THE SCIENCE AND PRACTICE OF CAPTIVE ANIMAL WELFARE

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THE SCIENCE AND PRACTICE OF CAPTIVE ANIMAL WELFARE

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EDITORIAL
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Editorial: The Science and Practice of Captive Animal Welfare

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Editorial on the Research Topic

The Science and Practice of Captive Animal Welfare

Animal welfare science is not a new field of study, but has gained immense traction in the past decades (Wilson, 1982; Novak and Suomi, 1988; Maple and Perdue, 2013; Sherwen et al., 2018). The study of animal welfare and wellness from a scientific perspective yields valuable improvements to captive care given the reliance on empirical data rather than anecdote or opinion. This shift to scientifically approaching welfare has been applied to a range of captive animal settings including farms, zoos, laboratories, and personal ownership. The extent to which the principles of animal welfare science are implemented in these settings ranges from strict, highly regulated guidelines such as those followed in research laboratories to the less or unregulated pet ownership or emotional support animals. Nonetheless, there is great potential for synergy across these settings if the data on captive animal welfare is collected in an empirical manner. Here we gather a number of studies spanning different zoo and aquarium settings with a range of species that builds our knowledge of how to adequately assess and ultimately advance animal welfare in captivity.

EXHIBIT DESIGN AND ENRICHMENT

The physical space or enclosure in which an animal lives is a universally important aspect of animal welfare (Hediger, 1950; Hancocks, 2001). This includes aspects of the structural design itself as well as components of enrichment that may be permanent or periodically included or removed. Browning and Maple offer novel perspectives on how to measure the actual space available in an animal enclosure beyond the standard measures of area. Spatial volume is rarely calculated when describing useable space, despite the fact that so many species are largely arboreal in their locomotor habits. Browning and Maple provide a methodology to measure complex space, acknowledging that there more sophisticated measurements are available to designers. Beyond the physical space, various forms of enrichment that are either permanently or temporarily added to environment have been found to have a substantial influence on animal welfare (Bacon, 2018). Fernandez and Timberlake offer an overview of how to select enrichment and evaluate its effectiveness in lemurs and find that conducting a preference assessment may be a fairly simple method for identifying food items to be used with enrichment devices. Moving beyond standard forms of enrichment, Regaiolli et al. draw from cognitive research and assess the effectiveness of visual illusions as a form of enrichment for lions. Clark et al. present a technique for providing cognitive enrichment while preserving the naturalistic design of the zoo experience and providing a "screen-free" enrichment experience for gorillas. These findings highlight the range of potential ways to measure and improve upon the physical space and enrichment offerings to captive animals.

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HUMAN-ANIMAL INTERACTIONS

In addition to the physical component of an animal's experience, it is well-established that social interactions have an important influence on welfare and wellness. Much of the research in this area has focused on social conspecifics, but human interactions can have potentially positive or negative effects on animal welfare and should be evaluated thoroughly (Sherwen and Hemsworth, 2019). An animal might experience contact with a caretaker, researcher, farmer, pet owner, or zoo visitor. These interactions should be carefully evaluated to minimize potential stress and maximize the potential value of these relationships. Clegg et al. investigate how a dolphin's willingness to participate in a form of interaction, specifically positive reinforcement training, might be related to the individual's overall health. Many animals have evolved to hide symptoms of illness, but willingness to participate in interaction may provide a useful metric for identifying at risk animals before other symptoms emerge.

Conversely, interactions with animals can have significant effects on visitor perceptions and attitudes toward animals. Godinez and Fernandez review the literature on how experiences at the zoo can influence perception, behavior, and conservation opportunities both on-site and post-visit. They also highlight the importance of having a true control group of non-zoo visitors in future assessments of this kind. Chiew et al. manipulated aspects of visitor experience, including proximity to animals on exhibit and extent of engagement, to assess the influence on visitor attitudes. Notably, the penguin behavior itself was related to several aspects of visitor attitudes whereas the treatments themselves were less influential in influencing the measured attitudes.

VARIETY OF SPECIES STUDIED

Historically, a fairly limited range of species have contributed the most to our knowledge of captive animal welfare. For a variety of historical and practical reasons, much of the early research in this domain focused on farm animals such as cows and chickens, lab animals such as rats and mice, as well as non-human primates such as monkeys (Hill and Broom, 2009). More recent animal welfare science has drastically expanded upon the range of species studied. This diversity will yield better insights into the nature and study of animal welfare as well as the development of practical animal welfare guidelines for many different species.

For example, Hill and Nollens summarize the existing research on beluga whale welfare and highlight the importance and value of relationships between universities and zoological facilities. Allard et al. apply principles of welfare assessment and investigate the link between personality assessment in Blanding's Turtles and outcomes of reintroduction efforts. This work illustrates an important effort to bridge the gap between captive animal welfare and conservation. Overall, these articles, together with others in the special edition focusing on lemurs, lions, dolphins, penguins, highlight the potential for great diversity in the questions asked about animal welfare and the wide range of species that have the potential to contribute to this field as well as benefit from the findings.

CONCLUSIONS

Animal welfare science is a rapidly growing and critically important field in our society. As illustrated in this special edition, a wide variety of approaches to measuring, improving upon, and implementing welfare exist. The most critical pathway forward is to rely on empirical evidence and strong experimental design. By doing so, we can improve our knowledge and understanding of animal welfare and optimize the lives of the animals in our care.

AUTHOR CONTRIBUTIONS

BP, SS, and TM shared responsibility of the editorial process and wrote, reviewed, and edited the editorial summary. All authors contributed to the article and approved the submitted version.

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ORIGINAL RESEARCH
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Developing a Metric of Usable Space for Zoo Exhibits

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The size of animal exhibits has important effects on their lives and welfare. However, most references to exhibit size only consider floor space and height dimensions, without considering the space afforded by usable features within the exhibit. In this paper, we develop two possible methods for measuring the usable space of zoo exhibits and apply these to a sample exhibit. Having a metric for usable space in place will provide a better reflection of the quality of different exhibits, and enhance comparisons between exhibits.

Keywords: usable space, exhibit, zoo, animal, welfare, wellness

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INTRODUCTION

One of the most important environmental features for captive animals is the space they are provided. This was explored in Hediger's pioneering work on zoo exhibit design (Hediger, 1950) and has been the focus of research and discussion since. Increased space can improve animal welfare through allowing for movement and exploration, expression of natural behaviors, room to provide a variety of exhibit furnishings, ability to make choices regarding social companions and environmental conditions, and for distance from public and group members as required.

Increased exhibit space for animals allows for performance of more natural behaviors and decreases occurrence of negative behaviors. Poor captive environments can cause welfare problems such as stereotypies and self-injurious behaviors (Goerke et al., 1987). Improving exhibit spaces helps relieve these problems as well as promoting positive behaviors, increasing overall behavioral repertoire (Hebert and Bard, 2000) and allowing for a fuller range of natural locomotive behaviors (Poole, 1991). An increase in usable space can also prompt an increase in activity, as adequate exercise can be difficult for animals held in small or simple environments (Hebert and Bard, 2000).

Exhibit size can also impact the social behavior of the occupants. Early hypotheses about overcrowding from decreased space leading to aggression were not borne out (de Waal, 1989; Miller et al., 2011). However, providing more space allows animals the ability to express their social preferences. Clark (2011) found that when a group of chimpanzees were given a new larger exhibit space, animals chose who to spend time near, with individuals seeming to spend more time near their "friends" (as evidenced by affiliative behaviors) and less time near those they disliked. Goerke et al. (1987) suggest that an increase in usable space may decrease social interactions overall; presumably because this is chosen by the animals. Supporting this, Kitchen and Martin (1996) found that common marmosets in larger cages spent less time in proximity to cage-mates, suggesting that in smaller cages, time spent in contact may not have been voluntary. The way the space is organized is also an important factor. Provision of areas to hide and escape can reduce aggression, and a simple increase in space alone may have little or no effect on rates of aggression within a group without attention to these factors (de Waal, 1989; Herrelko et al., 2015).

Amount of space is still relevant, however, as more space allows for more provision of these features and, as indicated, also provides more choice as to proximity of social partners. Increase in usable space gives individuals more options for privacy and personal space, as well as the ability to provide more resources and decreasing competition for preferred areas (Hebert and Bard, 2000), all of which should provide social benefit to the exhibit occupants.

Beyond just the social benefits, availability of choice within their environment is of central importance to the welfare of captive animals. Increase in exhibit space can provide additional choice and control for animals. Coe et al. (2009) point out that increased usable three-dimensional space gives the animals more choice between different environmental gradients, such as light, temperature and humidity. Ross et al. (2009) suggest that increased space allows for spacing of preferred enclosure features, which can reduce competition for their use. Ross et al. (2011) found that gorillas and chimpanzees were highly selective of which space they used within their enclosure; indicating that they were making use of the choice available. As discussed above, space also allows animals to make social choices to meet or avoid one another when required. It can also allow animals to make the choice to avoid being too close to visitors when they find proximity distressing (see e.g., Hosey, 2005; Sherwen et al., 2015).

Exhibit size is thus valuable to animals for many reasons. Usually space is measured in terms of the floor space of the enclosure – a measurement in square meters that can be compared between exhibits. Guidelines and requirements for animal housing typically lay out space requirement in these terms (see for example EAPA, 2000). However, there is more to enclosure space than simply floor space. For example, consider two orangutan exhibits, both with the same size "footprint" in terms of floor space. One of these is a flat grassy exhibit, while the other contains a tall climbing structure of poles, ropes and platforms. As well as the obvious improvement in enclosure quality, this second exhibit also provides more space than the first for the orangutans to utilize for locomotion. The presence of additional exhibit furniture increases the internal space of the exhibit (Burton, 2004). Available exhibit spaces must be accessible to the animals, through the presence of furniture such as ropes, platforms and other pathways. These sorts of features "open up" the vertical space for use by the animal and increase total usable space. Many current enclosure modifications for arboreal animals, particularly primates, are centered around an increase in usable space through improving access to the vertical dimension (Anderson, 2014). Of central importance is ensuring that animals are able to use the space available to them. Quantity of space is generally less important for animal welfare than the complexity and usability of the space (Kitchen and Martin, 1996; Ross et al., 2011). By adding furniture which makes central and upper cage spaces accessible, this converts these areas into usable space and increases total availability (Maple and Perkins, 1995).

The importance of increasing usable vertical space for arboreal primates has been identified for decades (e.g., Maple, 1979, 1980) and is the focus of many recent enclosure modifications and studies. Historically, the vertical dimension was underutilized, as Maple and Finlay (1989) describe: "the last generation of captive environments for apes were deficient in providing for a vertical dimension of space. These generic ape grottos typically contained few climbing structures of insufficient height and complexity... the space available for locomotion is greatly expanded by building upward. Apes can use climbing structures to locomote through vertical space by brachiation or more cautious means" (1989, pp. 105–106). Increasing vertical space may be one of the best ways to improve the environments of great apes (Maple, 1979; Goerke et al., 1987), as well as other primates, allowing arboreal animals to display more of their natural behaviors. Orangutans, as the most arboreal of the great apes, have a particularly high requirement for vertical space (Maple, 1980). Hebert and Bard (2000) found that orangutans showed different behaviors at different heights within their enclosure; with more solitary and rest time in the higher strata, and more social and active time in the lower. They conclude that "usable space for orangutans is said to include adequate enclosure size as well as horizontal and vertical space" (2000, p. 249). Perkins (1992) found that orangutan activity level increased with enclosure size. Exhibit improvements for other primate species have had similar effects. Anderson (2014) examined the use of space by gibbons before and after the addition of hammocks, enrichment pulleys and log bridges to increase accessibility and create opportunity to use vertical space. This was successful, with the animals spending more time in the upper segments of the enclosure. Kitchen and Martin (1996) found that common marmosets showed increased activity and variety of behaviors in response to increases in enclosure size and complexity. Although most work so far has focussed on primates, increasing usable vertical space could also benefit other types of animals that are also vertically active, such as felids (Mellen and Sheperdson, 1997).

Volumetric space of this type can be described in a metric of usable space. The usable space of an enclosure includes not only the floor space, but all the exhibit features that the animals may use to move around and spend time on or in. It is a measure of the total usable surface area, or volume, that the animals can access. Maple and Finlay (1986) call for a measure of usable space that would allow unbiased comparison between complex zoo exhibits. There are many reasons to think that increasing usable space will benefit animal welfare, in terms of an expanded behavioral repertoire and an increase in social and environmental choice. Thus, a measure of usable exhibit space can stand in as a proxy measure for animal welfare and exhibit quality. Measurement of all usable exhibit features and the development of a function to combine these measures into a single "usable space" score would provide a valuable way of quantifying the space within exhibits and enabling a comparison between exhibits. This sort of measurement of spatial volume can provide a more meaningful index of space than simple exhibit size.

We differentiate here between usable space, as a measure of the potential space afforded by an exhibit in virtue of its design, and the actual use of space by its inhabitants, as shown by their behavior. Once usable space has been characterized by a metric such as the ones we provide, there is then a further question as to how the animals will use it. Not all usable space within an exhibit may be used by animals, for reasons of individual preference or temperament, but this does not mean that this should not count as usable space for the purposes of measurement. This distinction and its implications will be discussed in more detail further on. This paper will be concerned with usable space as a metric for evaluation of exhibits, rather than on the behavior of the animal inhabitants.

MATERIALS AND METHODS

The process of creating a usable space metric occurs in three parts: determining which exhibit features should be counted as part of the usable space, measuring these features and creating a formula that can combine the various measurements into a single metric that can be used to assess and compare enclosures. In the rest of the paper we will examine these steps through application to a real-world example, comparing two possible formulas that might be used in creating a usable space metric, before addressing some potential problems with the process and outlining its benefits. The exhibit chosen was the pygmy marmoset (*Cebuella pygmaea*) enclosure at the National Zoo and Aquarium in Canberra, Australia (**Figure 1**). This exhibit was chosen for ease of measurement, due to its small size, as well as the presence of complex vertical environmental features, which were necessary for best testing the calculations. As the animals were not present in the exhibit at the time of measurement, the study did not have the potential to impact animal welfare and as such no ethics approval was required, as per Australian National University and NHMRC guidelines.

Determining Which Exhibit Features to Include

The first step in coming up with a measure of usable space, is deciding which exhibit features should be included within the measurement and calculation. As opposed to traditional measures of exhibit size, which simply take floor and wall dimensions, usable space measures will take into account all accessible exhibit features. General discussion of application of this method can be found in the discussion section. For this study, as the sample exhibit was for an arboreal primate the measured exhibit features incorporated the floor dimensions as well as all the vertical climbing surfaces. This included mesh cage sides and ceiling, ropes, poles, platforms and branches. Because of the small size of pygmy marmosets (body length around 15cm), all the smaller features of the exhibit (small branches, tree canopies) were considered usable space for these animals.

Measurement

After identifying the relevant exhibit features to measure, the next step was to enter and measure them. Measurements for this exhibit were taken manually in cm, using a tape measure. Floor and wall dimensions were taken along edges; as were platform and nest box dimensions. One problem with measurements of usable surface area is calculations involving nearly one-dimensional linear pathways, such as ropes. Wilson (1982) came up with one solution, making measurements of such objects "as if the objects were flat planes" (1982, p. 204). It is unclear whether this meant using the diameter of the object as the flat surface dimension, or the circumference. In this work, we used the diameter for features the animals were likely to only use one side of (e.g., climbing along the top of ropes) and circumference for features they may use all sides of (e.g., climbing up and around poles). Trees, perches, ropes and poles were measured for length and circumference. For branching trees, all individual branches were measured, as these could all be individually occupied by the animals, due to their small size. Although branch circumferences varied slightly from base to tip, branches were treated as having

FIGURE 1 | Pygmy marmoset exhibit at National Zoo and Aquarium.

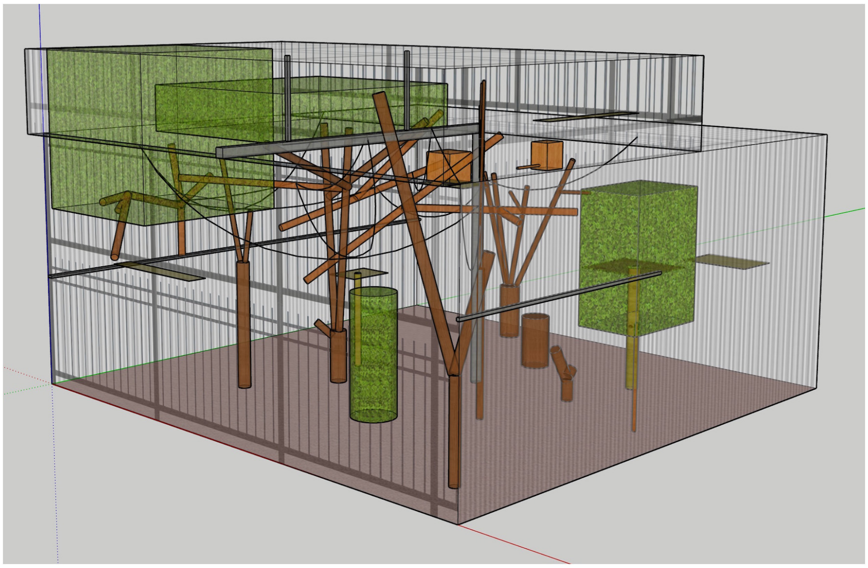

FIGURE 2 | Digital 3D model of the pygmy marmoset exhibit.

a single circumference, taken near the middle of their length. Future work could look at validating this assumption through comparing calculations using this measurement to those using a more complex formula to account for circumference change along the branch length. Complex canopies of numerous small branches and leaves were too difficult to measure individually and were instead measured as though they were solid blocks, with their exterior dimensions being recorded. This approach could also be validated in future through comparison of this measurement to one more accurately recording the interior complexity of the canopies.

Once all measurements were taken, these were then used to create a 3D model of the exhibit, using the program SketchUp Pro (2018 version)[1] (**Figure 2**). This model was extremely useful for visualizing different components of the exhibit and their relationship to one another, for taking any measurements that were missed in the initial exhibit measurement procedure, and for making volumetric space calculations (described in the next section).

Creating a Formula for Combining Measurements Into a Usable Space Metric

Once measurements were obtained, the final step was to create a formula to combine these, to give us a single number representative of the usable exhibit space. For terrestrial animals that only move along flat spaces, this would be a straightforward sum of the various floor spaces they can use. For arboreal animals, this becomes more difficult with the addition of linear pathways. For aquatic and flying animals (possibly also some arboreal animals likely to leap and swing), there will be additional volumetric measurements of three-dimensional spaces the animals can move around within that also must be added to the model. There are two methods by which we think a useful measure of usable space can be obtained – that of total usable surface area, and usable volume, and both were tested for this exhibit.

Usable Surface Area

Total usable surface area (m^2) is a sum of all the exhibit surfaces accessible to the animals – floor area, as well as platforms, ropes, mesh walls, exhibit furniture etc. (Wilson, 1982; Perkins, 1992; Lukas et al., 2003). For this exhibit, usable surface area was taken as the sum of surface areas of all the separate usable exhibit features. Flat surfaces, including floor, wall mesh, ceiling mesh and platforms, were calculated as the product of their side lengths. Other climbing structures, such as poles, ropes and branches, were calculated as the product of their length and their circumference. This treated the usable surface area for these objects as essentially the flattened surface area if they were to be rolled out. As the marmosets could move around any side of these features (e.g., climbing along top or bottom of ropes, or any side of a vertical perch), the entire surface area was considered usable. In some cases, a feature may not be considered usable on all sides (for example, if an animal could move along the top but not the bottom of a rope, as with an arboreal animal like a tree kangaroo). In these cases, the usable surface area would have to be modified accordingly, perhaps by taking the diameter of the object and treating it as an otherwise flat pathway of this width. For the pygmy marmosets there were no objects like this. As mentioned, since tree canopies were too complex to take the measurements of all the small branches within, usable surface area of these spaces was taken as the surface area around the edges of the canopy, as though it were a solid prism with external usable surface area. These separate surface area measures were then combined to form a total usable surface area score.

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[1] www.sketchup.com/products/sketchup-pro

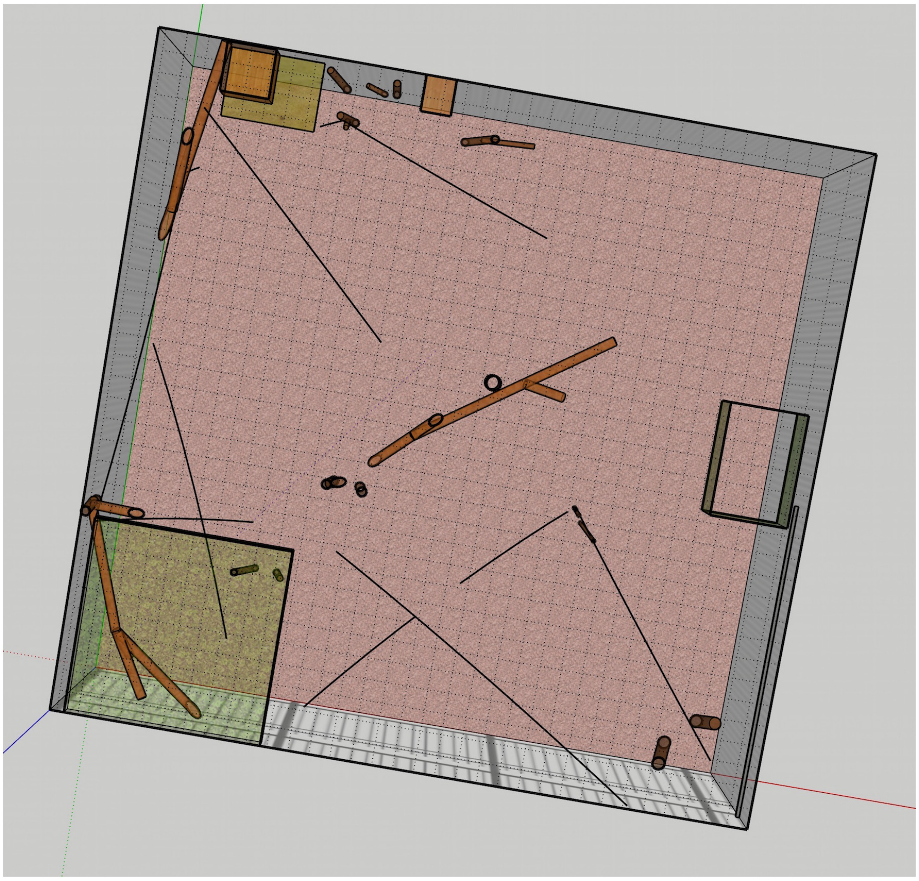

FIGURE 3 | Cross-section of the exhibit model, with grid overlaid.

Usable Volume

Usable volume is a different type of measure, one which calculates how much of the total exhibit volume (m^3) is accessible to the animals. Both Wilson (1982) and Perkins (1992) used a measure of exhibit volume, however this was not a measure of usable space as it was total exhibit volume and large parts of the total volume may be inaccessible to the animals. Ross et al. (2009) provided a useful way of thinking about usable enclosure volume. Their method was to divide the 3D space of the enclosure into blocks of 1 m^3 and then score which of these blocks the animals are able to occupy, based on which exhibit structures are nearby; counting out "empty" spaces between exhibit features. Burton (2004) uses a similar method when running student courses on assessing animal exhibits – drawing up the enclosure as a 3D grid (in this case, usually 9 segments – low, middle, upper; left, center, right; front, middle, back).

For the pygmy marmoset enclosure, usable volume calculations were taken by dividing the exhibit into many individual cubes, which were then scored for whether or not they could be used by the animal (i.e., whether exhibit features would allow the animals to access or use these spaces). Because of the small size of the animals, these cubes were taken as 15 cm × 15 cm × 15 cm (the body length of the marmosets). Essentially, the process involved dividing the enclosure into marmoset-sized boxes and counting those boxes which the marmosets could actually occupy. The 3D model produced in SketchUp made this process quite simple through the overlay of a grid onto the model. The model was then viewed as sections at each cut of 15 cm height (see **Figure 3**) and the number of boxes usable and not usable by the animals then individually counted through each section cut.

A cube was considered usable if it was adjacent to floor, mesh walls or ceiling, or if it contained a piece of exhibit furniture the animals were able to use. Usable volume did not include the usable spaces between objects that the monkeys could use to leap through; if these spaces were included as "usable" then the figure would be higher again. Where there was overlap between two different types of exhibit features within a single cube, this was only scored once. As well as being given a score for whether or not the cube was usable, it was also categorized according to which types of exhibit features it contained (floor, wall, ceiling, furniture). Due to substantial overlap between different objects (i.e., a single segment may have been made accessible to animals through both a branch and a rope), the general category "furniture" was used in calculations rather than specific sub-types of objects.

RESULTS

Usable Surface Area

The results for the usable surface area calculations are presented at **Table 1**.

The total usable surface area for this exhibit was found to be 116.14 m^2. This is almost 5 times the space of the floor surface area alone, illustrating the difference between using this measure and traditional exhibit dimensions. This table also shows the total surface area sums for the different types of exhibit features (mesh, floor, platforms, nest boxes, poles, trees and branches, and ropes), as well as the proportion of the total contributed by each feature. These results show that by far the greatest proportion of the usable surface area (42%) is made up by the meshed walls and ceiling, results similar to those found by Wilson (1982). The next highest surface area (30%) was provided by trees and branches. The majority of this was accounted for by the canopies, as canopies made up 77% of the total surface area for this group. Floor space was the next highest (21%). Linear climbing structures such as ropes, poles and tree branches made up a very small proportion of the total surface area (10%), despite their large cumulative length (over 87 m).

