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Zoo foraging ecology: development and assessment of a welfare tool for captive animals

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Abstract

*Foraging ecology and food patch studies are commonly used to elucidate the environmental perceptions of wild, free-ranging animals. Their application to captive animals, however, especially those in zoos, is still in its infancy. To illustrate some specific applications of zoo foraging ecology, we provide a study that evaluated: (i) whether patch use and giving-up densities (GUDs) can reveal areas of preference within an exhibit for zoo species; (ii) if food patches provide an effective form of behavioural enrichment; and (iii) if visitor interest and behaviour is affected by food patch presence. A combination of behavioural observations, and experimental food patches and giving-up densities were used to address these objectives in Parma wallabies (*Macropus parma*) and Patagonian cavies (*Dolichotis patagonum*) at Lincoln Park Zoo, Chicago, Illinois USA. GUDs revealed distinct areas of preference and aversion within the exhibit for cavies, but not so for the wallabies. For both species, presence of food patches increased foraging behaviours, decreased inactive behaviours, and increased within-exhibit movement, demonstrating that food patches serve as an effective behavioural enrichment technique. The use of food patches also revealed striking differences between individuals, particularly for the pair of cavies. There were encouraging trends toward increased visitor number and stay-time when food patches were present in each exhibit, but the effect was not statistically significant. These results suggest that utilising patch use, GUDs, and foraging theory in zoo populations may enhance animal welfare, and can inform improvements to exhibit design directly from the animal's perspective. We conclude with a broader discussion of zoo foraging ecology as an emerging field, with suggestions for future avenues of research.*

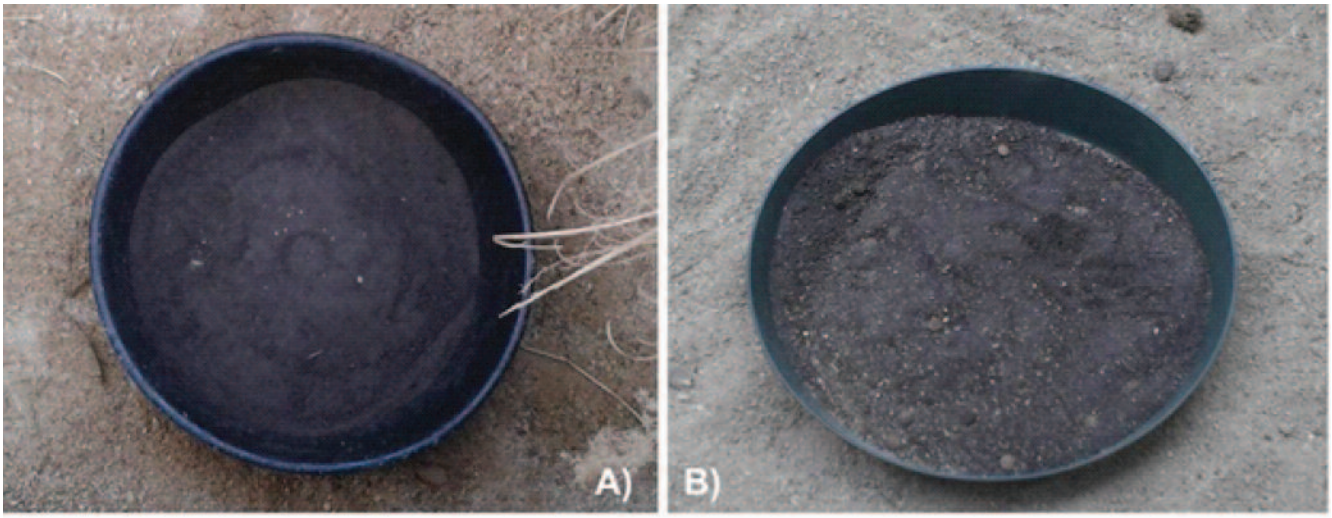
Keywords: *animal welfare, environmental enrichment, exhibit preferences, giving-up densities, Parma wallaby, Patagonian cavy*

Introduction

Zoological parks aim to improve the care and welfare of their animals. An animal's welfare is the integration of several inputs, including the individual's physiological, psychological and physical conditions. Numerous methods have been developed to assess animal welfare, most of which focus on either the physiology, behaviour, or general health of the focal animal(s) (Hill & Broom 2009; Melfi 2009; Whitham & Wielebnowski 2013). The effectiveness of any single method, however, may be limited, as each reflects only a portion of an animal's needs and perceptions (Swaisgood 2007; Barber 2009). Additionally, animal care decisions may be constrained by interpreting animal experiences from a professional, yet inherently subjective, human perspective that may not accurately reflect the experiences of the animals themselves (Veasey *et al* 1996; Rivas & Burghardt 2002). Therefore, new methodologies to assess and improve animal welfare are highly sought after (Barber 2009; Whitham & Wielebnowski 2013), particularly those that allow the animals to reveal their perspectives (Melfi 2009).

To improve animal care and improve welfare, zoos increasingly incorporate aspects of a species' natural history and behavioural ecology (Forthman & Ogden 1992). As animals in the wild often invest considerable time and energy in acquiring resources (Herbers 1981), zoos typically provide enrichment opportunities to mimic more natural foraging scenarios for their animals. For example, providing access to live fish significantly increased performance of natural hunting behaviours (Shepherdson *et al* 1993; Mellen *et al* 1998; Bashaw *et al* 2003), and supplemental carcase feeding reduced stereotypic behaviours (Bond & Lindburg 1990; McPhee 2002), for captive felids. When given the option, captive grizzly bears (*Ursus arctos horribilis*) spent more time actively manipulating objects to acquire food compared to when it was freely available (contra-freeloading; McGowan *et al* 2010). Hiding food throughout the exhibit also increased foraging time and decreased stereotypic behaviour for chimpanzees (*Pan troglodytes*; Baker 1997), walrus (*Odobenus rosmarus*; Kastelein & Wiepkema 1989), and several species of bear (Carlstead *et al* 1991). Furthermore, implementation of an unpredictable feeding schedule increased foraging behaviour and activity for sun bears (*Helarctos malayanus*; Schneider *et al* 2014), fennec foxes (*Vulpes zerda*; Watters *et al* 2011) and chimpanzees (Bloomsmith & Lambeth 1995). These

Figure 1



Pictures of species-specific food patches showing A) cavy food patches consisting of 20 pieces of food mixed into 2 L of topsoil inside a black rubber foot tub and B) wallaby food patches with 35 pieces of food mixed into 1 L of topsoil inside a plastic saucer.

results demonstrate that providing captive animals with the opportunity to work for their food can have positive implications for animal behaviour.

