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(*Ursus arctos horribilis*)

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Effect of season and scatter feeder use on anticipatory behavior in two zoo grizzly bears  
(*Ursus arctos horribilis*)

By

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THESIS

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## **Abstract**

Anticipatory behavior (AB) has been reported to be a potential indicator of an animal's subjective affective state and is thought to be modulated by the animal's reward sensitivity and motivation to acquire a resource. In considering the role of evolutionary pressures shaping seasonal behavior (i.e., hyperphagia and torpor) and the significance of resource driven anticipatory behavior in many of the *Ursus* genus living in North America, we chose to investigate trends of AB: A) across the day in a baseline year in order to validate our focal behaviors as AB by definition and B) in response to allotment of treatment types varying in timing and number of daily food-related reward opportunities via use of a scatter-feeder across an experimental year in two resident grizzly bears at the San Francisco Zoo. Upon validating our behavior according to the definition (i.e., increase before predictable rewarding event and near-cessation post event), post-hoc analysis revealed a general seasonal effect on both of our dependent AB measures (total AB duration and average AB bout length, in seconds per observation session) in both bears and research years. Except for differences seen in total AB duration performed in the winter between baseline and experimental years, we found no other overall significant effects of scatter feeding treatment on total AB duration or AB bout length. Specific treatment type effects appeared to be highly influenced by season which speaks to the engrained motivation to participate in temporally significant behavioral patterns. In summary, our findings reveal that AB may serve as a potential indicator of motivation to acquire resources, but interpretation of AB patterns and implementation of enrichment must be taken with caution and with species-specific natural history in mind.

## 1 - Introduction

The science of observing and analyzing animal behavior in the use of understanding the lives of the billions of species that share space alongside us people continues to evolve. Perhaps one of the first extensive speculations that animals experience emotions similar to humans and the explanation of tentative measurements of these emotions was written in Darwin's 1872 collection of books as *The Expression of Emotions in Man and Animals* - the same collection that brought scientists the revolutionary work of *On the Origin of Species*. Today, animal behavior and welfare scientists persevere in the endeavor of looking deeper into the trends of behaviors and what these trends are telling us - things that animals cannot tell us directly themselves (Ward, Sherwen, Clark, 2018; Walker, Diez-Leon & Mason, 2014; Watters, Margulis & Atsalis, 2009). It becomes particularly important to consider welfare in situations where human caretakers are responsible for the wellbeing and quality of life of animals (i.e., those living in captivity). With the creation of general frameworks in considering the treatment of animals in our care such as the Five Freedoms outlined in the 1965 Brambell Report and the first Animal Welfare Act written into legislation in 1966, researchers have continued the pursuit to create optimal welfare conditions for zoo, laboratory, and agriculture animals alike.

In addition to physiological indicators of welfare, behavioral indicators may help to paint an overall picture of an animal's quality of life and its corresponding affective state (Dawkins 2003; Watters, Krebs & Eschmann, 2021; Whitham & Wielebnowski, 2013). Over the decades, various behavioral metrics with the potential for use in welfare assessments have been suggested and tested, including, but not limited to: behavioral diversity (Miller et. al., 2020, Miller et al., 2021), repetitive abnormal behavior (Broom, 1983; Garner, 2005; Mason & Latham, 2004; Rose, Nash

& Riley, 2017), play (Oliveira et al., 2010; Mintline et al., 2013), human-animal interactions/relationships (Bertenshaw et al., 2008; Claxton, 2011; Mellor et al., 2020), and anticipatory behavior (Neave, Webster & Zobel, 2021; Spruijt, van den Bos & Pijlman, 2001; Van der Harst & Spruijt, 2007; Watters, 2014). Results have been enlightening, yet heterogeneous, as specific interactions involved between these behaviors and underlying mechanisms related to motivation and affective state are complex, not directly observable, and thus difficult to measure (Mason & Latham, 2004; Mason & Mendl, 1993; Veasey, 2017).

Methodological strategies must then be scrutinized in the ability to accurately measure the constructs they are meant to reflect. For example, criticisms have been made over the Shannon-Wiener Diversity Index (H-index) used to measure behavioral diversity in welfare assessments as a main indicator of affective state. In using this method, researchers must assume direction of “goodness” (e.g., larger behavioral diversity as an indicator of “good” welfare) and makes assessments fallible to biased researcher categorization and subsequent statistical analysis (Cronin & Ross, 2019). Furthermore, measures of welfare states focus heavily on the presence or absence of stress-related indicators (i.e., cortisol, stereotypic behavior); however, simple presence or absence of these things do not necessarily indicate that an animal is in poorer or better welfare state (Boissy et al., 2007; Melfi, 2009). For instance, although general presence of play behavior in species previously known to be playful is associated with good welfare and reduction of play behavior may be found in situations of poorer welfare, there are examples in which these assumptions are violated. In fact, evidence has been found that in some instances of maternal care deprivation leads to *increased* object play in domestic kittens – as you can see, it is important to consider the definition of potential indicators of welfare, in this case play behavior,

and how we may make distinctions between potential different subgroups of those indicators, in this case object play versus, say, social play (Alloy-Dallaire, Espinosa & Mason, 2018; Held & Špinka, 2011).

On top of all these variables, species across taxa behave differently according to differing natural histories and biological nuances that make these measures difficult to generalize and caution must be taken when creating assessments with careful attention to context (Binding et al., 2020; Wolfensohn et al., 2018). Finally, researchers must also keep in mind the significance of the possible influence of individual experience and personality on the veracity of suggested indicators of welfare and the effectiveness (or harmfulness) of potential enrichments (Carere & Lucurto, 2011; Izzo, Bashaw & Campbell, 2011; Richter & Hintze, 2019). In light of all these considerations, researchers may approach assessments of welfare and underlying affective states through the use of behavioral indicators, albeit with caution. Continued investigation into the reliability and accuracy of potential indicators (individually and in concert) is imperative in exploring what is important to individuals in captive settings and evaluating individual motivation to behave and/or access resources (e.g., food, social interaction, enrichment).

### ***1.1 - Defining welfare and affective state***

The first step in using potential behavioral indicators of welfare (e.g., play behavior or behavioral diversity) to create a successful means of assessing animal welfare is to consider the definition of *welfare*: the overall balance between positive and negative events an animal experiences in an instance and accumulated over time (Fraser & Duncan 1998; Spruijt, van den Bos & Pinlman, 2001; Watters & Krebs, 2019). This balance contributes to the individual's

overall subjective perception of its affective state (sometimes referred to as emotion/emotional state) – that is to say, its overall mood-like “feelings” (e.g., anxious, relaxed) (Boissy et al., 2007; Broom, 1991; Fraser, 2008; Hill & Broom, 2009; Mellor et al., 2020). In more relatable terms, if a person has a bad day filled with unpleasant experiences, such as waking up late for work and missing an important staff meeting, the person is going to *feel* unpleasant because he/she now exists in a negatively-valenced affective state; the same goes for positively balanced experiences and a positively-valenced affective state. It is to this *affective state* that behavior and welfare researchers have directed their attention as one construct to gain insight into welfare (Dawkins, 1990; Fraser, 2009; Mellor, 2012). As a quick note, these longer lasting states are distinct from the idea of fleeting emotional responses to certain stimuli (e.g., fear response to a startling noise) which are primarily directly related to immediate survival (Panksepp, 2005). An animal in a relatively positive affective state may still experience short-term negative feelings such as disgust to an aversive tasting food item as this serves as an important function in conserving fitness.

More formally, affective state can be broken down into two dimensions: arousal and valence (Mendl, Burman & Paul, 2010; Russell & Barrett, 1999). In the interconnected biological and behavioral circuitry systems involved in seeking rewards and avoiding punishment (i.e., primary avenues in increasing fitness), individuals can theoretically move between the continuum of negatively-valenced states of low or high arousal (e.g. depression and anxiety, respectively) to positively-valenced states of low to high arousal (e.g. content and joy) based on the balance of quality and quantity of previous experiences. By approaching these affective states in such a dimensional framework as functional and with adaptive value, welfare scientists can begin to

break down the various discrete emotions animals may experience throughout their lives (Anderson & Adolphs, 2014; De Waal, 2011; Rolls, 2002; Shariff & Tracy, 2011). In simple terms, affective states can range from absolute suffering to unadulterated pleasure with a spectrum of states in between, possibly fluctuating from one moment to the next. In order to assess where in this system an animal exists, researchers have launched numerous strategies encompassing the study of potential indicators of these “feelings” and how animals perceive them.

### ***1.2 - What are they telling us: indicators of affective state and welfare***

As mentioned above, there exists an adaptive function built into the existence of affective states and the decisions that an individual makes during his/her lifetime. The central dogma of species evolutionary biology and the economics of decision-making stipulates that one should weigh costs and benefits of behaviors in order to avoid potentially threatening situations - situations that would likely lower fitness (Gilbert, 1988; Parker & Stuart, 1976; Real & Caraco, 1986; Sih et al., 2015; Winterhalder, Lu & Tucker, 1999). The driving force behind this evolutionary strategy is a result of multiple coordinated motivational systems built into the central nervous system and the interactions with external circumstances (Spruijt, van den Bos & Pijlman, 2001). For example, when physiological cues trigger feelings of hunger (e.g., low circulating glucose), an individual is motivated to perform appetitive behavior (i.e. searching for food) in order to engage in consummatory behavior (i.e. consuming of food) which brings the system back to homeostasis (e.g., release of insulin). However, these actions may be modulated by exogenous contexts such as presence of perceived threat or inability to perform appropriate behaviors (e.g., injury or barren captive environments – i.e., loss of agency). Based on whether an individual is able to



perform behaviors it is highly motivated to enact and satiate these needs, they will be either activating reward or distress systems which can ultimately lead to feelings such as relaxation or frustration. Researchers must keep in mind, however, that simple satiation of individual needs (e.g., hunger or reproductive motivations) is not the only factor that contributes to overall affective state (de Passillé and Rushen, 1997; Haley et al., 1998; Hammell et al., 1988; Meunier-Salaün, Edwards & Robert, 2001). One such factor is the quality of past experiences which may lead to creation of cognitive biases that influence information-processing and decision-making (humans - Chaby et al., 2013; Everaert, Koster & Derakshan, 2012; Smith & Bryant, 2000; Treadway et al., 2009). For example, both human and non-human animals, having been either self-reported as residing in negative affective states (i.e., depression/anxiety in humans - Gotlib & McCann, 1984; MacLeod & Byrne, 1996) or experimentally manipulated into presumed negative affective states (e.g., mice raised in barren housing versus enriched - Brydges et al., 2011; Douglas et al., 2012; Mendl et al., 2010; Ritcher et al., 2012), have responded negatively to otherwise ambiguous/neutral stimuli, demonstrating selective attention and decision-making to stimuli *perceived* as negative (non-human animals - e.g., Boissy et al., 2007; Clegg, 2018; Enkel et al., 2010a; Harding, Paul & Mendl, 2004; Hedlund, Palazon & Jensen, 2021; Krebs et al., 2017; Lagisz et al., 2020; Mendl & Paul, 2020; Mendl et al., 2009; Neave, Webster & Zobel, 2021; Papciak et al., 2013; Paul et al., 2020; Watters & Krebs, 2019). With the consideration of both internal and external circumstances over time, these states have the potential to communicate the overall balance of an individual's experiences and whether or not basic needs are being met (i.e., welfare - Bateson et al., 2011; Enkel et al., 2010b; Karagiannis, Burman & Mills, 2015; Rygula, Papciak & Popik, 2013; Rygula et al., 2015; Stephenson & Haskall, 2022).

