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RESEARCH ARTICLE

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Activity budget and spatial distribution of Bennett's wallabies (*Macropus rufogriseus*) in open versus closed exhibit designs

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Abstract

Although many studies investigating the impacts of zoo exhibit designs on captive animals exist, none have been performed on how they influence the behavior and welfare of captive Bennett's wallabies (*Macropus rufogriseus*). Here, we assess the impact of exhibit design on the activity budget and spatial distribution of Bennett's wallabies. We compared animal behavior in two open exhibits (i.e. physical interaction between animals and visitors permitted) to two closed exhibits (i.e. physical interaction between animals and visitors prohibited). Behavioral data were collected using focal sampling, and spatial distribution was recorded on exhibit maps at regular time intervals. We found a significant increase in feeding and interactive behaviors in closed exhibits in comparison to open exhibits. However, other behaviors such as resting, locomotion, and vigilance did not vary with design. Functional use of space was similar between both designs; however, the effect of habituation may be relevant to consider in future studies. Although some support for visitor effects were present, our study provided no evidence for strong impacts of exhibit design on Bennett's wallaby welfare. Our study emphasizes the need for additional research into the impacts of how zoo environments affect Bennett's wallaby behavior and welfare.

KEYWORDS
animal behavior, exhibit design, visitor effects

1 | INTRODUCTION

Studying animal welfare in captivity requires the use of welfare indicators that can be measured and experimentally tested (Broom, 1991; Dawkins, 1990). Common indicators include hormone levels, the presence of disease or injury, lifespan, reproductive success, and behavior (Broom, 1991). Assessments of behavior are noninvasive and can be useful to provide information on both physical and mental health of animals (Dawkins, 2004). For instance, patterns of behavior in captivity can be compared to the patterns observed for wild conspecifics (Broom, 1991). In the wild, wallabies have been found to increase their resting, while decreasing other behaviors such as foraging, vigilance, locomotion, and grooming as daylight increases (Stirrat, 2004). In captivity, observed trends that do not follow this tendency could be explained by welfare impacts caused by captivity, such as visitor presence or exhibit design (Broom, 1991). Therefore, behavioral observations used to generate activity budgets and spatial distribution can be valuable indices of zoo animal welfare.

The effect of visitor presence on captive animals has stirred much interest in zoo research (Davey, 2007). Unlike other captive settings (e.g. farms and laboratories), zoos welcome large crowds of visitors on a daily basis. Davey (2007) demonstrated that for many primate species, crowd density, activity level, noise level, and proximity are examples of visitor characteristics that affect zoo animal behavior. Sellinger and Ha (2005) demonstrated that an increase in visitor density and intensity can lead the *Panthera onca* species to increase pacing behavior, aggressive events, and time spent hiding. Indeed, 15 different species of primates were observed to be more active and aggressive but less affiliative in the presence of visitors, suggesting that visitor presence was associated with stressful excitement among animals (Chamove, Hosey, & Schaetzel, 1988). Others have argued that visitor presence may instead represent a beneficial source of

enrichment for zoo animals (Claxton, 2011). Some animals will expend large amounts of energy into increasing the probability of visitor interaction, which suggests that human–animal relationships are stimulating to some individuals or species (Nimon & Dalziel, 1992). Elsewhere, primates often voluntarily initiated interactions with visitors, especially when food was involved (Choo, Todd, & Daiqin, 2011; Cook & Hosey, 1995; Hosey, 2000). Nevertheless, conclusions about negative and positive visitor effects on zoo animals are still ambivalent since most of these studies were made using a limited range of study species (Davey, 2007).

In zoos, exhibit design can differ in the degree to which animal–visitor interaction can occur. In "closed exhibits", an impassable barrier keeps both parties physically apart and only auditory, visual, and olfactive interactions can occur. In contrast, there is a possibility of physical contact in "open exhibits", sometimes referred to as free-range exhibits (e.g. Sherwen, Hemsworth, Butler, Fanson, & Magrath, 2015). Most of the time, visitors are constrained to stay on a predefined path, allowing the animals the decision of choosing to approach the paths or not. The physical touch possible in open designs has been found to alter mammal behavior in past studies (Anderson, Benne, Bloomsmith, & Maple, 2002; Farrand, Hosey, & Buchanan-Smith, 2014). However, many past observations were performed in petting zoos, which are settings with goals even further inclined to encourage human–animal interaction. In some cases, *Capra hircus* and *Ovis aries* species exhibited undesirable behaviors that increased with visitor density in these designs (Anderson et al., 2002). In other species such as *Lama glama* and *Sus scrofa*, an increase in visitor density increased nonaggressive interaction with the public (Farrand et al., 2014). Therefore, whether the human–animal interaction possible in open exhibits is aversive or enriching is still being discussed (Anderson et al., 2002; Farrand et al., 2014; Sherwen et al., 2015).

