time per look ($p = .007$; Table 6, Figure 5) and in total duration per experimental trial during the course of the experiment ($p < .001$; Table 6, Figure 4). The average bout duration of looking at the camera before the staff member arrived decreased throughout the experiment ($p = .05$; Table 6, Figure 5), as did the total duration and frequency of scooting ($p < .001$ and $p = .03$, respectively; Table 6). The frequency and total duration of mesh holding before the staff member's arrival decreased with an increasing number of days since the previous trial ($p = .02$ and $p < .001$, respectively; Table 7).

Table 3. Frequencies and total durations of behaviors during 4-min periods between the buzzer and arrival of the person for the silverback gorilla.

	Bilabial Trill	Look Individual	Look Camera	Look Around	Mesh Hold	Rumble	Sit	Stand	Walk
Total Duration in Seconds	97	31	112	123	195	28	1,004	559	332
Frequency	6	6	29	21	24	6	57	27	66

Table 4. Number of times during 4-min periods between the buzzer and arrival of the person that the silverback gorilla exhibited each behavior in the four indoor locations.

Location	Bilabial Trill	Look Individual	Look Camera	Look Around	Mesh Hold	Rumble	Sit	Stand	Walk
1	6	6	28	21	23	6	46	10	33
2	0	0	1	0	1	0	1	3	6
3	0	0	0	0	0	0	1	2	9
4	0	0	0	0	0	0	9	12	18

Table 5. Total time during 4-min periods between the buzzer and arrival of the person that the silverback gorilla spent in each location and number of times any behavior occurred in each location.

	Outside	Area 1	Area 2	Area 3	Area 4
Duration in Seconds	1,732	4,148	160	326	1,096
Frequency	32	241	16	23	59

Table 6. Regression results of days since the beginning of the experiment on behavioral measures of the silverback gorilla in the 4 min prior to the person's arrival.

Behavior	Measure	Estimate	*p* value	Model
Mesh hold	Frequency	1.01	.03	Poisson
Look at Individual	Average Bout Duration	0.98	.007	Poisson
Look at Camera	Average Bout Duration	0.99	.05	Negative Binomial
Look Around	Total Duration	1.01	< .001	Negative Binomial
Mesh Hold	Total Duration	1.01	< .001	Poisson
Look at Individual	Total Duration	0.98	< .001	Poisson

Note. All estimates were back-transformed as the natural antilog of regression coefficients. Estimates greater than 1 indicate the behavior increased during the course of the experiment; estimates less than 1 indicate the behavior decreased during the course of the experiment.

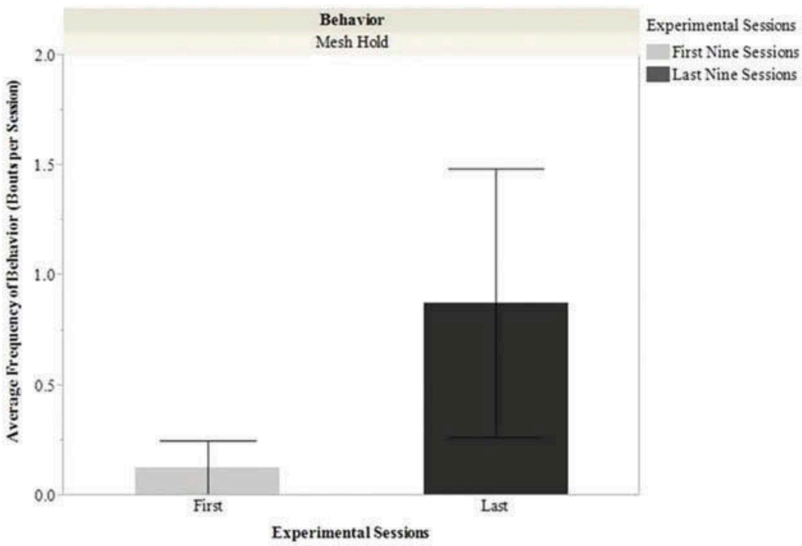

Figure 3. The average frequency of mesh holding by the silverback gorilla during the first 9 and last 9 experimental sessions. The 36 total experimental sessions were divided into four groups of 9 sessions to illustrate the change in behavioral frequency during the course of the experiment. Error bars are +/− 1 standard error of the 9 sessions included in the average.

The silverback gorilla sat and mesh held more frequently before the staff member's arrival than after the staff member's arrival (Table 8, Figure 6). The gorilla looked around less after the person arrived as determined by total duration and frequency (Table 8, Figures 6 and 7); however, he looked toward the camera (the same direction as the person, Figure 1) more as measured by both average bout duration and total duration (Table 8, Figures 7 and 8). Charging occurred less frequently on average after the person arrived; however, the average bout duration and total duration of charging were higher after the staff member arrived than before (Table 8). The male gorilla also rumbled more frequently after the person arrived (Table 8, Figure 6).