### *1.2.2 - Exploring motivational systems and interrelated reward-processing circuitry*

Areas responsible for evaluating environmental stimuli/conditions (i.e., perception) and the activation of actions in pursuing or avoiding these things (i.e., goal-directed behavior) are centralized in the corticolimbic region of the brain (Ernst & Paulus, 2005; Leknes & Tracey, 2008). The closely concerted system of reward sensitivity and motivation also have foundations within this region, specifically within the mesocorticolimbic dopaminergic system (Berridge, 2007; Mendl et al., 2009; Spruijt et al., 2001). There has been wide speculation of the origins of motivational systems and several different models of motivation proposed in relation to general decision-making as well as welfare of animals in captivity. Historically, arguments have been made mainly in two different forms: the natural history driven model (i.e., teleological basis of behavior) versus the more flexible subjective origin of motivation (i.e., individual motivation varies by context and previous experience) (Browning, 2020; Dawkins, 1990; Fraser, 2009; Fraser & Duncan, 1998). The debate amongst these models have been the focus behind motivation and decision-making of animals living in captivity, which is a setting that generally differs distinctly in context and selection pressures than those found in the wild. General consensus today, however, agrees that both aspects play a role – that the continuously interchanging dynamics between an individual's varying internal systems and external circumstances are responsible for an individual's perception of their environment, including factors directly related to fitness such as perceived costs and elasticity of demands. All of these things are considered in concert with feedback loops connecting performance of appetitive and/or consummatory behaviors – and the consequences of such – back to motivation (e.g., Hughes & Duncan, 1988).

For example, let us consider the goal-directed behavior of exploration and the motivations behind the performance of this behavior in captivity. As exploration is vital for survival in the wild as animals must explore for resource and information acquisition, researchers may cautiously assume that the motivation to perform this behavior will be highly conserved, regardless of context (Mellor, 2015; Wood-Gush & Vestergaard, 1989). However, evidence has highlighted the elasticity of motivation behind the behavior and that it can be influenced by natural history factors, such as trophic level (predator versus prey species) and endogenous rhythms (ultradian, circadian, seasonal), but also by interactions with factors related to specific captive contexts, such as quality of enclosures (barren or appropriately enriched) and human-animal interactions (positive versus negative) (Easton & Turek, 2003; Feenders, Klaus & Bateson, 2011; Learmonth, 2019; Mellor et al., 2020; Morgan & Tromborg, 2007; Price & Stoinski, 2007; Wells, 2009; Würbel, 2006). Furthermore, individual factors such as behavioral strategy type (e.g., bold versus shy) as well as group dynamics (e.g., social hierarchy) have also been shown to influence exploratory behavior (Horback, 2017; Laskowski & Bell, 2014; Perals et al., 2017; Spiegel et al., 2017). In extreme cases, researchers have shown that containment in impoverished captive environments may even lead to complete cessation of the behavior as these contexts manifest a state of anhedonia because of lack of opportunities to perform species-specific behavior and loss of agency (i.e., poor welfare).

These combinations of external circumstances and interconnected internal systems (e.g., hormonal regulation) modulate the flow of physiological messengers that trigger the release of dopamine - a neural substrate closely linked to reward and responsible for the state of “wanting”. This cascades to activate aspects of the motivational system, such as response allocation and

responsiveness to conditioned or ambiguous stimuli, which are determined by the perceived disparity between current and optimal physiological and/or emotional states (Mistleberger, 2009; Rolls, 2005; Spruijt et al., 2001). In other words, the strength of motivation to acquire a reward is shaped by the extent of demand to perform a behavior based on the interplay between physiological and emotional states and therefore, necessitates the intensity of sensitivity to potential reward. In saying so, stressed (negative affect) individuals (i.e., those existing in suboptimal physiological and/or emotional states) are going to be particularly sensitive to rewards and consequently, loss of rewards, compared to those not experiencing the same levels of stress. Studies have shown that both humans (Hajcak, McDonald & Simons, 2004; Wenzlaff & Grozier, 1988) and non-human animals (Burman et al., 2008; Luo et al., 2020) in negative affective states are more sensitive to reward loss than others. On the other hand, in severe cases of chronic stress, generally in which individuals have little to no control in daily life, may lead to learned helplessness and a state of anhedonia; humans and non-human animals experiencing this phenomenon show decreased to non-existent motivation to pursue reward due to the impairment of the reward processing systems (Der-Avakian & Markou, 2012, Berridge & Robinson, 2003; Silva et al., 2020; Treadway et al., 2012).

It is important to note here that there exists a reward in the performance of the appetitive behavior itself as well as at the completion of the goal-directed behavior (i.e., consummatory behavior) and the ability to perform only one of the two phases of behavior may lead to animal frustration and subsequent changes in reward sensitivity (de Jonge et al., 2008; Rozek & Millam, 2011; da Silva Vasconcellos, Adania & Ades, 2012). For example, dairy calves provided forage (i.e., hay) to manipulate and consume reduced the performance of oral-related abnormal

repetitive behaviors compared those not offered this opportunity to perform behaviors associated with feed intake (i.e., only grain provided) (Downey et al., 2022). Similarly, providing cognitive stimulation through appropriately challenging puzzles to individuals to solve has shown to be more enriching, and therefore more rewarding, than simple non-cognitive enrichment (e.g., tactile objects) (Meehan & Mench, 2007). With all these insights, researchers may use the constructs of reward-evaluating systems and corresponding behaviors (i.e., anticipatory behaviors) when assessing behavioral needs of individuals in captivity and whether or not these needs are being met appropriately.

### ***1.3 - Introducing a new tool in welfare assessment: anticipatory behavior***

Anticipatory behaviors (ABs) are goal-directed and performed in response to a cue or event, whether internal or external, that are most often associated with reward opportunities (Bolles, 1968; Mistlberger & Rusak, 1987; Richter, 1922; Van der Harst & Spruijt, 2007). Another characteristic – as a component of the appetitive phase – is the general cessation of the behavior once a certain rewarding event passes (de Groot & Rusak, 2004). As implied in the name, this behavior demonstrates the ability of animals to *anticipate* events based on repeated previous experiences and biological clocks (i.e., chronobiology – *further discussed in subsection, 1.3.2*) and behave in ways that facilitate the acquiring of associated rewards based on this predictability. Importance of being able to predict and anticipate in order to attain goals in the wild is often directly related to survival as well as optimizing fitness. For example, some animals have demonstrated anticipation of pulsed resources (i.e., differences in resource availability between years) through changes in behavior, such as increased activity and intensified reproductive strategies, before anticipated resource “boom” seasons (eastern chipmunks –

Bergeron et al., 2011; white-footed mouse – Marcello, Wilder & Meikle, 2008; American & European tree squirrels – Boutin et al., 2006).

Although selection pressures such as meeting basic survival needs are relaxed in captive settings, AB still occurs in daily animal routines. A common example of AB observed in zoological institutions is focused movement and attention towards a location that is often in proximity to where food is presented at feeding time. Because feeding is usually set on a predictable basis dependent on keeper schedules as well as planned visitor education schedules, animals generally learn to expect food at certain times and locations either based on endogenous timing mechanisms (i.e., circadian rhythm) or associated cues (e.g., keeper walking by enclosure) and consequently entrain on these schedules resulting in food-anticipatory circadian rhythms (Bassett & Buchanan-Smith, 2007; Mistlberger, 2009; Reeb & Lague, 2000; Verwey & Amir, 2009). Thus, the animal described in our example is most likely anticipating an imminent food reward through this biological clock. Once the food reward is allotted, the pacing will stop until it is feeding time again, when cued once more. Demonstrating the strength of these rhythms and the impact on psychological functioning, breaking the usual feeding schedules (i.e., predictable versus unpredictable) in several different captive-housed species have resulted in increased stress responses such as social disengagement, elevated levels of corticosterone, and increased performance of coping behaviors (rhesus macaques - Gottlieb, Coleman & McCowan, 2013; red knots - Reneerkens et al., 2002; brown capuchins - Ulyan et al., 2006). On this note, adding reliable signal to potentially startling/sudden events can help lower stress response and increase predictability, allowing animals to respond by anticipating and giving some sort of agency to individuals (Basset & Buchanan-Smith, 2007; Greiveldinger, Veissier & Boissy, 2007; Krebs et

al, 2017; Rimpley & Buchanan-Smith, 2013; Watters & Krebs, 2019). With these considerations, there is evidence that *too much* predictability may also be suboptimal, as shown through decreased species-specific behaviors and increased habituation to enrichment, and researchers and managers should keep this in mind when designing animal husbandry protocols (Bloomsmith & Lambell, 1995; Gilbert-Norton, Leaver & Shivik, 2009; Quirke & O’Riordan, 2011; Krebs & Watters, 2017). Thus, researchers have suggested employing a sweet spot in uncertainty of reward based on evolutionary significance of learning theory and optimal foraging theory – that is to say, balancing animal challenge and agency – that ultimately impact individual motivation to perform species-specific behaviors (Gilbert-Norton, Leaver & Shivik, 2009; Watters, 2009).

As stated, food-anticipatory rhythms have distinct neurobiology and have been shown to be robust. Furthermore, the cues involved in these rhythms (i.e., food/energy) are ubiquitous in its necessity to all life and therefore, can be considered the ultimate reward to be able to predict and pursue (Antle & Silver, 2009). Species across taxa have been shown to display ABs in response to predictable feeding schedules in captivity from fish (cichlids - Galhardo, Vital, & Oliveira, 2011; golden shiners - Reeb & Lague, 2000) to various primates (stump-tailed macaques - Waite & Buchanan-Smith, 2001; brown capuchins - Ulyan et al., 2006). Hitherto, we focus on AB in response to food rewards (as opposed to other reward opportunities, such as mating or social interaction) in this paper. It is important to keep in mind before further discussion that, although food anticipatory behavior is widespread, not all these behaviors look alike across taxa, and that researchers should proceed with caution in choosing behavioral variables to be measured in their experimental design (Mason & Mendl, 1997; Van den Bos et al., 2003).

### *1.3.1: A model connecting AB to welfare*

Literature has speculated that AB largely reflects *motivational states* and is closely tied to *reward sensitivity* circuits (Spruijt, van den Bos & Pijlman, 2001; Van der Harst & Spruijt, 2007; Watters, 2014). Behavioral conditioning paradigms using reliable cues using stimuli considered rewarding (i.e., food, social interaction with familiar beings), have been shown to successfully induce ABs (e.g., Anderson et al., 2015; Clegg et al., 2018; Krebs et al., 2017; Neave, Webster & Zobel, 2021; Vinke, van den Bos, Spruijt, 2004; Zimmermann et al., 2011). In a study involving dairy calves, researchers explored the effect of differences in housing conditions (i.e., basic versus enriched pens) on performance of AB in response to a conditioned cue associated with a rewarding opportunity (Neave, Webster & Zobel, 2021). Calves in the basic housing treatment group displayed more intense AB (i.e., increased frequency of behavioral transitions) when cued than those in the enriched treatment group. Furthermore, when quality of reward was unexpectedly changed (i.e., access to additional enrichment pen changed to access to additional basic pen), those in the basic group displayed decreased AB when cued, suggesting they experienced a “disappointment-like” state that has been found to be more pronounced in animals of poorer welfare state in response to sudden reward loss. Results such as these help illuminate the proposed connection between affective states, AB and the activation of reward-evaluating systems (i.e., release of dopamine) using predictable events associated with reward. Anticipation induced by a conditioned cue allows individuals to prepare for approaching events. In the process, this information is fed into motivational circuitry, as modulated by previously described interactions between varying internal and external circumstances as well as previous experiences,