Multienclosure studies are very useful for validating repeatability of results across similar captive contexts as well as for understanding the impacts of different environmental conditions on captive animals (Shepherdson, Carlstead, & Wielebnowski, 2004; Sherwen, Magrath, Butler, Philips, & Hemsworth, 2014). However, few studies have compared open and closed exhibit designs and none exists for Bennett's wallabies (*Macropus rufogriseus*). The aim of this study was to compare the behavior of Bennett's wallabies in open and closed exhibits using observed activity budgets and spatial distributions. In addition, we studied visitor effects to increase knowledge of the behavior of this species in captivity. Such research is important to contribute to future development decisions and improvement of zoo exhibits.

2 | MATERIALS AND METHODS

2.1 | Subjects and study areas

Bennett's wallaby was the chosen focal species for our study because it is housed in a variety of different exhibit concepts in captivity. All individuals included in the study were zoo-born. We studied wallabies in two open and two closed exhibits. Only one observer collected the data presented in this study.

Our open exhibits were at the Zoo de Granby, Granby, Canada (Figure S1) and the Roger Williams Park Zoo, Providence, RI (Figure S2). At the Zoo de Granby, wallabies were housed in a 5,425 m^2 open exhibit, designed with a 200 m visitor path delimited by roped barriers traversing the habitat. The wallabies could therefore interact with visitors by easily crossing these ropes and paths. The exhibit was specifically designed for the wallabies and was first opened in May 2014. A total of 14 adults and 3 joeys were housed in this habitat in 2015. In 2016, there were 15 adults and 2 joeys. At the Roger Williams Park Zoo, animals were housed in a 2,044 m^2 open exhibit with a roped visitor path traversing through the exhibit. A total of five adults were kept in this enclosure since the spring of 2014.

Our closed exhibits were at Riverview Park and Zoo, Peterborough, Canada (Figure S3) and again at the Roger Williams Park Zoo (Figure S4). At Riverview Park and Zoo, the exhibit has a chain-link fence delimiting the visitor paths. This 727 m^2 exhibit's last enlargement renovation occurred in 1998. During our 2015 field season, the zoo possessed a group of six adults and two joeys. At Roger Williams Park Zoo, the closed habitat was 280 m^2. There, visitors were separated from the wallabies by a wood fence and a raised platform. This population of six adults and one joey had been in this exhibit since the summer of 2014.

Feeding regimes were similar for all four exhibits. Unlimited quantities of food and water were provided daily in the same areas in the exhibits. However, extra enrichment foods such as fruits and vegetables would sometimes slightly vary in their quantities and timings on a day-to-day basis due to varying employee workloads and tasks.

2.2 | Behavioral observations

We collected activity budget data using the focal-animal sampling technique (Martin & Bateson, 2007), whereby single individuals were observed for a period of 10 min and their behavior, based on an established ethogram (Table 1), was recorded on every 15-s mark. The order in which we observed the animals varied according to a predetermined schedule, enabling all individuals to be studied at different times of day over the total data collection period. We also recorded additional information such as the date, time, individual ID, visitor density estimation, and weather conditions. We estimated visitor density after every focal sample by counting the number of visitors within eyesight of the observed wallaby.