Usable Volume

Results for the usable volume calculations are shown at **Table 2**.

The total usable volume for the exhibit was 20.14 m^3. The total exhibit volume was calculated at 68.27 m^3, so the usable volume represented around 30% of the total. This figure may seem low, but represents necessary empty space between exhibit features, both for keeper access and for animals to move around.

TABLE 1 | Usable surface area calculations.

Feature	Surface area (m^2)	Proportion of total
Mesh (walls/ceiling)	49.04	0.42
Floor	24.00	0.21
Platforms	1.51	0.01
Nest boxes	0.76	0.01
Poles	2.94	0.03
Trees/branches	35.10	0.30
- Canopy	26.96	0.18
- Branches	8.14	0.05
Ropes	2.79	0.02
Total	116.14	

TABLE 2 | Usable volume calculations.

Feature	Volume (m^3)	Proportion of total
Floor	3.56	0.18
Mesh	6.94	0.35
- Ceiling	3.79	0.19
- Walls	3.15	0.16
Exhibit furniture	10.19	0.57
Total	20.14	

TABLE 3 | Amount of volume overlap between exhibit features.

Features	Amount of overlap (segments)	Proportion of total
Floor and wall mesh	33	0.01
Wall and ceiling mesh	102	0.02
Floor and furniture	60	0.01
Walls and furniture	209	0.04
Ceiling and furniture	110	0.02
Total	514	0.10

The proportions in **Table 2** do not add up to 1, because they represent how many total segments each of these features types appear in and some of those segments have overlap between features, such as ceiling mesh and tree foliage. **Table 3** shows the amount of overlap between different exhibit features.

This overlap contributes to around 10% of the total usable volume, which means that 90% of the volume is accounted for by segments consisting of only a single type of exhibit feature (in this case, counting all exhibit furniture as a single type of feature – the proportions would be much higher if broken down by branches, ropes etc.).

Comparison

There are interesting differences between the breakdowns of the different measurement types, in terms of the contribution of the different types of exhibit features. While the usable surface area calculations showed 42% for meshed walls and ceiling, and 20% for floor; the usable volume showed 35% for meshed walls and ceiling, and 18% for floor. The usable surface area of exhibit furniture was only 37% of the total, while the usable volume provided by the furniture was 57% of the total. This suggests that the usable volume measure might be better at accounting for the contribution of exhibit furniture to usable space.

DISCUSSION

Methods

In this paper, we designed and tested two different methods for quantifying the usable space of an exhibit. Both features shared the same first two steps – determining which exhibit features to include and taking measurements – and differed in the final step, of creating a formula through which to combine measurements in a single usable space metric.

Determining which exhibit features to include requires knowledge of the natural history of the species within the exhibit, as different exhibit features will count as usable or not usable, depending on the species. Which features are relevant will depend on the biology of the animals involved – the types of features which are usable for a wombat will be vastly different than those for a capuchin monkey, or an owl. Both the size of the animals and behavioral repertoire of the species will determine which exhibit features will be usable by the animals. There will also be an effect of the individual personalities and capacities of the animals held on which exhibit features can be used. Animals with physical limitations may not be able to access all features, while smaller or younger individuals may be able to access additional features. Individual behavior and preferences will also affect which features animals will choose to use, though this will be reflected more in actual space use than in the usable space features of the exhibit. Despite this, we can come up with a generalized list of those features which are likely to be important.

- Floor space –the basic floor space of an enclosure is a large part of the usable space for that exhibit. For strongly terrestrial animals, such as a kangaroo, this might still be the primary measure of usable space. For arboreal species, it will play less of a role. For raised or uneven surfaces, the surface area will be higher than the simple enclosure dimensions.
- Elevated platforms – the surface area of elevated platform spaces.
- Rocks – perhaps a type of elevated platform, the sitting and climbing surfaces of rocks count for those animals that can use them.
- Arboreal pathways – the length of ropes/logs/other pathways between elevated spaces.
- Climbing structures – the height (and possibly diameter/circumference) of climbing poles/trees.
- Cage sides – for many primates and birds, the mesh of cage sides is usable space to move around on.
- Air volume – for flying (or leaping) animals, the total air volume of the enclosure could function as usable space for locomotion.
- Water volume – for aquatic animals, the volume of ponds and pools would count as usable space.
- Burrow volume – for burrowing animals, underground burrow systems would count as usable space.

Once the relevant features for any particular exhibit have been identified, they can then be measured and the total usable space calculated. Where there are areas in the enclosure that cannot be used because they are inaccessible to the animals though presence of barriers, or lack of accessible furniture, these should be subtracted from the total.

For pygmy marmosets, because of their small size and climbing ability, there were a very large number of separate usable exhibit features within their exhibit. For larger animals, or for animals with less agility, there may be fewer features included. This is an important step of the process for two reasons. First, because the accuracy of the usable space score will depend on inclusion of the right features – leaving out some usable features or including some inaccessible ones will give misleading scores. Second, in order to make comparisons between exhibits, the same types of features will need to be measured in each. There is a potential for future standardized lists of inclusions for each species to facilitate comparisons, but much is still likely to depend on individual discretion for each exhibit. A good understanding of the biology of the species in question will be crucial.

The second part of the process, measurement, took the most time. Manual measurement of all the individual usable exhibit features was time-consuming and labor-intensive. Measurement of straight floor and wall dimensions was relatively simple, but curved surfaces such as ropes and branches, were more difficult to measure accurately. Measurement of all the individual branches within the trees was the most intensive part of the process; though this would be easier for larger animals that would not separately use each of these small branches. In some cases it is likely to be impractical due to accessibility difficulties (not all tree spaces, for example, would be easy for a person to access and measure) as well as potential for inaccuracy. Once the measurements were taken, having the finished 3D model was useful for validating the accuracy of measurement through the depiction of exhibit features in relation to one another. Having such a model and would also be of use in the future for modeling potential changes to the exhibit.

For the measurement part of the process, a possible alternative method would be to create digital 3D exhibit models from which such measurements can be extracted. These can be created through a compilation of photographs (drone technology is particularly useful for gathering photographs from different heights and angles) or similar surveying methods (e.g., laser scan) through one of the many software programs available for such tasks – usually used in construction and engineering. Early attempts to use this procedure with photos of the pygmy marmoset exhibit were unsuccessful, with the models not stitching the photos together properly to create usable 3D models. However, this is a very promising area for future research, as use of this technology would significantly decrease measurement time, and increase accuracy, if used well; as it would combine both the measurement and model-creation into a single process, most of which would be done by the software rather than manually.

The final step was the calculation, and application of the two different formulas for quantifying usable exhibit space. Calculations of usable surface area did not require use of the 3D model, and were done easily within a spreadsheet containing the measurement data. Usable volume calculations were more complex, requiring first the building of the 3D model, and then manual counting of segments within the model. The same method could potentially be applied to counting segments through basic photos (ones not compiled into 3D models) or even visually assessing segments within the exhibit, but particularly at this scale, this would not be an accurate method. For large exhibits holding larger animals, where the scale of segmentation would be something more like 1 m^3, these might be more useful methods.

Of the two methods, usable volume seems the most promising as a metric of usable exhibit space. It is better in accounting for the contribution of all exhibit features and more flexible in the types of exhibits it can score. As mentioned in the results, the usable volume calculation gave a much higher weighting for the effects of exhibit furniture in opening up usable space. This is because, although furniture such as ropes may not have much surface area, they have a large impact on how much of the exhibit they can make available to animals.

This method is also more flexible, able to provide scores for a range of exhibit types. As demonstrated here, it can account for usable space of complex vertical exhibits. Although the method was only applied to one type of exhibit – an arboreal primate – the results should generalize to any type of exhibits with usable volumetric space. These include those used by other arboreal or climbing species, exhibits with burrows or pools, aviaries and aquarium tanks. Future work applying these methods to a variety of exhibit types will help to refine the methods for different enclosure types. As usable volume seems the preferable method in most cases, through the rest of the paper discussion will be of this method only, though usable surface area calculations may still be valuable in making quicker judgements of usable exhibit space, or when dealing with terrestrial animals such as ungulates, on largely flat exhibits.

Project Limitations

The primary limitation of the use of the usable volume calculation is that it may give misleading results in regards to the comparative assessment of enclosures. It does not necessarily contain all the information we require about exhibit quality and use. There will be cases in which a usable space score won't accurately represent the actual use of exhibits by the animals, and also cases in which enclosures of lower overall quality are still given high usable space scores. However, these limitations seem possible to overcome.

One potential issue is that actual exhibit use by the animals may not reflect the usable space score. This follows the distinction we made in the beginning of the paper, between usable space as an exhibit metric, and space use as a behavioral measure of animals. While an exhibit might have a large usable space, the animals may in actuality only ever occupy a small portion of this space. In these cases, the usable space score will be misleading. This is likely to occur in cases where the space is undesirable to the animals, such as areas which are too open, or too close to the public. We certainly do not deny that use of space is important. As Kelling and Gaalema (2011) argue: "analysis of use of space is an essential element to link exhibit design and animal welfare" (2011, p. 602). If animals aren't using portions of their exhibit, this may be reason to consider them not usable, or to try to find methods to make them more desirable. Ross et al. (2009) point out that studies of enclosure use help inform us about the preferences of the animals regarding the features of their available space, and can allow us to make modifications to encourage use of all areas. However, this is not the particular concern of this study: the usable space metric is not intended as a measure of actual enclosure use but of that space which is accessible by the animals and has the potential for use. Although actual use of space is important for animal managers and caregivers to pay attention to (not least because unused space is a waste of limited resources), it is not the focus here.

Additionally, a score of usable space may miss some important components of exhibit quality, particularly complexity. Environmental complexity has often been suggested as more important than exhibit space in terms of benefits to animals (Wilson, 1982; Goerke et al., 1987; Maple, 2007; Coe et al., 2009; Ross et al., 2011; Herrelko et al., 2015). However, this does not devalue the use of a usable space measure. Ross et al. (2011) point out that "these findings [regarding importance of spatial complexity over size] do not negate calls for larger spaces to improve captive wellbeing. Indeed, we are unaware of any reports that have empirically determined that providing too much space is detrimental to captive primate welfare" (2011, p. 203). Usable exhibit space and complexity will often be tightly connected, in both directions. Enclosure size affects the level of potential complexity – a larger enclosure has more space to add features which can increase complexity and use (Poole, 1991). As well, an increase in complexity will give an increase in usable space; and so usable space will reflect complexity as much as simply enclosure dimensions. There is the possibility of even constructing a score of exhibit complexity, as something like a ratio of total usable space to floor space. Much more so than traditional measures of enclosure size, usable space measures will give some representation of exhibit complexity.

Due to the nature of usable space calculations, a large but barren enclosure could still have a high usable space score while being low in quality. For example, when we include floor space (which we generally should, as it is a large part of the usable space), then one way of increasing the overall score is simply to add more floor space, without focussing on vertical complexity. For arboreal animals, such as orangutans, this seems like the wrong result, as elevated space is much more "usable" to them than ground space. This may simply be a separate issue of enclosure quality and provision of species-specific features (size isn't everything, after all), but is certainly worth keeping in mind. There will, however, generally be overlap – the sorts of features which increase usable space, particularly vertically, will also be the sorts of features which increase environmental complexity. Where this is not the case, we need to keep in mind that while usable space is a useful metric for scoring and comparing different exhibits, it should not necessarily be used in isolation from other assessments of exhibit quality.

Benefits of the Approach

There are several benefits to using the usable space metric developed in this paper. It allows for assessment of exhibit quality, comparisons between exhibits, assessment of potential exhibit improvements and the possibility to improve exhibit size guidelines and recommendations.

As discussed above, the usable space measure is not a perfect reflection of exhibit quality, as it does not entirely account for complexity, however, this measure will be closely linked with exhibit quality and certainly comes closer than existing basic measures of exhibit size. This method will also allow for comparisons between exhibits. Again, such comparisons are currently based either on basic exhibit size measurements, or on subjective assessments of how good or bad an exhibit seems to the observer. A usable space score provides an objective means of making more meaningful comparisons between exhibits. It must be kept in mind that such comparisons are only meaningful when comparing similar exhibits – those housing the same species (or species with the same requirements) and those for which the same sets of features have been measured and included in the score. There is no really meaningful way to perform an absolute comparison of, say, a Tasmanian devil and capuchin exhibit, except perhaps in regards to their relation to recommended or average usable space requirements for each species, as will be discussed further on.

Usable space calculations give us a means for assessing the benefits provided by possible exhibit improvements, as well as for coming up with the best ways to create improvements. By understanding the usable space calculation and which features contribute to it, we gain means to figure out how to increase the usable space of existing exhibits, or to build new exhibits that maximize usable space. One of the basic ways to increase usable space is still to increase exhibit size in terms of floor space. For entirely terrestrial animals, such as most hoofstock, this will be the primary method for increasing usable space. Another method for arboreal animals is through modifying walls or ceilings to allow for climbing – for example through use of mesh, hand-holds or cargo nets (Maple and Finlay, 1989). Mesh is often avoided, due to its unnatural appearance, but its contribution to usable space is important and methods of using climbable walls and ceilings while still maintaining a naturalistic appearance should be investigated. As seen in this study (and as found by Wilson, 1982), these factors can account for a high proportion of usable exhibit space and this means these values may represent the easiest way of increasing usable surface area within an exhibit. It is important again here to remember not to use usable space calculations without attending to the habits of the animals involved – for example, the pygmy marmoset exhibit showed 18% of the usable space as contributed by the floor area, but the monkeys rarely if ever use this space. Following Kitchen and Martin (1996) and Maple and Finlay (1989), finding ways of encouraging more use of this space – for example by providing woodchip for foraging – may help open up a lot of spatial opportunities for the animals.

Overall, it is likely to be more beneficial to increase usable space through increasing the complexity of an existing exhibit as opposed to replacing or upgrading. Due to space limitations within zoos, exhibit size will be restricted. It is, however, possible for zoos to increase the usable space available for animals by increasing use of the vertical dimension – adding platforms and pathways that create more spaces the animals are able to use and occupy. The exact methods used to increase usable space will depend on the particular exhibits and species, requiring the understanding of the species' natural history as discussed in the previous section, but this measure allows for calculation of the change in usable space under different exhibit modifications and provides an excellent way of quantifying the value of such changes.

Finally, this work could have important implications for exhibit size recommendations. Although this project was not one of determining what the ideal recommended exhibit sizes for animals should be – rather of improving the ways in which we measure current exhibits – these measures could be useful in building future recommendations. Though we are able here to give a measure of usable space, this is not particularly meaningful without comparison to recommendations of ideal exhibit size. As current recommendations are usually based on floor space rather than more complex usable space, this will not give us much of a basis for determining whether exhibits are suitable. However, usable space recommendations could be incorporated into future exhibit recommendations and guidelines. Kelling and Gaalema (2011) note that there are not enough quantitative recommendations for exhibit design. Although there is a general consensus that there should be large and complex exhibits, this has not often translated into specific recommendations. Ross et al. (2011) make a similar point regarding "questions about if and how enclosure size for captive primates should be regulated. Currently, there is a tremendous range of enclosure size guidelines.... While each of these documents specifically notes the importance of other considerations such as vertical height and environmental complexity, it is clear that there is very little consensus on how much space is necessary to provide to this and other species. Given the push to formulate scientifically based management standards, further research that accounts for a range of environmental variables is necessary, especially studies that help elucidate the value of all the space that captive primates are not using" (2011, p. 206). It is our hope that having a measure of usable exhibit space might go some way toward being able to develop such guidelines, though it will take separate research to determine the usable space requirements for different species.

We can compare the measures found in this study to the traditional enclosure dimension measures to see their advantage. Usual space measures for this exhibit would simply represent the floor space (24 m^2) and the exhibit height (3.05 m) without taking into account the use of these additional features. For example, the EAPA requirements for pygmy marmoset housing simply state that the animals require floor space of 2.5 m × 3.0 m (7.5 m^2) and a height of 3 m (EAPA, 2000). Although reference is made to suitable provision of climbing structures, this is quantified by number of platforms and pathways rather than the space afforded by these. If we were to only consider floor surface area in this way, we would be underestimating the usable surface area of the exhibit by a factor of almost 5. Using the traditional methods, we could say that this marmoset exhibit exceeds minimum requirements by more than three times, but if we include all usable surface area this is much higher. Using the minimum EAPA requirements, we come to a required volume of 22.5 m^3. The total exhibit volume was calculated at 68.27 m^3, which is over three times the required space. Using the measure of usable volume, this comes out at 20.14 m^3. This cannot be compared to the total required volume, as this volume would necessarily also include the empty space for keeper access and animal movement. Expression of exhibit requirements in terms of percentage of usable volume within the required space, or just an absolute value of minimum usable volume, would help capture this.

There are a number of methods by which usable space recommendations for exhibits could be developed, such as preferred social distance, animal body size, preference testing, and exhibit use studies (Innis et al., 1985; Petherick, 2007). Of some use may be information about home range or territory space in the wild, though zoos are often unlikely to have the resources to match this space, and as these can often reflect resource availability rather than space requirements *per se*, conclusions based on wild ranges may be misleading. Size requirements will depend on species-specific factors, as well as individual preferences of the animals involved. Preference tests can be a valuable tool in determining how much extra space is important to the animals – if the animals will work to gain access to extra space (as has been shown in studies on hens and rodents), then this space must be valuable to them; and at the point at which they would stop working for it, then it becomes welfare-neutral (Petherick, 2007). Finally, exhibit use studies can tell us how much of the space, and what type of space, the animals prefer to use, and can shed light on what would be an appropriate amount of usable space.

CONCLUSION

There are many reasons to think that the size of exhibits provided for zoo animals will have important effects on their lives and welfare, through allowing more opportunities for choice and control, to exhibit natural behavior, and to maintain social groups. Currently, most exhibit size recommendations only refer to basic exhibit dimensions, without considering the space afforded by usable features within the exhibit. Here, we used measurements of a sample pygmy marmoset exhibit to develop two possible methods for measuring the usable space of zoo exhibits – usable surface area and usable volume. For arboreal species like the marmosets, usable volume calculations seem to better capture the contribution made to usable space by different exhibit features. Usable surface area calculations are simpler and could be applied to most solely terrestrial species. Having a measure of usable space in place will give a better indication of the quality of different exhibits, and allow for comparisons between exhibits. Use of digital methods for modeling and measuring exhibits may help make the process faster and more accurate, and this is a promising direction for future research. The introduction of the construct "wellness" suggests that future zoo exhibits will be aspirational rather than simply regulatory in their scope and function (Maple and Perdue, 2013). With an increasing focus on positive animal welfare, zoo professionals aim to ensure animals are thriving in their environment, as opposed to merely coping (Maple, 2014). Increasing usable space is one way to promote this end. If we try to arrange exhibit features to encourage thriving, exhibits will need sufficient size and complexity to achieve these results. Measurement of usable volumetric space will permit zoos to enhance wellness by attention to the details of space and the usable features within that space.

AUTHOR CONTRIBUTIONS

HB conceived the method, performed the measurements and calculations, and wrote the manuscript. TM contributed to the idea and planning, and helped to shape the manuscript.

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High-Tech and Tactile: Cognitive Enrichment for Zoo-Housed Gorillas

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The field of environmental enrichment for zoo animals, particularly great apes, has been revived by technological advancements such as touchscreen interfaces and motion sensors. However, direct animal-computer interaction (ACI) is impractical or undesirable for many zoos. We developed a modular cuboid puzzle maze for the troop of six Western lowland gorillas (*Gorilla gorilla gorilla*) at Bristol Zoo Gardens, United Kingdom. The gorillas could use their fingers or tools to interact with interconnected modules and remove food rewards. Twelve modules could be interchanged within the frame to create novel iterations with every trial. We took a screen-free approach to enrichment: substituting ACI for tactile, physically complex device components, in addition to hidden automatic sensors, and cameras to log device use. The current study evaluated the gorillas' behavioral responses to the device, and evaluated it as a form of "cognitive enrichment." Five out of six gorillas used the device, during monthly trials of 1 h duration, over a 6 month period. All users were female including two infants, and there were significant individual differences in duration of device use. The successful extraction of food rewards was only performed by the three tool-using gorillas. Device use did not diminish over time, and gorillas took turns to use the device alone or as one mother-infant dyad. Our results suggest that the device was a form of cognitive enrichment for the study troop because it allowed gorillas to solve novel challenges, and device use was not associated with behavioral indicators of stress or frustration. However, device exposure had no significant effects on gorilla activity budgets. The device has the potential to be a sustainable enrichment method in the long-term, tailored to individual gorilla skill levels and motivations. Our study represents a technological advancement for gorilla enrichment, an area which had been particularly overlooked until now. We wholly encourage the continued development of this physical maze system for other great apes under human care, with or without computer logging technology.

Keywords: animal cognition, behavior, challenge, *Gorilla gorilla gorilla*, maze, puzzle, technology, welfare

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INTRODUCTION

Environmental enrichment refers to additions or alterations made to the environments of captive animals which enhance their physical and/or psychological well-being (Newberry, 1995; Shepherdson, 2003). Zoo-based enrichment has advanced over the past two decades, in tandem with general advancements in zoo animal welfare science (Alligood et al., 2017; Ward et al., 2018).

Two notable advancements in enrichment have been (1) an increased focus on cognitive enrichment, and (2) increased incorporation of technology into enrichment, particularly for great apes. These two advancements overlap; computer-based tasks are increasingly provided to zoo-housed great apes as a form of cognitive enrichment.

Cognitive enrichment is a subset of enrichment which "(1) engages evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of wellbeing" (Clark, 2011 p.6). It should also involve some form of reward for the animal, which could either be internal (such as a mental state of satisfaction), or external (such as food or another valued resource; Clark, 2017). Cognitive enrichment is gaining interest and uptake within the zoo community (Clark, 2017). "Traditional" enrichment can often cover multiple bases such as providing animals with sensory stimulation, extending foraging time, and permitting consummatory (i.e., feeding) behavior; yet little consideration is given to the cognitive mechanisms behind these behaviors and whether in fact the enrichment is particularly challenging to respond to, particularly over repeated uses over time (Clark, 2017). Cognitive enrichment aims to focus on the specific cognitive skills known for a species/individual, and how best to stimulate the expression of these skills. Cognition cannot be observed directly and therefore must be inferred through behavior (Shettleworth, 2010). Cognitive enrichment is supported by evidence that many animals are highly motivated to explore and acquire resources under a variety of conditions, even when resources can be acquired little, or no cognitive or physical effort (Wood-Gush and Vestergaard, 1991; Wemelsfelder and Birke, 1997). In other words, evidence suggests that animals often prefer to be challenged to acquire food, as long as the challenge can be overcome (Meehan and Mench, 2007; Špinka and Wemelsfelder, 2011).

Great apes under human care are compelling candidates for cognitive enrichment; their cognitive skills comparative to humans have been studied relatively intensively, and they can often habituate rapidly to novelty (for reviews see Ross, 2010; Tomasello and Herrmann, 2010; Clark, 2011). Recent attempts at great ape cognitive enrichment have included pipe maze puzzles for chimpanzees *Pan troglodytes* (Clark and Smith, 2013), and a chimpanzee pipe feeder aimed to simulate natural foraging patterns (Yamanashi et al., 2016). These are both low-tech approaches to cognitive enrichment, in the sense of not having associated computer technology or mechanical components.

Great ape enrichment increasingly uses computer technology; this includes touchscreens (via a static computer monitor or computer tablet), projected images, and embedded microchips (Perdue et al., 2012; Kim-McCormack et al., 2016). A review of published great ape enrichment focusing on "digital enrichment" up to 2016 (Kim-McCormack et al., 2016) reported six studies on orangutans *Pongo pygmaeus*, three on chimpanzees, and none on bonobos *Pan paniscus* or gorillas *Gorilla gorilla gorilla.* There were a further 27 cited studies on technology without a focus on enrichment; for example for pure animal cognition research. It is interesting to note that six of the nine studies on great ape "digital enrichment" were published in scientific journals within the remit of animal behavior, zoo science or related fields. The other three were published in ACI or human-computer interaction (HCI) conference proceedings; this is the convention for academics in these fields but means that some relevant technological advances may not be easily known by, or accessible to, the zoo community.

Computer touchscreen interfaces can be used to provide great apes with cognitively challenging tasks such as stimulus discrimination/matching and 2D maze navigation, and to automatically dispense food rewards. These interfaces can be used to study animal cognition, provide enrichment, or indeed both (Iversen and Matsuzawa, 2001; Tarou et al., 2004; Perdue et al., 2012; Egelkamp and Ross, 2018). Computer touchscreen systems can also help to evaluate other forms of enrichment; McGuire et al. (2017) recently employed a computer touchscreen system to measure the effect of browse presence on gorilla cognitive bias or "mood" (i.e., to evaluate browse as a form of enrichment). Hopper et al. (2018) used a computer touchscreen to assess food preferences in a single zoo gorilla, which could then inform which foods were used as rewards for this individual in future enrichment. Touchscreen systems can be extremely beneficial to enrichment efforts, because subjects' responses to virtual (on-screen) stimuli can be logged automatically, and many digital stimulus combinations can be provided without the need for cumbersome or expensive physical apparatus (Cronin et al., 2017). Recently, Schmitt (2019) proposed a new, portable computer touchscreen system known as the zoo-based animal-computer-interaction system (ZACI) for application in zoos, allowing dual-purpose cognitive testing and enrichment. Similarly, the Arena System (Martin et al., 2014) allows cognitive testing of captive great apes, with an inbuilt food reward dispenser.