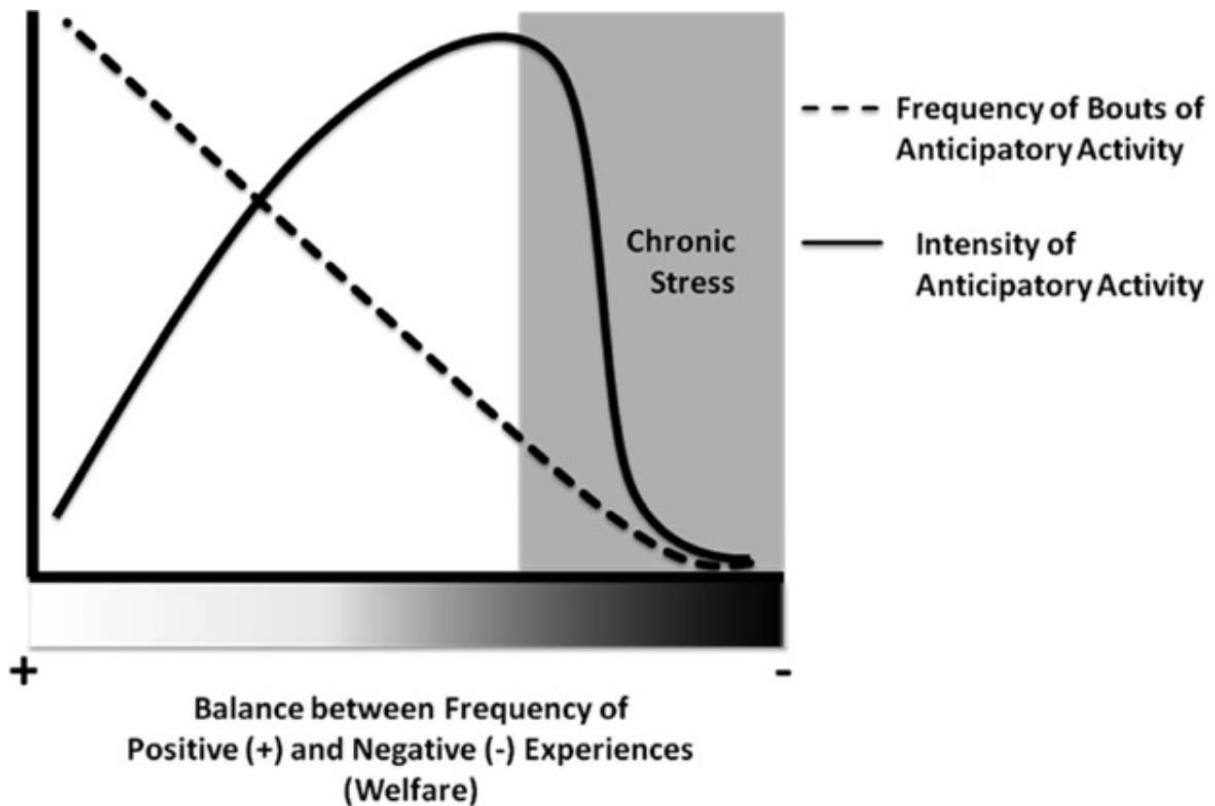


and into the consequent strength of the performance of behaviors needed to reach the perceived reward.

Following this theory, as an animal's motivation to access a resource increases, the longer and more intense the bouts of anticipation will be. In many cases, this may be simply reflecting biological rhythms (e.g., ultradian, seasonal) when increased sensitivity to food related goals naturally arise (e.g., when hungry), in both the wild and in captivity. However, there may also be circumstances in both contexts when AB is reflecting increased sensitivity to food related goals because of the potential lack of opportunities to perform related appetitive and/or consummatory behaviors. For example, it is possible that, in contexts of environments that are lacking opportunities to perform foraging and feeding behaviors, there will be increased sensitivity to imminent food reward (Van der Harst & Spruijt, 2007; Watters, 2014). Vice versa, when an animal's needs are largely satiated through multiple positive opportunities per day, resulting bouts are more frequent in number but shorter and less intense. In other words, if something is considered as a reward to an animal, it is going to "want" that reward more when they do not get the chance to have it regularly, whereas an animal that gets several chances to indulge in that reward in its day will not express the "want" as enthusiastically. In this case, an individual's motivation to acquire reward may be symptom of whether or not it is having its' "wants" met, which can be related back to individuals perceived balance of experiences (i.e., welfare state). One can then suggest the relationship between these states and AB trends (Figure 1).

In addition to the effect of overall frequency of rewarding opportunities experienced by an individual on AB, one may also consider the timing of these opportunities. Theoretically, sensitivity to predictable imminent food reward as shown through AB will be most reduced when

additional rewarding opportunities are experienced in time periods directly preceding the event (i.e., when balance of motivation to perform food-related behaviors is most currently tipped to increased satiety and positive experiences are most salient). As discussed before, however, there exists a complicated network of factors that play into individual motivation and the boundaries between these interactions are oftentimes unclear and difficult to dissect. Therefore, it is important to keep in mind at this point that our discussion of AB is not that the behavior be used as a singularity when assessing welfare and/or affective states, rather it be one of many diagnostic tools employed in the matter.



**Figure 1.** Predictive model of AB (Watters, 2014). The x-axis signifies the balance between overall positive and negative experiences, representing an animal’s welfare state. Lines shown on the graph represent the general increase in intensity of anticipatory activity with a higher ratio of negative experiences (e.g., animal experiences unreliable food availability) and a decrease in AB bout frequency. At a certain point, chronic stress results in a state of anhedonia, shown here in gray, when both frequency of bouts and intensity of AB drop off dramatically (e.g., animal is consistently food deprived).

With this caveat mentioned, multiple studies have demonstrated the effect of differing rearing environments and management styles on anticipatory behavior, which may be theoretically revealing the role of general welfare and the associated mechanisms of reward-sensitivity in the shaping of behavioral patterns. For example, studies with laboratory rats and dairy calves have shown that standard housed animals (i.e., barren housing, minimal enrichment) are more sensitive (reflected in the form of increased behavioral frequency) to food rewards than animals housed in enriched or semi-naturalistic enclosures (Makowska & Weary, 2016; Neave, Webster & Zobel, 2021; Van der Harst, Baars & Spruijt, 2003). A pharmacological study also done with rats revealed that administering antidepressants to food-deprived individuals would decrease anticipatory activity when presented with access to food, reflecting the potential influence of the drug on reward-sensitivity (Barbano & Cador, 2006). Another study suggests that the act of anticipation itself may be rewarding: in an experiment testing preference for feeding conditions meant to elicit varying levels of appetitive and consummatory behavior, piglets preferred conditions when access to food was announced beforehand with a delay between the announcement and the arrival of food rather than when access was given right after announcement (de Jonge et al., 2018). This finding potentially suggests that anticipation of acquiring a reward acts as a reinforcer on its own, apart from the acquisition of the reward alone. On top of these studies which focus on gathering data on the role of AB using different experimental groups amongst different individuals, there is additional data provided by studies modulating experimental conditions for the same individuals over time. One study conducted on a black rhinoceros showed that introducing a puzzle feeder (a mechanism that allowed for multiple reward opportunities per day) reduced anticipatory activity (i.e., increased walking and standing) before regularly scheduled afternoon feeding (Krebs & Watters, 2017). By using

anticipatory behaviors as indicators of welfare, we can begin to break down the role of motivation and reward sensitivity in captivity and use our knowledge in order to tailor our handling and care of animals to their needs.

### *1.3.2 – Ursus: chronobiology and AB*

As previously described, ABs are highly anchored to time and naturally occurring repetitions in it - after all, to be able to anticipate indicates the ability to predict. All life on earth, from single cell organisms (dinoflagellates - Roenneberg & Morse, 1993; cyanobacteria - Mihalcescu, Hsing & Leibler, 2004) to humans (Mills, 1966; Wager-Smith & Kay, 2000) depends on cues from temporally significant events that have direct effects on fitness (e.g., energy intake, reproduction). These reliable cues, such as day-length or temperature, allow an animal to evolve internal mechanisms (e.g., circadian rhythms) that elicit organized behavioral responses such as sleep-wake cycles and migration/hibernation (Berger, 2011; Halberg, 1969). These biological rhythms and the associated biological mechanisms, collectively referred to as chronobiology, allow individuals as well as entire species to optimize behavioral strategies within ecosystems. In turn, it becomes evident that internal clocks allow an individual to be able to predict and *anticipate* significant changes in opportunity for resources (e.g., food, mates, territory) (Antle & Silver, 2009). On this point, there may be differences in priority of these endogenous rhythms depending on the state of acting motivational systems and we will now begin to explore this concept in our focus species.

Grizzly bears, along with many others in the *Ursus genus*, undergo complex biological and metabolic changes during the phases of hyperphagia (increased eating) and hibernation and

waking-hibernation (Jansen et al., 2019; Nelson et al., 1980). Through several observational studies, these changes have been indirectly shown to be induced in the wild by seasonal weather conditions and associated forage availability – hyperphagia begins during the fall months when food is still available - yet dwindling - and prepares individuals for harsh winters when food becomes scarce and, subsequently, torpor begins (Evans et al., 2016). The physiological demands of torpor require that individuals substantially increase foraging activity during periods of decreasing light cycles (Nelson et al., 1983). A 2012 study involving the combined modulation of photoperiod and feeding schedules across seasons in captive brown bears found that individuals entrain on both light and food cues. More importantly, it was shown that entrainment to feeding schedules may mask sensitivity to photic cues which may lead to the behavioral flexibility seen in seasons when food becomes less readily available (Ware et al., 2012).

The existence of ecological time niches and the importance of temporally significant food entrained anticipatory behavior point to the power in creating and applying species-appropriate feeding schedules. As demonstrated by the study motioned above, sensitivity to intertwined factors naturally occurring in the wild may not be as obvious or easy to control in captive settings. By paying attention to anticipatory behavior as goal-directed action patterns highly reflective of motivational states and reward sensitivity, researchers and animal managers can utilize these as individualized reports in welfare assessments.

### ***1.5 - Current attempt to explore AB in two zoo grizzly bears***

Along with manual scattering of food, the use of automated scatter feeders has been employed in past studies to gauge its effectiveness in reducing abnormal repetitive behaviors and increasing behavioral diversity in bears and across taxa (Forthman et al., 1992; Grandia, van Dijk & Koene, 2001; Kistler et al., 2009; Swaisgood & Shepherdson, 2005). Focus has included the intention of creating more foraging opportunities reflecting natural feeding behaviors, with generally positive results (e.g., Andrews & Ha, 2014; Jenny & Schmid, 2002; Kistler et al., 2009). There has not been, however, much work around scatter feeder use with captive bears and none specifically examining anticipatory behavior related to the feeding method.

This study was aimed at examining effects of varying levels of reward acquisition on influencing AB patterns. Our objectives were to look at 1) potential differences in performance of our AB – in the form of total AB performed per observation session and average AB bout length – between the two individuals as well as changes in AB 2) over the day, in order to validate our definition of anticipatory behavior, 3) over the seasons 4) to general allotment of reward opportunities over the experimental year in comparison to our baseline year, both broken down into season and 5) in response to specific scatter feeder treatment within the experimental year.

We predicted that AB at our focal event would 1) look different between the two individuals based on previous keeper-reported anecdotal trends, 2) by definition, generally increase before shift times and drop of right after in both baseline and experimental years, 3) by definition, increase in months where reward sensitivity is heightened (i.e. in fall/winter – months where eating/foraging become more important due to seasonal behavioral demands), 4) decrease during the experimental year in relation to baseline levels, 5) decrease with increased *number* of reward opportunities based on specific treatment type (i.e. AM/PM only versus split AM + PM) when

analyzing across the experimental year and 6) change according to *timing* of reward allotment: highest decrease with complete allotment in time periods directly preceding the focal event (i.e., AM Only) compared to the lowest decrease when they are completely allotted after the focal event (i.e., PM only), with split allotment before and after the focal event having a medium effect on AB levels.