We recorded data for the animal spatial distribution within enclosures using the scan-sampling technique (Martin & Bateson, 2007). We recorded the position of all visible individuals on exhibit maps every second 10-min focal sample (once every 20 min). These maps were divided into different areas, representing specific functional uses and terrain types. The number of functional areas varied between 7 and 11 among the four exhibits in the study. The relative size of these areas was calculated using Google Earth and grid patterns. The areas included the pathways and, at the Zoo de

TABLE 1 Ethogram of Bennett's wallaby behaviors recorded during focal sampling periods, inspired by Russel (1968) and Stirrat (2000)

Behavior	Description
Resting	Absence of movement or activity. Individuals are sitting or lying down. Facial expression and general attitude show lack of vigilance, alertness or curiosity.
Vigilance	Individual is in an alert state to increase awareness of immediate surroundings. Head positions are always upright and can be either motionless (when observing a specific disturbance) or in rapid movement (when observing surroundings). Vigilance, alertness, curiosity or fear can usually be easily discerned on facial expressions.
Locomotion	Traveling from point A to point B by rapidly hopping with two hind limbs or slowly walking using four limbs and tail for increased stability.
Feeding/Foraging	Actively searching for or consuming food (includes chewing).
Grooming	The use of mouthparts, forelimbs or hind limbs for licking or scratching any body part for comfort or hygiene purposes.
Social interaction	Engaging in social behavior with a conspecific, another exhibit occupant or a visitor. Body positions include skipping, grabbing, sparring, hitting or kicking. Includes allogrooming, smelling or touching others.

Granby and Roger Williams Park, retreat zones that were only reachable by the wallabies. Retreat zones were defined as specific areas in the exhibits that provided wallabies with visual relief and increased distance from visitors.

We collected data during the high visitor season at all three zoos from June to August 2015 and during both the off-season (no visitor) and high visitor seasons at Zoo de Granby between May and July 2016. Observations began between 9:00 and 10:00 and usually ended between 15:00 and 16:00. We only observed adult individuals. They were identified using color tags and/or physical distinctions. Data collection was done in accordance with the Animal Care and Ethics Certificate provided by Concordia University (AREC 30003983) and with the research *Guidelines of the Zoo de Granby Committee on Conservation and Research Operations*.

2.3 | Statistical analysis

Our first analysis sought to assess how the frequency of behavior occurrence (a count variable) varied with exhibit design (open or closed). A follow-up analysis was additionally performed to assess the variation of the frequency of behavior occurrence with visitor presence (high or none), and field season (2015 and 2016) at Zoo de Granby. We analyzed these activity budget data using generalized linear mixed models (GLMM) with a negative binomial family distribution and the log link function. We used the logarithm of the total number of observations recorded within each 10-min period as an offset in the models to control for the variation in the total possible number of observations within each focal trial. The different individuals observed (Individual ID) in this study were set as a random factor in all models to appropriately control for the repeated measurements within single individuals.

We also used GLMM models to determine how all the individual behaviors varied with temperature, visitor density, time of day, and individual sex and age. We analyzed each behavior separately. We used the counts of the different behaviors as response variables. Since many predictors were included in the models, we selected the most parsimonious (lowest Akaike information criterion [AIC]) using AIC-based backward selection (Burnham & Anderson, 2002).

We used generalized linear models (GLM) to assess wallaby space use. We set models with quasibinomial distributions and with the proportion of individuals observed per area as the response variable. Our models assessed the variation in proportions of individuals observed per area with a time of day for all populations, and with visitor presence and field season for Zoo de Granby's population. Time of day was set as a two-level factor of either morning or afternoon period. To account for the difference in area sizes of the exhibits, it was included as an offset in our models.

After all models were generated (both GLMMs and GLMs), we performed pairwise comparisons of the involved categorical variables and their interaction using the Tukey–Kramer correction. We performed all tests in R 3.3.1 (R Core Team, 2016) at the 5% level of significance.

3 | RESULTS

3.1 | Activity budget

We found dependency between the observed behavior occurrences and the exhibit design when comparing activity budgets of open versus closed exhibit populations ($\chi^2 = 58.70$, $df = 5$, $p < 0.001$). More specifically, individuals in closed exhibit designs spent more time engaging in feeding behavior (proportion of occurrence ± standard error = 0.40 ± 0.12, $p = 0.04$) and social interaction behaviors (1.61 ± 0.23, $p < 0.001$; Figure 1). However, no significant differences between exhibit designs were found for other behaviors of interest such as vigilance, locomotion, and resting.