Red pandas

We recorded 44 experimental trials during the course of 156 days. The average time between trials was 4.4 days (± 4.2 days). The behaviors with the longest total duration and greatest frequency across all trials were walking, looking around, and looking at the camera (Table 9). Most behaviors occurred on the perch facing the camera or on the grass in front of the camera (Table 10) as determined by duration and frequency. Overall location patterns of each behavior were less clear; however, bipedal standing only occurred near the window where the interaction with the person

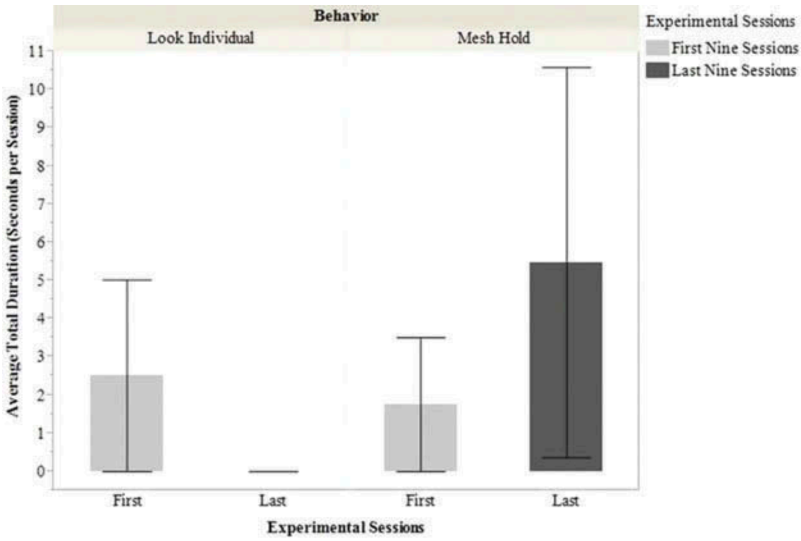

Figure 4. The average total number of seconds per session the silverback gorilla spent looking at other gorillas or holding the mesh during the first 9 and last 9 experimental sessions. The 36 total experimental sessions were divided into four groups of 9 sessions to illustrate the change in behavior during the course of the experiment. Error bars are +/− 1 standard error of the 9 sessions included in the average.

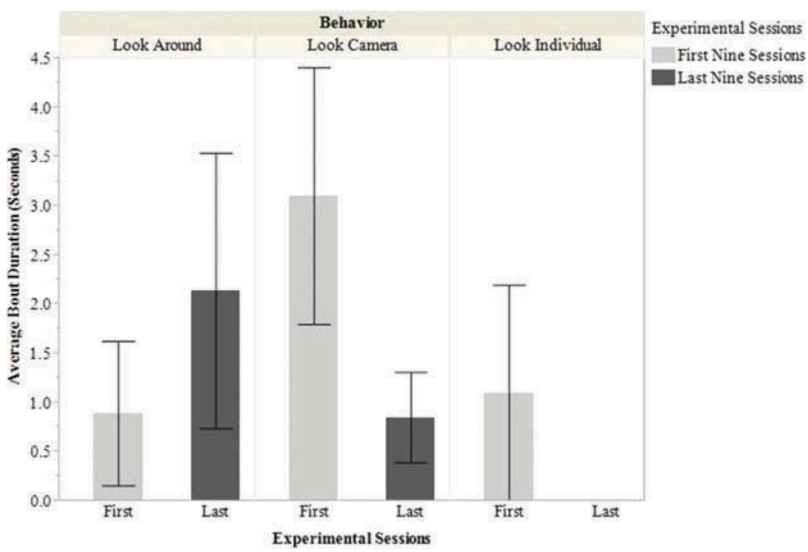

Figure 5. The average bout duration of each instance of looking around, looking toward the camera, and looking at other gorillas by the silverback for the first 9 and last 9 experimental sessions. The 36 total experimental sessions were divided into four groups of 9 sessions to illustrate the change in bout duration during the course of the experiment. Error bars are +/− the standard error of the 9 sessions included in the average.

occurred, trotting occurred near the windows where the interaction happened or on the ground, and all looking behaviors occurred most frequently from the perch facing toward the camera (Table 11).

During the course of the experiment, the red panda walked and trotted more frequently (p = .01 and p = .05, respectively; Table 12, Figure 9). The average bout durations of looking around and

Table 7. Regression results of days since previous session on behavioral measures of the silverback gorilla in the 4 min prior to the person's arrival.

Behavior	Measure	Estimate	*p* value	Model
Mesh hold	Frequency	0.67	.02	Poisson
Mesh hold	Total Duration	0.6	< .001	Poisson

Note. All estimates were back-transformed as the natural antilog of the regression coefficients. Estimates greater than 1 indicate the behavior increased with an increase in days since the previous experimental session; estimates less than 1 indicate the behavior decreased with an increase in days since the previous experimental session.

Table 8. Paired *t* test results comparing silverback gorilla's behavior before and after the person arrived.

Behavior	Measure	Mean Before Person Arrived	Mean After Person Arrived	*p* value
Charge	Average Bout Duration	0.08	1	< .01
Charge	Frequency	0.05	0.3	.01
Charge	Total Duration	0.08	1.1	< .01
Look	Frequency	0.6	0.02	.02
Look	Total Duration	3.5	0.2	.04
Look - Camera	Average Bout Duration	1.7	13.2	< .01
Look - Camera	Total Duration	3.05	15.5	< .01
Mesh Hold	Frequency	0.7	0.1	.01
Rumble	Average Bout Duration	0.75	6	.01
Rumble	Frequency	0.17	0.64	.02
Rumble	Total Duration	0.75	11.8	.03
Sit	Frequency	1.67	0.38	< .01

Note. Mean duration values are given in seconds; mean frequency values are given in occurrences.