## **2 – Material and Methods**

### ***2.1 – Subjects, material, and enclosure***

We conducted our study on the two available resident grizzly bears (n=2, adult females – Kachina and Kiona) at the San Francisco Zoo. We chose this species based on predictable and conspicuous pre-existing patterns of ABs as well as readiness to react to scattered food rewards. The entire enclosure (about 3,000 m<sup>2</sup> total) consists of two sides (the grotto and the gulch) separated by a singular shift door, forming an hourglass-like shape with the door as the narrow point in the middle (Figure 2). When the bears are on one side of the enclosure, the shift door is closed and access to the other side is not possible. The grotto (mostly concrete with indoor denning area) is where the bears spend their evenings and overnight into the mornings when their scheduled breakfast feeding occurs (around 1030 hours) with the opening of the shift door to allow bears access to the gulch where breakfast, consisting of assorted fruits and vegetables and occasionally bone and fish, is scattered. Post-shift, the door is closed again, and the bears spend the rest of the zoo open hours in the gulch, which consists of a large meadow with grass, foliage, rocks, and trees and a large swimming hole. On most days, there will be treats (e.g., carrots, lettuce, celery, yams) tossed into the gulch by the keepers from outside between major shift/meal hours. These treat-tossing events do not occur at a regular schedule and is performed during

scarce free moments in the schedules of keepers. Around 1600 hours, the bears once again shift back into the grotto to eat their dinner, consisting of Mazuri® Omnivore Diet kibble as well as some assorted fruit and vegetables, and den for the evening. It is important to note at this point concerning changes in behaviors in response to certain cues given to our resident bears, whether purposeful or unconsciously. As much as these two respond to the main feedings that occur at predictable times across the year (endogenous cues), they are also highly tuned to the actors that are associated with these feedings – the keepers (i.e., external cues). These keepers not only provide main feedings, but also previously described treat tosses as well as other duties such as enclosure cleaning or behavioral monitoring. In saying so, we must keep in mind that the SF Zoo bears may interpret any cues (intentional or unintentional) given by nearby keepers as related to feedings or perhaps other reward events. For an example, when the bears are both in their AM gulch enclosure, keepers will find some available time to go over to the PM grotto enclosure to clean the area and prepare it for dinnertime. When this happens, the bears react similarly in the way they would knowing that these keepers, who are usually associated with food, and start to wait at the shift door in anticipation of assumed reward-related outcome. This becomes important when interpreting some analysis later in the results and discussion sections.

We chose the placement of the feeder (FeedPod, UltimateAnimal™) so that it would experimentally scatter the bears' regular kibble pellets at times when members of the public were not around (i.e., before and after closing) in order to limit any visitor effect. Thus, the feeder contraption was positioned up on the keeper roof access overlooking the mainly concrete night quarters of the grizzly bear enclosure. When triggered by an automatic timing device, the feeder activated a spinner that dispensed the Mazuri® Omnivore Diet kibbles for five seconds which



amounts to about 5 -10 kibbles dispensed total for that event, of which there are 7 total events per treatment, varying on timing allotted (in the AM, in the PM, or split between the AM and PM, explained in detail below). To assess any changes in food-motivation and reward sensitivity to regular daily enclosure shifts as a result of scatter-feeder treatment, observations occurred at the metal mesh shift door (Figure 2). These specific locations were chosen in that behavioral responses occurred preceding a regularly scheduled event which 1) were directly connected to food/foraging events 2) were fairly consistent in timing over the year 3) were presumed to be an event when AB occurs and is conspicuous and directly observable.



Figure 2. Grizzly bear enclosure design at the San Francisco Zoo (via Google Maps). Focal events occur around 1000 hours (main focal event time) and 16300 hours at the shift door between night quarters (left) and afternoon quarters (right) daily. Both enclosures are fully viewable by the public and both meals are offered outdoors and during zoo open hours.

## ***2.2 – General Data Collection***

As mentioned, the behavior measured as AB consisted of a food-related waiting behavior that occurred at an area significant to attainment of food. This occurred at the enclosure gate separating the overnight quarters (Grotto) and on-exhibit daytime (Gulch) enclosures in which morning and evening meals would be waiting before major transition periods (i.e., twice-daily shifting from one enclosure to the other for feeding) (Figure 2). Both enclosures are fully viewable by the public and both AM and PM meals are offered outdoors and during zoo hours. We chose this particular AB for our study because of the conspicuousness of the behavior in both our subjects and the potential connection to daily feeding events that represent significantly rewarding occasions. All AB was collected as a continuous variable (seconds) and all other behaviors (see ethogram, Table 1) were collected instantaneously at intervals of 60 seconds. AB was analyzed as total duration per observation session and average door-focused bout length, both in seconds. Additionally, some behaviors potentially associated with anticipation of food (e.g., running, checking den door) were collected on all-occurrence basis.

We collected data in two phases: 1) experimental data from summer 2018 to winter 2019 and 2) baseline non-experimental observational data in the subsequent year from summer 2019 to winter 2020. Seasons were classified as follows: summer included days from June 1<sup>st</sup> – August 31<sup>st</sup>; fall included days from September 1<sup>st</sup> – November 30<sup>th</sup>; winter included days from December 1<sup>st</sup> – February 28<sup>th</sup>. Unfortunately, due to the Covid-19 pandemic as well as other complications in scheduling, we were not able to collect spring data in the baseline year; thus, spring was left out of comparisons between baseline and experimental years. We collected

behaviors of both bears simultaneously at each observation session. All live hour-long observation sessions for experimental seasons ( $n = 184$ ) were started one hour before shift time where door-focused behaviors were recorded up until actual enclosure shift with continuous sampling (duration in seconds). Door-focused behavior was defined as any directed lingering ( $> 2$  seconds) within 2 meters of the enclosure shift door. All other behaviors were also recorded as instantaneous at every 60 seconds (see Table 1). We chose to focus in on AB and not analyze general time budgets for the purposes of this study. We decided on this timing of observations as the performance of most food ABs are captured starting around an hour prior to shifting (Figure 5; Richter, 1927; Mistleberger, 1994) and allowed us to encapsulate almost all potential anticipatory behaviors in relation to the enclosure shift event in both the morning and the afternoon. An additional hour after the focal shift event was also recorded to assess changes in behavior from pre-shift to post-shift. On top of treatment data, we also recorded baseline data in the same fashion up to four randomly chosen hour-long sessions between 0900 – 1800 hours per day at least four times a month in order to capture any general AB activity throughout the day, which may or may not have included the focal event (baseline:  $n_{\text{total}} = 64$ ,  $n_{\text{focal}} = 19$ ). All observations were recorded on the ZooMonitor application (Lincoln Park Zoo, 2020) using an ethogram created for the grizzly bears (Table 1). Two observers collected data over the two years of the study. We estimated inter-rater reliability by having both observers record behavior from a random sample of 40 minutes of video using the study ethogram. Observers achieved  $>80\%$  agreement on interval behaviors across all videos.

Behavior	Description	Sampling Method
Eat/Forage	Bear consumes food. Includes processing behaviors like chewing, biting, tearing, pulling, or otherwise manipulating food. Also includes grazing.	Interval
Forage in Water	In water, actively pursuing food	Interval
Groom	Bear scratches, licks, picks at, shakes fur, or otherwise grooms itself. Includes stretching behaviors.	Interval
Interact with Enrichment	Any interaction with non-food enrichment in bear enclosure. Includes digging in dirt, non-foraging interactions with vegetation.	Interval
Interact with Keeper	Bear participates in training session or other interaction with keeper	
Lie Down	Bear is lying down on the ground	Interval
Out of View	Bear is not in view	Interval
Pace	Bear walks back and forth for at least one full loop (A to B to A) or walks the same complete circle at least once	Interval
Rub	Bear rubs body against structure or item in exhibit	Interval
Run	Bear moves from one location to another via running. Includes any form of locomotion where more than one paw is raised off the ground at one time.	Interval
Sit	Bear is sitting with upper body upright and rear on the ground. Paws can be in any position.	Interval
Stand-Bipedal	Bear is standing at full height on two rear paws	Interval
Stand-Quadrupedal	Bear is standing with all four paws on the ground	Interval
Wade/Swim	In pool, locomoting/swimming, standing, or lying down but not actively pursuing food or prey	Interval
Walk	Bear moves from one place to another via walking - at least 3 paws are on the ground at any given time.	Interval
Affiliative	Bear shows affiliative behavior towards other bear - e.g. grooms other, lays down next to, plays with, or any other non-aggressive interaction between bears	All Occurrence
Aggress	Bear aggresses towards other bear, includes swatting, hitting, chasing, snarling, biting	All Occurrence
In Bear Dens	Bear walks into den	All Occurrence
Interact with Enrichment	Bear interacts with any non-food enrichment item in exhibit. Includes digging in dirt/substrate, or non-foraging interactions with vegetation	All Occurrence
Pace	Bear walks back and forth for at least one full loop (A to B to A) or walks the same complete circle at least once	All Occurrence
Run	Bear moves from one location to another via running. Includes any form of locomotion where more than one paw is raised off the ground at one time.	All Occurrence
Vocalize	Bear vocalizes, unrelated to aggressive interaction with other individual	All Occurrence
Door-Focus Behavior	Bear approaches within 2 m of shift door and remains for > 2 seconds directed at the door	Continuous

**Table 1.** Grizzly bear behaviors and descriptions observed during hour-long live-coding observation sessions. Door-focused behavior recorded continuously, den-focused behavior all-occurrence and all other behaviors instantaneously at every 60 seconds, per bear. Observations are taken starting one hour before the daily shift event during experimental year along with three other randomly chosen hours in the baseline year.

## 2.3 – Experimental Design

### 2.3.1 – Objectives 1) Individual differences and 2) Changes across the days - AB validation

Our first proceedings were to complete objectives 1) and 2) to reveal any differences in our proposed AB between individuals and, respectively, to demonstrate validation of our measured behaviors as AB (referred to as door-focused behavior from here on) according to the definition of AB (i.e., goal-directed behavioral patterns responding to reliable cues, either endogenous, external or both) by observing changes in AB over the day for each bear. Collection of AB data

for objectives 1) and 2) consisted of 3 to 4 randomly chosen hour-long observation sessions over the day between 0800 – 1700 hours (at least 4 days/month) in a baseline year (summer, 2019 – spring, 2020). These measurements were to allow us to see any patterns in our door-focusing behavior across the day, which may or may not have involved our focal feeding event and use these findings to validate our door-focusing behavior as AB. Additionally, to further confirm the goal-directed nature of door-focusing and the theoretical drop-off of AB we expect to see, we also collected data in one-hour sessions following directly after the AM shift event. All measurements were collected for both bears simultaneously in each observation session in order to continue fulfilling objective 1) throughout the research phases.

### *2.3.2. Objectives 3) Seasonality of AB at focal event - Baseline and Objective 4) Comparison of seasonal breakdowns of AB at focal event between baseline and experimental year*

To address objective 3) examining seasonal trends of our AB, we broke down measures from the AM shift events into averages for summer, fall and winter months across our baseline year. We then performed the same analysis across our experimental year in order to address objective 4) of directly comparing seasonal trends against baseline to examine any general effect (i.e., not by specific treatment type but overall effect of providing extra opportunities for food-related reward via scatter feeder over the year).

### *2.3.3. Objective 5) Specific treatment effect on AB at focal event*

Finally, to fulfill objective 5) of examining specific effect of feeder treatment, we attempted to modulate expression of AB (i.e., total duration, average bout length) by regulating the number of rewarding opportunities apportioned throughout the day as well as when these rewards were

allotted (i.e., in the AM, PM, or split AM + PM) through application of a scatter-feeder as our treatment types. Data from our experimental year (summer 2018 – summer 2019) was collected once per day for at least one week of each treatment type given on a general continuous schedule of 1-2 weeks on treatment and 1-2 weeks off treatment.

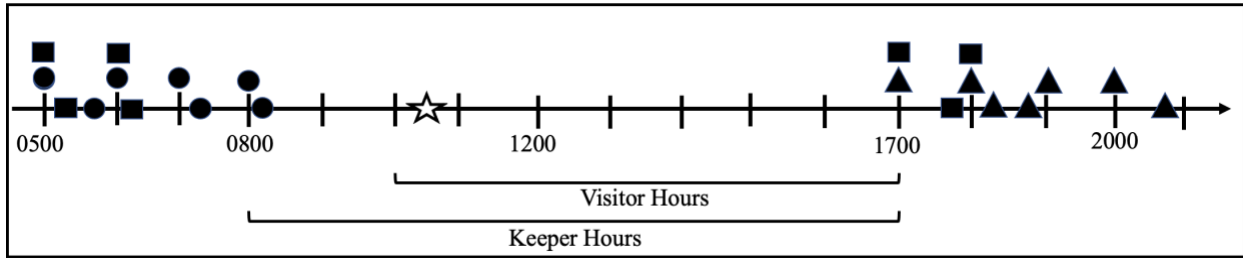
#### 2.4 - Treatment descriptions

To examine the effects on AB based on number of opportunities for reward acquisition as well as timing of these opportunities in relation to our main focal event (i.e., before, after or both), we created our three main types of treatment (AM only, PM only, and AM/PM split; Table 2).