The pattern of activity at Zoo de Granby did not vary with visitor presence (Figure 2) but did vary with year of study (i.e. 2015 vs. 2016; $\chi^2 = 24.08$, $df = 5$, $p < 0.001$; Figure 3). This was mainly due to feeding behavior occurrence being reduced in 2016 as compared to 2015 (−0.59 ± 0.15, $p = 0.007$)

The frequencies of all but one of the behaviors were significantly related to at least one of the other explanatory variables (Table 2). Vigilance behavior decreased with the time of day (−0.38 ± 0.11). Resting behavior was affected by the sex of individuals (higher for male individuals) and increased with age (0.03 ± 0.01), time of day

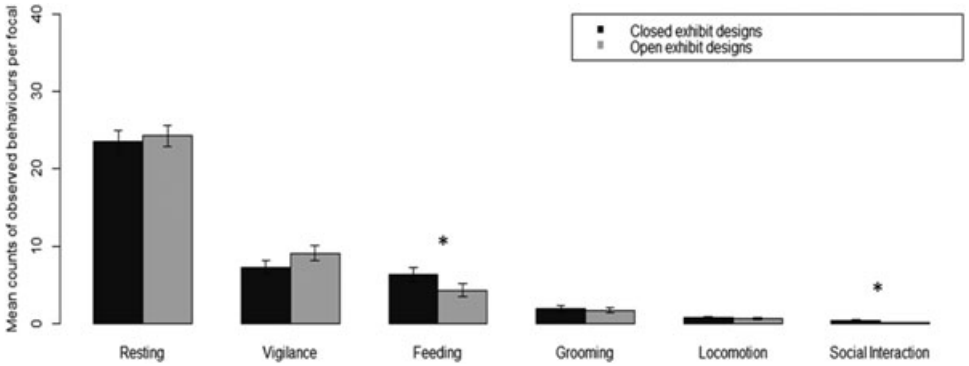

FIGURE 1 Mean activity budgets of individual Bennet's wallabies (*Macropus rufogriseus*) located in open versus closed exhibits. We collected data from four exhibits (two of each type) at three North American zoos. All focal samples (N = 890) were out of 40 total observation counts. Error bars were extended to ±2 standard errors from the mean values. The asterisk indicates significant differences

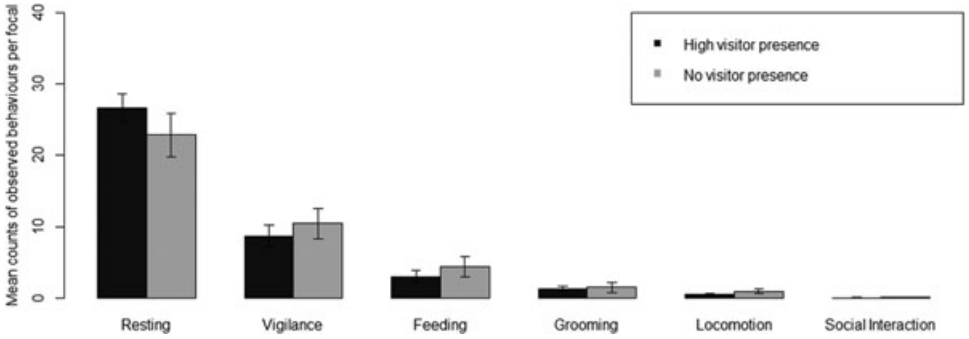

FIGURE 2 Mean activity budgets of the Bennet's wallabies (*Macropus rufogriseus*) Zoo de Granby population in the absence of visitors (May 2016) and in the presence of high visitor densities (July–August 2016). All focal samples (N = 342) were out of 40 total observation counts. Error bars were extended to ±2 standard errors from the mean values

(0.28 ± 0.02), temperature (0.03 ± 0.002) and visitor density (0.05 ± 0.002). Locomotion decreased with time of day (−0.47 ± 0.16) and increased with visitor density (0.005 ± 0.02). Feeding behavior decreased with time of day (−0.62 ± 0.17) and temperature (−0.09 ± 0.03). Grooming behavior also decreased with time of day (−0.34 ± 0.12), age (−0.08 ± 0.04) and temperature (−0.04 ± 0.02). Social interaction behaviors were not affected by any of the previously mentioned additional variables.