Beyond the previously stated behavioural implications, foraging behaviours can also reveal important information about how an animal perceives its environment. When provided with a number of experimental food patches that are equal in quality, an animal in a safe or more preferred spot or environment (ie, area with little probability of injury or death) will exploit a food patch more thoroughly (ie, leave less food behind) than an animal in a risky or less-preferred environment (Whelan & Maina 2005). Measuring the amount of food left by the forager in each food patch (the giving-up density: GUD; Brown 1988) provides a quantifiable metric of environmental perception, with extensive patch use (low GUD) indicating areas of preference, and low patch use (high GUD) indicating areas of aversion (Brown 1988). In the wild, these procedures have been used to develop species-specific 'landscapes of fear' (ie, an environmental 'map' of areas of preference and aversion; Brown *et al* 1999; Shrader *et al* 2008; Laundré *et al* 2010). We propose that similar methods can be used in captivity to develop an animal's 'landscape of comfort' within their exhibit. Such a map can provide valuable information to caretakers regarding how their animals perceive and use their exhibit space. For example, if GUDs reveal that individuals are too uncomfortable to forage extensively in several areas of their exhibit, the exhibit itself may be negatively impacting the welfare of the animals housed within it. Furthermore, food patches themselves may provide enrichment benefits to captive foragers by encouraging increased foraging and general animal activity.

For the purposes of this study, we define animal welfare as an intersection of an animal's internal state (eg, physiological condition), and its perception of the opportunities and risks provided by its current environment. GUDs provide a window into how the animal integrates its assessment based on its internal state (Sánchez *et al* 2008; Schwanz *et al* 2012) and its perception of the external environment (Brown 1988; Tuen & Brown 1996; Frid & Dill 2002). Working within this conceptual framework, we suggest that GUDs can also provide a tool with which to quantify animal welfare. Here, we investigate the utility of incorporating patch use as a tool to investigate questions related to animal care and welfare in captive populations. We combined measures of patch use with behavioural observations to determine: (i) whether patch use and giving-up densities can reveal landscapes of comfort for zoo species; (ii) if food patches are an effective form of behavioural enrichment; and (iii) is visitor interest and behaviour influenced by food patch presence? Finally, we aim to provide a more general discussion of zoo foraging ecology's potential as an emerging field.

This study was performed with two Patagonian cavies (*Dolichotis patagonum*), and two Parma wallabies (*Macropus parma*) at Lincoln Park Zoo (LPZ) in Chicago, IL, USA. Based on previous patch use studies with these species in the wild, we predicted that cavies prefer foraging in open areas (away from exhibit borders and blocked sightlines; Sombra 2011), whereas wallabies prefer areas close to cover (near bushes or exhibit borders; While & McArthur 2006). In regard to behavioural enrichment, we predicted that presence of food patches would increase natural behaviours, particularly time spent foraging and movement throughout the exhibit, and decrease inactive behaviours for both species. Finally, as active animals are known to attract more zoo visitors than resting/inactive animals (Margulis *et al* 2003; Watters *et al* 2011), we predicted that presence of food patches within an exhibit would increase the number of zoo visitors and visitor stay-time.

Materials and methods

Creation of a species-appropriate food patch is critical to achieving reliable GUD measurements (Bedoya-Perez *et al* 2013). Food patches typically consist of a measured amount of food mixed into an inedible substrate. The inedible substrate ensures diminishing returns: as an animal depletes the patch, its harvest rate declines as each piece of food becomes progressively harder to find (Brown 1988).

In our study, food patches consisted of 20 pieces (10 g) of species-specific food randomly mixed into 2 L of topsoil inside a black rubber foot tub for cavies (20.32 × 10.16 cm; diameter × height; Figure 1A), and 35 pieces (10 g) of food randomly mixed into 1 L of topsoil inside a plastic saucer for wallabies (40.1 × 9.6 cm; diameter × height; Figure 1B). Final foraging patches varied between the species because the wallabies would not forage from the same tub as the cavies, necessitating the change to a plastic saucer to ensure proper foraging. This study was approved by the UIC Office of Animal Care and Institutional Biosafety (OACIB; protocol # 12-181), and the LPZ Research Committee (protocol # 2013-025).

We let each species acclimate for approximately one month to the food patches before formal data collection began. At that time, food patches were placed in the exhibit in the morning (0830h) by keepers, and collected in the evening (1630h), allowing approximately an 8 h total foraging period. All food remaining in each patch was separated from the topsoil via a sieve and individual pieces counted, providing the GUD.

Subjects and housing conditions

Two exhibits were used for this study, one with two adult male Parma wallabies (Wallaby A and Wallaby B), and the other housing two adult Patagonian cavies (one male, one female). Parma wallabies and Patagonian cavies were chosen for this study because background information regarding how wild individuals use depletable food patches was already available, and both species inhabit similar small, indoor, exhibits with conspicuous heterogeneity in topography. The cavies and wallabies occupied adjacent, indoor exhibits in the Small Mammal-Reptile House at the LPZ. The wallaby exhibit was approximately 24.2 m^2, and the cavy exhibit approximately 12.5 m^2.

In the non-food patch condition, the wallabies were fed the same total ration of Mazuri Kangaroo/Wallaby diet® (PMI Nutrition International, Richmond, IN, USA) provided in the patches, however the ration was presented in two dishes only in the morning, plus chopped vegetables and/or fruits in the evening. Similarly, the cavies were provided their Mazuri Rodent diet® (PMI Nutrition International) in a single dish, plus chopped vegetables and/or fruits in the morning. When measuring GUDs and feeding behaviours from the depletable food patches, the pelletised diet ration for both species was provided only in the food patches (see below) in the morning. The cavies continued to receive their raw produce in the morning with the food patches, and the wallabies continued to receive their raw produce in the evening after food patches were removed.