Design of the timing of physical scattering of Mazuri ® Omnivore Diet pellets from the scatter feeder *within* each treatment time period is based on an optimal foraging theory suggesting that a mix of predictable (AM and/or PM) and unpredictable (random within AM and/or PM) enrichments stimulates behavior that helps promote higher levels of well-being (i.e., through the encouragement of motivation to acquire rewards or resources) (Watters, 2009). Combination of these factors can be seen in example timelines of treatment types and timing in Figure 3.

Treatment	Description
Pre Feeder	One month of baseline data to serve as a control – no scatter-feeder treatment
AM Only	Four-hour window in the AM, hourly from 0500-0800 and an additional 3 randomly chosen dispenses between 0500-0859 hours (i.e. total of 7 feeder dispenses)
PM Only	Four-hour window in the PM, hourly from 1700-2000 with an additional 3 randomly chosen dispenses between 1700-2059 hours (i.e. total of 7 feeder dispenses)
AM/PM Split	Two-hour window in the AM + 2-hour window in the PM with hourly dispenses at 0500 & 0600 and 1700 & 1800 with an additional 3 randomly chosen dispenses a day within the collective 4-hour dispense window (AM and PM) (i.e. total of 7 feeder dispenses)

**Table 2.** Scatter-feeder treatment types and descriptions. Every treatment continued for 14 days and live-observations were collected for 10 days in that time period on weekdays (Monday-Friday). Approximately fourteen days were taken off between treatments (any between-treatment periods longer than 14 days were results of the feeder breaking or animal management conflict). Experimental treatments took place over the course of one year (July 2018-March 2019).



**Figure 3.** Example timelines of different treatment types allotted in the experimental year. Axis ticks represent hours from 0500 to 2100. Different shapes represent the three different treatment types: ● = AM Only, ▲ = PM Only, ■ = AM/PM split. ☆ indicates focal event (AM door-shift) at which hour-long observations are taken.

It is important to note that no extra supplementation of regular feedings was provided with experimental treatment - regular portions were divided amongst the treatment types and experimental manipulation was solely based on varying opportunities to perform feeding and foraging behavior, not provision of extra feed. For example, on a typical day, each bear is fed a total of 1.13 kilograms of kibble for breakfast and another 1.13 kilograms for dinner (i.e., 2.27 kilograms total daily for both bears). Thus, if the AM Only treatment called for 0.57 kilograms of kibble to be dispensed from the scatter feeder, the keepers would subtract that 0.57 kilograms from the total of 2.27 kilograms (i.e., 1.7 kilograms) that was regularly schedules for each bear (i.e., 0.85 kilograms of kibble would be given for breakfast and 0.85 kilograms for dinner for each bear).

### ***2.3 - Statistical method***

All statistical analyses were performed using RStudio Version 1.3.1093. All behaviors recorded were summed (total time performing door-focused behavior) or averaged (door-focused behavior bout length) per hourly session for standardization for each of the two bears. We tested both variables of interest for normality using the Shapiro-Wilks test and found that data was not normal and continued analysis using nonparametric tests and following assumptions for non-normal data. We validated door-focused behavior as anticipatory by: 1) comparing the average differences between pre- and post-shift total door-focused behavior (per session in seconds) as well as the differences between pre- and post-shift average proportion of time spent eating/foraging per session using Wilcoxon rank sum tests for each bear, and, 2) applying a linear mixed effect model to examine door-focused behavior across each hour time slot (i.e. 0900 – 0959, 1000 – 1059, ..., 1700 – 1759 hours) as a fixed effect and season as a random effect. We then ran post-hoc pairwise comparisons using estimated marginal means from the model to reduce type 1 errors. Once door-focused behavior was validated as anticipatory according to our definition of AB (i.e., occurs before a predictably timed event and drops off after anticipated outcome is attained), we first broke down our two measurements by season, as this was a way to compare directly between our baseline and experimental year to examine overall experimental effect. Because we were not able to collect spring data in our baseline year, we only compared between summer, fall, and winter data.

To account for possible interactions between variables, we applied a linear mixed effects model (using the *nlme* package, *lme()* function) to each of the three measurements to analyze fixed



effects of A) season, B) research phase (i.e., baseline or experimental) C) research phase nested in season, and D) focal individual (Harrison et al., 2018):

A)  $AB(x2) \sim \text{Season, random} = \text{Phase/Focal}$

B)  $AB(x2) \sim \text{Phase, random} = \text{Season/Focal}$

C)  $AB(x2) \sim \text{Season/Phase, random} = \text{Focal}$

D)  $AB(x2) \sim \text{Focal, random} = \text{Season/Phase}$

Next, we then took the entirety of the experimental year – including data taken in spring – and broke data down by specific treatment in order to examine any treatment effects using a linear mixed effect model for each of the two bears:

E) Kachina:  $AB(x2) \sim \text{Treatment, random} = \text{Season/Month}$

F) Kiona:  $AB(x2) \sim \text{Treatment, random} = \text{Season/Month}$

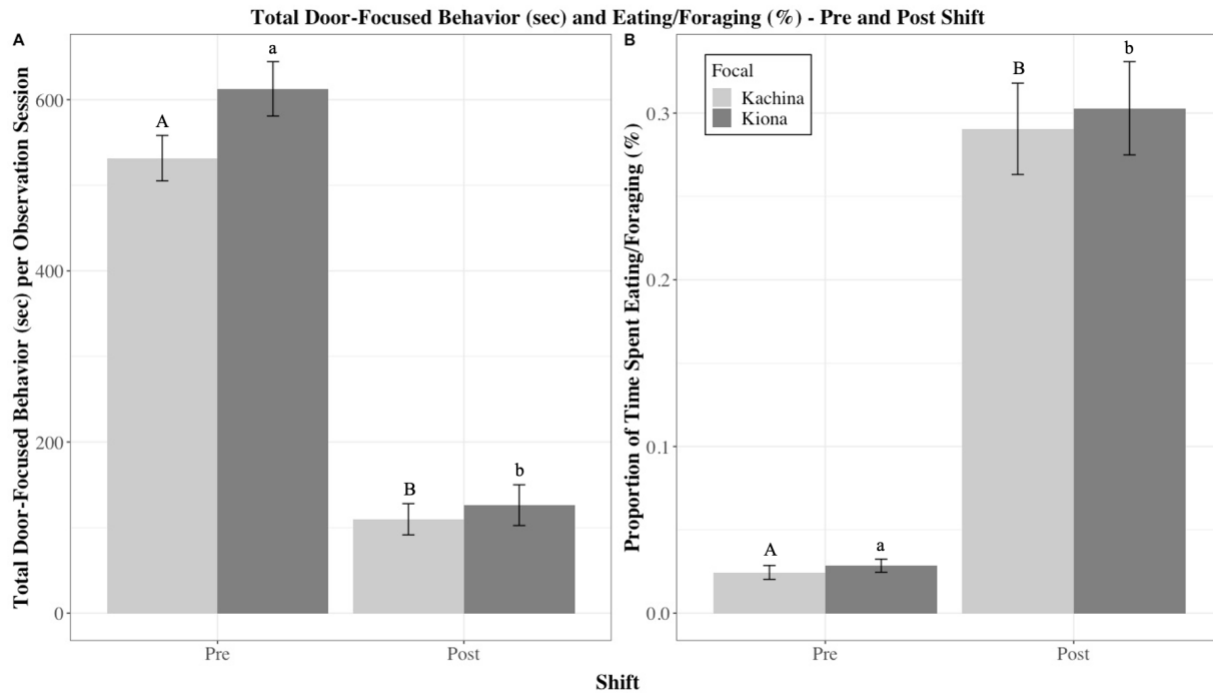
We ran post-hoc pairwise comparisons using estimated marginal means for models A), C), and D). Finally, for models E) and F), we ran post-hoc effect contrasts (against the grand mean) using estimated marginal means. All tests were conducted at  $\alpha = 0.05$ ; pairwise tests were adjusted by Tukey HSD correction and effect contrasts were adjusted by FDR correction, as default in the *emmeans* package.

### **3- Results**

#### ***3.1 – Daily Trends (Figures 4 &5)***

As seen in Figure 4, there is a significant decrease in anticipatory door-waiting behavior (Kachina:  $W = 1412, p < 0.01$ ; Kiona:  $W = 1470.5, p < 0.01$ ) and significant increase in

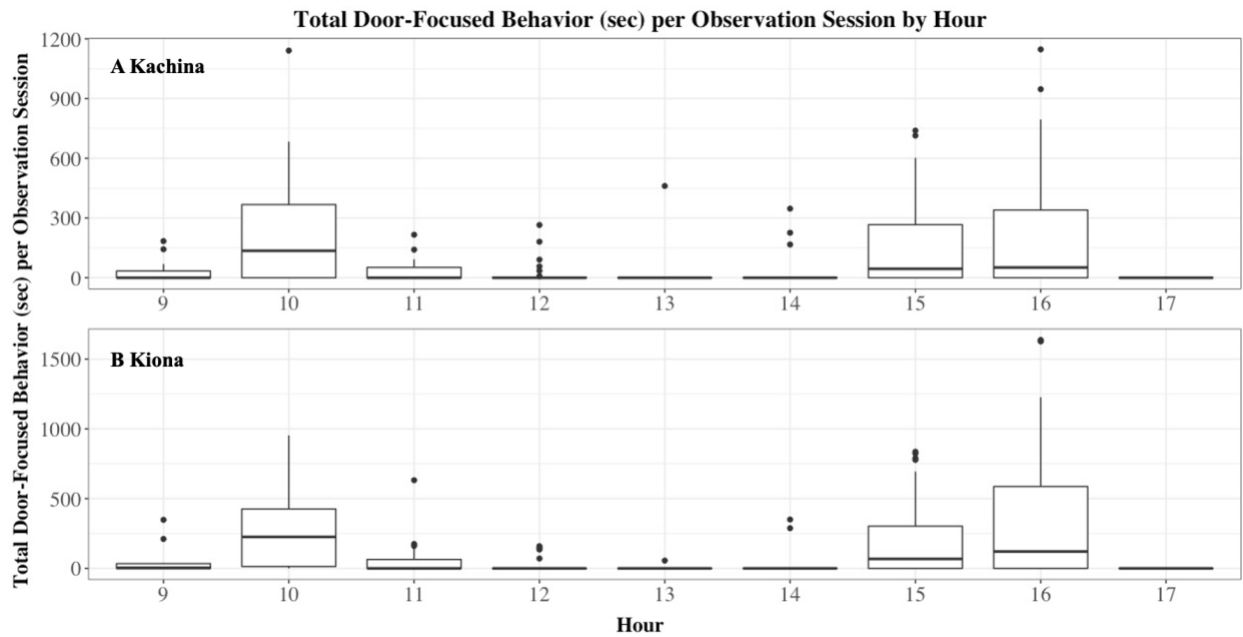
eating/foraging behavior (Kachina:  $W = 16473$ ,  $p < 0.01$ ; Kiona:  $W = 15968$ ,  $p < 0.01$ ) from pre-shift to post-shift.



**Figure 4.** **A)** Comparing total time performing door-focused behavior in seconds per hour-long observation session between pre-shift and post-shift sessions for each focal bear. **B)** Comparing average proportion of time spent eating/foraging per hour-long observation session between pre-shift and post-shift sessions for each focal bear. Letter case indicates significant differences between pre- (A/a) and post- (B/b) shift behaviors for each bear, respectfully ( $p < 0.05$ ). Standard error bars included.