3.2 | Spatial distribution

During the high visitor season of 2015, the wallabies housed at the Zoo de Granby did not use the different exhibit areas to the same extent and instead, favored the retreat zone of their enclosure (Figure S1: Area A; χ^2 = 3301.8, df = 10, p < 0.001). Time of day did not significantly alter the use of the different exhibit areas. There was a significant difference in the spatial distributions observed

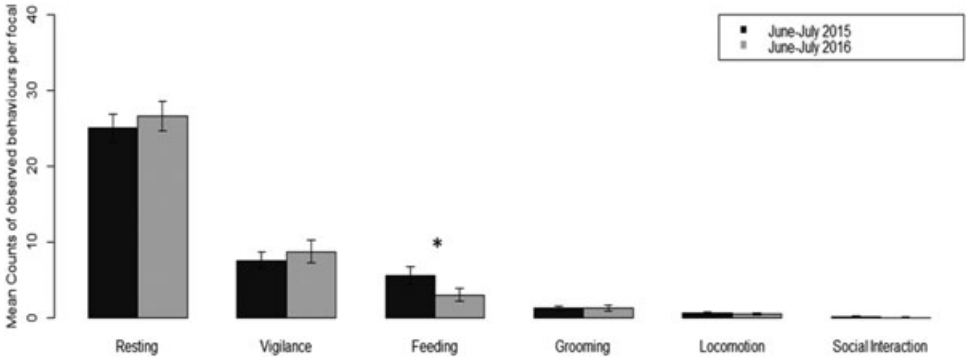

FIGURE 3 Mean activity budgets of Zoo de Granby's Bennet's wallabies (*Macropus rufogriseus*) population during high visitor zoo seasons in 2015 versus 2016. All focal samples (N = 521) were out of 40 total observation counts. Error bars were extended to ±2 standard errors from the mean values. The asterisk indicates significant differences

TABLE 2 Bennett's wallaby behavior response as a function of different explanatory variables as determined using the most parsimonious (lowest AIC) generalized linear mixed models with AIC-based backward selection (Burnham & Anderson, 2002)

	Vigilance		Resting		Feeding		Grooming		Locomotion		Social interaction	
	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*
Time of the day (a.m./p.m.)	13.33	<0.001	326.11	<0.001	12.80	<0.001	7.44	0.006	8.29	0.004	2.58	0.108
Sex (male/female)	3.47	0.062	8.07	0.0045								
Visitor density	2.86	0.091	66.50	<0.001	1.00	0.317	3.31	0.069	4.33	0.038	0.23	0.633
Temperature	0.80	0.370	155.56	<0.001	12.29	<0.001	5.14	0.023	3.62	0.057	3.57	0.059
Age	2.58	0.108	5.73	0.017			4.92	0.027				

Note. AIC: Akaike information criterion.

during the high visitor seasons of 2015 as compared to 2016 (χ^2 = 384.5, *df* = 10, $p < 0.001$). In 2016, animals spent less time in the retreat zone (Figure S1: Area A) and more time in areas allowing closer visitor spatial and visual proximity (Figure S1: Areas E and F) then they had in 2015. Also, in 2016, the Zoo de Granby population spent significantly less time in the retreat zone during visitor absence than they did during high visitor presence. (χ^2 = 160.12, *df* = 10, $p < 0.001$).

Animals selectively used different enclosure areas at Riverview park and zoo (χ^2 = 471.22, *df* = 6, $p < 0.001$). One of the areas farthest from visitors (Figure S3: Area C) was the most used and its use increased in frequency with time of day (0.74 ± 0.19, $p = 0.007$). The wallabies housed in the closed exhibit at Roger Williams Park Zoo similarly favored specific areas (χ^2 = 348.3, *df* = 7, $p < 0.001$). For these animals, most of their time was spent in the elevated portion of their habitat that provides shade and visual barrier (Figure S4: Area A). Wallabies at the Roger Williams Park Zoo's open exhibit also selectively used areas of their habitat (χ^2 = 998.43, *df* = 9, $p < 0.001$). Again, individuals there spent the largest amounts of time in retreat zones (Figure S2: Areas A and C).

4 | DISCUSSION

Activity budgets observed in closed versus open exhibit populations significantly differed for two behaviors. Animals exhibited feeding and social interaction behaviors more frequently in closed exhibit designs. However, resting, vigilance, locomotion and grooming behavior proportions remained similar in both designs.