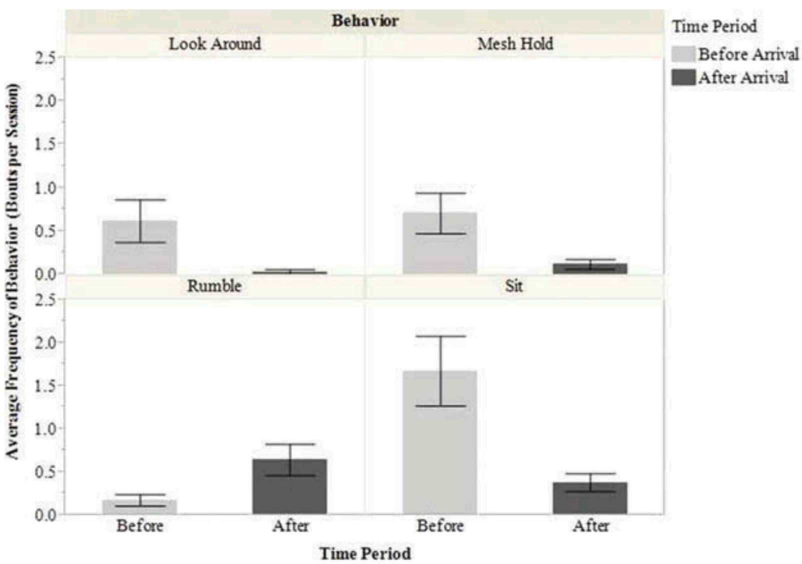

Figure 6. The average frequency of looking around, holding the mesh, rumbling, and sitting by the silverback in the 4 min before and the 4 min after the staff member arrived. Error bars are +/− 1 standard error.

looking toward the gate decreased throughout the experiment ($p < .001$ and $p = .02$, respectively; Table 12, Figure 10). The total durations of looking at the camera ($p = .04$; Figure 11), trotting ($p = .06$; Figure 11), and walking ($p < .001$; Figure 12) increased during the experiment, while the total durations of resting ($p = .03$, Figure 11) and looking at the gate declined ($p < .001$; Table 12, Figure 11).

As the number of days since the previous experimental session increased, the red panda spent more time in total looking at the camera ($p < .001$) and less time in total resting ($p < .001$),

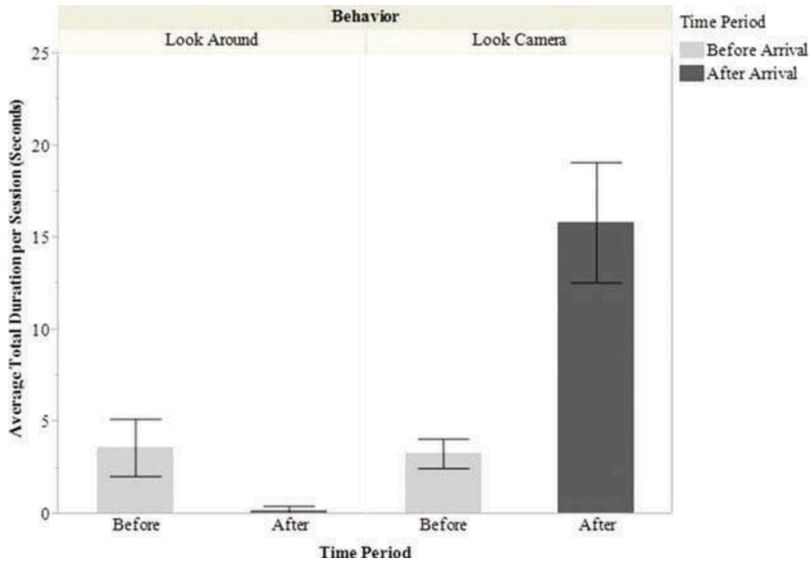

Figure 7. The average total number of seconds per session the silverback gorilla spent looking around and looking toward the camera in the 4 min before and the 4 min after the staff member arrived. Error bars are +/− 1 standard error.

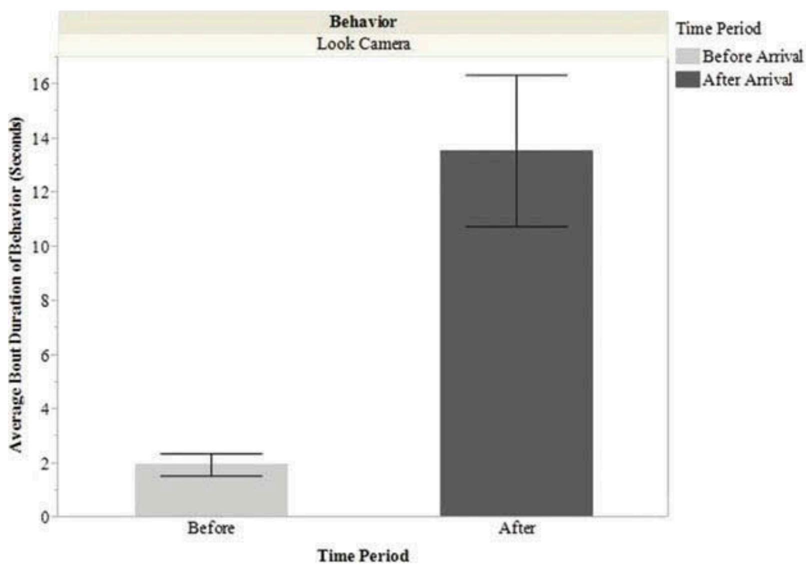

Figure 8. The average bout duration of each time the silverback looked toward the camera in the 4 min before and the 4 min after the staff member arrived. Error bars are +/− 1 standard error.