After breaking down hours of the working day between 0900 and 1700 hours from the baseline year, we found that both bears spent significantly more total time performing door-focused behavior preceding times when the morning shift event was expected to occur (i.e. starting around 0900 hours and peaking between 1000 – 1030 hours) with the AB dropping off quickly afterwards through around 1400 hours (Figure 5;  $t > 3.00$ ,  $p < 0.05$ ; at 1000 hours: Kachina - Med = 135.5 sec, SD = +/- 259.03 sec; Kiona - Med = 225.5 sec, SD = +/- 276.60 sec). Both bears tended to ramp up door-focused behavior around 1500 hours and peaking at 1600 hours (Figure 5;  $t < -3.00$ ,  $p < 0.05$ ; at 1600 hours: Kachina - Med = 51.5, SD = +/- 325.16 sec; Kiona - Med = 121 sec, SD = +/- 510.81 sec). There are a few outliers that occur during non-shifting

times associated with main feedings (i.e., 1200 to 1400), and we can attribute those back to afternoon treat tosses that occurred during those observation session – as described previously, the presence of keepers elicits the same door-focusing behavior, as they are generally associated with food.



**Figure 5. A) Focal bear Kachina. B) Focal bear Kiona.** Anticipatory behavior measured as average total time performing door-focused behavior per hour-long observation session (seconds) over the nine hours of the working day. Notice major peaks in AB around 1000 hours and later 1500-1600 hours. Any outliers presented between these peak hours represent anticipation directed as keeper presence at afternoon treat tosses or adjacent enclosure cleanings. Boxplots represent the median (black line within box) and first and third quartiles (25 and 75% of data). Whiskers extend to the lowest and highest values that are not outliers (values that are 1.5x the interquartile range), outliers are presented as dots.

### 3.2 - Individual patterns

Results show differences in anticipatory style between our two focal bears (i.e., model D). Kiona spent more time per observation session performing door-focused behavior (Kiona estimated marginal mean (EMM) = 601, Kachina EMM = 519,  $t = 2.07$ ,  $p = 0.04$ ) with longer bouts than her sister Kachina (Kiona EMM = 73.5, Kachina EMM = 62.6,  $t = 2.79$ ,  $p < 0.01$ ).

### 3.3 - Seasonal Trends (Tables 3A<sub>1,2</sub> & C<sub>1,2</sub>; Figures 6 & 7)

We found a seasonal effect across both of our AB measurements for both focal individuals, with total door-focused behavior increasing from summer into fall and staying consistent into winter (Table 3A<sub>1</sub>, C<sub>1</sub>), and average door-focused bout increasing continuously through summer to winter (Tables 3A<sub>2</sub>, C<sub>2</sub>).

<b>A</b>	<b><sub>1</sub>Total Door-Focused Behavior (sec)</b>					<b><sub>2</sub>Average Door-Focused Bout Length (sec)</b>				
	<b>SD</b>					<b>SD</b>				
~1 Experiment	41.23					0.008				
~1 Experiment/Focal	44.50					6.06				
<i>Residual</i>	389.56					37.64				
<b>Fixed Effects</b>	<b>Value</b>	<b>SE</b>	<b>DF</b>	<b>t</b>	<b>p</b>	<b>Value</b>	<b>SE</b>	<b>DF</b>	<b>t</b>	<b>p</b>
<i>Intercept: Fall</i>	605.59	57.48	374	10.54	0.00	77.59	5.23	364	14.82	0.00
Summer	<b>-163.83</b>	<b>49.77</b>	<b>374</b>	<b>-3.20</b>	<b>0.002*</b>	<b>-41.00</b>	<b>4.86</b>	<b>364</b>	<b>-8.43</b>	<b>0.00*</b>
Winter	-1.77	56.84	374	0.16	0.87	<b>15.33</b>	<b>5.57</b>	<b>364</b>	<b>2.75</b>	<b>0.006*</b>

<b>B</b>	<b><sub>1</sub>Total Door-Focused Behavior (sec)</b>					<b><sub>2</sub>Average Door-Focused Bout Length (sec)</b>				
	<b>SD</b>					<b>SD</b>				
~1 Season	82.62					28.25				
~1 Season/Focal	62.04					7.02				
<i>Residual</i>	388.75					37.57				
<b>Fixed Effects</b>	<b>Value</b>	<b>SE</b>	<b>DF</b>	<b>t</b>	<b>p</b>	<b>Value</b>	<b>SE</b>	<b>DF</b>	<b>t</b>	<b>p</b>
<i>Intercept: Experiment</i>	583.77	58.48	373	9.98	0.00	66.71	16.70	363	3.99	0.0001
No Experiment	-94.15	69.61	373	-1.35	0.18	8.18	6.70	363	1.17	0.24

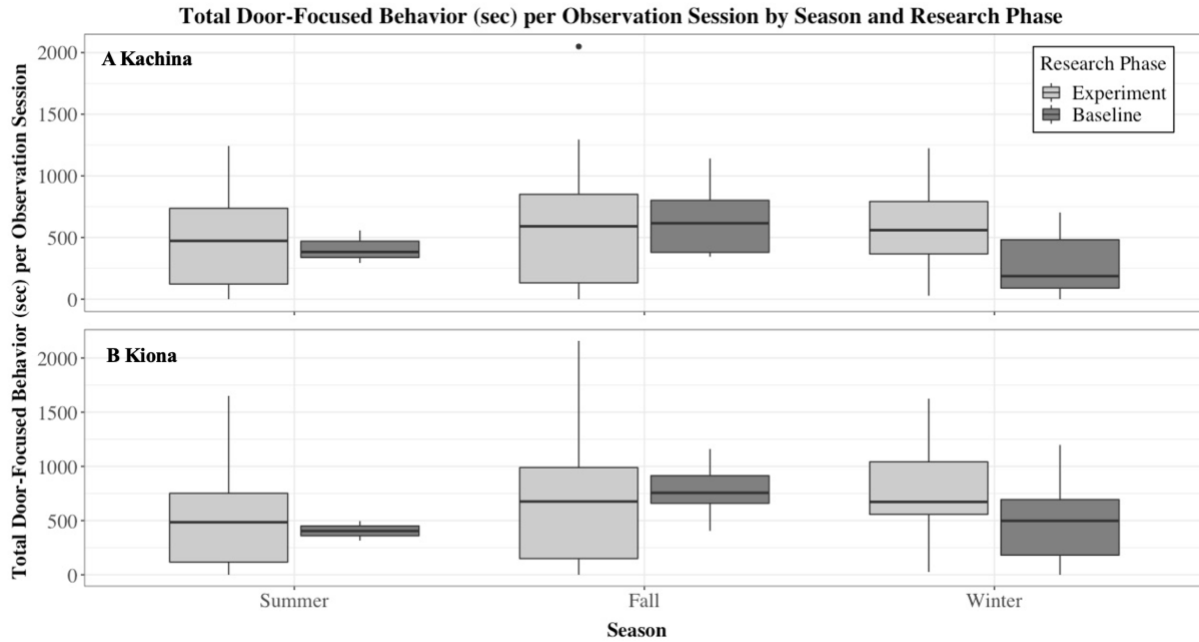
<b>C</b>	<b><sub>1</sub>Total Door-Focused Behavior (sec)</b>					<b><sub>2</sub>Average Door-Focused Bout Length (sec)</b>				
	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t. ratio</b>	<b>p</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b>t. ratio</b>	<b>p</b>
Fall - Winter	-8.99	56.8	374	-0.16	0.99	<b>-15.3</b>	<b>5.57</b>	<b>364</b>	<b>-2.71</b>	<b>0.02*</b>
Fall - Summer	<b>159.07</b>	<b>49.8</b>	<b>374</b>	<b>3.20</b>	<b>0.004*</b>	<b>41.0</b>	<b>4.86</b>	<b>364</b>	<b>8.43</b>	<b>&lt;0.0001*</b>
Summer - Winter	<b>-168.06</b>	<b>49.2</b>	<b>374</b>	<b>-3.42</b>	<b>0.002*</b>	<b>-56.3</b>	<b>4.80</b>	<b>364</b>	<b>-11.73</b>	<b>&lt;0.0001*</b>

**Table 3. A<sub>1,2</sub>) Results of model A:** the linear mixed effects analysis of dependent variable measurement (total door-focused behavior and average door-focused bout length) against season with focal individual nested in research phase as covariates. **B<sub>1,2</sub>) Results of model B:** the linear mixed effects analysis of dependent variable measurement (total door-focused behavior and average door-focused bout length) against research phase with focal individual nested in season as covariates. **C<sub>1,2</sub>)** Post-hoc pairwise comparisons of model A based on model estimated marginal means. Adjustment method for multiple comparisons: Tukey HSD. \* indicates significant effect on AB ( $p < 0.05$ ).

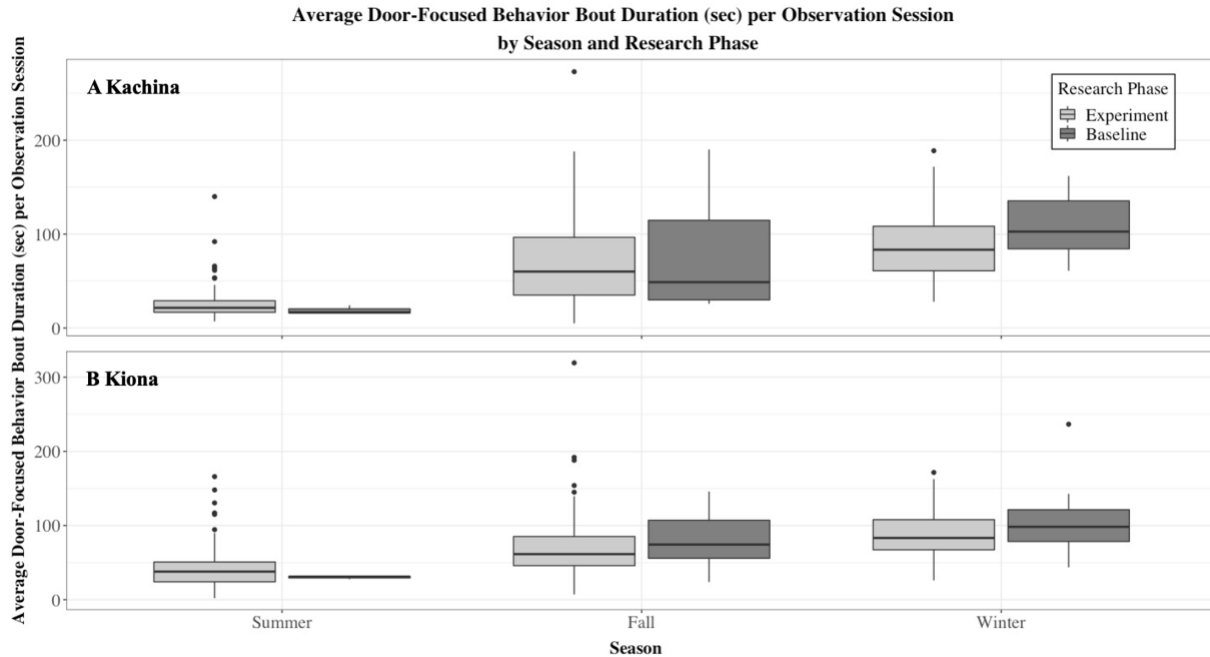
### 3.4 - Experimental Effects (Table 3B<sub>1,2</sub>; Figures 6 & 7)

We did not find any experimental effects (i.e., effect of general treatment application on AB performance as compared to baseline performance across the seasons) in both our AB measures according to season (Table 3B<sub>1,2</sub>). However, when comparing experimental effects within seasons, we found significantly more total door-focused behavior per session within winter of the

experimental year compared to the baseline year when controlling for focal individual effect (Model D; Figure 6;  $t = 2.81$ ,  $p = 0.05$ ).



**Figure 6. A) Focal bear Kachina. B) Focal bear Kiona.** Comparison of anticipatory behavior measured as total door-focused behavior per session broken down by season between the two year-long phases of the study. The two research phases consisted of one year of baseline data and another year of experimental data in which we applied treatments varying in the number of reward opportunities allotted per day via scatter-feeder. No overall effect of treatment via scatter-feeder on total door-focused behavior over the experimental year was found in comparison to the baseline year, except for winter (See Table 3B<sub>1</sub>). Boxplots represent the median (black line within box) and first and third quartiles (25 and 75% of data). Whiskers extend to the lowest and highest values that are not outliers (values that are 1.5x the interquartile range), outliers are presented as dots.