Technology can also provide great apes more interactive opportunities within their exhibits; Microsoft Kinect® motion sensors, depth-sensing cameras and projectors have recently allowed zoo orangutans to control and interact with colored lights and images (Webber et al., 2017; Scheel, 2018). Touchscreen computer tablets with "painting" packages have also been provided to great apes in several zoos via the "Apps for Apes" program (Smith, 2011). Recently, Grunauer and Walguarnery (2018) found that digital painting (on a tablet) had the same efficiency at reducing some stereotypical and stress-related behaviors in zoo-housed chimpanzees as having access to a real brush and paint, but the latter activity had longer term effects. More conservative uses of technology have included providing great apes in North American zoos with food dispensers, water sprays or air canons, thus giving them more choices and control over environmental resources (reviewed by Clay et al., 2011).

Despite their many benefits, computer touchscreen systems are impractical or undesirable for many zoos housing great apes. In terms of practicality, touchscreen tasks usually require extensive animal training, modification to the existing enclosure (mesh, access, and power supply), and ongoing maintenance of the system (Clay et al., 2011). Unlike more controlled laboratory settings and dedicated research centers, animals in typical zoo settings have variable and unpredictable diets, husbandry schedules, and distractions such as visitors (McGuire et al., 2017).

Furthermore, there is mixed evidence that computer touchscreen tasks are consistently enriching for great apes. Yamanashi and Hayashi (2011) found that the activity budget of chimpanzees participating in touchscreen tasks were comparable to that of wild chimpanzees, and Perdue et al. (2012) found no negative behavioral effects of a computer touchscreen system for orangutans. In contrast, performance of stress-related behaviors increased in great apes when touchscreen tasks were relatively more complex (chimpanzees: Yamanashi and Matsuzawa, 2010), when a subject made errors on tasks (chimpanzees and gorillas: Wagner et al., 2016), or when a subject was uncertain about whether their response was "correct" or not (orangutans: Elder and Menzel, 2001; chimpanzees: Itakura, 1993; Leavens et al., 2001). It is therefore important not to automatically assume all computerized tasks are enriching to great apes, but rather evaluate the animal's wellbeing in response to these tasks.

Regardless of the benefits of touchscreens discussed above, many zoos do not wish to display their great apes interacting directly with computer screens or other digital technology, due to the ethos of the zoo itself or public perception. The level of desired environmental (and enrichment) naturalism is a subjective choice that should be respected, and interestingly this may differ significantly across different parts of the world. Clay et al. (2011) performed a survey of technology for great apes in a small sample North American zoos (N = 5), and found that respondents were broadly positive about technology and had a desire to increase its use. Positive visitor perceptions have also been found in response to great apes interacting with computerized systems in North American Zoos (Perdue et al., 2012). These are small samples and comparable data for other parts of the world are lacking; but the senior author's experience of working in United Kingdom zoos for over almost two decades suggests that they see more value in naturalistic enrichment (personal communication). This does not mean that technology cannot be used or cannot be useful in these zoos; rather it encourages us to investigate screen-free alternatives.

When reviewing literature on "cognitive" and/or "technological" enrichment for great apes, we identified an important gap in research efforts. Providing great apes with complex cognitive enrichment that does not require their direct interaction with computers (i.e., ACI) is relatively unexplored territory. In addition, the literature review by Kim-McCormack et al. (2016) revealed an absence of studies specifically on technological enrichment for gorillas. The overarching aim of the Gorilla Game Lab project was to develop cognitive enrichment for Western lowland gorillas housed at Bristol Zoo Gardens, a zoo which was in favor of the technological advancement of enrichment, but was seeking a screen-free option. Therefore, we wished to design a complex, physical interface for gorillas. The process of designing the device is summarized elsewhere (Gray et al., 2018), but in summary the key design features were:

I: Modular Maze

Studies demonstrating the cognitive skills required for maze navigation by great apes have mainly used virtual paradigms (i.e., computer screen tasks; for example Iversen and Matsuzawa, 2001; Beran et al., 2015) but also see manual finger mazes for chimpanzees (Völter and Call, 2014a,b). These studies tend to use the same repeating obstacle such as a ledge or wall, placed in different orientations within a 2D plane. Leading from previous research on 3D modular mazes for chimpanzees (Clark and Smith, 2013) we chose to create a modular cuboid puzzle maze, where different types of 3D obstacles could be placed in different locations within a 3D frame. We created 12 module designs (including the camera and blank modules) within 12 frame locations, giving rise to many thousands of possible arrangements.

II: Tactile (Otherwise Known as "Tangible," "Physical," or "Haptic")

The sense of touch is important to gorillas; they may not be as manually dexterous as other great apes and rely more on physical strength than manual skill, yet gorillas habitually use tools in captive settings (Boysen et al., 1999; Parker et al., 1999) and have been observed to interact with devices such as artificial termite mounds in zoos (Lonsdorf et al., 2009). Diverse and sometimes intricate food-processing behaviors involving the hands and mouth have been documented in wild mountain gorillas *Gorilla beringei beringei* (Byrne, 1999; Byrne and Byrne, 2001).

III: Extractive Rewards

We exploited the primate characteristic of extractive foraging; in other words their ability to process embedded food resources, with or without tools (Barrett et al., 2017). This complements the device being highly tactile, and it is relatively simple to use the frequency of reward items extracted as a gauge of an individual's "success" at the device.

IV: Playful Interaction

Play is a broadly accepted indicator of psychological well-being in primates (Held and Špinka, 2011; Ahloy-Dallaire et al., 2018; Yamanashi et al., 2018). The device was designed to promote playful interaction by drawing from aspects of human game play; particularly tactile arcade-type games where an object is extracted from a maze (Pons et al., 2015).

V: Hidden Technology

We decided to conceal technology within the device so that the gorilla-device interface remains tactile rather than digital. The majority of the technology is placed on the human side of the device; we can automatically and remotely log subject's interaction with the device using non-invasive sensors tracking the location of the gorilla's fingers/tools, the location of reward items, and facial recognition. Evaluation of the technological aspects of the device will be covered in future publications.

The current study is the first evaluation of the Gorilla Game Lab device as a form of cognitive enrichment. The effectiveness of a new enrichment item is typically evaluated by measuring the change in animal behavior, when the item is present and absent (an "AB" design; Young, 2013). To this end, we used the definition of cognitive enrichment by Clark (2011, p. 6): cognitive enrichment "(1) engages evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of wellbeing" (Clark, 2011 p.6). As stated earlier, cognitive enrichment should also involve some form of putative reward for the animal, which in our case was an external food reward. We predicted that the device would stimulate problem-solving behaviors; we also predicted that device presence and use would be associated with more playful and relaxed behaviors within the group as indicators of wellbeing. Furthermore, we predicted that device presence and use would not be associated with the performance of abnormal or aberrant behaviors. We predicted that the device would engage the gorillas' time, but that there would be significant individual differences in device use, with the silverback male using it the least and youngest adult females using it the most. In order to examine the effect of the device, we examined each gorilla's behavioral responses to the device: in terms of direct device use and broader behavioral changes, comparing behavior before the gorillas had any exposure to the device, and to post-exposure on days when the device was absent and present. We also assess whether the device was fit for purpose from a practical standpoint, which is not a part of the definition of cognitive enrichment but would limit its implementation in future.

MATERIALS AND METHODS

Study Subjects and Housing

Data were collected between July 2018 and January 2019 at Bristol Zoo Gardens, Bristol Zoological Society, United Kingdom. Subjects were a troop of six Western lowland gorillas (**Table 1**) living in the "Gorilla Island" exhibit. The exhibit comprised a large outdoor moated island (2,048 m^2) adjoined to a modern indoor enclosure (161.9 m^2) with nine interconnected on-show and off-show dens at ground level and a first storey. Enrichment trials took place in one ground level on-show den with the best lighting and visibility for filming (**Figure 1**). This den (8.8 m length, 3.7 m width, and 5.4 m height) was of concrete and brick construction, with a floor-to-ceiling visitor window, assorted smaller windows and skylights, a wooden climbing frame with beams and interweaving ropes, several nesting platforms and connections to other dens, and outdoors via steps and a bridge above the indoor public area.

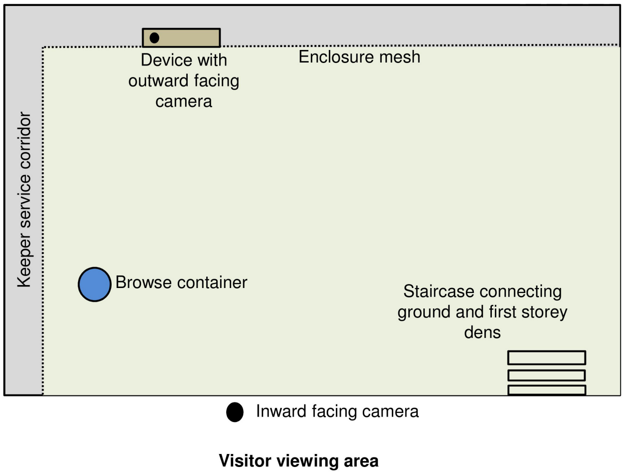

FIGURE 1 | Bird's eye view of the gorilla experimental den and camera setup.

The indoor enclosure was cleaned daily between 09:00 and 11:00 h. Subjects were fed two to five times per day, including an outdoor visitor talk and feed at 12:30 h, but feeding never took place during enrichment trials. The normal diet consisted of a wide variety of vegetables and fruit (approximately 90% root vegetables and 10% fruit and nuts), eggs, fresh browse (see description of stick tools below), and a commercial primate biscuit. Fresh water was available at all times from drinking pipes, and other drinks such as diluted fruit juice and herbal tea were offered by keepers throughout the day. Routine enrichment items provided daily by keepers (but not during enrichment trials) included cardboard boxes and tubes; large plastic barrels and balls; and different types of fabric. Some gorillas had previously experienced a "puzzle box" feeder in the same den as enrichment, but it was never formally evaluated and was placed in a different location to the new device. The puzzle box had been an acrylic-fronted wooden box with horizontal shelves, and food could be navigated from top to bottom using fingers or tools.

TABLE 1 | Details of gorillas housed at Bristol Zoo Gardens.

Name	Sex	Age at time of study (yrs)	Rearing type	Tenure in Bristol Zoo troop (years)	Kin within group	
					Mother	**Father**
Jock	M	35	Parent	15	–	–
Kera	F	13	Hand	10	–	–
Touni	F	10	Parent	3	–	–
Kukena	F	7	Parent	7	–	Jock
Afia	F	2	Hand	2	Kera*	Jock
Ayana	F	1	Parent	1	Touni	Jock

*Subjects arranged in decreasing order of age. All subjects were captive born. *Afia was also partially surrogate-reared by a 38 year old female (Romina) who died mid December 2018. Another adult female (Kala) arrived at Bristol Zoo Gardens toward the end of the study in October 2018. Both Romina and Kala were excluded from the current study; they were off show for most of allotted study period, had incomplete sets of baseline observations and did not use the enrichment.*

Enrichment Device

Summary

The device consisted of three parts: the frame, the modules, and computer technology backend. The technology within the backend was in development during the current study, and will not be discussed further here, except for footage captured from an internal camera. The operation of the device was independent from the technology meaning that it could be used without any automatic logging. The gorillas could not interact with the technology directly because the internal camera and sensors were protected behind physical barriers.

Device Frame

The frame was a box (outer dimensions: 850 mm length, 650 mm width, and 80 mm depth) made from 12 mm thickness plywood (**Figure 2A**). Twelve modules (arranged in 3 rows and 4 columns) slotted into the frame (**Figure 2B**). Most of the frame and module components (see section "Device Modules") were held together with wooden pegs inserted into slots, or using finger (comb) joints. The back of the frame was closed up using a hinged wooden door with a magnetic catch. All wooden and plastic components were laser cut, allowing fine detail, and precision sizing.

Device Modules

Each module was a rectangular cuboid (plywood, outer dimensions 200 mm length, 200 mm width, and 60 mm depth), and the inner components were wooden and/or acrylic plastic (**Figure 2B**). The front of each module was a 200 mm square face plate made from 5 mm thickness clear acrylic plastic. The module size was chosen to prevent module access holes being occluded by the mesh (gauge 100 mm length × 50 mm height). The faceplate either had circular holes cut into it (30 mm allowed gorilla finger access, 15 mm allowed stick tool access), or an elongated oval reward slot (80 mm length, 40 mm width for direct removal of food rewards). The hole diameters were determined from previous research at a different zoo (F Clark, unpublished).

The general concept of the device was for gorillas to interact with different connected modules and move food rewards through them, from the top row of the frame (pre-loaded with food at the beginning of the trial) to the bottom. This involved moving a food reward out of one module, via some sort of obstacle such as a ramp or several small shelves inside the module, and into another module which may either be to the side of, above or below the previous module. The side of each module contained circular holes (30 mm diameter), to allow the food reward to move horizontally, and vertically between connected modules.

The design of the twelve different modules used in the study, and their arrangement (frame location) for each enrichment trial, are provided in **Figure 3** and **Table 2**. One frame location was always occupied by an internally mounted outward facing camera (GoPro© HERO 7, GoPro, Inc., CA, United States) which the gorillas could not access. At least two other frame locations were blank modules (i.e., blank pieces of wood rather than plastic face plates). The first three enrichment trials had one column of modules down the center of the frame, and the columns on either side were blocked with blank face plates. In enrichment trials 4 and 5, the camera module was moved from the top row of the frame to the bottom, in attempt to improve footage capture of gorillas using the device. After trial 5 it was decided to put the camera back into the top row for the final trial 6. To ensure that gorillas could remove food rewards from the bottom row of modules only and not higher up, modules III, VI, and VII had interchangeable face plates that could either contain finger/tool holes or a reward slot, depending on where they were located in the device.

FIGURE 2 | Enrichment device. **(A)** Empty device frame. **(B)** Example modules within frame. The camera module is in the top right (frame location A3). The finalized module designs are shown in **Figure 3**.

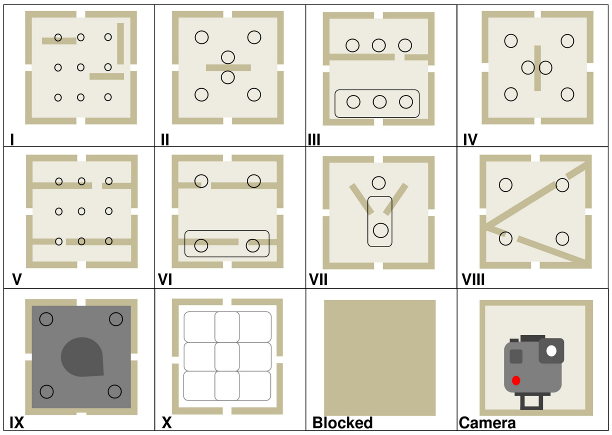

FIGURE 3 | Design of the twelve enrichment device modules. Round circles are finger or tool holes. Elongated ovals are reward slots. Modules I–IV contained vertical and horizontal wooden platforms inside. Modules VII–VIII had platforms slanted at 45°. Module IX was painted dark gray with a static wooden wedge inside. Module X contained three white hollow plastic boxes, and the holes inside each could be aligned by gorillas sliding the boxes left and right to allow the food reward to fall through. Modules III, VI, and VII either had a face plate with finger/tool holes *or* an oval reward slot. Refer to **Table 2** for frame locations per enrichment trial.

TABLE 2 | Location of modules in the enrichment device frame during six enrichment trials.

	Type of module					
Frame location	**Trial 1**	**Trial 2**	**Trial 3**	**Trial 4**	**Trial 5**	**Trial 6**
A1	Blocked	Blocked	Blocked	V	V	V
A2	II	V	III	VI	VI	Camera
A3	Camera	Camera	Camera	IV	IV	IV
B1	Blocked	Blocked	Blocked	IX	IX	IX
B2	IX	VIII	IX	VIII	VIII	VIII
B3	Blocked	Blocked	Blocked	X	X	X
C1	Blocked	Blocked	Blocked	III	III	VI
C2	IV	VI	VIII	I	I	I
C3	Blocked	Blocked	Blocked	VI	VII	VII
D1	Blocked	Blocked	Blocked	Blocked	Blocked	Blocked
D2	III	III	VI	Camera	Camera	VI
D3	Blocked	Blocked	Blocked	Blocked	Blocked	Blocked

Frame location is a two character code responding to the column and row position in the frame, e.g., the location A2 (top center) contained module II in Trial 1. Refer to ***Figure 3*** *for module designs.*

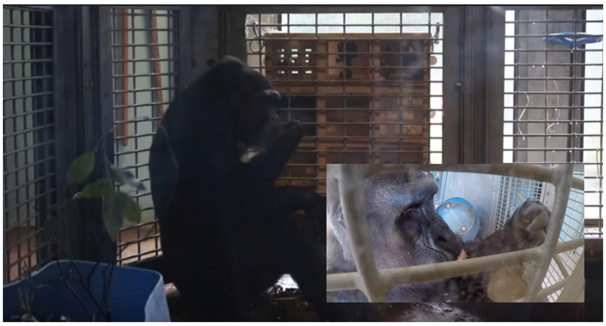

FIGURE 4 | Photographs of gorillas using the enrichment device. Main image: captured from inward facing camera, gorilla sat in front of the device with the browse bucket in the foreground. Inset: captured from outward facing camera, gorilla using a stick tool on one of the modules, and with browse container tipped over.

The device was "solved" when a gorilla moved a food reward into the bottom row of modules, where it could then be accessed from a reward slot and eaten. Unshelled peanuts supplementary to the daily diet were used as the food reward, because they were of an appropriate size (approximately 40 mm length, 15 mm width) and keepers anecdotally reported they were a valued food item. Given that the food rewards were available in one trial per month, the animal care team approved the additional calorific intake. At the keeper's request, we did not use non-food reward items such as tokens in the current study. Stick tools were available during all trials; fresh browse was provided on a daily basis inside a blue plastic container (220 L volume) approximately 1 m away from the device (**Figures 1**, **4**). The choice of browse included sticks and branches with a variety of lengths, diameters and degrees of flexibility, as well as straw.

Enrichment Trials

The device was presented for six trials, approximately once per month, on the following dates: (1) July 25, 2018, (2) August 16, 2018, (3) October 11, 2018, (4) November 29, 2018, (5) December 06, 2018, and (6) January 10, 2019. This schedule was chosen because it replicated how often the keepers felt they could feasibly implement this type of enrichment under normal (non-research conditions). It also allowed time for logger data to be evaluated between trials, and make any repairs or modifications to the device if necessary. It should be noted that, because the device operated well and was fit for purpose, it was not actually necessary to make any modifications between trials. Each trial was 60 min duration (11:00–12:00 h) following morning cleaning, and usually took place midweek to avoid conflicting with other keeper commitments. Trial setup took place during the last 10 min of indoor cleaning when gorillas were shut out of the den. One keeper and one researcher entered the keeper service corridor and installed the device on the keeper's side of the enclosure mesh. It was installed on the wall furthest away from the visitor window to minimize any potential distraction by visitors. Installation was achieved quickly using stainless steel D-shackles connecting the corners of the device to the enclosure mesh, while ensuring the mesh did not occlude module access holes on the gorilla's side.

In preparation for a trial, the unblocked modules along the top row were loaded by hand with fresh nuts (24 equally spread across the top row), being careful not to knock them down into the modules below. The outward facing camera was switched on and angled to capture a facial view of the gorilla(s) using the device. One researcher or a volunteer operated the inward facing camera (Sony HDR-CX405 Handycam Camcorder, Sony Corporation, Tokyo, Japan) positioned on a tripod in the indoor visitor viewing area. The camera operator made adjustments to the camera's location, tripod height and angle during a trial, in response to the gorilla's movements and changing natural light levels. Once the device was safely installed and loaded with nuts, the keeper let the gorillas back indoors, and the trial began at 11:00 or as soon as possible thereafter. At 12:00 h or as soon as possible thereafter, the device was removed from the enclosure mesh from the keeper's side. Any residual food rewards were removed using a stiff, dry brush, and the device was stored out of sight ready for the next trial.

All gorillas within an arm's reach of the device during a trial were coded from the recorded video. The outward facing camera was used to confirm which gorillas were observing the device within an arm's reach by looking at their head orientation and gaze. Recorded trials were played back using Windows Media Player® version 10 (Microsoft©, NM, United States) and scored by one observer using continuous sampling (Altmann, 1974; Martin and Bateson, 2007). The following data were scored for each gorilla that was within an arm's reach of the device and entered into Microsoft Excel: all frequencies and durations of device use (observing or contacting the device); type of device use (observe, poke with fingers or tool, shake, and mouth contact); the frame location contacted (**Table 2**); all successes (extraction of food rewards); and any abnormal behaviors performed while also touching or observing the device (Ethogram: **Table 3**). "Arm's

TABLE 3 | Ethogram of broad state behaviors observed in gorillas during focal follows around the exhibit, on days when the enrichment was present and absent.

Broad state behavior	
Forage/feed	Search for food. Or consume food/drink
Object exploration	Interact with enrichment device or routine enrichment such as cloth or cardboard
Locomotion	Walk, run, climb, or swing
Rest	Lie, sit, or stand. May be awake or asleep
Vigilance	Direct an alert, fixed gaze toward something in the environment including a conspecifc, keeper/staff, or observer
Play	Following Burghardt (2005), play is defined as behavior which is (a) not "fully functional" (i.e., not contributing to current survival needs); (b) self-rewarding; (c) is not a "serious" form of the behavior; (d) is performed "repeatedly." but not stereotypically; and (e) initiates when the subject is in a "relaxed field" (not in the presence of current threats). Can be lone or directed toward a conspecific or object
Affiliative	Allogroom. Or direct sexual behavior toward conspecific. Or friendly interaction with conspecific
Aggressive	Direct non-contact threat toward conspecific. Or direct hurtful contact toward conspecific
Abnormal/ aberrant*	Rock, repeatedly regurgitate and reingest food, pluck hair, rough-scratch, or perform other self-injurious or repetitive behavior
Other	Body maintenance including autogroom, defecate, or urinate. Or any other behavior which does not fall into one of the above categories. Rarely occurring
Out of sight	The subject cannot be observed within the exhibit

*Ethogram definitions based on Clark et al. (2012) and a longitudinal data collection protocol used at Bristol Zoo Gardens (unpublished). *Abnormal/aberrant behaviors were not observed in the study subjects.*

reach" referred to the gorilla's own arm, to take into account significant size and age differences in the troop.

Wider Behavioral Observations: Focal Follows

In order to examine if device exposure had a wider effect on gorilla behavior when they were not necessarily within arm's reach of the device (i.e., wider than captured by the video footage of device use), focal follow observations were made on the troop under three conditions. The first condition was a pre-exposure baseline when the gorillas had not received any exposure to the device. Observations took place on six dates over a 2 month period (May 2, May 7, May 22, June 12, June 29, and July 3, 2018). The second and third conditions alternated over time: the second condition was during the enrichment period when the device was implemented on that day (device present), and the third condition was during the enrichment period but when the device was not used that day (device absent). These observations took place over a 2 month period between November 2018 and February 2019, on three dates during the enrichment period when the device was present (November 29, 2018, December 06, 2018, and January 10, 2019), and three dates when it was absent (December 11, 2018, January 27, 2019, and February 05, 2019). These observations came at the end of the study (i.e., trial 4 onward), so the gorillas had received several months of exposure to the enrichment device by this point. Observations were made following an established behavior observation protocol used on the troop over the past 5 years (developed by Bristol Zoological Society, unpublished). One observer used focal animal sampling to observe each gorilla for 30 min per day, recording state behavior (**Table 3**) at 1 min intervals. Subjects were observed randomly without replacement (i.e., once per day in random order) between 11:00 and 15:00 h. Due to the long time period, it was necessary for one volunteer to make observations for the first condition, and a second volunteer made observations for the second and third condition.

Statistical Analyses

Analyses were undertaken using SPSS version 24 (IBM Corp, NY, United States). Data were inspected for normality and non-parametric tests were subsequently selected for analysis. Median averages are presented along with interquartile ranges (IQR).

Enrichment Trials

Using data coded from the camera footage, the total duration of device use across six enrichment trials was compared between subjects using a Kruskal-Wallis test with a p value set at ≤ 0.05, followed by multiple *post hoc* pairwise Mann-Whitney U-tests with a Bonferroni-corrected p value of ≤ 0.003.

Focal Follows

Between-condition comparisons

To examine the effect of three conditions [(1) pre-exposure; (2) post exposure, device present; and (3) post-exposure, device absent] on gorilla behavior, Friedman tests were used to compare the median proportion time spent performing behavior. This yielded 40 separate Friedman tests (6 gorillas × 8 behavior categories). Where there was a significant Friedman test result, *post hoc* analysis with Wilcoxon signed-rank tests was conducted with a Bonferroni correction applied, resulting in a significance level set at $p \leq 0.017$.

Between-gorilla comparisons

To examine whether there were differences in behavior between individual gorillas, Kruskal-Wallis tests were used to compare the median proportion time spent performing behavior. Each behavior was analyzed separately, yielding 8 separate Kruskal-Wallis tests. Where there was a significant Kruskal-Wallis test result, *post hoc* analysis with Mann-Whitney U-tests was conducted with a Bonferroni correction applied, resulting in a significance level set at $p \leq 0.003$.