Table 9. Total durations and frequencies of red panda behaviors during 4-min periods between the buzzer and arrival of the person.

	Bipedal Stand	Look Gate	Look Camera	Look Around	Rest	Trot	Walk
Total Duration in Seconds	45	148	249	1,012	143	36	1,317
Frequency	10	24	59	129	17	12	222

trotting (p = .06), and walking (p < .001; Table 13). The average bout duration of looking around increased with more time since the previous experimental session (p < .001; Table 13). The average duration, total duration, and total frequency of looking at the camera were greater before

Table 10. Total durations and frequencies of locations of the male red panda during 4-min periods between the buzzer and arrival of the person.

	Left Window and Camera Window	Window by Gate	Perch Toward Camera	Back Perch	Branch From Perch to Branches	Other Branches	Grass Left of Tree	Grass Right of Tree
Total Duration	133	253	1,193	131	217	125	425	636
Total Frequency	21	38	178	27	53	16	65	71

Table 11. Total number of times each behavior occurred between buzzer and arrival of the person in each location of the red panda exhibit.

Location	Bipedal Stand	Look Gate	Look Camera	Look Around	Rest	Trot	Walk
Left Window and Camera Window	9	0	0	0	0	1	11
Window by Gate	1	0	4	8	0	1	24
Perch Toward Camera	0	23	38	62	17	0	38
Back Perch	0	1	6	8	0	0	12
Branch From Perch to Branches	0	0	5	17	0	0	31
Other Branches	0	0	0	1	0	1	14
Grass Left of Tree	0	0	1	22	0	3	39
Grass Right of Tree	0	0	5	9	0	6	51

Table 12. Regression results of days since beginning of experiment on behavioral measures of the red panda in the 4 min prior to the person's arrival.

Behavior	Measure	Estimate	*p* value	Model
Walk	Frequency	1	.01	Poisson
Trot	Frequency	1.01	.05	Poisson
Look Around	Average Bout Duration	0.99	< .001	Poisson
Look at Gate	Average Bout Duration	0.98	.02	Negative Binomial
Look at Camera	Total Duration	1.02	.04	Poisson
Look Gate	Total Duration	0.99	< .001	Negative Binomial
Rest	Total Duration	0.99	.03	Negative Binomial
Trot	Total Duration	1.00	.06	Poisson
Walk	Total Duration	1.00	< .001	Poisson

Note. All estimates are back-transformed as the natural antilog of the regression coefficients. Estimates greater than 1 indicate the behavior increased with an increase in days since the previous experimental session; estimates less than 1 indicate the behavior decreased with an increase in days since the previous experimental session.

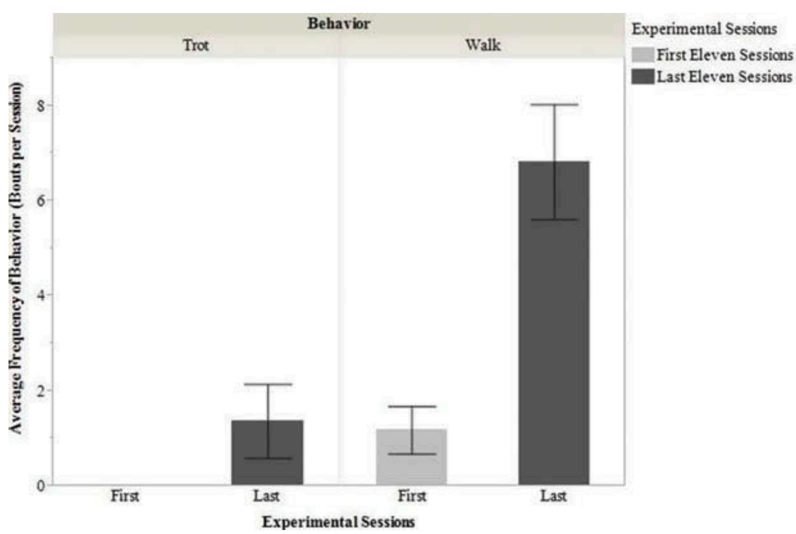

Figure 9. The average frequency per session the red panda trotted and walked during the first 11 and last 11 experimental sessions. The 44 total experimental sessions were divided into four groups of 11 sessions to illustrate the change in behavioral frequency during the course of the experiment. Error bars are +/− 1 standard error of the 11 sessions included in the average.

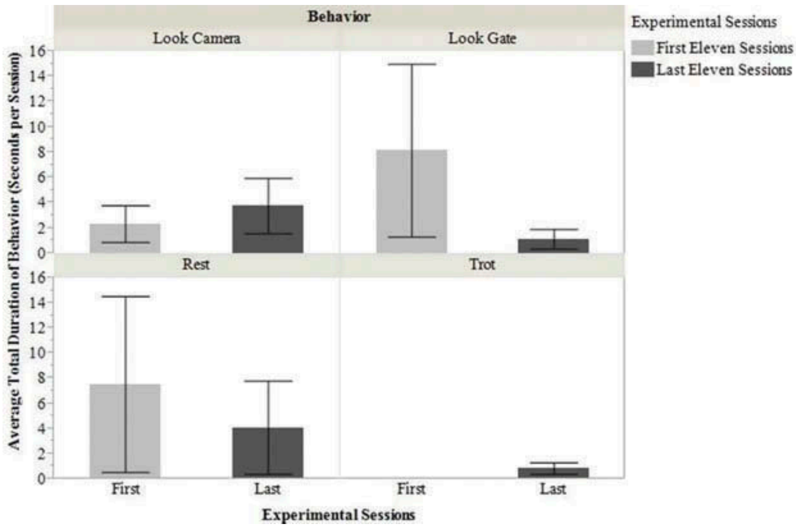

Figure 10. The average total number of seconds per session the red panda spent looking toward the camera, looking toward the gate, trotting, and resting during the first 11 and last 11 experimental sessions. The 44 total experimental sessions were divided into four groups of 11 sessions to illustrate the change in behavior duration during the course of the experiment. Error bars are +/− 1 standard error of the 11 sessions included in the average.