Environmental preferences

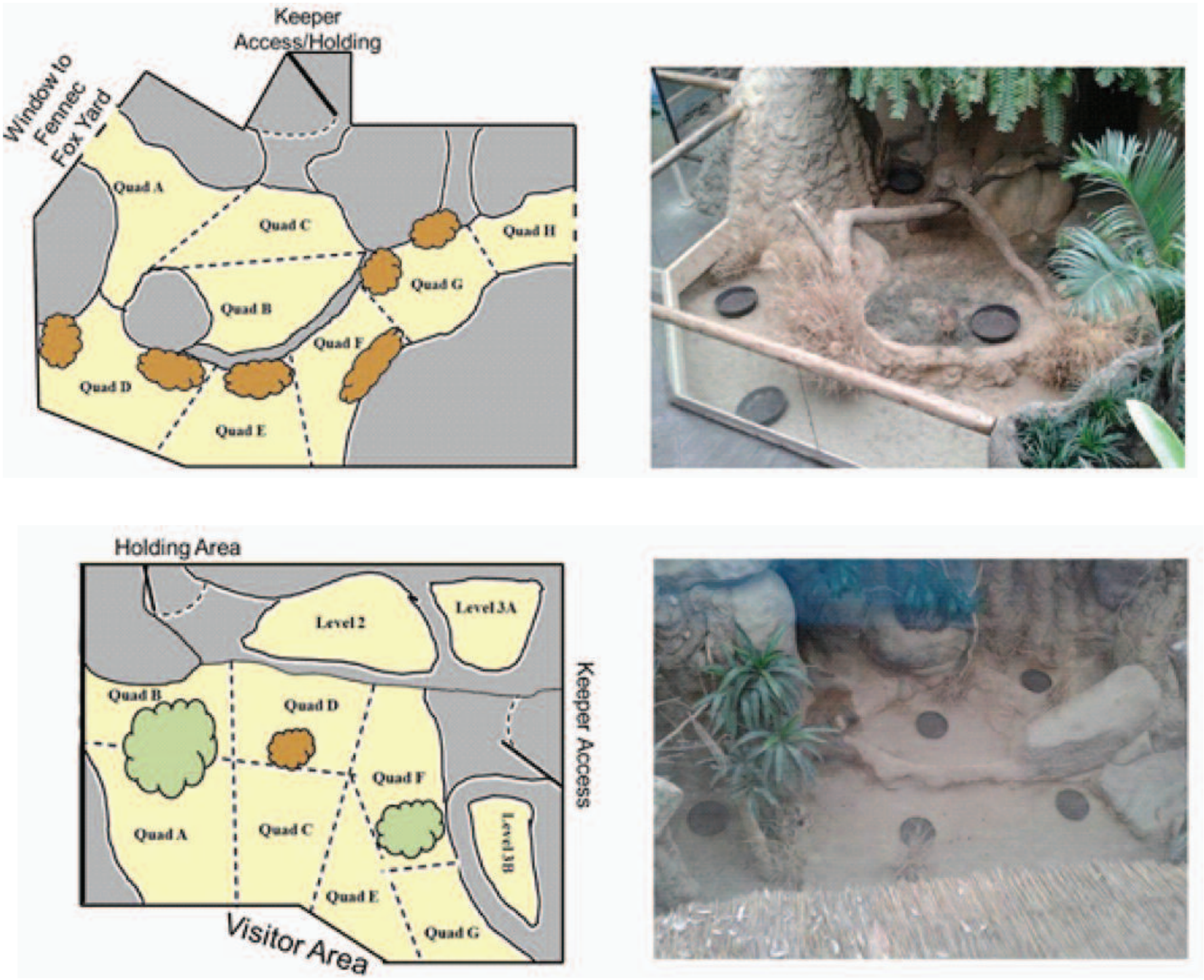
To investigate environmental preferences, the animals' locations within each exhibit were recorded during each observation period (see below) when patches were present and absent. The cavy yard was divided into eight quadrats (hereafter 'quads A-H') of approximately equal area (Figure 2 upper). Due to multiple levels within the exhibit, the wallaby exhibit had ten quads (Figure 2 lower). During the patch condition, a numbered food patch was placed in the centre of each quad. When patches were collected, the GUD for each quad was recorded to determine foraging location preferences within the exhibit. The wallabies had eleven total days with food patches, and the cavies ten. Patch design for cavies required iterative design modifications (ie, adjustment and reduction of food pellet size to prevent complete food patch depletion) that permitted five days of GUD data for analysis, while providing ten days of behavioural data with patches for behavioural analyses.

Behavioural enrichment

Behavioural observations were conducted on the cavies and wallabies prior to data collection to generate species-specific ethograms. The resulting cavy ethogram contained 20 behaviours, whereas the wallaby ethogram contained 18 (see Tables 1 and 2 in supplementary material to papers published in *Animal Welfare* on the UFAW website: http://www.ufaw.org.uk/t-ufaw-journal/supplementary-material). In both ethograms, all behaviours were collapsed into six main behavioural categories (active, inactive, foraging, social, maintenance, and other/out of sight). Once official data collection began, behavioural observations were conducted by the lead author, and consisted of 15-min periods using scan sampling at 1-min intervals (Altmann 1974). The location of each individual at each scan was also recorded. During observations, the lead author utilised the entire visitor area to ensure the best possible view of the animals at each scan. Four 15-min observation bouts were conducted per species in the morning (0830–1230h), and again in the afternoon (1231–1630h), generating eight observation periods (2 h of observational data) for each individual animal per day. A random number generator was used to assign observation times within morning and afternoon time-periods, and to determine daily assignment of patch treatment. All observations were recorded using the Animal Behavior Pro app for iPad (Newton-Fisher 2012, University of Kent, UK).