Ethics Statement

This study was carried out in accordance with the recommendations of Bristol Zoological Society and the University of Bristol Animal Welfare and Experimental Research Board (AWERB). The protocol was approved by Bristol Zoological Society and the University of Bristol AWERB Ref No. UIN/18/044. Gorilla interaction with the enrichment device was entirely voluntary, subjects were not deprived of their normal diet or access to other resources, and normal management conditions were maintained throughout the study.

RESULTS

Device Use: Engagement and Problem-Solving

The enrichment device was used during each of the six enrichment trials (**Figure 4**), but only five out of six gorillas physically contacted (used) it within arm's reach (**Table 4**). All of these users were females, whereas the silverback male observed the device within arm's reach as confirmed by the outward facing camera. The highest users were Touni and Kera, who used the device for around 2 h each in total (which is approximately 1/3 of the total time it was available). There was a significant difference in the total duration of device use by different gorillas ($U = 26.670$, $p < 0.001$, individual differences are shown in **Figure 5**). No self-directed behaviors or other abnormal behaviors were observed in individuals as they used the device. Only one case of device-related aggression was observed: within the first 10 min of trial 1, the highest user Touni pushed the infant Afia away from the device once to stop her accessing it.

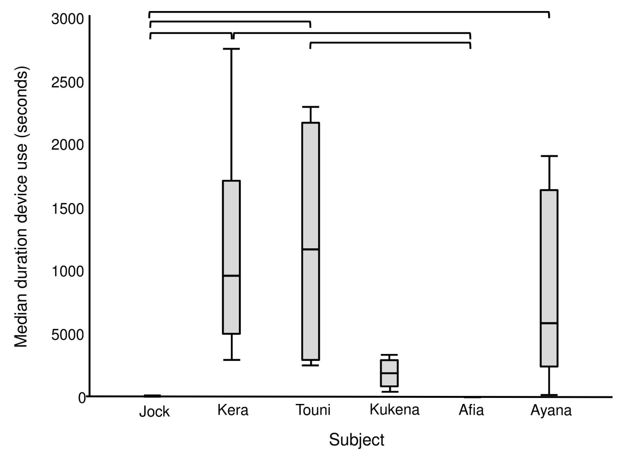

FIGURE 5 | Median duration of device use per individual gorilla summed across six enrichment trials. Includes observation and physical contact. Square brackets show significant differences between individuals, with a Bonferroni adjusted p value of ≤ 0.003.

Gorillas usually used the device in a seated position (**Figure 5**) with one hand using the device and the other hand used for postural support. The vast majority of device use involved poking into the module face plate holes, with fingers or stick tools (**Table 4**). Using the mouth (our view of the purpose of mouth use was impaired, but possible explanations include trying to suck or lick the nuts/fragments out of the holes, or to manipulate a stick tool) and shaking the device were relatively uncommon methods. We observed nuts being removed via the reward slots and never via the finger holes, although it is possible that broken nut fragments could have been removed through small holes. Tool use varied between gorillas; the percentage of use involving tools ranged from 0 to 64.2% (**Table 4**). The three tool-using gorillas (Kera, Touni and Kukena) were the only gorillas to successfully extract nuts from the device, removing a total of 22, 50 and 20 nuts from the device, respectively (**Table 4**). Touni, the highest user overall, was also the highest tool user and the most successful. In all cases but one, gorillas ate the nut rewards immediately after extracting them. The exception was during trial 3: we observed Kera extract 5 nuts from the device, and rather than eating these she formed a pile of them next to her and ate them all in one go, after a 36 min bout of device use beginning at approximately 22 min into the trial.

Device use did not appear to wane across the six trials. Duration of device use did not decline over successive trials, nor was there a clear link between the duration of use, and frequency of success extracting food rewards (**Figure 6**). Gorillas took turns to use the device alone; except for the youngest subject Ayana who was usually holding onto her mother Touni and therefore roughly occupied the same period of time. The order of taking turns was different for each trial (**Figure 7**). The infants Ayana and Afia played within an arm's reach of the device; this mainly involved playfully climbing and swinging around the device, or locomotory play on the floor next to it. The younger infant Ayana spent a total 1 h 8 min playing around the device, whereas the older infant Afia spent 12 s playing.

Focal Follows

No self-directed behaviors or other abnormal behaviors were observed during focal follows, in any condition. There were

TABLE 4 | Summary of enrichment device use by gorillas.

Subject	Total duration use (Σsix trials)	Average duration use (average six trials)	Problem-solving strategies*					Success frequency (nuts extracted)
			Physical contact				Observe (%)	
			Poke (tool) (%)	Poke (no tool) (%)	Mouth (%)	Shake (%)		
Jock	22.2	0 ± 4.8					100	0
Kera	7225.8	969 ± 1105.2	51.3	17.0	14.6	0.5	16.6	22
Touni	7332	1153.2 ± 1528.8	5.9	64.2	2.4	1.2	26.3	50
Kukena	1072.8	205.8 ± 129	20.9	64.5	0.5	0.1	14.0	20
Afia	94.8	0 ± 0		90.4			9.6	0
Ayana	4996.2	594 ± 1177.8		5.3			94.7	0

*Durations of enrichment device use are in seconds. Averages are medians ± IQR. Zero percentages have been removed for simplicity. *The percentage of time (Σsix trials) each problem-solving strategy was used.*

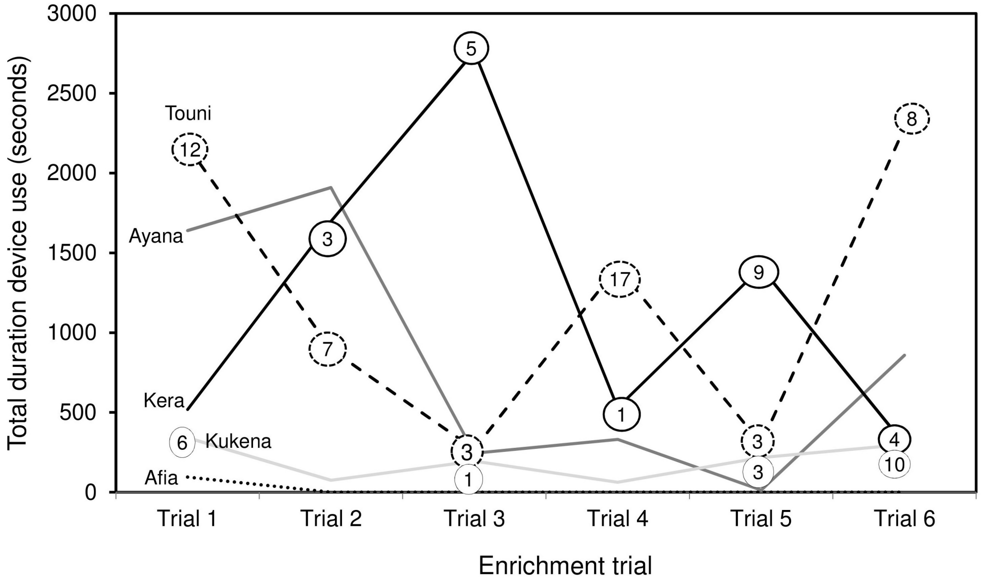

FIGURE 6 | Total duration of device use by individual gorillas over six enrichment trials. Includes observation and physical contact. Numbers in circles refer to the number of food rewards extracted at each trial (zero values not shown). Silverback male Jock is not shown, as use was negligible (Trial 1: 15 s observation, Trial 3: 7 s observation).

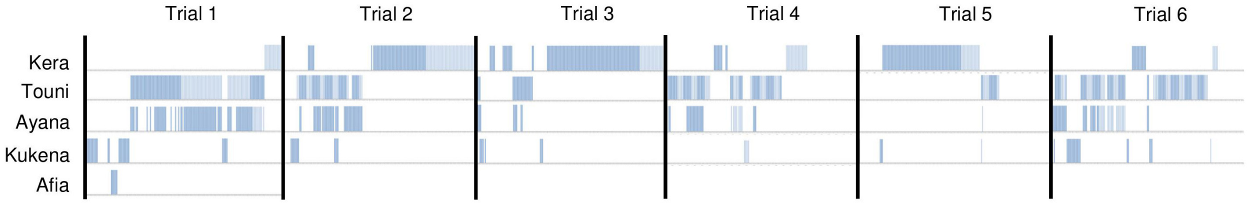

FIGURE 7 | Device use by individual gorillas within 1 h trials. Device use was scored as binary (vertical line, using device; no vertical line, not using device) every 20 s. Only physical contact with the device is shown.

several marginally significant overall effects of condition on behavior (**Table 5**), but when the data were subjected to *post hoc* pairwise testing and therefore a more conservative *p* value threshold they lost significance. When analyzing between-gorilla differences in behavior during the "post-exposure: device present" condition, there were significant individual differences in play and aggression (**Table 5**). The two youngest gorillas Afia and Ayana were both observed to play significantly more than the three oldest subjects Jock, Kera and Touni (Afia vs. Jock; Afia vs. Kera; Afia vs. Touni; Ayana vs. Jock; Ayana vs. Kera; Ayana vs. Touni; in all cases $U = -2.986$; $p = 0.003$). When aggression behavior was subjected to *post hoc* pairwise testing no significant differences were found between any pairs of gorillas.

DISCUSSION

Gorilla Engagement and Time-Share

Five out of six gorillas in the study troop engaged with the device by means of physical contact. Our prediction that the device would predominantly be used by younger adult females was supported, although it was the second and third youngest adult female. The lack of device use by the silverback male was also predicted, and keepers anecdotally reported that the male tended to avoid novel items. Our finding goes against a previous zoo study where a dominant male gorilla readily used and solved an extractive foraging task on the first trial (Lonsdorf et al., 2009). However, the location of our device could have affected use; the device was installed on an outer wall so that a gorilla needed to turn their back to the majority of the enclosure to use it. This could be a particularly undesirable position for a silverback male, whose role is to monitor the rest of the troop. In future we would suggest placing the device in a more outward facing position, making sure it does not dominate locations normally used for important activities such as rest and feeding. Given the high individual differences observed in the current study, and in previous great ape enrichment (Gilloux et al., 1992; Perdue et al., 2012; Clark and Smith, 2013), our findings should be treated conservatively and not generalized to the wider population of zoo-housed gorillas.

TABLE 5 | Summary of gorilla behavior pre- and post-exposure to the device.

Behavior	Between-condition comparison						Between-gorilla comparion
	Jock	Kera	Touni	Kukena	Afia	Ayana	
Forage/feed	χ^2 *3.70* *$p > 0.05$*	**χ^2 6.87** **p 0.032**	χ^2 0.78 *$p > 0.05$*	χ^2 4.80 *$p > 0.05$*	χ^2 3.60 *$p > 0.05$*	χ^2 2.00 *$p > 0.05$*	*U* 2.06 *$p > 0.05$*
Object exploration	**χ^2 6.00** **p 0.050**	χ^2 3.71 *$p > 0.05$*	χ^2 1.00 *$p > 0.05$*	χ^2 3.85 *$p > 0.05$*	χ^2 3.85 *$p > 0.05$*	χ^2 3.50 *$p > 0.05$*	*U* 1.45 *$p > 0.05$*
Locomotion	χ^2 5.06 *$p > 0.05$*	χ^2 0.33 *$p > 0.05$*	χ^2 0.11 *$p > 0.05$*	χ^2 3.90 *$p > 0.05$*	χ^2 4.80 *$p > 0.05$*	χ^2 3.90 *$p > 0.05$*	*U* 1.5 *$p > 0.05$*
Rest	χ^2 2.46 *$p > 0.05$*	χ^2 4.00 *$p > 0.05$*	**χ^2 6.35** **p 0.042**	χ^2 2.80 *$p > 0.05$*	**χ^2 8.40** **p 0.015**	χ^2 0.00 *$p > 0.05$*	*U* 7.53 *$p > 0.05$*
Vigilance	**χ^2 6.63** ***p 0.03***	**χ^2 6.82** ***p 0.03***	**χ^2 7.05** ***p 0.03***	**χ^2 7.05** ***p 0.03***	χ^2 4.59 *$p > 0.05$*	**χ^2 6.63** ***p 0.04***	*U* 4.74 *$p > 0.05$*
Play	No data	No data	χ^2 4.00 *$p > 0.05$*	χ^2 2.00 *$p > 0.05$*	χ^2 5.20 *$p > 0.05$*	χ^2 3.60 *p 0.04*	***U* 27.51*** **$p < 0.001$**
Affiliative	**χ^2 6.00** ***p 0.05***	No data	χ^2 4.35 *$p > 0.05$*	χ^2 2.60 *$p > 0.05$*	**χ^2 6.86** ***p 0.03***	χ^2 0.4 *$p > 0.05$*	*U* 9.55 *$p > 0.05$*
Aggressive	χ^2 4.00 *$p > 0.05$*	χ^2 1.00 *$p > 0.05$*	χ^2 2.92 *$p > 0.05$*	χ^2 4.35 *$p > 0.05$*	χ^2 1.00 *$p > 0.05$*	χ^2 4.00 *$p > 0.05$*	***U* 11.17*** **p 0.05**

*Between-condition comparisons: Friedman tests examined the effect of three conditions (pre-exposure; post exposure: device present, post: exposure device absent) on behavior. Significant Friedman tests (bold, $p \leq 0.05$) were followed by post hoc Wilcoxon signed rank tests with an adjusted p value of $\leq$0.017; there were no significant results from pairwise tests. Between-gorilla comparisons: Kruskal-Wallis tests examined the effect of gorilla ID on behavior (post-exposure: device present condition). Significant Kruskal-Wallis tests (bold, $p \leq 0.05$) were followed by post hoc Mann-Whitney U-tests with an adjusted p value of $\leq$0.003. *Significant post hoc results are described in the main text. "No data" refers to when the subject was not observed performing the behavior in any condition.*

Non-digital enrichment for great apes has traditionally suffered from a high level of habituation, particularly if food supplies can be rapidly depleted (Bloomstrand et al., 1986; Gilloux et al., 1992; Csatádi et al., 2008). For the Gorilla Game Lab device, it is worth considering habituation at two levels: habituation to the overall device and habituation to the challenges it provides. At the first level, the device was used by gorillas during every trial, and throughout each trial, suggesting that the device itself remained interesting to repeatedly approach and use. It could be argued that our monthly trial schedule made habituation very unlikely; this schedule was chosen because the Bristol Zoo Gardens keepers expect to implement the device on a monthly basis in future. Zoos such as Bristol Zoo Gardens, which are unfamiliar with technological enrichment, will understandably wish to start slowly, but zoos wanting to use the device more frequently, or for longer trials may expect to see higher rates of habituation. A trial duration of 1 h in combination with 24 preloaded food items allowed enough time for gorillas to extract nuts approximately once every 3 min, whereas a shorter trial or fewer food items could have encouraged rushing and competition over the device. At the second level, habituation was circumvented by providing different module arrangements between trials, meaning that the challenges always remained novel. Even though the same modules were used repeatedly, their order relative to each other changed, and therefore provides different levels of challenge to the gorillas.

Monopolization and resource-related aggression can often occur with great ape enrichment (Celli et al., 2003; Tarou et al., 2004; Ryan et al., 2011), but we found the opposite phenomenon. Our device was large enough to permit social use but gorillas chose to take turns using the device; it was always used alone or by Touni and her infant Ayana who was riding on her back or nearby. We would classify this as gorillas choosing to "time-share" the device rather than serial monopolization, because apart from one instance of aggression on the first trial (Touni directed to Afia), there were no indications of gorillas competing with each other for access. Similarly, a recent cognitive study on chimpanzees found that individuals in mother-offspring dyads spontaneously took turns to work at a computerized task on one screen (Martin et al., 2017). In fact, the ability of gorillas to efficiently take turns on our device indicates that at least some of the females were keeping track of each other and/or the device over the course of a trial. Confirming whether the gorillas were consistently engaged by the device at long distance (i.e., beyond arm's reach) would be a useful avenue for future study. From the data available, we do not know whether "spectator" gorillas observed conspecifics using the device for short or long periods of time, or indeed where they positioned themselves to do this (i.e., particular vantage points, or while patrolling the enclosure). The concept of animals choosing to be spectators in conspecific's enrichment, and furthermore how they may benefit from this, is of particular relevance to cognitive enrichment. Visual access to conspecifics using tasks is known to significantly affect learning success in great apes under laboratory conditions (Whiten et al., 2007). Our results justify using a single copy of the enrichment device for the Bristol Zoo gorilla troop in future, which will save on the zoo's resources. However, some facilities may prefer to use several copies of the device at one time, allowing simultaneous use by several troop members.

To our knowledge, there has never been a duration or proportion of time proposed as an "acceptable" level of enrichment use (i.e., below which the putative enrichment is deemed ineffective). Indeed, one individual within a group may benefit from a short bout of use whereas another individual may benefit from more prolonged uses. The fact that two of the six members of the study troop each used the device for a third of the time it was available (i.e., 2/6 h) is promising in terms of the general level of engagement. This is in contrast to another recent attempt at great ape non-digital cognitive enrichment, where chimpanzees were exposed to a pipe maze. Chimpanzees used the device significantly more when it was pre-loaded with tokens (red wooden cubes) than nuts, but spent on average only 2.5% of their time using the device (Clark and Smith, 2013). The static nature of the maze (one shape), and potentially a lack of moving components, could have contributed to low use over a 2 month period.

Gorilla Problem-Solving and Success

The Gorilla Game Lab device is distinctive from other physical mazes tested on great apes, because each module within the frame is different. Previous mazes have used repeated components such as pipes or shelves; for example Clark and Smith (2013) created a vertical pipe maze for chimpanzees from modular sections of opaque tubing, and only one spatial arrangement of pipes was tested. A "paddleboard" maze for bonobos and orangutans contained three vertical levels of shelves which could be rotated clockwise or anticlockwise allowing food items to fall through (Tecwyn et al., 2013). Völter and Call (2014a,b) tested a manual finger-maze task for great apes; this had different levels of shelf and traps (blockages) could be arranged in different locations. While the apparatus in the previous studies are easier to evaluate in terms of identifying what cognitive skill(s) are required to solve them, the paddleboard and "shelf maze" have not been evaluated as enrichment devices to our knowledge.

Gorillas solved the device in a number of ways, but most often used their fingers, or tools to probe into module access holes. Subjects did not use physical force to break into the device, or show other signs of physical frustration. The "shaking" strategy was gently executed, and seemed to occur when a piece of mesh was occluding one of the module access holes. Even though placing the device behind the mesh restricted full access, it protected the device against physical damage and increased the level of cognitive challenge by imposing manual manipulation with or without tools (Prétôt and Brosnan, 2019).

It was interesting that only the tool-using gorillas could successfully extract food rewards from the bottom of the device. This is at odds with previous research where great ape performance on physical tasks has been confounded by stick tool use (Seed et al., 2009; Völter and Call, 2014a). Because the access hole diameter (15–30 mm) varied across module locations, tool use was not mandatory but facilitated overall success. Touni was the most engaged subject, used tools the most and was also the most successful. Our small sample size precludes a deeper analysis of the relationships between success, tool use and overall duration of device use. We could envisage there being a positive feedback loop, where gorillas that are more effective at solving the task find it more rewarding, and are therefore more engaged.

There were signs that the device may have been rewarding to gorillas irrespective of the food reward inside. First, the gorillas were never food-deprived during trials and therefore did not "need" to obtain the food inside the device. Second, on one occasion, one gorilla (Kera) retrieved and stored 5 nuts during a bout of device use, and ate them in one batch afterward. This suggests that a food reward was of low value to Kera at the time. As a consequence of this food-storing behavior, we think it would be interesting to trial the device with non-food rewards similar to the chimpanzee cognitive enrichment study of Clark and Smith (2013). This would be best achieved with a new study group now that the Bristol Zoo gorillas are familiar with food rewards. Critically, it must be clear to the gorillas that the item inside the device is not a food reward. Other ways to test the value of the device would be to present other forms of enrichment at the same time, and look at relative preference.

Other Indicators of Well-Being

Until relatively recently, animal welfare science has focused on measuring the absence of negative wellbeing indicators rather than the presence of positive wellbeing indicators (Yeates and Main, 2008; Mellor, 2015). Traditionally, the proportion of time spent in negative behaviors such as over-grooming, self-injury, or stereotypy has been used as a measure of the "inverse of wellbeing" in primates (Washburn, 2015), but does acknowledge the great improvement in captive welfare standards in recent years, and therefore, as with our study troop, an absence of abnormal/aberrant behaviors within the baseline repertoire. A shift toward considering "positive" welfare states is emerging within the zoo community, as evidenced by the adoption of the Five Domains model of animal welfare assessment by the World Association of Zoos and Aquariums (WAZA) which places emphasis on recording positive mental experiences in animals as well as negative ones (Mellor and Beausoleil, 2015; Mellor et al., 2015).

Other than direct engagement with the device, there are few other significant behavioral changes to discuss. Against our predictions, gorillas were not observed to be significantly more playful or restful on days when the enrichment device was present. The two infants played significantly more than their conspecifics when the device was present, which is highly likely a function of age. As discussed previously, we suggest more closely monitoring the behavior of individuals at times when the device is present in the enclosure but they are not using it. At these times, subjects may remain vigilant of the device, or take advantage of more space or freedom when other gorillas are occupied by the device. A lack of statistically significant results also highlights the discrepancy between statistical and biological significance; now that we have tested the concept of the enrichment device with one troop it is pertinent to increase the sample size across different facilities.

Overall Evaluation as Cognitive Enrichment

According to the definition proposed by Clark (2011), cognitive enrichment should (1) engage evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) should be associated with one or more validated measures of well-being. Furthermore, it should provide some form of reward for the animal, be it a positive mental state and/or receiving an external resource such as food (Clark, 2017). According to these definitions, the current Gorilla Game Lab device can be conservatively classified as a form of cognitive enrichment for the study troop of gorillas. It certainly provided problem-solving opportunities related to food access. It also gave the gorillas more autonomy, through choosing and using stick tools. The gorilla's voluntary engagement over time was also a very positive result, since the time an animal spends with something can be viewed a measure of its value (Kirkden and Pajor, 2006). Finally, three out of six gorillas were successful in removing food rewards from the device, and even unsuccessful gorillas may find the experience of using the device internally rewarding (as evidenced by continued use, and a lack of stress or frustration-related behaviors).

We believe that individual differences observed in the study troop of gorillas, both in terms of focal observations around the exhibit and direct responses to enrichment, are an important justification for a continued modular approach to enrichment. A "one size fits all" approach to cognitive enrichment for a social group is not credible, given that individuals within that group will have different levels of cognitive skill and motivation. The overarching benefit to a modular approach is that the modules can be changed according to the levels of challenge they provide, and cumulative difficulty if connected into a maze.

Finally, although it is not part of the definition of cognitive enrichment, we also have to consider the practicalities of the device for its future use. The device operated safely for the study troop, and device use was possible in a variety of postures. The fact that the subject's actions directly affected the movement of the reward item, in real time, meant that no prior training was required, in contrast to virtual and physical mazes used in cognition studies (e.g., Tecwyn et al., 2013; Völter and Call, 2014a,b; Beran et al., 2015). The device was easy to implement without needing access to the gorilla den, and it could be pre-loaded with food rewards; this makes it highly practical for continued use by keepers. A design modification we feel would be useful going forward is to construct the entire frame and modules from acrylic plastic. This would be more durable in a humid enclosure, easier to clean, and would also aid data collection. As inspiration, Völter and Call (2014a,b) designed a transparent finger maze task to compare the cognitive skills of all four great ape species; they used rubberized material and narrowed channels to help cushion food rewards as they fell through the maze. Previous studies on great apes interacting with computer touchscreen tasks highlight the importance of making sure that a subject's progression on a task, and whether or not they have succeeded, is made clear to the subject (Itakura, 1993; Elder and Menzel, 2001; Leavens et al., 2001). Making modules out of transparent acrylic could help the subjects to witness their own progress, and also help researchers to track this progress (although see section "Automatic Logging Technology" for automatic logging).

Future Directions for Research

To our knowledge, the Gorilla Game Lab device is the only scientifically evaluated, published great ape enrichment with a modular cuboid design. Now that the first evaluation is complete, we aim to further develop the current device, focusing on (1) evaluating gorilla's use of individual modules, and (2) developing the technology backend.

Meta-Task Use

The Gorilla Game Lab device is a task at large, but each module is also a task it its own right, i.e., a "meta-task." We now wish to investigate, in a more experimentally controlled manner, how gorillas use each module. Currently, we do not have data to accurately evaluate which modules were preferred by gorillas, or which modules they may have found more difficult. This is because module location impacted use; modules placed lower down in the frame were likely used less than modules placed higher up because food rewards were navigated from the top to the bottom. We also wish to investigate whether some individuals may find unconnected modules more enriching; for example individual modules placed in different locations around the enclosure rather than one large static maze. This could be more engaging for the silverback male, who could have been unwilling to use the current device because it involved him turning his back to the rest of the troop.

Automatic Logging Technology

Our future plan for Gorilla Game Lab is to develop the technology backend which was partially developed alongside the current study. We have been working on using small sensors to track the movement of food rewards within the modules, and feed this information back to a web page in real time, offering researchers, and keepers a summary of device use. This is combined with facial recognition of gorillas, captured by the outward facing camera, and building upon previous facial recognition research on great apes (Brust et al., 2017). Once developed and validated, these types of technology will save researchers immense time coding behavior from video footage. Furthermore, they allow keepers to find which modules work well so they can continue to create novel and interesting mazes for the gorillas.