Social interaction accounted for 0.82% of the activity budget for closed exhibit populations and 0.16% for individuals housed in open exhibits. One explanation could be that open exhibits were larger in surface area, reducing the opportunity for interaction between individuals when compared to the smaller closed exhibits. However, although the difference between the enclosure types was statistically significant, both proportions account for less than 1%, a very low portion of the wallabies' daily activity pattern. This supports the activity budget tendencies of wild macropod species (Stirrat, 2004). In nature, groups of Bennett's wallabies are relatively unstable and small in size (Johnson, 1985). In fact, they are one of the least social marsupial species, with a tendency to remain solitary (Johnson, 1985). When they do engage in social events, it is usually associated with courtship, play fight, aggression or passive tactile communication behaviors (Johnson, 1985; Russell, 1984). In the present study, the few observed fights were playful in nature (i.e. they did not involve access to a limited resource). Other observed interactive events were most often in the form of passive touch. Although social behavior differed significantly between open and closed exhibits, overall social behavior occurred infrequently in both exhibit types. This is representative of normal behavior, as social interaction events are relatively uncommon among wild wallabies (Stirrat, 2004).

Although relatively independent, Bennett's wallabies often aggregate into small groups, a tendency interpreted as part of their antipredator strategy (Coulson, 1999). Indeed, wallabies have evolved to adapt their behavior according to levels of perceived threat risk in their environment (Blumstein, Evans, & Daniel, 1999; Coulson, 1999). Another example of their behavioral adaption is through their feeding times (Blumstein et al., 1999; Coulson, 1999). In our study, feeding behavior occurrence was significantly higher in closed exhibits. The lack of obvious physical barriers delimiting the animals from the visitors in the open exhibits may have augmented the potential visitor threat risk perceived by the wallabies, causing more frequent interruptions in feeding bouts during visiting hours. Indeed, wild animals have to evaluate the costs and benefits of time spent feeding versus time spent monitoring their environment for potential threats (Barnier et al., 2016; While & McArthur, 2005). However, vigilance did not vary significantly with exhibit design in this study. It is therefore unclear if the difference in feeding behavior was the result of perceived threat risk due to lack of physical barriers separating the animals from the public or some other influence. Husbandry practices related to enrichment food timings may have influenced feeding behavior more than an elevated risk perception. Nevertheless, the feeding behavior proportions and patterns observed in all four populations still remained within the ranges of what is typically observed during daylight in the wild (Stirrat, 2004).

Although the remaining behaviors did not significantly vary with exhibit design, our results demonstrated an increase in resting behavior with visitor density. This is contrary to the decrease in captive kangaroo resting behavior with increasing visitor numbers observed by Sherwen et al. (2015). Whether the decrease in resting state was caused by fear or by the curiosity of humans was not conclusive in their study (Sherwen et al., 2015). Our interpretation of

the increase in resting with visitor number is also ambivalent. Locomotion, a behavior interpreted as contrary to resting, also increased with visitor density. This may potentially be indicative of stress in high-density situations (Morgan & Tromborg, 2007) as animals may have been seeking out new locations away from people, followed by increased resting behavior after having reached their new chosen location for that time of day. However, resting behavior proportions observed in this study were very similar to the trends observed in the wild, an environment with no visitors and captivity-related stressors (Stirrat, 2004). Evidence has shown that this increase in inactivity in the wild is linked to heat avoidance and thermoregulation strategies because of warmer daytime temperatures (Stirrat, 2004). Our results showed an increase in resting behavior as a function of time of day and ambient temperatures which coincides with wild wallaby behavior. Therefore, environmental factors likely played a role in wallaby resting behavior either in conjunction with or despite increased visitor density.

Previous studies show that marsupial vigilance varies due to visitor effects such as visitor number, noise, and proximity (Larsen, Sherwen, & Rault, 2014; Sherwen et al., 2015). These visitor effects could be perceived as amplified in open designs. However, vigilance proportions did not vary with exhibit design in our study. In the wild, marsupials are preyed upon by various predators and therefore use vigilance to survey their environment for potential threats (Pentland, 2014; Stirrat, 2000; Stirrat, 2004). In our study, no visitor-related variables such as visitor presence versus absence or visitor number influenced vigilance proportions. Therefore, the idea that visitors cause a significant disturbance to the wallabies' environment, much like predators do in the wild, was not supported for the vigilance behaviors we observed. In summary, we believe the vigilance levels observed in this study more appropriately reflect the idea that vigilance was used to gather social and environmental information on their surroundings (Favreau, Pays, Goulard, Best, & Goldizen, 2015), irrespective of exhibit design or visitor presence and density.