Experimental observations occurred for eight weeks (March 10, 2014–May 14, 2014) generating approximately 40 h of behavioural data for cavies, and 39 for wallabies. Cavies had ten observation days (totalling 20.6 h) with the food patches, and eleven days (19.8 h) with traditional food presentation methods. Wallabies had eleven days (21.8 h) with food patches and ten days (17.9 h) with traditional methods. Differences were due to weather and maintenance-related building closures on two separate observation days.

Figure 2



Schematics and corresponding photographs of the cavy (upper) and wallaby (lower) exhibits at Lincoln Park Zoo. Dark brown areas indicate bushes or dry foliage and green areas indicate live foliage within the exhibits. Grey areas indicate rock formations and exhibit walls and borders that were inaccessible to the animals. In the food patch condition, patches were placed in the approximate centre of each section. The cavy exhibit depicting the eight environmental preference sections (tan), and photograph depicting food-patch placement within the exhibit. Quads A, B, and C are approximately 0.2 m higher than the rest of the sections. Schematic of the wallaby exhibit with the ten environmental preference sections (tan) delineated, and photograph depicting food patch placement within the exhibit. Level 2 was approximately 0.5 m higher than Quads A–G, and Levels 3A and 3B were approximately 1 m higher than Level 1.

Visitor effects

Following documentation of animal behaviour at each 1-min scan, the number of zoo visitors at the exhibit were estimated and noted in the following increments: no visitors, 1–5, 6–10, 11–15, 16–20, 21–25, 25+ (Margulis *et al* 2003). Visitor interest in the exhibit was also documented by recording length of stay. If the majority of visitors (approximately 75% of group) present at the time of the scan spent < 20 s actively looking at the animals or into the exhibit, that observation received a rank of 'low'; 21–40 s ranked 'medium', and 41–60+ s ranked 'high' (Margulis *et al* 2003).

Data analysis

Environmental preferences

To test for effects of patch location on GUD for each species, GUD data were analysed using randomised block ANOVAs under the general linear models of SYSTAT 13 (SYSTAT SOFTWARE Inc, San Jose, CA, USA). We conducted separate analyses for each exhibit space (or species). GUD was the dependent variable, and patch location and date of treatment served as independent variables. We used days of each experiment as replicates rather than repeated measures since the GUD measurement on one day is independent of the GUD of the next. We also satisfy conditions of sphericity (von Ende 1993). A Fisher's Least Significant Difference (LSD) *post hoc* test was used to evaluate which feeding locations differed significantly.

To evaluate whether the patch treatment influenced how the animals used their exhibit space, we performed goodness-of-fit test comparing the number of instances each animal was observed in each exhibit quad when patches were present or absent. Associations between exhibit location preferences and GUDs were also tested using a Spearman rank order correlation. Finally, we used descriptive statistics to compare proportions of time spent in preferred vs unpreferred quads with and without patches.

Behavioural enrichment

As we were specifically interested in how effective food patches were as an enrichment option, we focused on the two salient behavioural categories — foraging and inactive. Time spent foraging and inactive (in min) was calculated for each animal on each day of observation as a proportion of time the animal was visible to the observer. Similarly, to test for patch treatment effects on movement throughout the exhibit, we calculated the total number of times each animal moved from one quad to another (hereafter called 'transitions') as a proportion of the total number of observational scans for each day. We then used a MANOVA to test whether individual animal ID and patch treatment (with or without patches) influenced the proportion of time each animal spent in the two behavioural categories and on proportion of transitions. Proportion of time spent foraging and inactive, and proportion of transitions were the dependent variables, and individual animal and patch treatment were the independent variables. We did not attempt to test for differences in effects between the two exhibits, as we had just four individuals (of only two species) that were nested within exhibit spaces, different patch designs, and the potential for between individual interactions.

Visitor effects

To determine whether patch treatment influenced visitor interest and stay time at each exhibit, we first converted our descriptive data into coded, qualitative scores for both visitor number and stay time at the exhibit (0 visitors = 0, 1–5 visitors = 1, 6–10 visitors = 2, and 0–20 s = 1, 21–40 s = 2, etc). Each scan's qualitative visitor scores were then averaged within day to obtain a daily visitation and duration rate. We then used two-sample *t*-tests to compare the daily visitor number and stay-time rates to detect possible effects of patch treatment on visitor behaviour.