**Figure 7. A) Focal bear Kachina. B) Focal bear Kiona.** Comparison of anticipatory behavior measured as average door-focused bout length per session broken down by season between the two year-long phases of the study. The two research phases consisted of one year of baseline data and another year of experimental data in which we applied treatments varying in the number of reward opportunities allotted per day via scatter-feeder. Boxplots represent the median (black line within box) and first and third quartiles (25 and 75% of data). Whiskers extend to the lowest and highest values that are not outliers (values that are 1.5x the interquartile range), outliers are presented as dots.

### 3.5 Treatment Effects

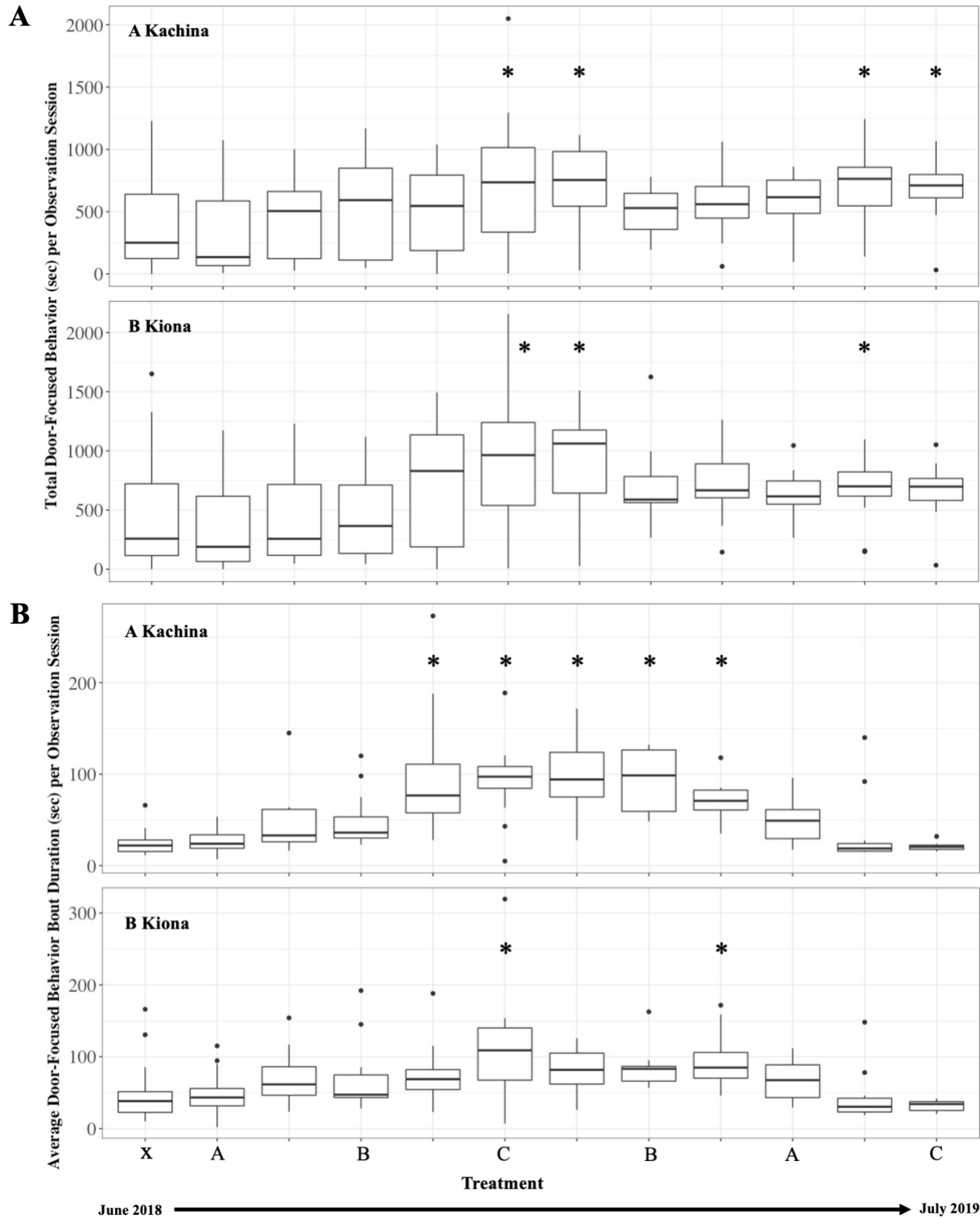
<b>A<sub>1</sub> – Kachina</b>				<b>B<sub>1</sub> – Kiona</b>			
Total Door-Focused Behavior (sec)				Total Door-Focused Behavior (sec)			
Fixed Effects	DF	t	p	Fixed Effects	DF	t	p
Intercept: Pre Feeder	162	2.23	0.03	Intercept: Pre Feeder	162	2.42	0.02
AM Only	162	-0.46	0.65	AM Only	162	-0.50	0.61
No Feeder 1	162	0.17	0.86	No Feeder 1	162	0.03	0.97
AM and PM	162	0.35	0.73	AM and PM	162	2.42	0.87
No Feeder 2	162	0.42	0.67	No Feeder 2	162	1.14	0.26
<b>PM Only</b>	<b>162</b>	<b>2.11</b>	<b>0.04*</b>	<b>PM Only</b>	<b>162</b>	<b>2.70</b>	<b>0.008*</b>
No Feeder 3	162	2.25	0.03*	No Feeder 3	162	2.75	0.007*
AM and PM 2	162	1.28	0.20	AM and PM 2	162	1.87	0.06
No Feeder 4	162	1.39	0.17	No Feeder 4	162	1.78	0.08
AM Only 2	162	0.53	0.60	AM Only 2	162	0.55	0.58
No Feeder 5	162	2.05	0.04*	No Feeder 5	162	1.95	0.05*
PM Only 2	162	2.20	0.03*	PM Only 2	162	1.59	0.11

<b>A<sub>2</sub></b>				<b>B<sub>2</sub></b>			
Average Door-Focused Bout Length (sec)				Average Door-Focused Bout Length (sec)			
Fixed Effects	DF	t	p	Fixed Effects	DF	t	p
Intercept: Pre Feeder	159	2.03	0.04	Intercept: Pre Feeder	158	3.08	0.003
AM Only	159	0.67	0.51	AM Only	158	0.47	0.64
No Feeder 1	159	1.57	0.12	No Feeder 1	158	1.73	0.09
AM and PM	159	0.74	0.46	AM and PM	158	0.17	0.86
No Feeder 2	159	3.33	0.001*	No Feeder 2	158	0.66	0.51
<b>PM Only</b>	<b>159</b>	<b>3.92</b>	<b>0.0001*</b>	<b>PM Only</b>	<b>158</b>	<b>3.18</b>	<b>0.002*</b>
No Feeder 3	159	3.56	0.0005*	No Feeder 3	158	1.79	0.08
AM and PM 2	159	3.47	0.0007*	AM and PM 2	158	1.91	0.06
No Feeder 4	159	2.78	0.006*	No Feeder 4	158	2.41	0.02*
AM Only 2	159	0.87	0.38	AM Only 2	158	0.96	0.34
No Feeder 5	159	0.56	0.57	No Feeder 5	158	-0.06	0.95
PM Only 2	159	-0.26	0.80	PM Only 2	158	-0.81	0.42

**Table 4. A<sub>1,2</sub>) Focal individual Kachina – results of models E. B<sub>1,2</sub>) Focal individual Kiona - results of model F.** Results of linear mixed effects analysis of dependent variable measurement (total door-focused behavior and average door-focused bout length) against treatment with month and season as the covariates. Fixed effect values of treatment type are in relation to pre-feeder (baseline) values. \* represents significant treatment effect on anticipatory behavior ( $p < 0.05$ ).

Results continue to illuminate season as a strong influencer across all three of our ABs for both bears when experimental data is further broken down by treatment (Figure 9). Total door-focused behavior peaked around treatments occurring during November/December and June the following year. These treatments included PM Only, No Feeder 3 and No Feeder 5 in both bears as well as PM Only 2 for Kachina (Figure 4. A<sub>1</sub>, B<sub>1</sub>). Length of door-focused bouts peaked at significantly longer bouts throughout more treatments for Kachina from October to March in the following year with treatments: No Feeder 2, PM Only, No Feeder 3, AM + PM 2 and No Feeder 4 (Figure 4. A<sub>2</sub>). Kiona performed longer door-focused bouts around December and later around February with treatments of PM Only and No Feeder 4 (Figure 4., B<sub>2</sub>).



**Figure 9. Treatment effect** –Anticipatory behavior measurements per observation session by treatment and focal individual, across treatment application by chronological time to elucidate interaction between season and treatment: **A) total door-focused behavior (sec); B) average door-focused behavior bout length (sec)**. X-axis represents the treatment schedule given in chronological order over the experimental year: x – pre-feeder/baseline, A – AM Only, B – AM/PM Split, C – PM Only. **Unlabeled spaces in between are periods of no treatment**. See Table 2 for treatment descriptions. Boxplots represent the median (black line within box) and first and third quartiles (25 and 75% of data). Whiskers extend to the lowest and highest



values that are not outliers (values that are 1.5x the interquartile range), outliers are presented as dots. *Note:* data was not recorded for May 2019 due to scatter-feeder maintenance issues.

## **4 - Discussion**

### ***4.1 – General AB Styles – Individual Differences***

It is important to note the individual differences seen in our results before discussing overall experimental findings. Our results show that the SF Zoo resident grizzly bears have statistically different anticipatory styles based on how much total time dedicated to performing door-focusing behaviors and how long bouts of those behaviors last on average per hour-long observation session. Kachina anticipates in a more “active” pattern than her sister, spending less time sitting and waiting at the shift door, and instead, spending her mornings wandering about the overnight enclosure and making short visits to the shift door. On the other hand, Kiona chooses to spend more time waiting at the shift door each time she visits it - a “sit and wait” method.

We could speculate that this difference in behavior reflects Kachina’s anticipation of the PM shift as a result of the influence of current conditions on her as an individual. One such condition may be the ever-present social hierarchy and competition between the sisters – Kiona is the dominant individual among the pair, displayed in the outcomes of various agonistic interactions such as physical altercations. *In-situ* grizzly bears generally live as single individuals or as small family units (i.e. mother and cubs), although GPS studies have shown that home ranges do overlap and that there are frequent encounters between individuals, with female-female interactions being short in duration (McLellan & Hovey, 2001; Stenhouse et al., 2005). There is, however, a noticeable gap in literature on the social hierarchies of these bears within captivity. In our case, Kiona (i.e. dominant) is a faster eater than her sister Kachina, meaning that there are times she will finish her meal and then push Kachina away from hers in order to finish hers as

well. Thwarted access to feed or perform other behaviors that individuals are highly driven to perform can result in frustration behaviors, including aggression, increased activity, and potentially in our study, increased goal-directed behavior associated with the thwarted opportunity (i.e., door-waiting earlier for food) (Carbonaro, Friend & Dellmeier, 1992; Olsson & Keeling, 2000). Future studies employing scatter-feeder treatment may consider controlling for intra-group competitions in order to clearly see trends in anticipatory behavior.

Researchers and managers must keep these – sometimes subtle – idiosyncrasies in mind when collecting data and when creating potential enrichment programs for their animals. Empirical findings of differences in individual behavioral trends such as ours, along with anecdotal evidence from zookeepers and visitors, have been documented. Researchers have studied these “personalities” (i.e., behavioral tendencies that are consistent across time and situations) (Réale et al., 2007; Sih et al., 2004) amongst individuals of the same species and have tested and quantified these behavioral correlates through careful observation across longitudinal studies (Finkemeier, Langbein & Puppe, 2018; Tetley & O’Hara, 2012; Watters & Powell, 2012). Just like with any other measure of behavior and its potential use as indicator of welfare, it is imperative to ensure the correct type of measurement is used based on the unique individuals, as individuals of different personality types may behave, react, and cope differently to their environments. Consequences of disregarding individual differences in management may result in varying levels of welfare amongst one single population (Richter & Hintze, 2019). For example, Asher and colleagues (2016) found that not only did housing quality (i.e., more enriched versus less enriched) affect performance in cognitive bias tests for pigs, they also found that pigs which were rated as more “reactive” in coping/personality type were more pessimistic when placed in

less enriched housing than their more “proactive” cohorts. Thus, animal caretakers must continue to factor unique behavioral types into general management and enrichment programs to meet individual needs.