All four populations significantly favored specific areas in their habitats. However, the functional uses of the favored areas did not differ with exhibit design. In all four populations in 2015, the areas located farthest from visitors, often providing partial visual barrier and shade were the most frequently selected areas. Retreat areas are often found in zoo exhibits to provide relief from interaction with the public (Anderson et al., 2002). Offering zoo animals the opportunity to control their exposure to visitors using retreats has been suggested as being beneficial for animal welfare (Morgan & Tromborg, 2007). The retreat options available for the four populations of this study were therefore most likely used with the purpose of either visitor relief, acting as a buffer for undesirable behaviors that might have otherwise occurred (Anderson et al., 2002), or as a heat-relief mechanism by using the shade they provided. Our results therefore suggest that regardless of enclosure design type, providing retreat areas are important to maintain adequate welfare standards for Bennett's wallaby species.

Sherwen et al. (2015) calculated the mean kangaroo distance from visitor paths as a function of visitor density. They demonstrated that kangaroos did not show an increase in visitor avoidance by modifying their mean distances from visitor paths as visitor numbers increased (Sherwen et al., 2015). It was therefore concluded that the visitor effects present in open exhibit designs did not present significant adverse effects for the welfare of their occupants. In our study, the areas closest to and most visible from visitor paths were the least used by all four populations, regardless of design type. One possibility is that the areas closest to the visitor paths lacked desirable attributes such as shade or food. Moreover, although Sherwen et al's population did not demonstrate negative visitor effects, the individuals spent most of their time in areas 5–15 m away from visitor paths. Therefore, another alternative for our population is that the animals could have chosen to remain within preferred buffer distances while generally avoiding visitors. This may suggest that visitor interaction is not particularly enriching to Bennett's wallabies and possibly, that open exhibit should not be designed with visitors as a source of enrichment in mind.

Our results also showed that Zoo de Granby wallabies' space use varied between years. In 2016, there was an important increase in the use of the centralized area where visitors can view animals with ease. Also, they spent less time in their retreat zone when compared to the previous year. This may be explained by a lengthy exhibit habituation process where the wallabies slowly discovered their enclosure and developed different favored areas through time. Past research studying captive gorilla adaptation to new exhibits revealed a slow onset of exploratory behavior after exhibit transfer, which was interpreted as a possible reaction to the unfamiliarity of their new environment (Ogden, Finlay, & Maple, 1990). Even after 1 year of observation in the new enclosure, some individuals still had not explored 40% of the available exhibit space (Ogden et al., 1990), which is very similar to the results at Zoo de Granby. It is important to point out that at Zoo de Granby, the least used areas represent approximately half of the exhibit. As seen by Ogden et al. (1990), this may be due to the exhibit's novelty. Zoo de Granby's current wallaby exhibit was first opened in 2014. It is therefore possible that the year 2015 was still too soon after the wallabies' entry into their new exhibit to observe conclusive space use trends. However, the retreat zone still remained the most used in 2016, 2 years after its opening. Therefore, despite showing an increase in the use of the central area of the exhibit in 2016, the areas with the most and the least interest remained unchanged. Further observations would need to be performed over a longer period to see if Zoo de Granby's exhibit is used to its full potential.

There was also a difference in space use with varying visitor conditions (presence or absence) within the same season at Zoo de Granby. Wallabies spent significantly less time in the retreat zone during visitor absence than they did during high visitor presence. Captive animals have been known to increase their time spent hiding with increased visitor density and intensity (Sellinger & Ha,

2005). In our study, the high visitor presence later the same year could have further motivated wallabies to spend increased amounts of time in a retreat area (Sellinger & Ha, 2005).

5 | CONCLUSION

Bennett's wallaby activity budgets differed between closed versus open exhibit populations for two behaviors. Although social and feeding behaviors did vary across exhibit design, resting, locomotion, and vigilance did not vary with design. Moreover, space use trends were very similar when comparing both enclosure designs. Our results did not provide evidence for major differences in the impacts of open versus closed exhibits on Bennett's wallaby welfare. However, our results did provide support for a visitor effect on Bennett's wallaby activity budgets and spatial distributions; a topic we consider worthwhile investigating in future studies.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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