Results

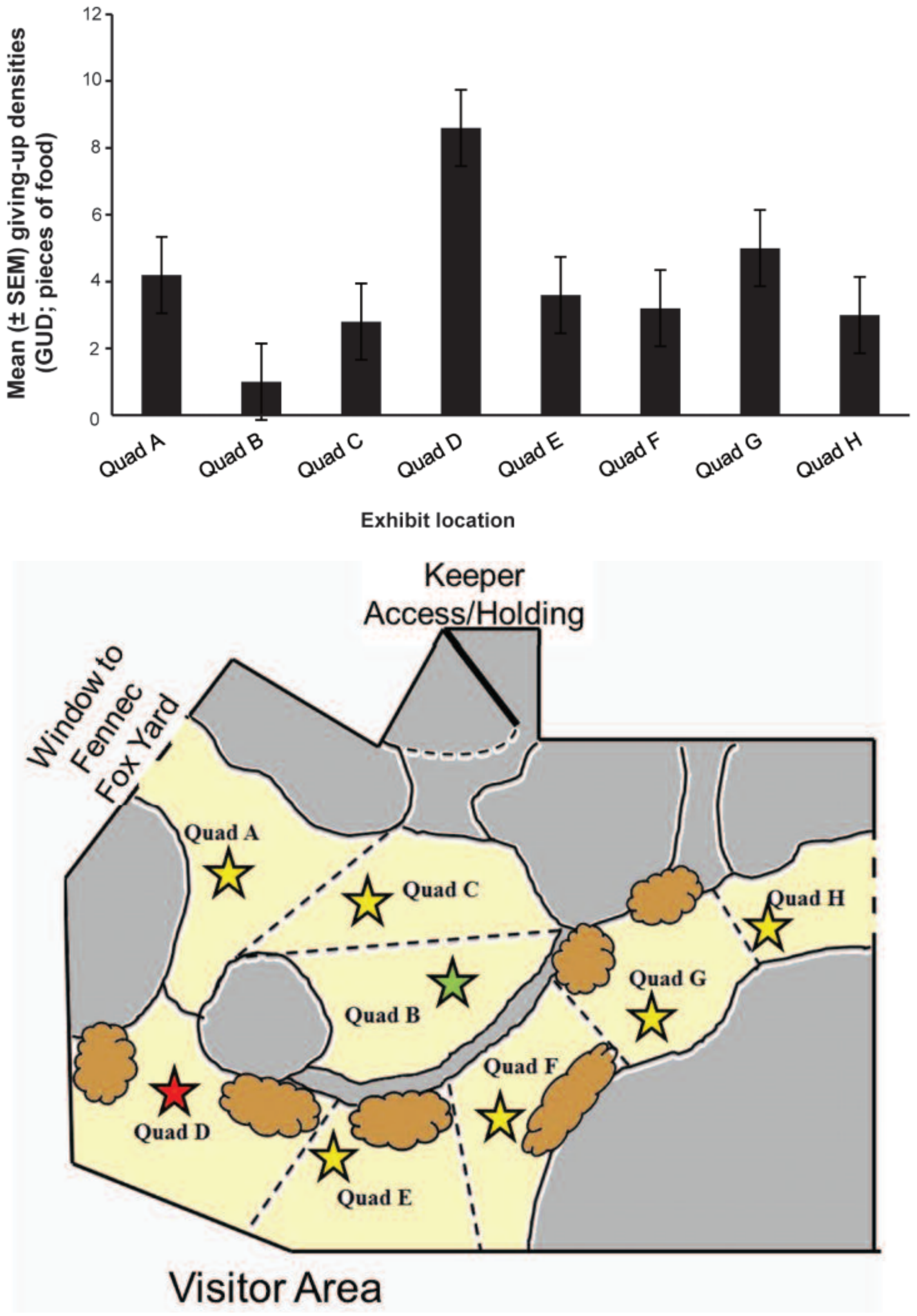
Environmental preferences

For cavies, the location of food patches had a significant effect on GUDs ($F_{7,28} = 3.59$; $P < 0.01$; Figure 3 upper). Fisher's LSD revealed that GUDs in Quad D were significantly higher than any other section, and GUDs in Quad B were significantly lower than most other sections (Figure 3 lower). Date had no significant effect on GUDs ($F_{4,28} = 1.90$; $P > 0.05$). While the wallabies showed strong trends toward low GUDs in Quad B and high GUDs in Levels 3A and 3B, the effect of patch location on GUDs was not significant ($F_{9,90} = 1.35$; $P = 0.07$; Figure 4). Date also had no significant effect on GUDs ($F_{10,90} = 1.57$; $P > 0.05$) for wallabies.

Goodness-of-fit tests revealed that food patch treatment significantly influenced where the cavies spent their time in their exhibit ($\chi^2 = 51.22$, df = 7; $P < 0.001$). Analysis of residuals indicates that quads previously under-utilised without patches became more utilised when patches were present, indicating an increase in exhibit space use. For cavies, GUDs were lowest in quads where they spent most of their time, however, the association was not significant (Spearman rank correlation: $r = -0.37$; n = 16; $P > 0.1$). When patches were available, the cavies spent most of their time in Quad B (60.1%), followed by Quad C (13.8%) and Quad A (12.2%). The cavies spent less than 5% of their time in the five remaining quads: Quad D (3.3%), Quads E, F, G (2.8%), and Quad H (2.2%). When patches were absent, cavies again spent the majority of their time in Quad B (68.2%), followed by Quad C (13.8%), and Quad A (9.0%), with less than 5% of time spent in Quads G (2.6%), E (2.3%), F (2.0%), H (1.3%), and D (0.8%). Cavies left the lowest GUDs in Quad B, followed by Quad C, which correspond to the locations where they spent most of their time. However, the next lowest GUDs occurred in Quad H, followed by Quads F, E, A, G, and D (Figure 3 upper).

Goodness-of-fit tests revealed that food patch treatment significantly influenced where the wallabies spent their time in their exhibit ($\chi^2 = 116.22$, df = 9; $P < 0.001$). As with the cavies, analysis of residuals with the wallabies indicates that quads previously under-utilised without patches became more utilised when patches were present, again suggesting an increase in exhibit space use. For wallabies, there was a significant association between quads where GUDs were lowest and where they spent most of their time (Spearman rank correlation: $r = -0.65$; n = 20; $P < 0.025$). When patches were present, the wallabies spent most of their time in Quad A (41.2%), followed by Quad G (33.7%) and Level 2 (6.0%). The wallabies spent less than 5% of their time in the seven remaining quads: Quad E (4.7%), Quad B (4.0%), Quad D