#### ***4.2 - Daily Changes***

As shown in the results, we did indeed see that the door-waiting behavior occurred at specific times of the day – at shift times when bears were allowed access into the adjacent enclosure where food (either breakfast or dinner) would be waiting. The schedule on which these shift events occurred are predictable, occurring at 1030 in the morning and around 1530 - 1600 hours in the afternoon every day, year-round. Because of this, as reasons stated in the introduction, our resident bears have been able to entrain on the temporal predictability of these events most likely using a combination of endogenous clocks and external cues (i.e. keeper walking by enclosure) and formed reliable food-anticipatory behavior, as many species have shown to do when fed on a circadian schedule (Mistlberger, 1994; Mistlberger, 2009). Even outside of regularly timed events, such as our major shift change, associated external cues may be enough to elicit the same anticipation, as seen in the minor occurrences of our AB behavior during non-shift hours (Figure 5). In these cases, door-focusing behavior in both our bears were triggered simply by the keepers passing by the shift door area, sometimes followed by the tossing of an afternoon treat. All of this points to the significance of scheduling, predictability and intentional (as well as unintentional) cues in the influence on anticipation of important events, which will lend a helping hand in informing managers around which events to assess behavior when using anticipatory behavior as an indicator of welfare.

Furthermore, we see that door-focused behavior occurs at significantly higher durations around an hour before the first shift of the day occurs and then drops off to almost non-existent after shift. On the other hand, the bears spend little proportion of their time eating and foraging before shift (foraging is still possible because of potential leftover bits of food from the night before) which then significantly increases after the shift as the bears get their main meals. Any instances of our AB during times outside of our focal event were results of other food-related rewards in the form of random afternoon treat tosses. These findings are consistent with the definition of anticipatory behavior (i.e., cued by an event associated with reward and cessation of behavior once reward is attained) and thus allow us to continue with our study with door-waiting validated as anticipatory behavior for these bears.

#### ***4.3 - Seasonality***

As predicted, both bears increased total time spent performing AB as well as average bout length from summer into fall during both research phases; however, we did not expect the bears to sustain the level of total door-focusing and continue increasing in door-focus bout length into winter. As described in the introduction, grizzly bears are motivated to perform temporally-cued behaviors that allow individuals to adapt to seasonal changes in food availability and prepare for the physiological demands of torpor/hibernation. As these behaviors are highly conserved, the motivation and sensitivity to increase foraging and eating in specific seasons persists *ex-situ*, as shown by our bears through increased anticipatory behavior for foraging and feeding opportunities in fall months. However, the natural scarcity in food in the winter is not a constraint in the zoo and animals continue to eat on regular schedules, which may be why the bears continued to entrain on and anticipate feeding opportunities in the winter. Furthermore,

while some zoological institutions encourage or even force hibernation, others (such as SF Zoo) allow their bears to continue on with normal activity, although there still exists a marked reduction in activity during the winter months. Perhaps this is another reason why we see the sustained increases in door-waiting behavior through winter – individuals are receiving mixed signals from the increased physiological demand triggered in the fall but the occurrence of torpor when those demands are “shut off” never happens. In addition, it should be considered that our bears reside in California, where fluctuations in temperature and climate are not nearly as dramatic as seen in the wild (habitat ranges limited to some areas of Montana and Yellowstone national park, western regions of Canada, and up into Alaska) when full hibernation may be necessary. Future directions to explore the interaction of food anticipatory behavior and hibernation/torpor management across institutions may illuminate more findings.

#### ***4.4 - Overall Experimental Effect***

As the first step in examining potential experimental effects, we assessed whether having *any* sort of extra treatment allowing for increased opportunities to forage and feed apart from regular feeding and treat tosses (i.e., little batches of food offered between main meals) would affect levels of our three measure of AB (Figures 6-8). To our surprise, we did not see any overall treatment effect in any of our three measures, with the exception of an increase in total door-focused behavior in winter going from baseline year to experimental year for both bears (Figure 6). This may have been an unintended consequence of a change in management style that season; the grizzly bear managers had decided to try out a new tactic in handling by allowing more animal agency during this ecologically-sensitive time period. In doing so, they permitted all-day access to both enclosures once the shift door was opened (and not closed back up afterwards) for

the first time in the morning after cleaning was complete and food was set up in the adjacent enclosure (The Gulch, Figure 2). Thus, instead of being isolated in the enclosure fully visible to the public during zoo open hours, the pair were given the choice to den-up during the day (in the bear dens of The Grotto, Figure 2). An increase of AB during the experimental year – when this management decision was not applied – may have serendipitously lent a hand to our predictions that this change in management may have tipped the scale of experiences to be more positively balanced (through providing more agency) leading to less door-focused AB. This is, however, purely speculative and would need further testing to assess this idea.

#### ***4.5 - Specific Treatment Effect***

Our attempt in looking at specific treatment effects on AB once again revealed a quick look into the impact of evolutionarily engrained behavioral drives. It seems as if the treatment effects on anticipatory behavior were highly tied to any seasonal effect on AB (reflected in change of AB between summer into fall and winter), as demonstrated by longitudinal design of our study (scheduled and applied continuously over the year as listed in Table 5) seen in Figure 9. This finding highlights the importance of considering feeding and behavior management in grizzly bear welfare assessments, seeing as the evolutionary drive to perform hyperphagia-related behaviors (demonstrated by increase in our food AB – door-focused behavior) continues to be relevant *ex-situ*. This also reiterates the important point that behavioral observations are not equivalent across time and researchers must keep this circumstance in mind when considering methodological procedures in their experimental design.

As mentioned in Section 4.3, both bears fluctuate similarly in respects to seasonal timing (i.e., changes seen between summer, fall, and winter) with total door-focused behavior and average

door-focused bout length. When we break down AB data further into treatments across seasons, we continue to see similar responses in total door-focused behavior in both bears, with significant treatment effects of PM Only, No Feeder 3, and No Feeder 5 (additionally PM Only 3 for Kiona) increasing total door-focused behavior per session. The first two of these treatments occur right before (November) or during the time of major transition (December) to a state of torpor whilst the last two occur around when the bears would be naturally coming out of torpor (June) (Haroldson et al., 2002). These time periods happen to mark the yearly processes during which sensitivity to food are significantly heightened: pre-torpor and post-torpor. As a result, the *timing* of access to food-related reward opportunities and the potential *removal* of access may play a role in AB performance. We predicted that treatments that allotted reward through the scatter feeder in the PM only would most likely decrease performance in our AB (compared to baseline) but not as much as it would for AM treatments given right before the focal event, as the effect of the reward is still salient whereas reward given hours beforehand may have lost effect by the shift time the next morning. However, because PM Only happened to fall during the height of pre-torpor transition, perhaps introducing a reward the previous night and an *absence* of reward in the morning of the focal event may have functioned as a *removal* or *decrease* in environmental enrichment quality as perceived by the bear in its increased sensitivity to reward. Various studies have found that removal of enrichment after having been exposed to said enrichment has resulted in pessimistic decision-making in cognitive bias tasks, this could potentially explain the surprising increase in AB, opposite of our initial predictions (Bateson & Matheson, 2007; Burman et al., 2008a; Burman et al., 2008b; Neave, Webster & Zobel, 2021). Akin to these thoughts, although we did not make any predictions for No Feeder periods as these functioned as breaks to control bleed-over effects of our different treatments, we can speculate

that removal of reward opportunities during these 2-week intervals acted similarly as the PM Only treatments.

When looking at average door-focused bout length across the year, we found that patterns were less similar between the two bears than those seen with total door-focused behavior, with Kachina focusing for longer bouts across most winter and spring months and Kiona focusing for longer bouts only at the beginning of winter and spring. There can be a multitude of reasons as to the marked difference in average bout length of AB seen between the individuals starting around September to the following February/March. One important note to keep in mind is, although the instinctual drive to acquire food is high starting in the fall (as shown in the increase of door-focused behavior in both individuals), there is general decrease in activity starting late fall, through winter and into the following summer experienced by bears as they head into torpor (as shown through an increase in door-focused bout length for both bears). In other words, sensitivity to food reward remains high throughout temporally significant seasons, however, anticipation may be shifted away from more active forms to more passive, i.e., sitting and waiting at the door. In saying so, we may speculate that this shift may be seen on a larger scale in Kachina because her anticipatory style is more active in general as a baseline while Kiona already works in a wait and see pattern.

Although we do see a few significant treatment effects on our AB measures, we remain wary of these findings as these were shown in mainly those treatments given in the winter months, when the bears were most sensitive to seasonal effects. With unfortunately only one year of experimental data collected, it is unsure that our model was able to reliably discriminate between



treatment and seasonal effect and further data collection is needed to determine treatment effect. It is important to note, however, that based on Figure 9B, our measure of total door-focused behavior may be the most insightful measure – at least for our resident two bears – of the two measures in that it is the one behavior performed similarly between the individuals across the year and according to treatment, which can help us eliminate effects of individual behavioral types in future analysis. This highlights the importance of preliminary observations and analysis of behavior and anticipatory styles before designing studies in order to ensure aptness of measurements and robustness of findings.

Moreover – and possibly most importantly – sensitivity of AB to season and treatment emphasizes the fact that managers should always proceed with caution when implementing enrichment programs. It may be that it is much easier to “bump” an animal from more negative experience to more positive experience, or vice versa, in times when that animal’s reward sensitivity is most pliable. In our case, as described before, the unique seasonality of behavior in grizzly bears creates major peaks in motivation to forage and feed in response to food availability and physiological mechanisms (i.e., in fall). In saying so, researchers must explore more into the potential of influences of individual, group, and species characteristics such as animal personalities, social dynamics, and ecological pressures on behavior when assessing welfare. If there are indeed such interactions, further work needs to be done in order to tease these conditions apart so that managers can reliably predict enrichment treatment effects accurately when applying them in the real world.

## 5 – Conclusions

We were able to complete all objectives of examining door-focused behavior as our AB in two different grizzly bear individuals A) across the day, B) over the seasons and C) in response to specific scatter feeder treatment. Findings from our study followed our initial predictions while some surprised us. We were able to confirm our chosen behavior of door-focused behavior follows the definition of AB (i.e., increase in duration preceding a predictable scheduled food-related event and drop off after allowed access to food through the event) and that our two bears presented door-focused behavior in statistically different ways (i.e., active versus sit-and-wait). Furthermore, both bears, despite individual styles, did indeed increase total door-focused behavior as well as how long they held these waiting bouts in fall and winter months for both phases of the experiment (i.e., baseline year and experimental year). To our surprise, however, we did not find a general experimental effect during the experimental phase of our study when comparing AB levels back to baseline levels, except for the winter season which may have been an unattended consequence of management changes during the baseline winter. Additionally, specific treatment effects (i.e., number of reward opportunities timing of allotment), ended up being harder to tease apart from potentially interconnected seasonal drives - findings did not show the predicted levels of AB based on treatment type and, in fact, showed the opposite effect with our PM Only treatment.

Overall, however, our study demonstrates to us that our resident grizzly bears have the ability to readily direct us towards what is important to them in their daily lives; in other words, they show us what they want through their anticipatory door-focused behavior. The quality of door-focused behavior fluctuates most clearly over the seasons when feeding and building up physiological

energy reserves become biologically imperative. This finding emphasizes the significance of behavioral monitoring in welfare assessments, particularly in species who naturally experience large biologically relevant transitional events, such as hibernation or migration, which may result in temporally significant changes in motivation to perform certain behaviors. Using anticipatory behavior as an indicator of motivation and reward sensitivity, animal caretakers can piece together the bigger picture of affective states in their animals in the process of gauging welfare and tailoring species-specific management protocols to the individuals in their care.

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