There are perhaps two other options worthy of consideration, for automatically logging gorilla device use. First, eye-tracking technology has recently been used on zoo-housed gorillas without the need for animal training or reinforcement (Chertoff et al., 2018). The authors found that gaze data could reliably be collected from subjects via apparatus mounted on top of a television monitor, so the same technology could feasibly be used to track which Gorilla Game Lab device module a gorilla was looking at; in fact we have already successfully trialed a camera inside the device. This being said, gorillas typically have dark eye sclera making it difficult to track their eye movements (Mayhew and Gómez, 2015). It is more feasible to log the movement of objects (maze obstacles, fingers, and stick tools) in the device itself, than to log eye movement or the movement of the animal external to the device. The second option is to use radio frequency identification (RFID) microchips embedded within subjects, to recognize which individual is using a device at any time. This has already been achieved with success on bonnet macaques *Macaca radiata* (Andrews and Rosenblum, 1994); Guinea baboons *Papio papio* and rhesus macaques *Macaca mulatta* (Fagot and Paleressompoulle, 2009); and chimpanzees: (cited in Clay et al., 2011). This could be viewed as a drastic and invasive option by some zoos, especially as it becomes increasingly feasible to log the device itself. However, microchips could be a very effective and appealing way to automate animal care programs if animals are already microchipped for husbandry reasons (Hoy et al., 2006).

Alternative Technology and No-Technology Options

For the benefit of zoos and sanctuaries who do not wish to use touchscreen systems or other types of obvious computerized enrichment, it is important to explore further touchscreen-free enrichment options. Other applications of technology into our existing device may include ways to provide task feedback to the gorillas without a food reward. This could, for example, be achieved through haptic feedback in the form of vibrations. Gorillas communicate socially through low rumbles (Stewart and Harcourt, 1994; Salmi et al., 2013) and therefore making the device modules vibrate to signal a correct (or incorrect) action could be relevant feedback for this species. As shown by previous great ape touchscreen research, an individual's understanding of their success on a task contributes to wellbeing; for example Leavens et al. (2001) found that the rate of self-directed behaviors performed by chimpanzees decreased when an auditory tone signaled if the subject's response was correct or incorrect.

Our prevailing belief is that cognitive enrichment is maximized by allowing subjects to learn the solutions to the problem(s) themselves. Training subjects to use an apparatus (for example how a lever can be operated, or how pressing a button leads to a certain outcome) takes away a degree of cognitive challenge. Certainly, the animal will be challenged by needing to make correct responses to an apparatus, even if they have been trained to use certain components, but the challenge will not be as great. Contrast this to the ability to experience novel physical problems that require a substantial tangible element, and learn what different components "do." Therefore, we suggest researchers avoid incorporating any technology that has to be intensively demonstrated to subjects. It would also be interesting to compare and contrast the enriching effects of the Gorilla Game Lab device, which operates by itself (no humans needed), with other apparatuses which require human input including training sessions.

Having discussed the technological developments we wish to pursue in future, it is worth a reminder that the Gorilla Game Lab device does not actually require technology to function. Device evaluation in the current study used camera technology. A no-tech version of the device could be used by facilities where technology is not an option; for example in smaller zoos, great ape sanctuaries, or where the device is used within an enclosure rather than protected behind the mesh. Facilities who are interested in our design are encouraged to contact the primary author for design plans.

DATA AVAILABILITY

The datasets generated for this study can be provided upon request.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Bristol Zoological Society and the University of Bristol Animal Welfare and Experimental Research Board (AWERB). The protocol was approved by the Bristol Zoological Society and the University of Bristol AWERB Ref. No. UIN/18/044. Gorilla interaction with the enrichment device was entirely voluntary, subjects were not deprived of their normal diet or access to other resources, and normal management conditions were maintained throughout the study.

AUTHOR CONTRIBUTIONS

FC, SG, PB, and KB designed the enrichment device, conducted the experimental protocol, and conceptualized the framework. LM coded the video footage data. FC handled and analyzed the baseline and video footage data. FC wrote the first draft of the manuscript. All authors contributed to the manuscript revision, read, and approved the submitted version of the manuscript.

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REVIEW
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What Is the Zoo Experience? How Zoos Impact a Visitor's Behaviors, Perceptions, and Conservation Efforts

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Modern zoos strive to educate visitors about zoo animals and their wild counterparts' conservation needs while fostering appreciation for wildlife in general. This research review examines how zoos influence those who visit them. Much of the research to-date examines zoo visitors' behaviors and perceptions in relation to specific exhibits, animals, and/or programs. In general, visitors have more positive perceptions and behaviors about zoos, their animals, and conservation initiatives the more they interact with animals, naturalistic exhibits, and zoo programming/staff. Furthermore, zoo visitors are receptive to conservation messaging and initiatives at zoos and are more likely to participate in on-site conservation opportunities as opposed to after their visits. The research also suggests that repeat visitors are even more inclined to seek out conservation efforts compared to those visiting zoos for the first time. While current research suggests that repeat visitors are more likely to engage in conservation efforts, little is known about causal factors related to such findings, and almost no research exists to-date comparing the conservation efforts of visitors vs. non-visitors. This latter comparison will likely play a greater role in future zoo visitor research, since it poses one of the most important metrics for evaluating the specific effects visiting a zoo can have on people engaging in conservation efforts in general.

Keywords: human-animal interactions, zoo visitors, zoo research, visitor perceptions, visitor behaviors, visitor education, conservation

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INTRODUCTION

Modern zoos have a variety of functions both relative to the species exhibited and the conservation of wildlife in general. According to the Association of Zoos and Aquariums (AZA), some of these goals are: (1) the care and welfare of the animals they exhibit; (2) educating and engaging public, professional, and government audiences; (3) species/habitat conservation; and (4) internal and academic research that increases our knowledge of animals and promotes AZA's other goals (Reade and Waran, 1996; Fernandez et al., 2009; Association of Zoos and Aquariums, 2013). In addition, zoos have a legacy of being a form of entertainment and are primarily a destination for visitors to attend in their leisure time (Carr and Cohen, 2011). Approximately 700 million people visit zoos and aquariums worldwide annually (Moss et al., 2014), with a 2011 survey indicating that participating zoos and aquariums spent at least $350 million on wildlife conservation internationally (Gusset and Dick, 2011). In a 2012 report by the AZA, 2,700 conservation programs spent approximately $160 million on field conservation for 650 individual species, in addition to ecosystems (Association of Zoos and Aquariums, 2012). It is these high attendance levels and their associated income that gives accredited zoos the ability to fulfill their mission statements.

While zoos are expanding their missions and welcome a large number of visitors, these institutions also have their critics. Animal rights activists and others argue that many zoos contribute little to conservation efforts and also impair zoo animals' welfare by placing them in captive environments (Hancocks, 2001; Rose et al., 2009; O'Connor, 2010). It is crucial to measure the impact of zoos' education and conservation initiatives to both indicate the extent of how these organizations are fulfilling their missions and continue to demonstrate the importance of the role of zoos in society despite their critics.

Ultimately, whether an opponent or a supporter of zoological institutions, it is critical to ask: How effective are zoological environments for meeting the welfare, conservation, education, and research goals of accredited zoos? More specifically, what can we learn about how particular captive environments help or hinder these goals? And what can visitors tell us about our ability to successfully meet these goals?

The following paper is a literature review of many peer-reviewed studies that examine how the zoo environment impacts visitors, as well as how these visits impact conservation efforts, both within and outside the zoo. We accomplish this by looking across a variety of disciplines and bodies of work that examine zoological institutions and visitor studies including psychology, museology, animal welfare, and environmental education. Keyword searches of "zoo visitor behaviors," "zoo visitor perceptions," "zoo visitor conservation," "zoo visitor learning," "animal-visitor interactions," and other terms occurred in the University of Washington Library's search engine, in Google Scholar, and in search engines of major publications across these fields. We specifically looked for articles where different factors of the zoo environment (the animals themselves exhibit design, programming/interacting with staff) affected visitor behaviors and perceptions. Articles that examined conservation awareness, attitudes, and behaviors with zoo visitors were also prioritized. In addition, reviewing references cited in relevant articles aided in compiling the studies cited in this literature review. Articles that did not look at visitor learning, post-visit outcomes, or observable zoo visitor behaviors were deemed irrelevant. Specifically, we examine (1) what visitors learn from their zoo experience, with an emphasis on how their behaviors and perceptions are changed and (2) how such visits change those visitors, specifically their conservation efforts. Specifically, we examine how visit frequency affects conservation actions and the need for more research on comparisons between visitors and non-visitors in terms of overall conservation support.

DISCUSSION

What Do Visitors Learn at the Zoo?

Zoos are by design an informal learning environment; unless visiting as part of a formal programmatic experience like a school tour, visitors are coming to zoos during their free time and choose which aspects of the zoo they engage with. Visitors to zoos come in with particular motivations like entertainment, bonding time with their families and friends, and also educational experiences (Falk, 2005; Roe and McConney, 2015). For learning to occur, attention is an important pre-cursor for learning (Altman, 1998), as well as connecting with visitors based on their prior knowledge (Dove and Byrne, 2014) and providing entertaining or enjoyable experiences (Spooner et al., 2019).

In order to establish the effectiveness of zoos as a learning environment, it is important to look at a variety of factors that influence visitor learning. Several studies have examined observable behaviors, as well as verbal responses from zoo visitors. These studies have looked at a variety of factors, including the social makeup of visitor groups, educational programming, and the animals in exhibits.

It is also important to understand how visitors cultivate perceptions and attitudes, in addition to studying their behavior, in order to evaluate the effectiveness of a zoo's education, conservation, and recreation goals (Anderson et al., 2003). Clayton et al. (2009) support the point that educational goals can be improved *via* perceptions. Specifically, positive perceptions can lead to a visitor who is interested in learning more about animals.

Effects of the Zoo Environment on Visitor Behaviors

One way to examine a visitor's response to a zoo exhibit is by measuring observable behaviors displayed by visitors. Specifically, (1) time spent in front of or near an exhibit; (2) attention toward an exhibit (e.g., facing and/or talking about an exhibit); and (3) overall crowd size has been used as measures of interest and satisfaction (Anderson et al., 2003; Margulis et al., 2003; Fernandez et al., 2009; Godinez et al., 2013). Attention is an important measure for visitor studies for which attention can suggest what information visitors are potentially processing and is a precursor to learning (Altman, 1998).

Previous studies suggest that visitor behaviors are influenced by both the presence of a zoo animal and the behaviors it displays. These studies have analyzed and tested the "visitor attraction model"; the theory that active animals attract visitors and have used observable measures such as pointing, stopping, and length of time is facing the exhibit. Results suggest visitors attend more to animal behaviors the more visible and active the animal is and also tend to spend more time in exhibits when an animal is visible and active (Bitgood et al., 1988; Altman, 1998; Anderson et al., 2003; Sellinger and Ha, 2005; Davey, 2006a; Godinez et al., 2013).

Debate over visibility of an animal and its influence on visitor behavior has risen from previous research. Bitgood et al. (1988) found that zoo visitors stopped more often and spent more time at exhibits where the animal was more visible. Whereas Philpot's (1996) study (as cited in Davey, 2006a, pp. 94–95) found that visitors spent more time searching for animals in naturalistic enclosures, which turned the exhibit and observing animal behaviors into an interactive experience.

In addition to the debate, over animal visibility is the size of the animal. Some studies suggest that visitors prefer larger-bodied animals (Bitgood et al., 1988; Ward et al., 1998). These findings have the potential to influence zoo decisions on the types of animals they display, even considering larger species typically cost more to care for and exhibit. However, Balmford (2000) re-analyzed the results of the Ward et al.'s (1998) study at the Zurich Zoo, which suggested that zoo visitors preferred viewing larger-sized animals. After re-analyzing the data along with additional data collected from the London Zoo, Balmford argued that in terms of visitor length of time at exhibits, there was no discernible difference between time spent at large-bodied animal exhibits and small-bodied animals. Balmford cautions that measures of visitor attention such as time spent attending to an exhibit and crowd size are not necessarily indicators of popularity or preference; smaller animals are typically housed in smaller exhibits, which may make the exhibit itself less appealing, as well as making it difficult for larger visitor groups to form.

Visitor conversations have also been studied in order to examine the influence of animal presence on visitor attention. Altman (1998) analyzed zoo visitor conversations at three bear exhibits as an indirect measure of attention. Conversations were recorded and later categorized as one of four types: (1) animal-directed; (2) human-focused; (3) animal behavior (directed); and (4) other. The study found that animal activity levels appeared to influence visitor conversations, particularly highly animated behaviors. Animal behavior conversation increased and human-related conversation decreased when animals were "highly animated" and the opposite occurred when the animals were pacing or not visible.

Studies examining the impacts of exhibit designs suggest that the transition to naturalistic exhibits in recent decades improves the animal's well-being as well as visitor behaviors (Nakamichi, 2007; Fernandez et al., 2009). Although the majority of zoo visitors do not interact with signage (Clayton et al., 2009), the context in which an animal is displayed can convey a wealth of information, increase visitor interest, and potentially create a more enjoyable experience. Research also suggests that naturalistic exhibits can increase visitor length of time at an exhibit (Shettel-Neuber, 1988; Davey, 2006a,b). These stay times are constant, even without the presence of an animal (Davey, 2006a; Nakamichi, 2007).

Effects of the Zoo Environment on Visitor Perceptions

While interacting with the zoo environment, visitors form perceptions of their surroundings. Previous research argues that zoos can encourage empathy in visitors for the care of zoo animals and, in turn, their wild counterparts and the ecosystems where these animals live. The catalyst for this empathy is positive experiences with animals in zoo environments (Clayton et al., 2009; Kutska, 2009).

Previous studies examining visitor perceptions suggest that perceptions can be influenced and changed by their experiences at zoos. Factors that influence visitor perception can include exposure to and interactions with zoo animals, the exhibit's design, and elements found within the exhibit space (e.g., signage, enrichment items, and feeding stations), public programming around the exhibit, the ability of visitors to interact with volunteers and staff, and preconceived notions of what certain behaviors (e.g., pacing and other potential stereotypic activity) suggest about the overall welfare of that animal. These aspects have the potential to equally foster or hinder respect and appreciation for zoo animals and the institutions that care for them.

Reade and Waran (1996) conducted a study of how zoo visitors and non-zoo visitors perceived zoo animals in general. The results of this study provided baseline data when examining visitor perceptions across many aspects of zoo operations. The study found that there were significant differences between non-visitors and zoo visitors' perceptions of animals in zoos. Zoo visitors viewed zoo animals more positively in all questions in the study and thought of them as more attractive, happy, and well-kept. Non-visitors tended to have more negative views of zoo animals across all questions and were significantly more likely to perceive zoo animals as "bored." In addition, non-visitors also viewed enrichment as less important than zoo visitors. The authors therefore concluded that this difference in perception suggests that the general public is not fully aware of the physical and psychological benefits enrichment has for zoo animals.

Exhibit design also appears to influence visitor perceptions. Zoos have undergone a substantial transformation over the past few decades in exhibit design, with a greater emphasis on naturalistic exhibits, both in terms of their appearance and functionality for the exhibited animals (e.g., ability to hunt and forage). Much of the support for displaying zoo animals in natural contexts is based on behavioral science and theory. In an article about achieving optimal visitor experiences in zoos, Coe (1985) argued that designs, or contexts, of zoo exhibits can reach visitors on both conscious and unconscious levels. These carefully planned contexts can grab the visitor's attention, and strong multi-sensory exhibit environments have the potential to create strong behavioral responses, such as greater empathy and desire to conserve the exhibited species. This transition to naturalistic exhibits improves visitor perceptions and encourages appreciation and respect for zoo animals (Maple, 1983; Finlay et al., 1988; Reade and Waran, 1996; Nakamichi, 2007).

Visitor perceptions can also be influenced by animal, keeper, and overall exhibit interactions they have while visiting a zoo. When analyzing how visitor perceptions were influenced by small-clawed otter activities, Anderson et al. (2003) found that public animal training and public animal training with interpretation produced more positive zoo experiences and perceptions of exhibit size than passive exhibit viewing or interpretation-only sessions. The educational approach to animal training programming has also been found to be an important factor in influencing visitor learning. A study by Visscher et al. (2009) found that after being told the same facts about Black Rhinoceros during two different types of animal training programs, the school group who received the interpretive presentation (i.e., audience encouraged to ask questions and could touch training tools) answered more post-program questions correctly than the students who attended a less interactive, fact-based presentation. In addition, a study by Lindemann-Matthies and Kamer (2005) found that visitors who attended a staffed "touch table" at a

Bearded Vulture exhibit at the Goldau Nature Park and Zoo were more likely to know more about the biology, ecology, and conservation of vultures both immediately after their visit and 2 months post-visit than those who visited the exhibit but only had access to exhibit signage. In addition, educational zoo theater programming performed by staff with no animals present resulted in both children and adult visitors answering more survey questions correctly after attending the performance than answering the same questions before the theater program began (Spooner et al., 2019).

How visitors perceive their experience, as well as the overall welfare of exhibited animals, can be greatly influenced by what behaviors they see the animals engaged in. Captive animal behavior is often broadly defined as positive, healthy behaviors (e.g., searching, foraging, and non-repetitive activity), and negative, "abnormal" behaviors (e.g., hiding, inactivity, and repetitive behaviors, such as pacing). While an operational classification and functional understanding of these behaviors goes beyond the scope of this paper, how such behaviors affect the visitor experience is critical to an overall understanding of what visitors learn at the zoo.

Bexell et al. (2007) examined visitor perceptions of Giant Pandas while playing or not playing. Those who witnessed Giant Panda play were significantly more likely to rate their experience more positively and have a more satisfying experience than those who did not observe playing. As noted previously, Altman (1998) found visitor conversations changed based on bear behaviors, with animal behavior conversations occurring the most when the bears were active compared to pacing and out of sight.

Another factor that influences visitor perceptions of animal behavior is stereotypic activity, broadly defined as repetitive, invariant behavior patterns with no obvious goal or function (Ödberg, 1978; Mason, 1991). In a study by Godinez et al. (2013), the researchers examined how different jaguar behavioral categories correlated with visitor activity and their ratings of the animals' predominant behavior displayed, well-being, exhibit quality, and the visitor's enjoyment. Overall, visitors were able to accurately describe a jaguar's behavior as inactive, active, or out of sight. However, approximately half of all visitors questioned (~47%) defined pacing and other repetitive behaviors as stereotypic, while the other visitors questioned simply described those behaviors as active and non-repetitive. For visitors who described a pacing pattern or other repetitive behaviors as stereotypic, they were also significantly more likely to rate the jaguar's well-being, exhibit quality, and visitor enjoyment lower than those who described the behavior as non-repetitive, active behavior. Therefore, it appears that acknowledgement of a behavior as a stereotypy can negatively impact multiple perceptions of a zoo visitor's visit. Similarly, Miller (2013) found that participants rated the overall care of a tiger as lower when the animal engaged in pacing than inactivity. In addition, the participants who observed a tiger pacing were significantly less likely to support zoos after witnessing this behavior when compared to those who observed an inactive tiger. Furthermore, visitors reported have the most positive emotions regarding zoo animals they observed after experiencing up-close animal encounters with animals displaying active behaviors compared to when the animals were out of sight or engaged in other behaviors (Luebke et al., 2016).

While zoos have made significant strides in reducing stereotypic activity displayed by their animals, these studies suggest that public education about such efforts is also necessary. It may be that part of the bias against such stereotypic activity on the part of the observing visitor is due to a lack of knowing what zoos and similar facilities do to deter such activity. Future studies could examine how educating visitors about behavioral enrichment and other welfare-oriented procedures affects their views of exhibited animals, in terms of both how they view the displays of potentially adverse behaviors and how they view the ability of zoos to care for animals.

Zoo Visitors Conservation Behaviors

Recent studies have focused on quantifying the effect of zoo visitation on the conservation efforts of those visitors. Most studies to-date have examined a visitor's conservation knowledge related to a specific exhibit or program before and after interacting with those programs (Hayward and Rothenberg, 2004; Lindemann-Matthies and Kamer, 2005; Lukas and Ross, 2005; Bexell et al., 2007; Chalmin-Pui and Perkins, 2017), as opposed to greater conservation awareness or analyzing a variety of exhibits and programs (Reade and Waran, 1996; Yalowitz, 2004; Falk et al., 2007; Adelman et al., 2010; Moss et al., 2017a,b). Research is emerging to suggest that visitors can have a relatively extensive awareness of human impacts on biodiversity conservation, even when they hold misconceptions regarding concepts about biodiversity and ecosystems (Dove and Byrne, 2014).

When analyzing how zoo visitors respond to conservation efforts within zoos, several studies suggest that one of the most significant factors influencing zoo visitors' conservation knowledge, attitude, and behaviors is repeat visitation. Repeat visitors retain significantly more conservation information, have more positive attitudes about conservation, and conduct more conservation-related behaviors than visitors who are attending the same zoo for the first time (Yalowitz, 2004; Lukas and Ross, 2005; Miller et al., 2013; Clayton et al., 2017; Moss et al., 2017a). Thus, while we have some knowledge about how repeat visitors differ from first-time visitors, the extent to which this occurs is not known.

In order to evaluate the overall impact zoos may have on increasing visitor interest and activity in conservation efforts, we examine (1) the conservation perceptions, behaviors, and actions taken by the visitor during a given visit; (2) what type of conservation behaviors and perceptions visitors have after their visit; and (3) how do all of these conservation-related efforts differ in zoo visitors compared to those who do not attend zoos.

Visitor Conservation Opportunities at the Zoo

In situ opportunities for conservation activities provide visitors with a tangible way to contribute to conservation efforts, especially since previous work suggests that visitors are uncertain how to become involved beyond donating money (Ojalammi and Nygren, 2018). On-site conservation activities may also reaffirm conservation behaviors and encourage long-term changes in zoo visitors. When comparing visitors' conservation actions on-site versus off-site, Stoinski et al. (2002) found that visitors were 20 times more likely to do on-site conservation activities than after their visit to the zoo. Furthermore, facilitating conservation actions *via* staff and programs as opposed to passive visits may increase the potential for visitors to participate in conservation efforts during a visit. In a study conducted during an elephant program at Zoo Atlanta, 350 of 471 visitors studied signed petitions and took solicitation cards. Those who had the highest levels of interaction with the exhibit and elephant program were significantly more likely to return the solicitation cards than those who had lower interaction (Swanagan, 2000).

Another way to encourage *in situ* conservation behaviors is by offering sustainably made items in zoo gift shops, where proceeds go to support conservation efforts (see Sigsgaard, 2009, for a case study of one such effort, and the sustainability issues to consider when stocking souvenirs and other goods in zoo gift shops). An additional on-site conservation action is at the point of admission through the "Quarters for Conservation" program. In this program, the zoo adds 50 cents onto the price of admission and gives their visitors a chance to choose which conservation project they would like their quarter to support. This simple program can help frame the visitor's entire zoo experience and has been implemented in over a dozen US zoos since the program was founded in 2007 (Hance, 2015).

If zoos continue to strive to demonstrate their effectiveness as conservation organizations, then it is crucial that zoos provide on-site opportunities for their visitors to participate in conservation. *In situ* conservation actions allow zoos to fulfill their missions and demonstrate their impact now. This can also be of great importance when justifying the role of zoos as conservation contributors when critics and others question the effect of zoos on various conservation efforts.

Zoo Visitor Conservation Post-visit

When analyzing conservation knowledge retention, some studies have found that visitors' conservation knowledge and interest persisted after a zoo visit (Jensen, 2014; Moss et al., 2015), but this new understanding rarely results in new conservation actions (Adelman et al., 2010; Miller et al., 2013). However, other studies suggest zoos prompt visitors to rethink their roles in conservation issues after their visit (Falk et al., 2007; Clayton et al., 2017; Jensen et al., 2017). While this is an emerging area of research interest, several studies support that the level and type of engagement with conservation and animals during the zoo experience affect not only visitors' knowledge retention but also post-visit behavior. Visitors who engaged with films and signage about biodiversity and conservation scored higher on biodiversity knowledge and intent to take part in post-visit conservation actions than those who did not interact with these elements (Moss et al., 2017b). Similarly, a study by Hacker and Miller (2016) indicated up-close encounters with elephants and witnessing active behaviors from the animals had positive effects on visitors' intent to engage with conservation actions post-visit. In a multi-institutional study of dolphin programs in zoos and aquariums by Miller et al. (2013), participants who witnessed dolphin programs retained much of their conservation knowledge learned from the shows and reported doing more conservation-related behaviors 3 months after witnessing the show than 3 months prior to their visit. Another study examining the effectiveness of touch tables on visitor's knowledge of bearded vulture biology, ecology, and conservation issues found that visitors who used the touch tables knew more about these items both immediately after their visit and 2-month post-visit than visitors who had not attended the table (Lindemann-Matthies and Kamer, 2005).