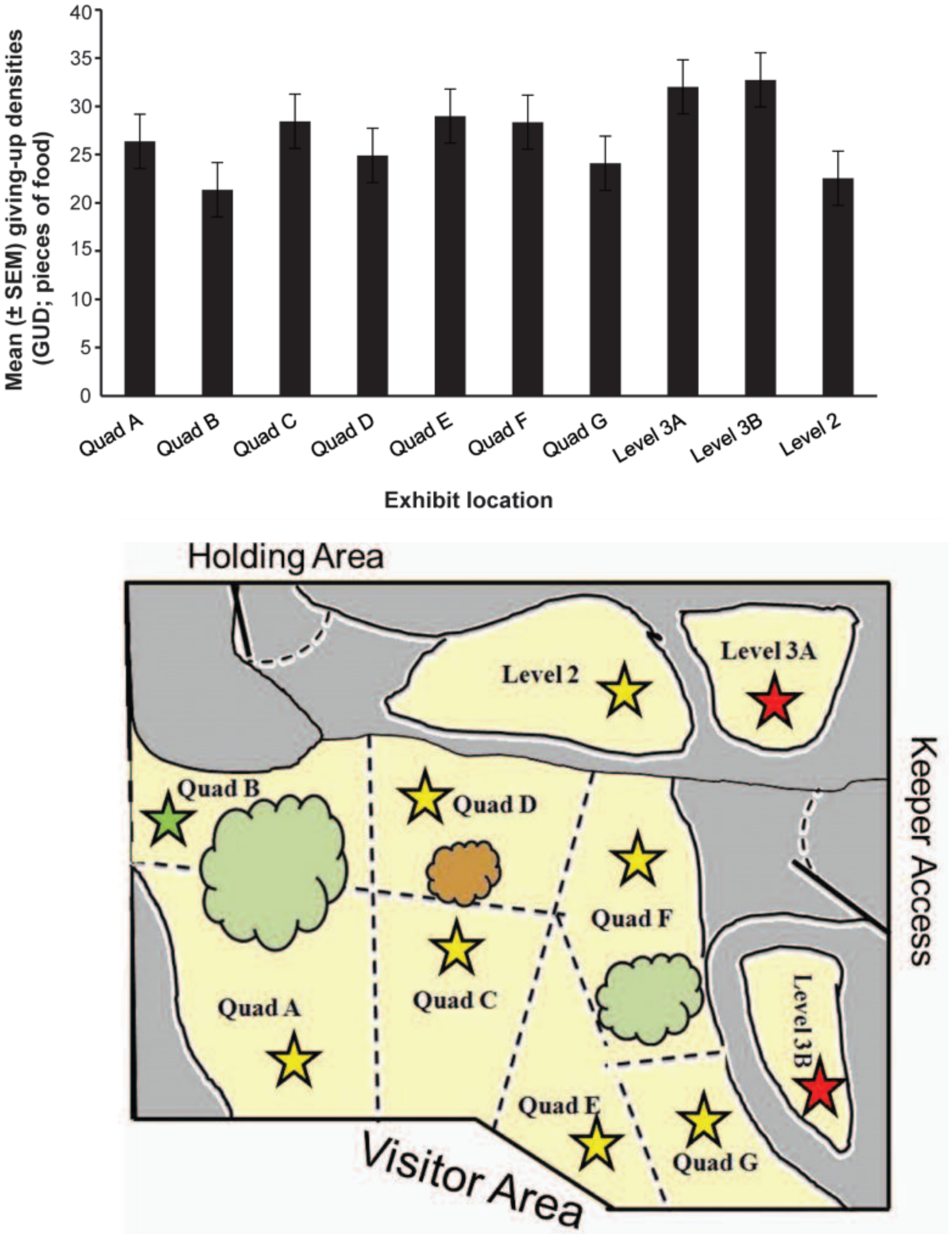
Figure 3



Showing (upper) mean (± SEM) GUD for the eight patch locations in the cavy exhibit. Patch location had a significant effect on GUDs ($P < 0.01$). GUDs in Quad D were significantly higher than other locations, and GUDs in Quad B were significantly lower than most of the other locations and, (lower), the corresponding exhibit graphic map of the cavies' 'landscape of comfort'. The red star indicates areas of aversion (highest GUDS), yellow stars indicate areas of intermediate preference (intermediate GUDs), and the green star indicates the area of highest preference (lowest GUDs).

(3.5%), Quad F (3.0%), Quad C (2.2%), Level 3B (1.0%) and Level 3A (0.7%). When no patches were present, wallabies again spent the majority of their time in Quad A (39.3%), followed by Quad G (38.2%). The wallabies spent less than 5% of their time in the seven remaining quads: Quad E (4.5%), Quad B (4.4%), Level 3A (3.8%), Quad D (2.9%), Level 2 (2.8%), Quad F (1.3%) and Level 3B (1.0%). The wallabies left the lowest GUDs in Quad B, followed by Level 2, which correspond to the locations where they spent most of their time. The next lowest GUDs occurred in Quad G, followed by Quads D, A, F, C, E, Level 3A and Level 3B (Figure 4 upper).