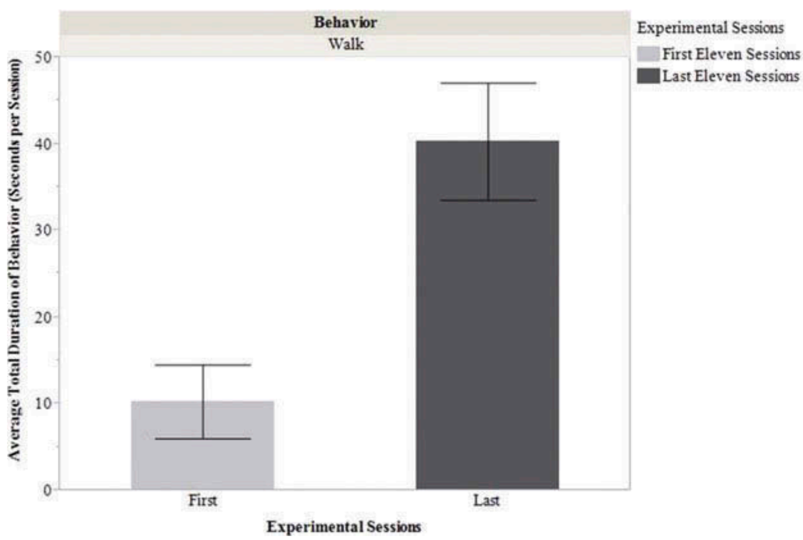

Figure 11. The average total number of seconds per session the red panda spent walking during the first 11 and last 11 experimental sessions. The 44 total experimental sessions were divided into four groups of 11 sessions to illustrate the change in behavior during the course of the experiment. Error bars are +/− 1 standard error of the 11 sessions included in the average.

the person arrived than after ($p < .01$; Table 14, Figures 13, 14, and 15). Resting also occurred more frequently ($p = .05$; Table 14) and for longer total durations ($p < .01$; Table 14) before the staff member arrived. Eating, grooming, standing, and trotting all increased in frequency, average duration, or total duration in the period after the staff member arrived compared with before (Table 14).

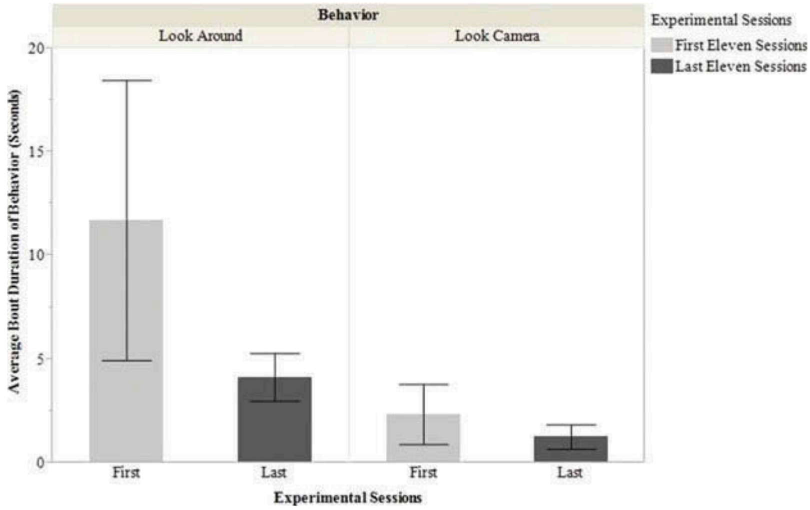

Figure 12. The average bout duration of each instance of looking around or looking toward the camera by the red panda during the first 11 and last 11 experimental sessions. The 44 total experimental sessions were divided into four groups of 11 sessions to illustrate the change in bout duration during the course of the experiment. Error bars are +/– one standard error of the 11 sessions included in the average.

Table 13. Regression results of days since previous experimental session on behavioral measures of the red panda in the 4 min prior to the person's arrival.

Behavior	Measure	Estimate	*p* value	Model
Look at Camera	Total Duration	1.04	< .001	Poisson
Rest	Total Duration	0.91	< .001	Negative Binomial
Trot	Total Duration	0.89	.06	Poisson
Walk	Total Duration	0.97	< .001	Poisson
Look Around	Average Bout Duration	1.05	< .001	Poisson

Note. All estimates are back-transformed as the natural antilog of the regression coefficients. Estimates greater than 1 indicate the behavior increased with an increase in days since the previous experimental session; estimates less than 1 indicate the behavior decreased with an increase in days since the previous experimental session.

Table 14. Paired *t* test results comparing the red panda's behavior before and after the keeper arrived.