In a 2014 study by Jensen analyzing the conservation concerns and conservation self-efficacy of school children both pre- and post-visit, Jensen found an increase in students' personal concerns about the extinction of species, but marginal differences in if the students felt they could do something about it. Furthermore, a study by Skibins and Powell (2013) suggests that visitors are more inclined to take conservation action for an individual species they connect with, as opposed to conservation of biodiversity on a larger scale. To combat this issue of awareness but lack of action (or widening the impact of said action), others who recommend zoos can take on stronger approaches to motivating visitors to do pro-conservation behaviors that are relevant and easy to implement for a diverse range of zoo visitors (Smith et al., 2012; Grajal et al., 2018). However, providing materials for visitors to participate in post-visit conservation actions has occurred in only a few studies. Analysis that has been conducted to-date suggests that materials that coincide with visitors' daily lives tend to be more effective in encouraging conservation-related behaviors than those that are less frequent and more in-depth actions. For example, at the Monterey Bay Aquarium, 51% of visitors who picked up a Seafood Watch Pocket Guide tried to use the guide when purchasing seafood after their visit to the aquarium. On the other hand, only 10% of visitors tried to use an "Ocean Allies Card" (a list of conservation organizations to join) after their visit, and no participants joined an organization (Yalowitz, 2004).

Zoo Visitors Versus Non-visitor Conservation Actions

To understand fully the degree of impact zoos has on visitors' conservation efforts, comparisons between zoo visitors and non-zoo visitors are necessary. However, most studies look at zoo visitors alone (Swanagan, 2000; Yalowitz, 2004; Falk et al., 2007; Miller et al., 2013). At least one study to-date indicated that non-zoo visitors viewed zoos as playing an important role in conservation, although non-zoo visitors' conservation knowledge and attitude were not measured (Reade and Waran, 1996). Because of the importance of comparing differences between zoo visitors and non-zoo visitors to determine the impact zoos have on increasing conservation efforts in general, our final section draws on directions zoos could go in to make such assessments.

FUTURE RESEARCH

Much of the studies done to-date examine changes in visitor behaviors and their perceptions in regard to exhibit design, the presence of animals and their displayed behaviors, and how visitors engage with singular exhibits and/or programs in individual zoos (see "Zoos and Visitors" section of this paper for examples of these studies). This work has laid the foundation for a variety of in-depth questions to be examined moving forward. Specifically, the nuances of how the zoo environment may influence zoo visitors' appreciation for the animals exhibited, their species' associated conservation needs, and how the zoo visitors themselves can take conservation actions to support conservation initiatives for the animals' wild counterparts and their habitats.

As studies continue to examine the conservation impacts zoos have on their visitors, much of the research done to-date can be summarized in an assumed paradigm that zoo visitors go through that are a series of sequential steps with the intended outcome to be conservation-related actions.

Visit → Knowledge → Concern → Intent → Post-visit action

However, this paradigm assumes that knowledge is strongly linked to conservation actions. Recent research indicates that other factors like where you live and demographically related factors are more strongly correlated with conservation behaviors than knowledge (Moss et al., 2017a). Based on what studies cited in this literature review indicate, the paradigm could be reframed as follows:

Visit with in situ action → Knowledge → Concern → Intent → Post-visit action

Given the variety of factors influencing visitors in the free-choice learning environment of zoos and the variety of methodologies used to examine the impact zoos have on their visitors, there is a question beckoned to be asked: *Is it possible to empirically measure the impact zoos have on their visitors?* Many studies mentioned in this review have taken great strides in answering this question—especially when examining how the environment of the zoo (e.g. exhibits and programs) affects behavioral learning and general knowledge of both animal species and the individual animals housed.

Our recommendations are to continue measuring the impact—or to begin measuring the impact—of the following:

1. having a true control group (non-visitors) to understand the full impact zoos may or may not have on zoo visitor knowledge, perceptions, and behaviors;
2. increasing opportunities for on-site conservation activities that visitors can do during their visit; this could potentially improve their conservation knowledge and future conservation actions, as well as be a measurable impact of how zoos are contributing to conservation efforts;
3. providing more opportunities for tangible takeaways for visitors that directly contribute to conservation initiatives post-visit (i.e., Seafood Watch cards, pre-drafted letters to send to legislators, take-home electronic recycling kits) – and then measure the effectiveness of these tools; and
4. studying the phenomena of repeat visitors being more conservation-oriented than one-time visitors. Also begin to study how repeat zoo visitors compare to those who do not visit zoos at all.

On this last point, knowing that research to-date suggests that repeat visitation is a significant factor in conservation knowledge and appreciation for wildlife, we wonder: are repeat visitors continuing to visit zoos because they are already conservation-oriented and see zoological institutions as places to fulfill this area of interest? Or do they become more concerned with conservation issues over time as a result of the information and experiences they have in zoos? Additional studies that delve deeper into motivations of repeat visitors, and how these attitudes and behaviors develop, could shed light on these questions. Regardless of their motivation, these studies suggest that zoos are fostering conservation with this key group of visitors and that those who come to zoos appear to be receptive to and interested in conservation in the first place (Falk et al., 2007).

Zoo membership is a key tool that is readily available to all zoological institutions to help foster the transition from infrequent to frequent visitors. Looking at the motivation, visitors have when signing up for zoo memberships (cost saving, entertainment, interest in animals, interest in conservation, etc.,), and comparing these motivations to conservation-related knowledge, attitudes, and behaviors of members could provide a critical insight into the field.

Although we have described an array of studies for this review, most of them do not address an important aspect to the effectiveness of zoos—how visitors compare to those who do not attend these types of institutions. With the exception of the few studies mentioned earlier in this paper, we have not been able to find peer-reviewed, published research that compares zoo visitors to non-visitors. A plethora of topics, including conservation attitudes, knowledge of wildlife, and other environmental resources, or how these two groups perceive zoos themselves beckons further examination. We suspect that future visitor research will focus more directly on comparisons between zoo visitor and non-visitor conservation efforts, since this is one of the most important metrics for assessing the impact zoos have on increasing the conservations efforts of their visitors, and a necessary measure for evaluating the effect zoos have on the public supporting conservation efforts in general.

AUTHOR CONTRIBUTIONS

AG and EF co-wrote and edited the manuscript, as well as researched literature for this review. AG formatted the manuscript in accordance with Frontiers in Psychology guidelines. EF submitted the manuscript for publication.

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Providing Belugas (*Delphinapterus leucas*) in Controlled Environments Opportunities to Thrive: Health, Self-Maintenance, Species-Specific Behavior, and Choice and Control

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The health and welfare of animals in controlled environments continues to improve as evidence-based practices inform best care processes (Ward et al., 2018; Wolfensohn et al., 2018). Zoos and aquariums play an integral role in educating the public about Earth's fauna and flora (Maple and Perdue, 2018). Zoo and aquariums are learning environments for visitors and scientists, who come because of their appreciation for the animals and who trust that they are provided with the best possible welfare. Zoological facilities must continue to systematically and empirically measure animal welfare so science can inform decisions ensuring the optimal health and veterinary care practices along with creating environments that promote species-specific behavior and interactions, choice, and variability (Maple and Perdue, 2018; Ward et al., 2018; Wolfensohn et al., 2018). With increasing partnerships between external researchers and zoological facilities, the scientific investigation, and understanding of the components of animal welfare continues to expand (Fernandez and Timberlake, 2008; Ward et al., 2018). For example, academic-zoological partnerships have established that naturalistic exhibits can promote species-specific behaviors (e.g., Finlay et al., 1988; Ogden et al., 1990; Yilmaz et al., 2010; Chih Mun et al., 2013), and the placement of different types of enrichment promotes investigative behavior and greater habitat use (e.g., Vick et al., 2000; Clark, 2017; Makecha and Highfill, 2018). Research has also indicated that the needs of a given species and the individuals making up the facility's population must be considered when utilizing different types of enrichment, social groupings, or habitat configurations (Rose and Croft, 2015; Wolfensohn et al., 2018; Nollens et al., 2019).

The behavior and social interactions of a relatively stable white whale, or beluga (*Delphinapterus leucas*) population at a North American facility has been studied systematically since 2007. From long-term weekly documentation calf behavioral development and maternal care, behavioral milestones, such as nursing, swim positions, locomotor development, social interactions, and play behaviors have been established and validated with belugas from other facilities and in their natural habitat (Krasnova et al., 2006, 2009; Hill, 2009; Karenina et al., 2010, 2013; Hill et al., 2013, 2018a; Hill and Campbell, 2014; Hill and Ramirez, 2014). Maternal care behaviors are conserved across both habitats (Krasnova et al., 2006, 2009; Hill, 2009; Karenina et al., 2010, 2013; Hill et al., 2013, 2017), but show individual variation much like bottlenose dolphins in human care or the wild (Hill et al., 2007; Gibson and Mann, 2008; Stanton and Mann, 2012).

Results illustrated that dynamic social groupings decreased time spent swimming alone and provided opportunities for species-specific behavior, such as engaging with the environment whether it was interacting with different objects (e.g., enrichment devices, permanent fixtures, organic materials, or water) or with each other (Hill and Ramirez, 2014; Hill et al., 2015b, 2018b).

Pool configuration also influenced the actions of the belugas (unpublished data). When multiple pools were available, the belugas engaged in more dynamic and variable swim patterns. Moreover, access to multiple pools provided opportunities for choice and self-maintenance: individual belugas could move out of sight of conspecifics or choose a specific area in which to swim. More recently, based on data from three different facilities, male-male interactions (whether interspecific or intraspecific) have emerged as a significant element in beluga socialization, appearing early in the juvenile years and solidifying as the males age (Glabicky et al., 2010; Hill et al., 2015a, 2018b; Mazokowski et al., 2018). These socialization patterns appear to be conserved as well based on genetic work on beluga distributions in several beluga stocks (reviewed by Colbeck et al., 2013; O'Corry-Crowe et al., 2018).

Social composition, complexity of environment through pool configurations, opportunities for intra- and inter-species interactions, and variable access to different forms of enrichment have produced measurable behavioral and physiological outcomes that are indicative of enhanced welfare of belugas in human care. These findings corroborate those found with a number of terrestrial species in zoological environments (Finlay et al., 1988; Ogden et al., 1990; Vick et al., 2000; Yilmaz et al., 2010; Chih Mun et al., 2013; Clark, 2017; Makecha and Highfill, 2018; Maple and Perdue, 2018; Wolfensohn et al., 2018). Overall, dynamic and variable experiences increased the belugas' activity (i.e., intra- and inter-species interactions, play, engagement with environmental stimuli), reduced periods of solitary swims, and provided opportunities to thrive.

The physiological health of the majority of the belugas present in the population has remained stable and strong, and as such, the population has served as a baseline reference for evaluating free-ranging belugas (Norman et al., 2012, 2013). Belugas are a species of great interest because of their vulnerability to climate change, role as a sentinel species, importance to subsistence, and for understanding threats to at-risk populations. Not only do belugas in controlled environments serve as control populations, but the beluga husbandry expertise provided from aquaria has, in part, allowed for the safe and expedient collection of blood, feces, gastric contents, skin, blubber, blowhole swabs, breath exhalations, as well as morphological, auditory, and ultrasound measurements from 56 belugas in Bristol Bay, AK. Combined, the information gained has advanced our understanding of free-ranging beluga health, physiology, disease exposure, immunology, body condition, hearing, habitat use, and the risks free-ranging belugas face.

After almost 12 years of consistent weekly observations, this academic-zoological collaboration has produced a substantial body of behavioral evidence indicating that beluga welfare is enhanced through variability and complexity with regard to social compositions, enrichment, and habitat configurations. This evidence has been further substantiated by physiological parameters that have been used as controls for assessing the health status of free-ranging belugas. However, as summarized by both Maple and Perdue (2018) and Wolfensohn et al. (2018), individual differences and preferences must be considered in any welfare assessment. Responses to enrichment attempts are variable and subject to the individuals themselves, their current motivational state, and other environmental factors that may or may not be identifiable (e.g., social status change, subclinical illness). Between learning about the needs of the animals themselves and how that knowledge might benefit both captive and wild populations, this long-term study of a reproductively active beluga population that simulates the natural composition of beluga social groupings has demonstrated that variability and choice in different aspects of the daily environment are more central to beluga welfare than the permanent habitat itself. Active collaborations between external researchers (academic researchers in this case) and zoological facilities, such as in the case of this long-term beluga behavioral study, are essential for maintaining and improving animal welfare in human care and educating current and future generations on the need to care for and conserve our planet's resources.

AUTHOR CONTRIBUTIONS

HH drafted the text regarding the body of behavioral research summarized in the article. HN edited and summarized the research discussing the physiological and biological contributions of research performed with belugas in controlled environments and applied to their wild counterparts.

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Selecting and Testing Environmental Enrichment in Lemurs

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Environmental enrichment has become a standard tool for improving the welfare of animals in zoos. Two critical steps in the manipulation of environmental enrichment are (1) selection of objects/procedures and (2) evaluation of their effects. In this study, we examined the selection and evaluation of feeding enrichment for four species of lemur. Experiment 1 used a paired-choice preference assessment to divide eight food items into high- and low-preferred categories. Experiment 2 separately assessed the effects of high- versus low-preferred items (placed in bamboo dispensers) on the behavior of two of the species in the preference assessment. Both high- and low-preferred items increased general activity and overall enclosure use, with high-preferred items having a greater effect than low-preferred items on most measures. The results suggest that preference assessments can serve as useful tools in selecting potential enrichment and that enrichment testing is important in evaluating the significance of these preferences.

Keywords: animal welfare, enrichment, lemur, paired-choice, preference assessment, zoo

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Over the past several decades, the use of environmental enrichment to promote the health and well-being of animals in zoos and other captive settings has increased (Markowitz and Aday, 1998; Shepherdson, 1998; Mellen and MacPhee, 2001). Advantages of environmental enrichment include (1) reducing stereotyped and aberrant behaviors, (2) improving the general health and increasing the longevity of captive species, and (3) promoting more naturalistic behaviors (Markowitz, 1978; Carlstead, 1996). In addition, the display of naturalistic behaviors in zoo animals (the goal of enrichment) has been correlated with increased visitor attention and perceived likability of the animal/exhibit by the visitor (Finlay et al., 1988; Altman, 1998).

Examples of environmental enrichment include the presentation of food items to felids (Shepherdson et al., 1993; Lyons et al., 1997) and bears (Law et al., 1990; Carlstead et al., 1991; Forthman et al., 1992). Artificial foraging objects have also been presented, including acoustic "prey" for African leopards (Markowitz et al., 1995) and manipulable objects for bears (Altman, 1999). Modifying the captive environment has been tried as well, including presenting a species with a new exhibit or rotating a species through different exhibits (Chang et al., 1999; Little and Sommer, 2002; Lukas et al., 2003).

Introducing environmental enrichment for captive animals has two critical aspects: enrichment selection (choosing potential enrichment) and enrichment evaluation (measuring the effects of the enrichment). In the case of enrichment selection, choices are often made based on keeper/caretaker opinion and anecdotal reports of past successes. Only a few researchers have suggested a systematic basis for the selection of potential enrichment items (Mellen and MacPhee, 2001; Fernandez et al., 2004; Alligood et al., 2017). In the case of enrichment evaluation, researchers have emphasized the systematic assessment of enrichment in relation to the psychological well-being and behavior of captive animals (Crockett, 1998; Morgan et al., 1998; Shepherdson, 1998), but this remains a relatively newer component of animal welfare assessment, with a growing need for data-driven enrichment evaluation.

The present study investigated systematic procedures for selecting and evaluating feeding enrichment manipulations in several species of captive lemurs: ring-tailed lemurs (*Lemur catta*), red ruffed lemurs (*Varecia rubra*), collared brown lemurs (*Eulemur collaris*), and blue-eyed black lemurs (*E. flavifrons*). Lemurs are exclusively found in the island of Madagascar, off the southeastern coast of Africa. They are highly social primates, evading predation by foraging in groups, and are primarily nocturnal and arboreal. (Jolly, 1966; van Schaik and Kappeler, 1993; Scheumann et al., 2007). While most lemur species are nocturnal and arboreal, ring-tailed lemurs are known to forage diurnally and terrestrially (Gould and Sauther, 2007; see General Discussion). As such, we were additionally interested in differences that might exist in the latter enrichment evaluation for the ring-tailed lemurs.

To select our enrichment manipulation, we systematically assessed preferences for various food items (Young and Chaplin, 1945; Young and Kappauf, 1962; Thompson and Grant, 1971). Applied researchers have used similar assessments to determine human preferences for potential reinforcers (Pace et al., 1985; DeLeon and Iwata, 1996; Roscoe et al., 1999). These assessments include single-, paired-, and multiple-stimulus methods (see Fisher and Mazur, 1997 for a review). We chose the paired-choice procedure because it can rapidly rank order stimulus preferences and can readily be administered to non-human animals. In this method, items are repeatedly and concurrently presented in pairs to an individual who selects one of them. After all possible combinations are presented, the researchers rank the items based on the percentage of times an individual selected each item (Fisher et al., 1992).

The paired-choice procedure has been applied previously in zoo settings. For example, Fernandez et al. (2004) used the procedure to determine food preferences of five cotton-top tamarins. Similar studies documented browse preferences for five colobus monkeys (Tovar et al., 2005), preferences among three species of bamboo in a pair of giant pandas (Tarou et al., 2005), preferences for training or enrichment in wolves (Dorey et al., 2015), object and interaction preferences and enrichment efficacy in Galapagos tortoises (Mehrkam and Dorey, 2014), scent preferences in giraffes (Fay and Miller, 2015), preferences for potential enrichment items with several species of zoo-housed animals (Mehrkam and Dorey, 2015), and with domestic cats and dogs in other applied animal settings (Vicars et al., 2014; Vitale Shreve et al., 2017). However, apart from Mehrkam and Dorey (2014), these studies did not attempt to evaluate the relationship of enrichment selection through preference assessments to the success of subsequent enrichment introductions, and none of the above studies directly compared preference order to their resultant enrichment effectiveness.

In this study, we assessed paired-choice preferences for food items, ranking the items as high-preferred (HP) or low-preferred (LP). We then evaluated the enrichment effects of these items on the lemurs' foraging behavior and general activity. Experiment 1 assessed preferences for paired selection and consumption of eight food items in four species of lemurs. Experiment 2 placed high- and low-preferred items (based on Experiment 1) in bamboo dispensers and tested the effect of presenting filled versus empty dispensers to a mixed group of ring-tailed and collared lemurs (*Lemur catta* and *Eulemur collaris*, respectively) in their outdoor exhibit.

We hypothesized that enrichment effects should be greater for high- vs. low-preferred conditions, and higher for food vs. non-food [Baseline (BL)] conditions. We expected this greater enrichment effect to be observed *via* (1) increased foraging and general activity, and (2) greater overall enclosure use.

EXPERIMENT 1: ENRICHMENT SELECTION

Method

Subjects and Enclosures

Nineteen adult lemurs (age range: 4–10 years) across four species were included in the study: seven ring-tailed (two male, five female; *Lemur catta*), seven red ruffed (five male, two female; *Varecia rubra*), three collared (one male, two female; *Eulemur collaris*), and two blue-eyed black lemurs (one male, one female; *E. flavifrons*). All lemurs were captive-born and housed at the Indianapolis Zoo. All lemurs were approved for use in this study by the Indiana University – Bloomington Institutional Animal Care and Use Committee (IACUC; Study # 04-116), as well as through the Indianapolis Zoo's internal research review process.

The seven red ruffed and two blue-eyed black lemurs resided in a 185 m^2 enclosed outdoor island exhibit during the day. Three of the ring-tailed and all three collared lemurs resided in a 97 m^2 outdoor island exhibit during the day. The ring-tailed/collared lemur exhibit contained a 2 m × 1.5 m × 1 m artificial rock that was hollow in front, allowing the lemurs to move under the structure yet remain visible to the public. The red ruffed/blue-eyed black lemur exhibit contained several 0.5 m × 1 m × 0.5 m hollow logs. Both exhibits contained trees, branches, or similar fixed hanging structures for the lemurs to move across while being viewed by the public.

At night or when the temperature remained below 21°C, lemurs were separated by species and placed in holding enclosures. The red ruffed and blue-eyed black lemur holding enclosure was approximately 155 m^2. The ring-tailed and collared lemur holding enclosure was approximately 123 m^2. The final four ring-tailed lemurs were a breeding group and were maintained in a similar holding enclosure throughout the day. All trials were run in the holding/night enclosures.

Materials

Eight food items were used during the preference assessment: zucchini, cauliflower, red pepper, green beans, corn, yams, eggplant, and squash. These food items were selected because they were part of the lemurs' standard diet and were desired by the management/staff to be used in enrichment procedures. Each food item was cut into 2–3 cm^2 × 2–3 cm^2. During a trial, two items were placed on a 50 cm × 25 cm tray approximately 35–40 cm apart. Data sheets listing order and choices for each trial were used to record the food selections.

Data Collection and Procedures

The paired-choice preference assessment in this study used methods like those of Fisher et al. (1992) for presenting stimuli in concurrent pairs. All lemurs were initially allowed to approach and sample each of the eight food items as a keeper presented each one individually on the tray. A list of pairs for all eight items was generated, presenting each food item on the left against all seven other food items and again for the right side; therefore, each food item was equally presented with each other food item on both the right and left sides (14 presentations for each food item, and a total of 56 food presentation trials for each lemur). To minimize potential order effects and experimenter bias, the list of possible pairs was randomized and run in either forward or backward order, with order being counterbalanced across gender and species.

During each trial, a researcher placed two food items on the tray and handed it to a keeper. The keeper entered one of the night/holding enclosures and presented the tray to the designated lemur. A selection was determined when the focal lemur grasped and removed one of the two food items from the tray. Other lemurs rarely attempted to approach the keeper during a trial. If a lemur did attempt to interfere with a trial, the keeper would adjust their position so that only the designated lemur could select one of the food items. The lemur was given several seconds to make a choice. If the lemur did not make a choice within several seconds or moved away from the tray, the tray was re-presented to the lemur. If no choice was made after three presentation attempts, that trial was recorded as "no choice." Up to 30 trials were run for each lemur in a day, and typically at least 5–10 trials were run consecutively for any one lemur at a time. Each trial took approximately 30 s to run (total of 20–30 trials each day per lemur; 2–4 lemurs tested each day).

Data were collected by recording both the food item selected and the position of that item for any given trial. The experimenter also recorded whether a lemur consumed the food item after selecting it. To minimize both experimenter and presenter bias, prior food selections were not discussed between the experimenter and presenter, and presentations of all food items were randomized for order and position. Each preference assessment took 2–3 days for each lemur, and the entire study took a total of 26 days.

Because of the small sample size for two of the four species included in the study, differences in food selections were determined by comparing the means and standard errors of the means for each species. Reported differences were based on non-overlapping standard errors of the means.

Results and Discussion

Figure 1 illustrates the food selections for each of the four species. Food items are listed across the x-axis, and percentage of times each item was selected are listed. Overall, a consistent pattern emerged across species for how often a food item was selected. Corn, yams, and red peppers were ranked, respectively, the first, second, and third most selected items overall. Green beans, squash, and zucchini were ranked, respectively, the least, second least, and third least selected items overall.

Table 1 provides the average and standard error for the number of times a food item was selected for each of the four species in the study. In addition to the obvious similarities in food selection among species shown in **Figure 1**, there are also differences in food selections. For instance, while corn

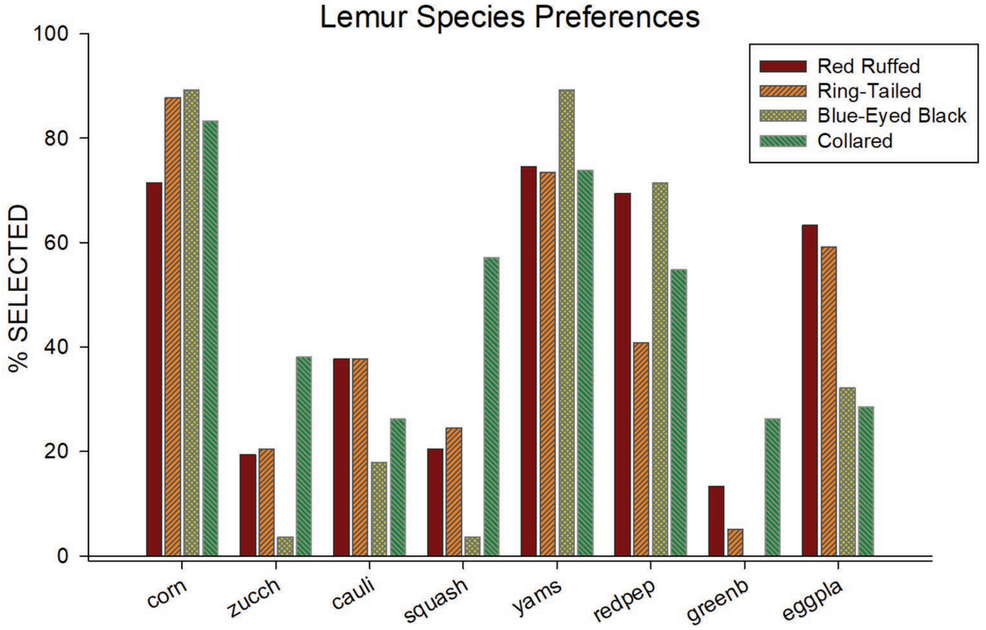

FIGURE 1 | Percentage of selection (out of 14 times presented) for all eight of the food items used in the paired-choice preference assessment across all four species.

TABLE 1 | Average number of times a food item was selected (out of a possible 14 presentations) by each of the four lemur species.