Figure 4

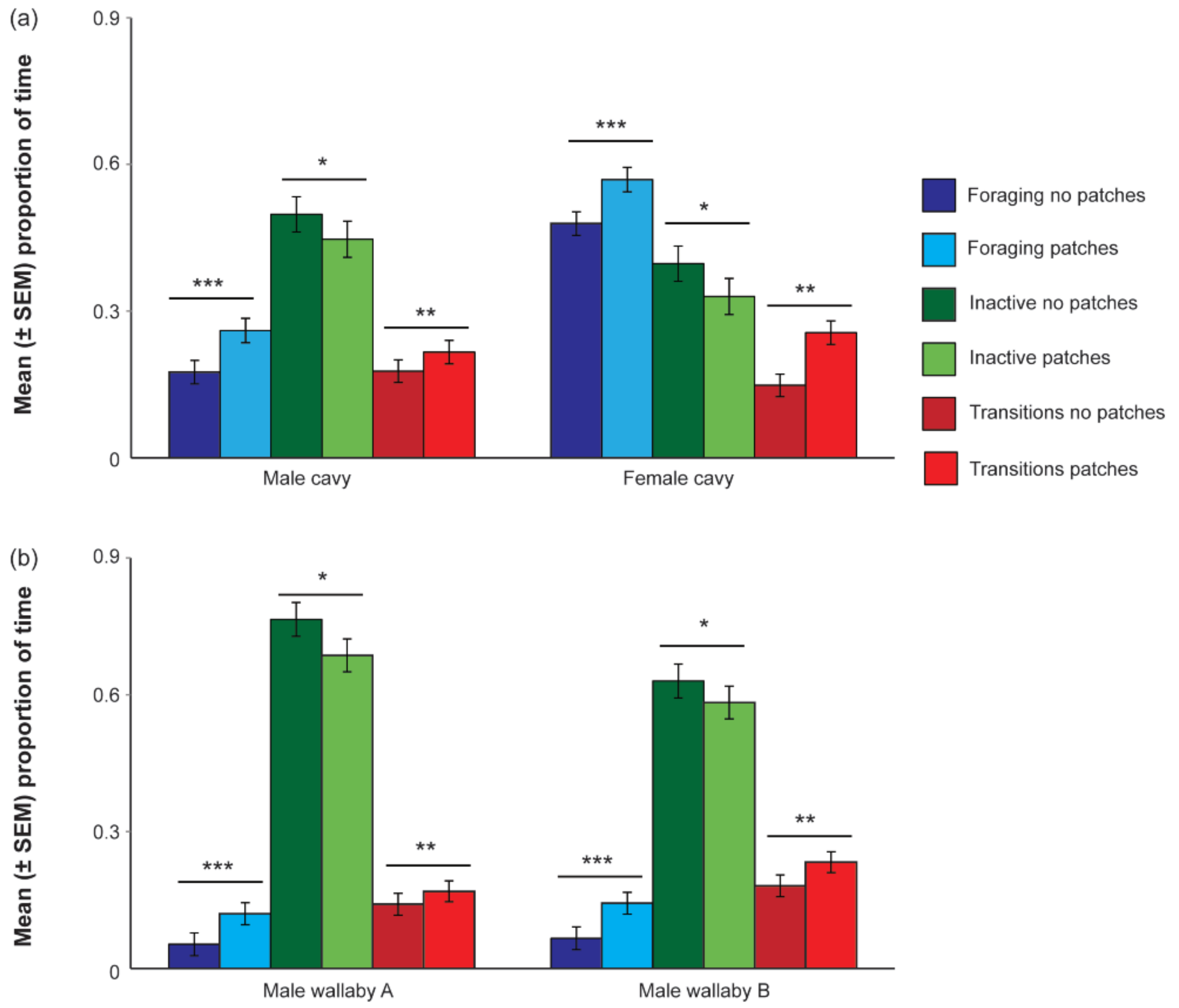


Showing (upper) the mean (± SEM) GUD for the ten different patch locations in the wallaby exhibit; while trends did exist, the effect of patch location on GUDs was not statistically significant ($P = 0.07$) and, (lower), the corresponding exhibit graphic map of the trends of wallaby 'landscape of comfort'. The red stars indicate areas of aversion (highest GUDS), yellow stars indicate intermediate preference (intermediate GUDs), and the green star indicates the area of highest preference (lowest GUDs).

Behavioural enrichment

The presence or absence of food patches had significant effects on proportion of time spent on particular behaviours ($F_{3,74} = 13.13$; $P < 0.001$; Wilk's $\lambda = 0.65$). Univariate tests showed that the presence of patches significantly increased proportion of time spent foraging ($F_{1,76} = 21.31$, $P < 0.001$), significantly decreased proportion of time spent inactive ($F_{1,76} = 5.55$; $P < 0.05$), and significantly increased proportion of transitions within the exhibit ($F_{1,76} = 11.31$; $P < 0.01$; Figure 5[a]) for all individuals. Individuals also significantly varied in behaviours ($F_{6,150} = 51.69$; $P < 0.001$; Wilk's $\lambda = 0.11$). Univariate testing found that the female cavy spent significantly more time foraging than any other individual, followed by the male cavy, then by the wallabies ($F_{3,76} = 137.51$; $P < 0.001$). Proportion of time each individual spent inactive also differed, with male Wallaby A spending more time inactive compared to all other individuals, followed by male Wallaby B, the male cavy, and

Figure 5



Mean (± SEM) proportion of time spent foraging, inactive, and the proportion of exhibit transitions in each treatment condition (with and without food patches) for (a) the cavies and (b) the wallabies. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

finally the female cavy ($F_{3,76} = 37.25$; $P < 0.001$). There was no individual effect on proportion of exhibit transitions ($F_{3,76} = 1.99$; $P > 0.05$; Figure 5[b]). There was also no significant interaction between each individual and patch treatment on any of the studied behaviours ($F_{9,180} = 0.78$; $P > 0.05$; Wilk's $\lambda = 0.91$).

Visitor effects

Despite trends toward higher visitor number and stay-time during days with food patches compared to days without, there were no significant effects of patch treatment at the cavy exhibit, on either visitor number (one-tailed *t*-test: $t_{19} = 0.33$; $P > 0.05$) or stay time (one-tailed *t*-test: $t_{19} = -0.08$; $P > 0.05$). Similarly, at the wallaby exhibit, patch treatment had no significant effect on visitor number (one-tailed *t*-test: $t_{19} = 0.14$; $P > 0.05$) or stay time (one-tailed *t*-test: $t_{19} = 0.78$; $P > 0.05$).

Discussion

Captive animal welfare is currently assessed using a variety of methods. Typically, these methods require either human interpretations of animal perception, or reveal only a portion (eg, physiological vs psychological state) of an animal's welfare. Quantification of foraging effort via patch use and GUDs, in contrast, has the potential to reflect both the psychological and physiological states of the forager as it assesses and responds to its environment. This information can ultimately assist caretakers in making caretaking decisions based directly on the animal's revealed preferences and perceptions. Integrating principles of foraging ecology, enrichment use, and behavioural observations can produce a comprehensive view of how animals perceive *their* environment directly from their perspective, while contributing important behavioural benefits for captive animals. We therefore envision zoo foraging ecology (employing food patches that allow quantification of GUDs) as a practical, inexpensive and useful method with which to address a variety of animal welfare-related questions.

Application to captive cavies and wallabies

We expanded upon previous research (Mogerman 2011; Howell-Stephens 2012) to examine three specific applications of zoo foraging ecology: (i) determine landscapes of comfort within exhibit space using patch use and giving-up densities; (ii) assess whether food patches increase animal foraging time and activity, thus providing an effective form of behavioural enrichment; and (iii) quantify whether food patch presence impacted visitor interest. Despite having only four individuals of two species participating in the study, food patches (a) revealed fine-scale exhibit preferences for foraging, (b) increased foraging and active behaviours while decreasing inactive behaviours of animals, and (c) demonstrated a potential to increase visitor interest.

Regardless of the relative safety of living in an indoor zoo environment, the results indicate that the cavies perceive areas of preference and aversion within their exhibit. Unlike most rodent species, wild cavies forage preferentially in open areas away from bushes and blocked sight lines (Sombra 2011). We therefore predicted that captive cavies would likewise prefer exhibit areas with unobstructed visual fields, and would avoid areas with impeded views. While other aspects of the exhibit also varied among foraging locations, such as proximity to visitors, we found that the exhibit space most avoided by the cavies (Quad D) had several large visual obstructions (tall grasses, large boulders, etc), which likely limited the cavies' sightlines to the rest of the exhibit area and visitor area. The most preferred foraging area, in contrast (Quad B), had arguably the best field of vision to these other areas. These results indicate that even though these cavies were bred and born in captivity, they retain environmental preferences similar to their wild counterparts (Troxell-Smith *et al* 2016).