Behavior	Measure	Mean Before Keeper Arrived	Mean After Keeper Arrived	*p* value
Eat	Total Duration	1.38	15	.03
Eat	Frequency	0.02	0.54	< .01
Groom	Average Duration	0	1.3	.03
Groom	Frequency	0.04	0.23	.03
Look	Frequency	3	1.4	.01
Look - Camera	Average Duration	1.6	0	< .01
Look - Camera	Total Duration	5.64	0	< .01
Look - Camera	Frequency	1.38	0.26	.03
Look - Gate	Average Duration	1.3	2.5	.05
Stand	Average Duration	0.52	1.57	.03
Stand	Total Duration	0.59	2.8	.01
Trot	Average Duration	0.52	1.88	< .01
Trot	Total Duration	0.76	5.26	< .01
Trot	Frequency	0.52	1.4	< .01
Walk	Average Duration	4.8	6.8	.03

Note. Mean duration values are given in seconds; mean frequency values are given in occurrences.

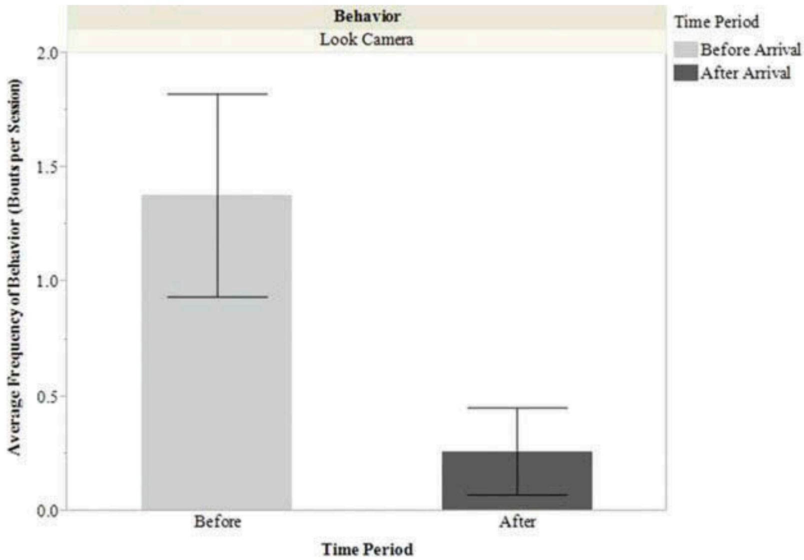

Figure 13. The average frequency of looking at the camera by the red panda in the 4 min before and the 4 min after the staff member arrived. Error bars are +/– 1 standard error.

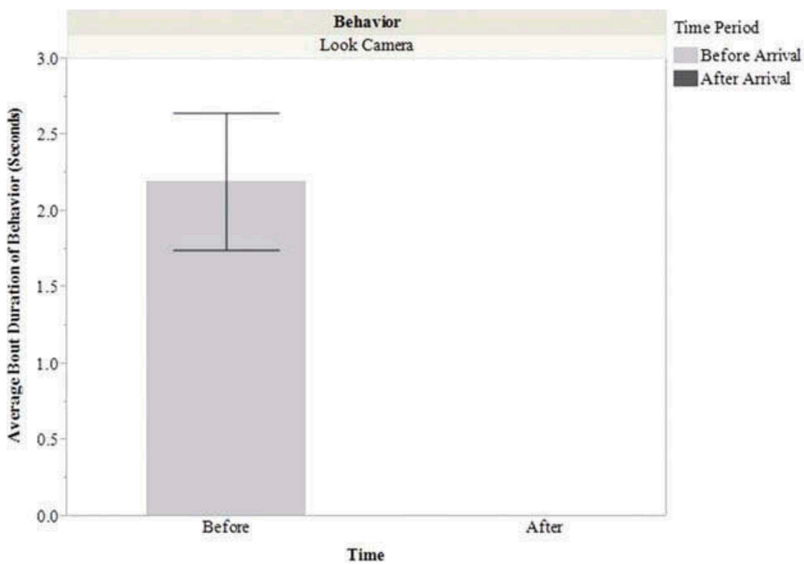

Figure 14. The average bout duration of each instance of looking toward the camera by the red panda in the 4 min before and the 4 min after the staff member arrived. Error bars are +/– 1 standard error.

Discussion

Gorilla

The silverback gorilla appeared to anticipate the arrival of the person by sitting or holding onto the mesh of the enclosure in the area closest to where the person arrived. The increase in mesh holding and looking around from the 1st day of the experiment to the last day suggests the gorilla anticipated the arrival of the person. Both mesh holding and looking around occurred most frequently in Area 1

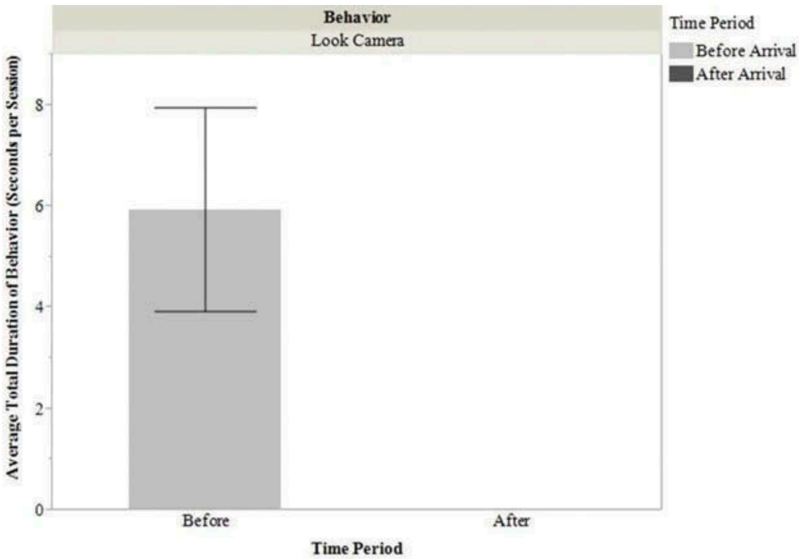

Figure 15. The average total number of seconds per session the red panda spent looking toward the camera in the 4 min before and the 4 min after the staff member arrived. Error bars are +/− 1 standard error.