Food item	Red ruffed	Ring-tailed	Blue-eyed black	Collared
Corn				
Mean	10.00^{B}	12.29	12.50	11.67
(SE)	(0.44)	(0.64)	(1.50)	(0.88)
Zucchini				
Mean	2.71	2.86	0.50^{B}	5.33^{A}
(SE)	(1.27)	(1.24)	(0.50)	(1.20)
Cauliflower				
Mean	5.29	5.29	2.50	3.67
(SE)	(1.06)	(0.52)	(2.50)	(1.33)
Squash				
Mean	2.86	3.43	0.50^{B}	8.00^{A}
(SE)	(1.18)	(0.90)	(0.50)	(1.00)
Yams				
Mean	10.43	10.29	12.50^{A}	10.33
(SE)	(0.65)	(0.18)	(0.50)	(0.67)
Red pepper				
Mean	9.71^{a,b}	5.71^{b,c}	10.00^{c}	7.67^{a,c}
(SE)	(0.71)	(1.51)	(0.00)	(1.20)
Green bean				
Mean	1.86^{a}	0.71^{a}	0.00^{B}	3.67^{a}
(SE)	(0.77)	(0.47)	(0.00)	(1.20)
Eggplant				
Mean	8.86^{a}	8.29^{b}	4.50	4.00^{a,b}
(SE)	(0.70)	(1.43)	(4.50)	(1.73)

For remaining food selections, differences between species are marked with the same lower-case letters, either$^{a,\,b}$ *or*^{c}. ^{A}*Species that selected a food item more than all other species (based on non-overlapping standard errors of the means).* ^{B}*Species that selected a food item less than all other species.*

was one of the most often selected food items for all four of the species, it was selected less often by the red ruffed lemurs (M = 10.00, SE = 0.44) when compared to the other three species (ring-tailed, M = 12.29, SE = 0.64; blue-eyed black, M = 12.50, SE = 1.50; collared, M = 11.67, SE = 0.88). Squash was selected in more than half of the trials for the collared lemurs (M = 8.00, SE = 1.00), but was selected in less than a third of the trials for the other three species (red ruffed, M = 2.86, SE = 1.18; ring-tailed, M = 3.43, SE = 0.90; blue-eyed black, M = 0.50, SE = 0.50). Yams were one of the most often selected food items for all four species (red ruffed, M = 10.43, SE = 0.65; ring-tailed, M = 10.29, SE = 0.18; blue-eyed black, M = 12.50, SE = 0.50; collared, M = 10.33, SE = 0.67). Green beans were one of the least selected items for the red ruffed, ring-tailed, and collared lemurs (red ruffed, M = 1.86, SE = 0.77; ring-tailed, M = 0.71, SE = 0.47; collared, M = 3.67, SE = 1.20), and were never selected by the blue-eyed black lemurs.

A similar pattern of selection was also present within each species. As evidence for similarities in selection, more than half of all standard errors of the mean food selections for each species were less than 1, and another third were less than 1.5. Two exceptions occurred, however, within the blue-eyed black lemurs: eggplant was selected nine times and cauliflower was selected five times by one lemur but never by the other.

It is worth noting that the position of the presented food items (on the right or left) appeared to have little effect on the food selections. For all 19 lemurs, items on the left were selected 47.95% of the time. The strongest position bias for any one lemur was a left item selection of 61.7%. Finally, when a food item was selected, it was almost always consumed (97.48%). Therefore, the preference for food items was based on their appeal as consumable food.

EXPERIMENT 2: ENRICHMENT EVALUATION

Experiment 1 produced systematic paired rankings of food items that allowed them to be arranged in a preference order and used to select potential enrichment items. The purpose of Experiment 2 was to evaluate the relative effects of high- and low- preferred enrichment items, with a control (Baseline) condition in which the bamboo feeder was presented with no food items. Previous research demonstrated that food enrichment placed in hanging devices was effective in producing increased foraging and natural foraging postures in black and white ruffed lemurs (Britt, 1998). Based on this report, we hung bamboo dispensers in two trees in the lemurs' enclosure during 1-h evaluation periods. The dispensers contained high-preferred food items, low-preferred food items, or no items. Evidence that food items increased interactions with the dispenser, enclosure use, and general activity was taken as evidence of enrichment, while differences between the effects of high- and low-preferred items provided evidence that the paired-choice assessments were useful in selecting enrichment items.

Method

Subjects and Enclosures

Subjects included three of the seven ring-tailed lemurs, two new ring-tailed lemurs, and all three of the collared lemurs from Experiment 1 for a total of eight lemurs. Lemurs were chosen for Experiment 2 because they were the animals exhibited where the study was conducted. Due to limited direct access to the two new ring-tailed lemurs, no additional preference assessments were conducted. However, because there was low variability in the items selected across the ring-tailed lemurs during Experiment 1, this was not a major concern. In addition, for the first session, only four of the five ring-tailed lemurs were on exhibit. Five ring-tailed lemurs were on exhibit until session 14, when the fifth lemur was removed for the remainder of the study due to illness. Therefore, half of all the sessions (sessions 1 and 14–24) were run with four rather than five ring-tailed lemurs. All lemurs were observed in the outdoor island exhibit previously described in Experiment 1.

Materials

Materials included the eight food items assessed in Experiment 1. During experimental conditions, the food items were cut in 2–3 cm × 2–3 cm squares and placed in one of two 61 cm × 10 cm bamboo dispensers. Each bamboo dispenser had eight 4-cm diameter holes that allowed food to be withdrawn from it. Other materials included Palm® handhelds used to record behavioral data, an Event-PC program that was run on the Palm® handhelds and designed specifically for this experiment by Dr. James Ha at the University of Washington, and a notebook used to record potential errors and additional observations/field notes that occurred during a session.

Design and Procedure

A modified scan sampling procedure (Altmann, 1974) was used to record behaviors during all sessions. The exhibit was divided into six possible coding areas. **Figure 2** shows the ring-tailed/collared lemur exhibit, with the coding areas labeled A through F. One of seven mutually exclusive and exhaustive behaviors listed in **Table 2** was recorded for each animal present in that location during each sample. In other words, only one behavior was recorded for each animal in the coding area being sampled. A coding area was sampled each 30 s over 1 h for a total of 120 area-behavior samples.

Because we were not able to observe all of the exhibit from any one area while distinguishing reliably between individuals within a species, for each area sample, we recorded instead the number of animals within a species that engaged in any of the coded behaviors in the sampled area. For example, at the start of the session, the observer(s) recorded the number of ring-tailed and collared lemurs engaged in any of the seven possible behaviors for Area A. Only behaviors occurring within Area A were recorded for that interval. During the following sampling interval, the same procedure was followed for Area B. The sample area was successively changed from A to F, and then the cycle was repeated beginning with Area A each time, creating a total of 20 samples per area for each session (3 min to cycle through the six areas).

A potential limitation of this technique is that individuals could be observed in more than one area during each scan. For instance, between 30-s observations, a lemur could move from Area A to Area B and thus be observed in both areas. To determine how often this may have happened, the total number of behaviors observed per species was counted for all 24 sessions. If a lemur was observed only once during each of the 3-min intervals required to observe all six areas, a total of 20 behaviors × the number of individuals in a particular species would be produced [60 observations for collared lemurs, 80 or 100 observations (depending on whether four or five individuals were on exhibit) for ring-tailed lemurs per session]. A number greater than this would suggest that one or more lemurs were counted more than once during a successive sample of the six areas, while a smaller number would suggest the animal moved so as not to be measured or was missed altogether. On average, both collared and ring-tailed lemurs were observed during 96% (SE = 1%) of all possible intervals recorded during all 24 sessions, suggesting that only a small number of possible observations per species

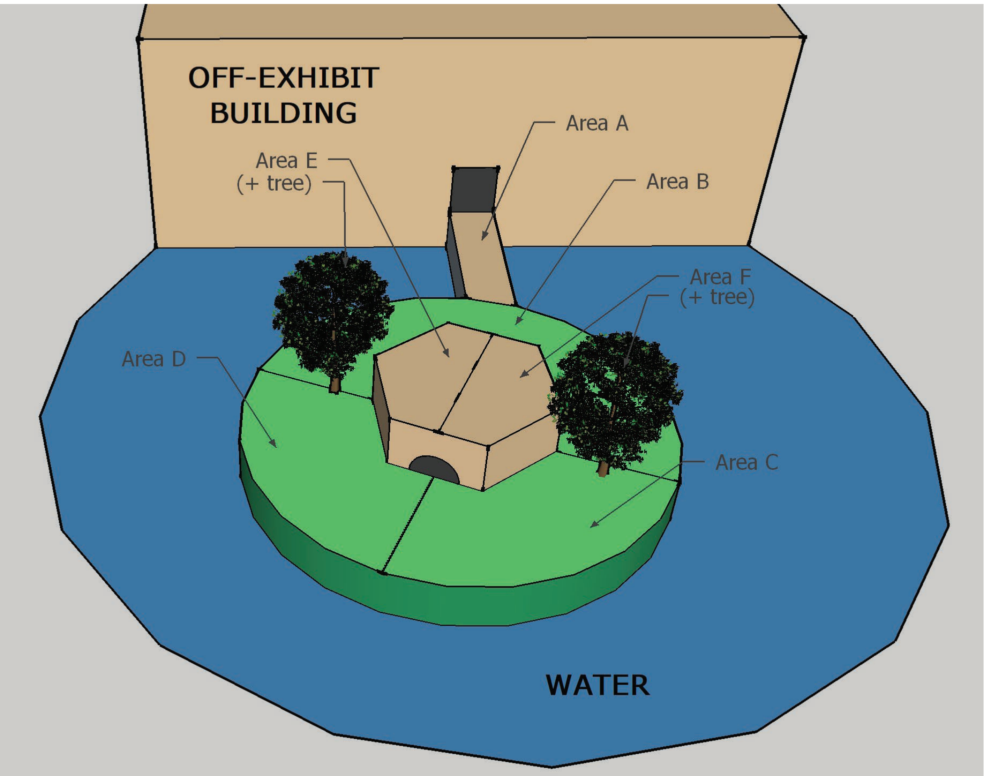

FIGURE 2 | Diagram of the ring-tailed/collared lemur exhibit, as viewed from above. Capital letters represent each area, and lines represent their boundaries. The structure above Area A shows the holding/nighttime exhibit (lemurs reach the island exhibit by crossing Area A). The trees in Area E and Area F are where the devices were placed during all three conditions (BL, LP, HP).

TABLE 2 | Behaviors and definitions for each response categorized in the ethogram.

Behavior	Definition
Active (A)	Movement around the enclosure, eating any edible items, or interacting with objects within the enclosure (other than the bamboo dispensers).
Dispenser-Directed (DD)	Manipulating one of the two bamboo dispensers used in the study. If a lemur is contacting a bamboo dispenser while eating, it is still recorded as DD.
Inactive (I)	Lying down or sitting in the enclosure. If lemur is contacting another lemur inactively (e.g., while lying down with no motion), this is still considered inactive.
Grooming (G)	Licking or manipulating own body (usually involving licking of body).
Interacting with Same Species (SS)	Orienting towards and/or actively contacting a lemur of the same species.
Interacting with Different Species (DS)	Orienting towards and/or actively contacting a lemur of a different species.
Other (O)	A behavior not listed above, or not being able to observe what a lemur is doing.

were missed (2.4 observations for collared lemurs, 5.6 or 6.4 observations for ring-tailed lemurs per session). This result was due to either a lemur not being visible in an area or transitioning between areas during a sampling interval. Additional support for this assertion is evidenced by the fact that only two of the 24 sessions for both species produced a number greater than the total number of behaviors × the number of individuals observed.

Several minutes prior to each session, a keeper would place both bamboo dispensers in the exhibit. Each dispenser was tied approximately 1 m high to one of the two trees within the exhibit: one located in Area E and the other in Area F. There were three possible conditions during the experiment:

Baseline

During this condition, no food was placed in the bamboo dispensers. The empty bamboo dispensers were only placed on exhibit during the Baseline condition to avoid any potential habituation effects to the devices.

Low-Preferred Condition

Based on the preference assessment conducted in Experiment 1, the four least selected items (based on the combined means for the six ring-tailed and collared lemurs from Experiment 1 that were involved in Experiment 2) were determined. The four food items consisted of zucchini, cauliflower, red pepper, and green beans. During this condition, 50 g of each item was placed in each of the bamboo dispensers for a total of 200 g of food per dispenser. The two dispensers in this condition were placed on exhibit in the same manner as during the Baseline condition. It should be noted that while red pepper was the third most selected food item for all lemurs in Experiment 1, it was the fifth most selected item for the six lemurs in this experiment, hence why it was considered a low-preferred food item.

High-Preferred Condition

This condition was the same as LP, except using the four most selected items: corn, yams, eggplant, and squash. As per the Baseline and low-preferred (LP) conditions, the two dispensers were placed on exhibit as noted above.

A reversal design was used with each condition being returned to once. Following the second BL condition, the LP and HP conditions were run in reverse order to control for potential order effects (ABCACB reversal design). Eight sessions per condition were run—four sessions for each of the two times a condition was presented—for a total of 24 sessions. All sessions were run between 10:00 and 11:30 am on a Monday, Wednesday, or Friday. The entire study was conducted between June 25, 2004, and August 18, 2004.

Because of the small number of sessions (four) included in each of the two food-enrichment conditions, differences between the first and second time a condition was run were inspected visually. All differences showed changes of no greater than 30% between each time a condition was run, except for a 34% difference in same species interactions with the collared lemurs during the LP condition. This difference is discussed in the results and discussion section.

Interobserver agreement (IOA) was calculated based on total agreement (Poling et al., 1995) for 21% of all sessions conducted. All measures of total agreement were above 90%. However, because total agreement is calculated by determining the number of total observations for each observer, there is no guarantee that two observers were ever able to observe the same event during the same sampling interval. To estimate reliability without this possibility, we randomly sampled 20 observations from each of the five sessions where IOA was calculated and generated both percentage agreement and Kappa (percentage agreement corrected for chance agreement) for the 100 observations (Lehner, 1996).

The two independent observers agreed on all 100 ring-tailed lemur observations, which generated a Kappa value of 1. They agreed on 86.27% of the collared lemur observations, with a Kappa value of 0.68. Fleiss (1981) suggests that Kappa values > 0.6 are good, while values >0.75 are excellent.

SigmaStat 3.1® was used to run all the statistical analyses. The data for the behaviors and areas observed were split into 1/2-h bins (0–30 min, 31–60 min), and both 1/2-h bins and species were analyzed separately. Behaviors were split into 1/2-h bins because most of the food was removed within the first 1/2 h of introducing the food conditions, and therefore behavior after that point typically returned to Baseline levels of activity. All analyses reported passed normality and equal variance tests; therefore, we used a repeated-measures ANOVA with experimental condition as the blocking variable to examine the data. When significant differences ($p < 0.05$) were found, *post hoc* pairwise comparisons (Tukey test) were used to compare differences among the three experimental conditions.

To examine overall enclosure use, a measure of entropy (Shannon, 1948) was generated for each session. Entropy measures randomness across a set of variables and therefore produces a single measure of the total variability of enclosure use across the six possible areas. The measures of entropy were calculated by the formula

$$H = -\Sigma p(i) \log p(i),$$

where $p(i)$ is the proportion of time spent in i_{th} area. This formula produces a number from 0 to 1, with a higher value of H demonstrating more variability in overall enclosure use. Entropy was selected as a measure of variability in enclosure use [over a spread of participation index (SPI); Dickens, 1955; Hedeen, 1982; Plowman, 2003] because it is sensitive to small sets of variables and does not require a modified formula to accurately handle unequal enclosure zones. The same statistical analyses as listed above were then tested on the values of entropy.

Results and Discussion

Figure 3 shows the overall distribution of behaviors in the first 1/2 h for both species across all three conditions. Two of the behaviors that could be coded [Interacting with a Different Species (DS) and Other (O)] were never observed during the study, and therefore were not analyzed or graphed (see **Table 2** for definitions of these responses).

Active and Inactive Behaviors

Ring-tailed lemurs showed a significant change in active behaviors ($F_{2,21}$ = 5.30, p = 0.019), d = 0.65. Active (A) behaviors significantly increased during the HP condition compared to the BL condition (p = 0.015). There was also a significant change in Active behaviors for the collared lemurs ($F_{2,\,21}$ = 10.57, p = 0.002), d = 0.955. Active behaviors significantly increased during the HP condition compared to the BL condition (p = 0.001). For both species, the data therefore suggest that the greatest increase in Active behaviors was observed during the HP condition in the first 1/2 h.

The collared lemurs spent much of their time in the first 1/2 h of BL engaged in Inactive (I) behaviors. This changed significantly during the experiment ($F_{2,\,21}$ = 80.36, $p < 0.001$), d = 1.0, with Inactive behaviors decreasing during the LP condition ($p < 0.001$) and the HP condition ($p < 0.001$). Ring-tailed lemurs showed no significant changes in Inactive behaviors in the first 1/2 h. However, their Inactive behaviors decreased from 89.8% (SE = 2.4) to 73.2% (SE = 9.1) and 65.8% (SE = 6.5) for the LP ad HP conditions, respectively. For the collared lemurs, both food conditions had similar effects in reducing Inactive behaviors in the first 1/2 h compared to BL. For the ring-tailed lemurs, the data suggest that the HP condition had a greater effect than the LP condition in reducing Inactive behaviors during the first 1/2 h.

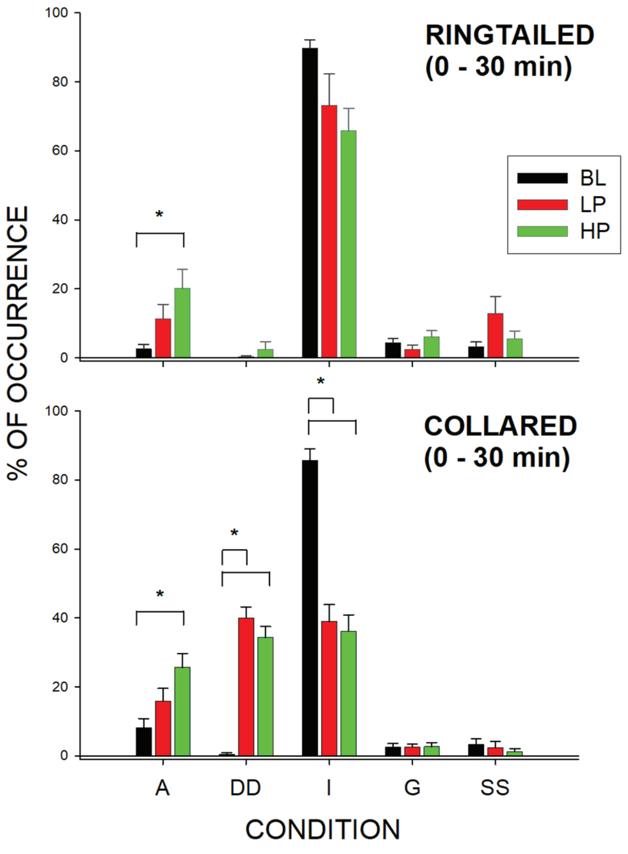

FIGURE 3 | Mean percentage of occurrence (with SE bars) in the first 1/2 h for the Active (A), Dispenser-Directed (DD), Inactive (I), groom (G), and Same Species (SS) behaviors across all three conditions (BL, LP, and HP). The top graph shows the ring-tailed lemurs' behaviors, and the bottom graph shows the collared lemurs' behaviors. Asterisks and solids lines indicate significant differences between two conditions ($p < 0.05$).

Dispenser-Directed Behaviors

The collared lemurs significantly increased their Dispenser-Directed (DD) behaviors in the first 1/2 h ($F_{2,\,21}$ = 71.14, $p < 0.001$), d = 1.0. During BL, the collared lemurs engaged in few Dispenser-Directed behaviors, although the frequency increased significantly during the LP condition ($p < 0.001$) and the HP condition ($p < 0.001$). Like the change in Inactive behaviors for the collared lemurs during the first 1/2 h, both food conditions increased Dispenser-Directed behaviors. Therefore, the presence of food within the dispensers produced the Dispenser-Directed behaviors, rather than the type of food present. The ring-tailed lemurs showed no significant changes in Dispenser-Directed behaviors for any of the behaviors during the first 1/2 h.

Second 1/2-h Effects

The only significant differences observed in the second 1/2 h were for Same-Species interactions (SS) with the collared lemurs ($F_{2,\,21}$ = 7.47, p = 0.006), d = 0.837. These Same-Species interactions were significantly higher during the LP condition

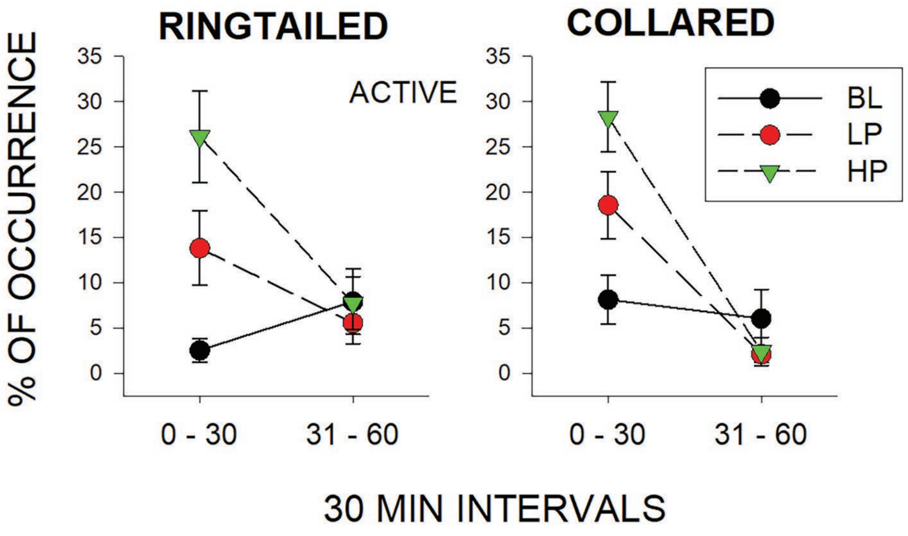

FIGURE 4 | Mean percentage of occurrence (with SE bars) for the Active behaviors across all three conditions (BL, LP, and HP). The graph on the left is for the ring-tailed lemurs and the graph on the right is for the collared lemurs. The x-axis is split into 1/2-h intervals for the full hour of observation.

when compared to both the BL condition (p = 0.009) and HP condition (p = 0.02). Therefore, the effects of both food conditions appeared to be short lived. Almost all changes in behaviors compared to Baseline were no longer observed by the second 1/2 h of observation. **Figure 4** demonstrates this trend for the Active behaviors. As described previously, there were increases in both the LP and HP conditions when compared to BL for both species in the first 1/2 h. However, Active behaviors returned to Baseline levels of occurrence for both species during the LP and HP conditions in the second 1/2 h.

It was unclear why Same-Species interactions among the collared lemurs increased in the second 1/2 h, and more specifically, for the LP condition and not the HP condition. It was unlikely that the fewer desirable food items in the LP condition resulted in increased aggression, since the observers noted few instances of aggressive displays, and there was no demonstration of similar Different-Species interactions. The lower number of desirable items in the LP condition possibly increased later social foraging strategies, or there may have been an order effect. Most of the Same-Species interactions occurred during the second LP condition (first LP: M = 8.34, SE = 8.34; second LP: M = 42.26, SE = 10.37), when the LP condition followed the HP condition.

Overall Enclosure Use

Figure 5 shows the entropy values for both species and during both 1/2-h bins. As described previously, entropy was used to measure the total variability of enclosure use across the six possible areas within the lemur exhibit. A higher value of entropy indicates greater overall enclosure use for that species. There was a significant change in the entropy values for the collared lemurs ($F_{2, 21}$ = 10.387, p = 0.002), d = 0.951. There was a significant increase in the entropy value from BL to both the LP condition (p = 0.008) and the HP condition (p = 0.002). For the ring-tailed lemurs, during the first 1/2 h,

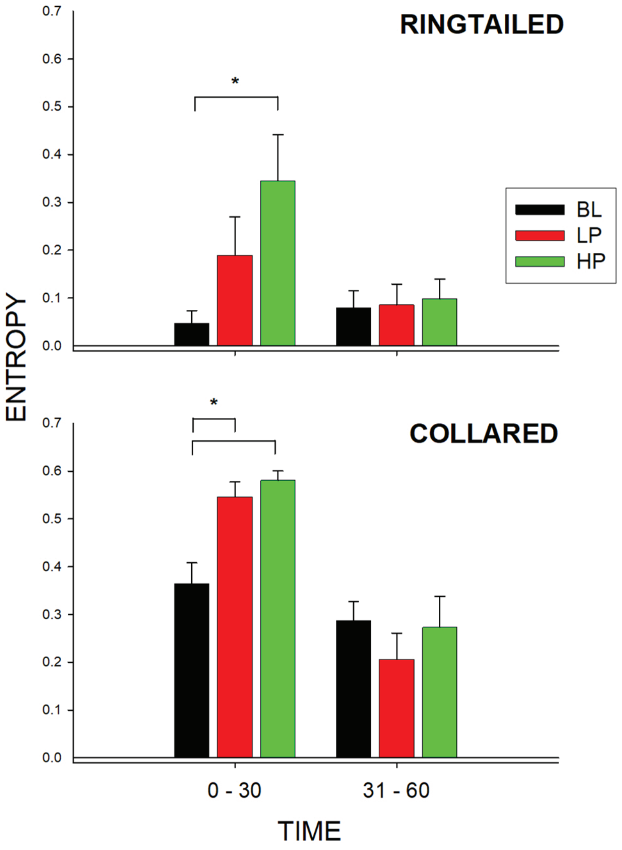

FIGURE 5 | Mean entropy value (with SE bars) for the three conditions (BL, LP, and HP). The x-axis is split into 1/2-h intervals for the full hour of observation. The top graph shows the ring-tailed lemurs' entropy values, and the bottom graph shows the collared lemurs' entropy values. Asterisks and solids lines indicate significant differences between two conditions (p < 0.05).

there was also a significant change in the entropy values ($F_{2,21} = 4.109$, $p = 0.039$), $d = 0.498$. There was a significant increase in the entropy value from the BL condition to the HP condition ($p = 0.031$). For the collared lemurs, both food conditions had similar effects on increasing overall enclosure use in the first 1/2 h compared to Baseline. For the ring-tailed lemurs, the data suggest that the HP condition had a greater effect than the LP condition in increasing overall enclosure use during the first 1/2 h of observation.