Foraging location preferences for the Parma wallabies also followed wild foraging studies. Wild Parma wallabies live in forested areas with dense ground cover (Read & Fox 1991), and previous patch-use studies with other wild wallaby species found a preference for foraging near areas of cover (hedges and forest edges) compared to open areas (While & McArthur 2006). We therefore anticipated that our wallabies would also preferentially forage in areas that provided cover and near exhibit borders. We found a nearly significant trend toward greater GUDs/greater aversion ($P = 0.07$) in the tallest exhibit levels (Levels 3A and 3B), and lowest GUDs/greater preference in Quad B. Quad B contained a large live plant and exhibit borders that may have created a sense of cover and safety for the wallabies. In contrast, Levels 3A and 3B, where wallabies left higher GUDs, were substantially higher (approximately 1 m above the ground quads) and more exposed than the other exhibit areas, which may have resulted in the wallabies feeling vulnerable. Overall, wallabies foraged less compared to the cavies. We attribute this result to the unique natural history of each species — unlike diurnal cavies (Taber 1987), wallabies are primarily nocturnal, and thus are unlikely to forage extensively during the day (Ord *et al* 1999). Due to concerns from animal care staff, however, we were not able to leave the food patches for the wallabies in the exhibit overnight, consequently limiting results to daytime foraging only. Comparing day and night foraging location preferences for nocturnal species in zoos could be an interesting area for future study.

A common goal of behavioural enrichment can be to increase species-specific behaviours, making the captive environment more biologically relevant to the housed animals (Mellen & MacPhee 2001; Swaisgood & Shepherdson 2005). Despite individual variation in the proportion of time spent foraging, inactive, and proportion of exhibit transitions, all participants of our study responded to food patches as predicted — patches significantly increased proportion of time spent foraging, decreased proportion of time spent inactive, and increased movement throughout the exhibit for both species. Consequently, creating biologically realistic foraging opportunities via food patches and GUDs increased the time spent foraging and the overall use of the exhibit spaces. Natural foraging opportunities are less predictable, requiring greater searching and handling of food items than in captivity (Newberry 1995). Therefore, providing captive animals with opportunities to work for food improves behavioural and physiological indicators of welfare (Morgan & Tromborg 2007). Food patches also require animals to move from patch-to-patch to search for and acquire their food, increasing within-exhibit movement, thus providing opportunities for choice and flexibility in foraging decisions. Animals are able to forage according to their own schedules, may choose to leave and return to a patch at any time throughout the day, and can avoid foraging in areas of perceived vulnerability. As a result, provisioning exhibits with food patches may more accurately replicate natural foraging conditions.

Visitor number and stay-time at each exhibit increased slightly when animals were provisioned with patches compared to traditional methods, suggesting that food patches can alter animal behaviour in a manner that may influence the interest of human visitors. It is possible that an increase in sample size (ie, number of days with each treatment) could reduce some of the variance in daily scores, allowing for more definitive detection of effects. Studies of more active or charismatic species may also result in a greater visitor effect. Regardless, food patches may influence the behaviour of not only the animals, but also the human visitors that come to the zoo.

Future applications of zoo foraging ecology

Our case study demonstrated that GUDs can be used to determine foraging location preferences and exhibit perceptions, are a useful behavioural enrichment tool for animals in captivity, and have the potential to increase visitor interest and experience. Further testing and validation of zoo foraging ecology is required to realise the full potential of food patches as a tool to assess animal welfare in captivity, and provide many opportunities for future research. For example, longitudinal patch use studies can examine temporal changes in an animal's welfare state via changes in their foraging habits (ie, seasonal differences, changes in physical and psychological health, pairing of new individuals in a single exhibit space, establishing and evaluating preferences in food types, etc). Food patches can be utilised to help alleviate stereotypic behaviours by providing increased opportunities for animals to perform productive foraging and active behaviours (Troxell-Smith *et al*, unpublished data). Similar to a goal of scatter-feeding (Ryan *et al* 2012), provisioning of food patches may also help alleviate aggressive interactions in situations where species' dominance hierarchies and access to resources are a concern, as the dominant animal cannot monopolise all food patches at the same time. Further, researchers can investigate visitor effects on animal preferences and perceptions without having to invest significant amounts of time in behavioural observations by comparing animal foraging location preferences via food patches on days with and without large numbers of visitors. Similarly, for immersive free-range exhibits, food patches can be used as a preference indicator to determine 'landscapes of comfort' for animals in constant proximity to humans, and inform further management decisions regarding placement of visitor footpaths, providing areas of cover for the animals, etc. Individual differences in environmental preferences via patch use can be noted and accounted for to customise exhibit design toward the preferences of the animals living in the exhibit, and can aid in tracking long-term health and wellness by revealing changes in food consumption to caretakers. For facilities engaged in wildlife rescue programmes, the use of the same food patch methodology in the wild and in captivity can allow researchers to compare the preferences and foraging abilities of rescued animals to their wild counterparts, providing a quantifiable evaluation of adequate and appropriate responses to environmental stimuli for rescued individuals.

Conclusion

We present an opening application that illustrates some of the potential of zoo foraging ecology with the goal of inspiring additional validation and application of patch-use techniques in captive environments. In particular, we encourage continued studies to more directly link food patches and GUDs to more traditional approaches for measuring animal welfare. With further validation, foraging ecology, patch use and GUDs can provide a simple, affordable, and practical tool to assess aspects of animal welfare that can be utilised by anyone working with captive animals. Caretakers in zoos, wildlife rehabilitation/conservation centres, laboratories, and even pet owners can all actively engage in ecological and behavioural research with their animals. Widespread implementation of foraging ecology principles to aid captive animal care can greatly contribute to the fields of animal welfare and behaviour by providing caretakers with a quantifiable metric to objectively answer a wide variety of welfare-related questions.

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