(Table 4), which was the area directly in front of the camera and the door by which the person entered the holding area.

The gorilla looked around more frequently and for longer total durations in the 4 min prior to the arrival of the person than during the 4 min after the person arrived, suggesting he was looking for something after the buzzer that he was not looking for once the person arrived. He also sat more frequently and held onto the mesh more frequently prior to the person's arrival than after, with both of these behaviors focused in Area 1. Thus, based on behavioral duration, frequency, and location, it seemed the silverback gorilla involved in this study developed anticipatory behavior directed toward a positive social interaction with a noncaretaking human.

The decrease in average bout duration and total duration of looking at other gorillas during the 4 min before the person arrived was an unexpected finding of this case study. The silverback spent less total time looking at other gorillas and less time per bout of looking at other gorillas as the experiment progressed. During the period after the buzzer sounded, it seemed the gorilla was more focused on the arrival of the person than he was on the activities of the other gorillas. Despite the availability of other social interactions, the silverback appeared to wait and watch for the opportunity to socialize with the person.

The increase in frequency, average duration, and total duration of charging after the person arrived compared with before may indicate the silverback was unsure how to react to the unfamiliar situation of the experiment. The gorilla may have felt the need to challenge the unfamiliar staff member initially before determining he was interested in the socialization opportunity, or perhaps he was excited by the visit. In addition, charging occurs in social situations, and the time prior to the social interaction with the person may have included social interactions with other gorillas, as they were free to come and go and sometimes left the silverback alone in the building. Despite the overall increase in charging, the "rumble" vocalization increased significantly by all measures after the person arrived compared with before (Table 8). In wild mountain gorillas, this vocalization is associated with positive social activities and overall contentment (Fossey, 1972), suggesting the silverback gorilla perceived the social interaction with the person as a positive event.

Red panda

The red panda's behavior changed during the course of the study, with an increase in overall activity level in the form of walking and trotting and a decline in resting. Although the frequency of walking and the total time spent walking both increased throughout the experiment, the average bout duration of walking did not increase. Each instance of walking was similar in duration at the beginning and end of the experiment, but the red panda performed more individual bouts of walking toward the end of the experiment.

The increase in bouts of walking before the arrival of the keeper may present similarly to pacing—repetitive, short bouts of activity—however, the overall increase in activity and diversity in behaviors the red panda exhibited after the arrival of the keeper do not suggest this apparent pacing was stereotypical in nature. The increase in trotting during the course of the experiment suggests the red panda was interested in the interaction with the person, as trotting happened on the ground near the socialization area or near the windows where the person would arrive. Bipedal standing also only occurred near the windows from where the person would approach. In this study, bipedal standing is a more intense form of looking around, suggesting the red panda was looking around for the person before he arrived.

Although it is possible the red panda's increase in trotting and bipedal standing were related to anxiety about the upcoming interaction, it is unlikely for several reasons. First, the red panda had access to all parts of his yard during the period between the tone and the arrival of the staff member. Despite this, a majority of the behaviors observed in between the tone and the staff member's arrival occurred in the area where the staff interaction would occur (Table 10), suggesting the red panda moved toward the location of the staff member after the tone sounded. If the interaction was aversive to him, we would have expected the red panda to stay in an elevated location, move away from where the staff member would arrive, or avoid the location entirely. Similarly, if bipedal standing occurred out of a desire to see and avoid the approaching staff member, we would expect this behavior to be accompanied by a pattern of moving away from the location of the undesired event.

Although we cannot say for certain whether the red panda's increased activity levels were related to anxiety or anticipation, reliable signals of disruptive or stressful events can actually improve animal welfare by letting the animal know when an unpleasant event will occur (Bassett & Buchanan-Smith, 2007; Hall, Robinson, & Buchanan-Smith, 2015; Rimpley & Buchanan-Smith, 2013). In this case, the reliable signal preceding the arrival of the staff member could have helped alleviate the potential stressor by letting the red panda know when to expect it. The decline in the average duration of looking at the gate and looking around during the course of the experiment was unexpected. The total overall duration of looking at the gate also declined.

The social interaction occurred between the window near the camera and the gate, so a decline in interest in this area was not expected in light of the other findings. One explanation may be that it was difficult to determine from videos where the red panda was looking. As a majority of the "looking" behaviors occurred from the perch facing toward the camera (Table 9), it seems unlikely, as the red panda was in clear view of the camera from this vantage point. An alternate explanation is that as he learned the meaning of auditory cue, the red panda spent less time looking for the person and moved toward the area where the socialization would occur.

Although the red panda's overall activity level increased in the 4-min period before the keeper arrived over the entire course of the experiment, his average activity level was greater after the keeper arrived than before, as trotting and walking both increased in duration (Table 14). He also exhibited several behaviors after the keeper arrived in which he rarely engaged during the 4 min prior to the keeper's arrival, such as eating and grooming (Table 14). The lack of these behaviors before the keeper arrived may indicate the red panda's focus on the impending arrival of the keeper to the exclusion of these behaviors. Alternatively, he may have been more motivated to engage in these behaviors after receiving the social reward of the keeper's arrival. Before the keeper arrived, the red panda looked at the camera for longer average durations, for longer total durations, and more frequently (Table 14). The camera-looking behavior may have been due to the positioning of the camera—the location of the camera was next to the path from which the keeper would approach.

Conclusion

Overall, we found support for the red panda and gorilla anticipating positive social interactions with a noncaregiving human, indicating the described method was sufficient for producing anticipatory behavior in both species. We also observed different anticipatory behaviors in different animals. The red panda showed a more "classic" anticipatory pattern of increased activity between the signal of an impending reward and receiving the reward, while the silverback gorilla exhibited a more subtle "sit and wait" pattern previously described in other great apes (Bloomsmith & Lambeth, 1995) and dolphins (Jensen et al., 2013). Despite differences in how the behaviors presented between species, the case studies demonstrate changes in behavior consistent with an anticipatory response to a nonfood reward.

Our results support the development of anticipatory patterns in both animals; however, our specific behavioral findings are not broadly applicable to all animals of the same species. The male red panda at the time of the study was young and comparatively more social with keepers compared with the female red panda in the same exhibit. Had the same study been conducted with the female red panda, her anticipatory patterns may have differed from those of the male. Similarly, the gorilla holding area at the San Francisco Zoo is enclosed with metal mesh, where other facilities may have glass or barred enclosures. Under other management conditions, the "mesh hold" behavior observed in this study could be impossible.

Anticipatory behaviors can vary based on species, management, personality, or learned behaviors (van den Bos et al., 2003), and individuals may exhibit different anticipatory responses under different conditions (Knutson & Greer, 2008). Thus, although general activity patterns (e.g., increased or decreased activity overall) may be broadly applicable, understanding individual behavior or differences in motivation or temperament may ultimately be more useful when studying anticipatory behavior as a welfare indicator.

The method described here for generating anticipatory behaviors can be applied to studying patterns of anticipatory behavior as a "self-report" of an animal's welfare. Animals provided with enrichment tend to exhibit less frequent or less intense bouts of anticipatory behaviors (van der Harst et al., 2003), suggesting providing multiple positive experiences in an animal's day decreases dependence on any single positive event (Watters, 2014). In this sense, patterns of anticipatory behavior can help animal care staff assess how an animal perceives his/her own welfare. By applying our method, animal managers can describe general patterns of anticipation in an animal on a day-to-day basis. If an animal's normal anticipatory patterns change in response to changes in an animal's husbandry, social situation, or other potentially stressful event, such changes could inform animal care staff of potential welfare concerns or improvements. Future research should aim to correlate management changes to changes in anticipatory patterns.

The technical definition of classical conditioning involves eliciting a reflexive behavior based on a cue (Pavlov, 1927), and operant conditioning involves rewarding or punishing a behavior to enhance or extinguish it (Skinner, 1938). Although a case could be made for defining the conditioning in this study as a form of classical conditioning as the term is used colloquially, the behavioral responses of the animals were not reflexes in the physiological sense. We also did not reward or punish any behaviors the animals exhibited between the audio tone and when the staff member arrived. Furthermore, the animals had the choice to participate in the interaction or avoid it.

As no behaviors between the signal and the event were shaped by humans and participation in the interaction was controlled by the animal, the behavioral responses after the tone were determined by the animal's perception of the reliably signaled event. Thus, we propose this method of conditioning be considered as a similar but distinct form of conditioning, "perception-driven conditioning." By using this method of conditioning, animal managers may be able to assess how an animal perceives a signaled event in addition to assessing anticipatory behaviors. Although our results support the anticipation of the social interaction for the individual animals involved in the study, this study only included a single individual of each species. Despite this small sample size, our results support the validity of this methodology in several ways.

First, behavioral conditioning such as the methodology described here has been demonstrated in many species from cockroaches (Watanabe & Mizunami, 2007) to humans (Antle & Silver, 2009) and has been successfully applied in training and husbandry applications across taxa (Augustsson, Lindberg, Hoglund, & Dahlborn, 2002; Moe et al., 2009). As such, there is no reason to believe the observed changes in behavior were related to anything other than the conditioned cue. Second, for both animals, we observed differences in the behaviors before and after the human arrived to interact with the animal. In addition, we observed changes in individuals' behavior during the course of several months (6 months for the red panda and 4 months for the gorilla).

Most importantly, we are not advocating for the use of specific behaviors used in this study as anticipatory measures in all red pandas or in all gorillas. We are providing evidence for the development of anticipatory behavior in response to a reliable cue in specific animals. Using a human–animal interaction as a reward may not work for all animals (Augustsson et al., 2002; Franks et al., 2013), and future work may expand on this methodology to include food or conspecific social interactions as the signaled reward. Nonetheless, given the broad applicability of behavioral conditioning across species (Amiez, Procyk, Honore, Sequeira, & Joseph, 2003; Watanabe & Mizunami, 2007), these case studies provide a proof of concept for a method generating and describing anticipatory behaviors in animals in captivity.

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