Figure 6 represents the percentage of area use for all six areas across all three conditions during the first 1/2 h. During Baseline, the ring-tailed lemurs spent 84% (SE = 12.18) of their time in Area B. This time decreased to 53.26% (SE = 16.97) and 56.53% (SE = 14.01) during LP and HP, respectively. Most other areas increased in use during the LP and HP conditions compared to Baseline. During the first 1/2 h of Baseline, the collared lemurs spent 24.71% (SE = 6.97) of their time in Area C, 52.27% (SE = 9.77) in Area D, 11.77% (SE = 7.58) in Area

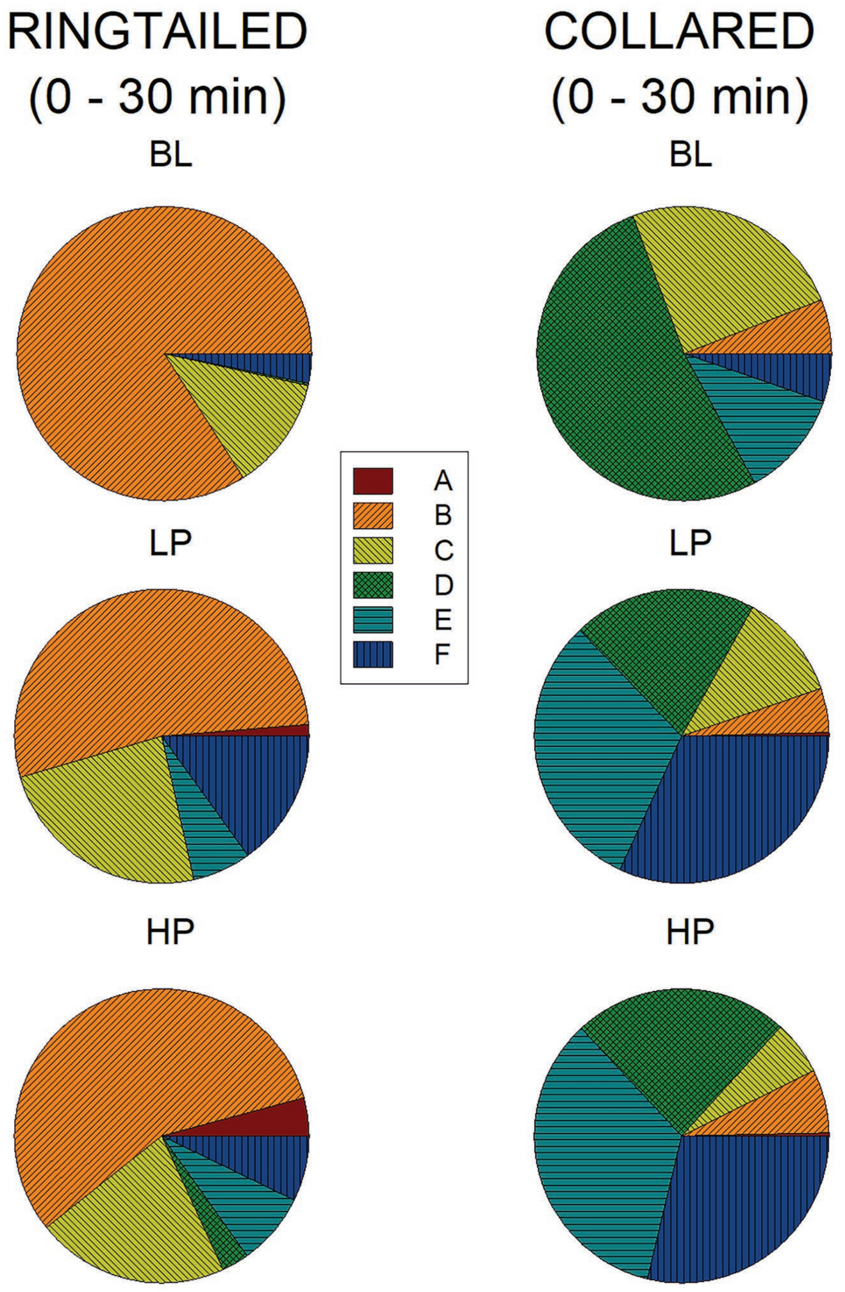

FIGURE 6 | Mean percentage of area use in the first 1/2 h across the three conditions for both species. The graphs on the left are for the ring-tailed lemurs and the graphs on the right are for the collared lemurs. The top graphs are for the Baseline (BL) condition, the middle graphs for the low-preferred (LP) condition, and the bottom graphs for the high-preferred (HP) condition. Area E and F included the trees, where the devices were placed.

E, and 5.31% (SE = 2.41) in Area F. During both the LP and HP conditions, area use was more evenly distributed, with Area D decreasing (LP: *M* = 20.18%, SE = 4.69; HP: *M* = 23.67%, SE = 2.85), and Area E and F (which held the devices) increasing (Area E, LP: *M* = 30.97%, SE = 5.30; HP: *M* = 34.36%, SE = 5.22. Area F, LP: *M* = 31.89%, SE = 6.72; HP: *M* = 28.74%, SE = 2.93).

GENERAL DISCUSSION

Experiment 1 was successful in rapidly and systematically ranking the preferences of eight food items for all four species of lemur in the study, showing a high degree of similarity in food preferences within and between species. As noted previously, except for minor exceptions (e.g., blue-eyed black lemurs' selection of cauliflower and eggplant), there were several similarities in the food selections both within and between a species. Because the food selections showed a clear and consistent ranking across all the lemurs, we were able to divide the choices into two categories: high- and low-preferred items. These categories facilitated testing the effects of food preferences on enrichment activities in Experiment 2.

In Experiment 2, presenting the high-preferred food items decreased Inactive behaviors and increased Active behaviors in the first 1/2 h, both with respect to BL. Presenting the low-preferred food showed similar trends with respect to the BL condition, but only the decrease in Inactive behaviors in the collared lemurs was significant. Although the average changes in behavior in the HP condition were consistently higher than those in the LP condition, there were no significant differences between the two experimental conditions.

Similarly, during the first 1/2 h following the presentation of food items, there was greater use of the enclosure (as measured by entropy values) for both species during one or both experimental conditions when compared to the Baseline. During Baseline, the ring-tailed lemurs spent almost all their time in Area B, while the collared lemurs spent more than half of their time in Area D. During both food conditions, times in Area B for the ring-tailed lemurs and Area D for the collared lemurs decreased, while there was an increase in most of the other areas within the enclosure. This change was due directly to the lemurs increasing the time they spent interacting with or remaining near the bamboo dispensers during the food conditions.

That food enrichment effects were largely confined to the first 1/2 h following the introduction of the bamboo dispensers indicates that the effect of our enrichment manipulation was limited to a relatively short time around the presentation of food. A larger amount of food (a total of 400 g of food was present in both dispensers) may have increased activity beyond the first 1/2 h. Since changes in the behaviors of the lemurs were directly related to the time it took the lemurs to consume the food, it seems worthwhile to investigate the effects of providing enrichment manipulations that require more extensive foraging activities. Distributing the bamboo dispensers more widely or making extraction of the food more difficult may have greater long-term effects.

It is worth noting that the presentation of the food may have interacted with the niche-related foraging repertoires of the two species. Ring-tailed lemurs are the most terrestrial of all lemur species in their habits and foraging activities (Duke University, 2005). Although the ring-tailed lemurs showed similar findings to the collared lemurs in terms of increased Active behaviors, decreased Inactive behaviors, and increased overall enclosure use, they rarely interacted with the suspended bamboo dispensers. Instead, during both high- and low-preferred experimental conditions, the ring-tailed lemurs remained below the hanging dispensers, picking up food that the collared lemurs dropped while manipulating the enrichment devices. This behavior suggests that for the ring-tailed lemurs, putting the bamboo holders on the ground might encourage more direct feeder interaction. Future research could be directed at comparing hanging vs. floor feeding enrichment for ring-tailed lemurs, as well as assessing preferences for both types of placement.

Ring-tailed lemurs are also known to shift their foraging patterns from fruit or leaves hanging on trees to fruit on the ground, depending on whether fruit and leaves have recently bloomed (Mertl-Millhollen et al., 2003). Therefore, it is possible that lemurs in captivity also change the percentage of time spent terrestrially based on the time of year. Future studies could examine differences in the effectiveness of hanging vs. non-hanging enrichment in ring-tailed lemurs during different seasons. Regardless, it is worth noting that one important component of naturalistic enrichment is that it interacts with species-typical behavioral repertoires, which is particularly true for foraging behavior. Environmental enrichment provides functionally related foraging opportunities for all species, which means that a better understanding of the natural history of any animal should facilitate the implementation of any enrichment practice.

Enrichment Selection and Systematic Assessment

Our data support the use of paired-choice preference assessments for comparing multiple small, easily presented stimuli such as food items. Systematic comparisons of a limited number of alternatives produce empirically evaluated differences in a relatively short period of time, allowing multiple individuals to be assessed in a way that can apply to the preferences of groups. Preferences for available foods or other items could easily be run daily using a sample of the captive population and would help guide the type of enrichment to be used for that group. Preference assessments also can be used to determine differences between individuals in a group and thus help individualize the types of enrichment used. The main point is that preference assessments such as these can bypass the trial-and-error process of enrichment selection, and instead focus on using data to guide the selection of possible enrichment to better improve their effectiveness.

Finally, we examined environmental enrichment only as it applied to small manipulable food sources. As other researchers have noted, enrichment can also refer to physical and social stimuli and human-animal interactions (Mellen and MacPhee, 2001; Alligood and Leighty, 2015). It seems likely that these more abstract forms of enrichment could also be selected based on successive pairings of alternatives and inspection of choice behavior. Even with enrichment procedures not directly testable through paired choices, such as access to keepers or husbandry training procedures, stimuli selected during a preference assessment could be paired with these events and therefore make it possible to select and test most types of potential enrichment systematically.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animals in this study were reviewed and approved by the IU – Bloomington IACUC and the Indianapolis Zoo Research Committee.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Dolphins' Willingness to Participate (*WtP*) in Positive Reinforcement Training as a Potential Welfare Indicator, Where *WtP* Predicts Early Changes in Health Status

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Welfare science has built its foundations on veterinary medicine and thus measures of health. Since bottlenose dolphins (*Tursiops truncatus*) tend to mask symptoms of poor health, management in captivity would benefit from advanced understanding on the links between health and behavioural parameters, and few studies exist on the topic. In this study, four representative behavioural and health measures were chosen: health status (as qualified by veterinarians), percentage of daily food eaten, occurrences of new rake marks (proxy measure of social activity), and willingness to participate (*WtP*) in Positive Reinforcement Training sessions as qualitatively measured by their caretakers. These data were collected multiple times a day, every day over the course of a year from a multi-facility, large sample size ($n_{dolphins} = 51$), allowing powerful analyses of the relationships between measures. First, it was found that dolphins with a higher *WtP* score also had a significantly better health status, ate a higher percentage of their daily food, and a lower occurrence of new rake marks. In addition, the *WtP* score was significantly lower up to 3 days before the weekly veterinary diagnosis of a decrease in health state; the percentage of daily food eaten and new rake mark measures did not show any significant change before such a diagnosis. These results suggest that *WtP* in training sessions is a potential behavioural measure of dolphin welfare, and an indicator of early changes in the dolphins' health state. We therefore suggest measurement of *WtP* as a more practical and non-invasive tool to support veterinary care and general management. More work needs to be conducted to elucidate the influence of social behaviour on health, and to identify other potential welfare indicators, but this long-term study has shown that qualitative measures can be both practical and valid when assessing dolphin welfare.

Keywords: animal welfare, bottlenose dolphins, positive reinforcement training, reward motivation, qualitative welfare measures

INTRODUCTION

Welfare science, the objective measurement of animals' affective states (Mason and Veasey, 2010; Hemsworth et al., 2015; Veasey, 2017), had its genesis in veterinary medicine (Dawkins, 2006). Health-related measures of individual welfare include assessing parameters such as body lesions, disease, immune response, body condition, and stress physiology. Over half a century ago when animal welfare issues started to capture the general public's attention, health parameters were simple, accurate indicators of the severity of suffering of farm animals (Wemelsfelder and Mullan, 2014; Veasey, 2017). As reflected by the perception of 'well-being' in human society at the time, efforts were firmly focussed on measuring and improving the physical as opposed to psychological health of animals.

An increase in both general husbandry standards and our knowledge of human and animal affective states led welfare scientists to consider behavioural and later cognitive measures of animal welfare. The initial behavioural measures studied were those associated with poor health, primarily 'sickness behaviour' which usually manifests as lethargy, anhedonia, inappetence, and social isolation, and which can be a key indication of poor welfare in animals that have adapted to mask overt signs of injury and disease (Johnson, 2002; Millman, 2007; Sneddon et al., 2014). Other behavioural indicators include play, affiliative behaviour, aggression, abnormal and resting behaviours, and are now thought to be just as informative as health measures in terms of overall welfare (Dawkins, 2004; Joseph and Antrim, 2010). Welfare science has moved on from considering good welfare as simply the absence of suffering and is now focussed on defining and measuring positive affective states, with behavioural measures being a key element in their evaluation (Boissy et al., 2007; Yeates and Main, 2008). Support for "feelings-based" welfare definitions is strong, stipulating that health only impacts welfare if the animal's feelings are affected (e.g., feeling sick), and therefore encouraging research on identifying welfare indicators associated with health conditions (Mason and Veasey, 2010; Watters, 2014; Hemsworth et al., 2015; Clegg et al., 2017b; Veasey, 2017).

This is not to say that health-related welfare measures are redundant: they are readily quantifiable, easy to standardise, and continue to be used in welfare assessment frameworks for a range of species (Welfare Quality®, 2009; Mononen et al., 2012; Clegg et al., 2015). Since there is no single, perfect measure of welfare, the most accurate method for scientists and managers who aim to measure the overall welfare of an animal or population is to develop a multidisciplinary assessment, comprised of a combination of health, behavioural and cognitive measures (Pritchard et al., 2005; Webster, 2005; Mason and Veasey, 2010). It is worth noting that these categories represent 'animal-based' measures, i.e., direct outputs that can be measured from the animal, and are thought to be more accurate welfare indicators than using 'resource-based' measures which focus on the resources we provide (Webster, 2005; Roe et al., 2011).

Among many different species, animal-based welfare measures developed so far have predominantly been quantitative (Wemelsfelder, 2007), where behavioural or health parameters are defined and measured among certain contexts. Some key individual welfare measures that have been validated against other indicators are: stereotypic behaviours (Mason and Rushen, 2006; Mason and Rushen, 2008), sustained agonistic behaviour (Shively et al., 1997; Papciak et al., 2013), close social bonds (Kikusui et al., 2006; Hennessy et al., 2009), cognitive bias (Mendl et al., 2009; Roelofs et al., 2016), skin condition (Pritchard et al., 2005; Mononen et al., 2012), stress response (Cockram, 2004; Palme, 2012) and body lesions (Broom, 1991; Robinson et al., 2018). There are many advantages to quantitative welfare measures: namely the high reliability and validity of the data (Martin and Bateson, 1986; Veasey, 2017). However, welfare scientists often aspire to measure inherently more holistic phenomena, such as attitude, personality and indeed when trying to integrate multiple indicators to evaluate overall welfare itself. Fortunately, human social science provides some guidance for how to most accurately measure these constructs, where qualitative measures have been used to capture this data for decades (Wemelsfelder, 2007). Recently, such qualitative techniques have been applied to animals in captivity and have been found to correlate to quantitative measures, indicating that they have "biological validity" (Rousing and Wemelsfelder, 2006; Wemelsfelder, 2007). Qualitative information also complements the quantitative through its interpretative role, providing comprehensive data on the situation which is critical when assessing welfare, but hard to realise (Wemelsfelder, 2007; Whitham and Wielebnowski, 2009). The most commonly used qualitative methodology thus far is the Qualitative Behavioural Assessment (QBA), where an observer evaluates an animal's emotional expressivity by considering and integrating many aspects of its behaviour (Wemelsfelder, 2007). QBAs have been used to assess welfare during transport of farm animals (Stockman et al., 2011), in measuring their social behaviour (Rousing and Wemelsfelder, 2006), and were included in the well-received Welfare Quality® assessments (Welfare Quality®, 2009), the largest Europe-wide project of its kind (Blokhuis, 2008). One of the key advantages of QBAs and general qualitative behavioural measurement is that data collection is feasible and inexpensive, and has therefore been shown to be preferred by animal managers for *in situ* monitoring of welfare (Napolitano et al., 2010; Maple and Perdue, 2013). However, despite these advances in qualitative measures of welfare, they are still often regarded as subjective and even anthropomorphic, and therefore are not as commonly used and thought to have lesser value than other presumed more objective measures (Hall et al., 2013; Wemelsfelder and Mullan, 2014).

Regular monitoring by animal caretakers themselves is thought to be the key to making actual improvements in welfare, especially in zoos and aquaria (hereafter zoos) (Maple, 2007). Zookeepers have a unique relationship with many of the animals under their care since they generally provide individualised care: they spend many hours each day in proximity to the animals, are their primary food providers, may engage in training with them, and sometimes have been present in their lives since birth (Hosey and Melfi, 2010; Szokalski et al., 2013). Therefore the keepers certainly have a high chance of capturing the subtle emotional and behavioural attitudes of the animals which might otherwise be inaccessible to researchers, and especially when using qualitative approaches (Weiss et al., 2006; Whitham and Wielebnowski, 2009; Gartner and Weiss, 2013). Inter-observer agreement on ratings between keepers in these studies has been shown to be high and the qualitative results have been significantly associated with quantitative data, as with farm animals (Whitham and Wielebnowski, 2009). Zookeepers' potential to monitor and influence welfare is further strengthened by the fact that many zoos are increasingly engaging in Positive Reinforcement Training (PRT) with their animals in order to conduct husbandry procedures, cognitive enrichment and increase exercise. Conducting PRT increases the time spent with the animals, and has been shown to increase behavioural diversity, and to lower cortisol levels and stereotypic behaviours (Bloomsmith et al., 2003; Carlstead, 2009; Pomerantz and Terkel, 2009; Da Silva Vasconcellos et al., 2016).

Cetacean species kept in zoos around the world have recently been the focus of increased welfare discussions and research (Clegg et al., 2015; Brando et al., 2016; Butterworth, 2017; von Fersen et al., 2018), acting as proxies for the general debate on animals displayed in zoos. Regarding bottlenose dolphins (*Tursiops truncatus*), studies are starting to suggest single potential welfare indicators such as synchronous swimming (Clegg et al., 2017a), play (Serres and Delfour, 2017), and cortisol measurement (Ugaz et al., 2013; Monreal-Pawlowsky et al., 2017; Mercera, 2019). As with other socially complex animals such as primates (Morgan and Tromborg, 2007; Buchanan-Smith et al., 2013; Schino et al., 2016), close social bonds seem to promote positive welfare in dolphins, but on the same token social stress has strong potential to reduce welfare (Waples and Gales, 2002; Clegg et al., 2017a,b). Social tensions have even been reported as causing chronic health problems and death in a few cases, although data were anecdotal (Waples and Gales, 2002). Notably, when cetacean species are experiencing poor health, they often mask symptoms and 'sickness behaviour' until the pathology is well developed (Waples and Gales, 2002; Castellote and Fossa, 2006). There is therefore a need to identify any behavioural indicators which reliably signal the early stages of health problems (Clegg et al., 2017b). These might be related to the animal's social behaviour, appetence or interaction with its environment. Thus far in the field of cetology, qualitative techniques have been used to measure dolphin personality, but not emotions or welfare. Such measures use the expertise of knowledgeable observers to integrate multimodal information over time and contexts in a way that one-dimensional quantitative data cannot (Meagher, 2009; Wemelsfelder and Mullan, 2014), are relatively cheap and easy to conduct, and are highly sensitive to the animals' immediate environment (Fleming et al., 2013).

Captive cetaceans live in a unique environment regarding their relationship with their trainers/caretakers: they often spend hours daily completing tasks with familiar humans during training sessions, sometimes in close physical contact, within a type of working relationship framework (Brando et al., 2016; Clegg et al., 2018). The effect on dolphin behaviour of these training sessions, which may include shows, human-animal interactions, medical behaviours or research tasks, has been the focus of several welfare studies, with some concluding the animals view the training sessions positively (Trone et al., 2005; Miller et al., 2011; Sew and Todd, 2013) and others suggesting they have led to agonistic behaviours (Frohoff and Packard, 1995). Behaviour before predictable events such as training sessions, termed anticipatory behaviour, has been considered in other animals as well as dolphins: a recent study found that bottlenose dolphins positively anticipate both training sessions where food is provided, as well as familiar trainer interactions where no food rewards are given, with the authors suggesting that dolphins' varying responses to both contexts could indicate their welfare state (Clegg et al., 2018). However, these studies are measuring the dolphins' response to the sessions indirectly, through associated behavioural repertoires: there is no existing research measuring the animals' level of motivation during the sessions. An animal's motivation is defined as its tendency to engage in an activity and is adaptively shaped with the goal of increasing biological fitness, where the associated behaviours are often linked to positive and negative affective states (Manteuffel et al., 2009). Therefore motivation was considered a significant phenomenon to study in terms of welfare (Kirkden and Pajor, 2006). In modern facilities, Positive Reinforcement Training (PRT) sessions are exclusively used to condition the animals to tasks, within which they receive their daily rations of food (Kuczaj and Xitco, 2002; Brando, 2010). PRT sessions provide food rewards conditional on the performance of certain tasks, and thus a dolphin's motivation during these sessions may relate to the acquisition of food or the performance of the tasks: previous studies on 'contrafreeloading' (preferring to work for rewards as opposed to obtaining them for free) suggest it is likely a combination of the two (Salamone et al., 1994; de Jonge et al., 2008). Although there is likely much inter- and intra-individual variation in the dolphins' motivation for PRT sessions, several significant influencing factors can be suggested. For example, chronic stress and social isolation were found to decrease motivation for rewards in laboratory rats (*Rattus norvegicus*) (Kleen et al., 2006) and domestic pigs (*Sus scrofa*) (Pedersen et al., 2002) respectively. In other animals, health status has been shown to impact motivation to work for rewards, e.g., an increase in pro-inflammatory cytokines signalling an immune response, i.e., departure from good health, induces decreased motivation for rewards in various species (Larson, 2002; De La Garza, 2005). If the above findings were also applicable to captive dolphins, measuring the motivation in PRT sessions could be a valuable early identifier for health and chronic stress conditions, allowing proactive management and reducing the need for invasive interventions further down the line.

Despite increased efforts into measuring dolphin welfare, scientists have not yet applied multiple health and behavioural measures to a large sample size with repetitions over time: this is essential for capturing the true variation and validating welfare measures. While this is easily achievable in farm and laboratory studies (Blokhuis et al., 2013; Wemelsfelder and Mullan, 2014), in the zoo setting small population sizes and animal management logistics are often limiting factors (Botreau et al., 2009; Whitham and Wielebnowski, 2013). The only study that combined health and behavioural measures looked at 3 case studies, reporting in mainly anecdotes that the dolphins' health problems were preceded by changes in social behaviour, appetence and their interactions with the trainers (Waples and Gales, 2002). If validated with a much larger number of animals, such measures would be extremely useful to managers for early prediction of dolphins in poor health and welfare [e.g., 48,49], and could also be applicable for wild animal research (e.g., understanding social context through rake mark prevalence, Cords and Mann, 2014). A multi-institutional study applying multidisciplinary welfare measures has recently been conducted with rhesus macaques (*Macaca mulatta*), successfully exploring the relationships between health and individual differences in personality, behaviour, and social status (Robinson et al., 2018). This study also used a concise set of representative welfare measures, which is an important step toward improving feasibility of assessments and increased industry uptake (Main et al., 2012; Wemelsfelder and Mullan, 2014).

The current study was therefore designed with the aim of collecting long-term, multidisciplinary welfare data from a large sample of captive bottlenose dolphins in multiple facilities, focussing on a small but representative number of qualitative measures that could be conducted by the caretakers themselves. The objectives of the project were to investigate four health and behavioural welfare measures, focussing on the potential links between motivation for rewards, health and welfare, and using both quantitative and qualitative approaches. The principal behavioural measure was willingness to participate during training sessions ("*WtP*"). This was chosen as the key potential welfare indicator based on findings that other animals' motivation to work for rewards has been closely linked to their emotional, welfare and health state (Spruijt et al., 2001; De La Garza, 2005; Rygula et al., 2005), and given that the training sessions represented a significant element of the dolphins' environment. We aimed to correlate *WtP* to three other measures in order to investigate the link between behavioural and health measures. Health status was qualitatively assessed as part of examinations by on-site marine mammal veterinarians, who gave a simple evaluation of the individual health status on a weekly basis. A qualitative score evaluating the social context was also developed, where the occurrence of new rake marks (caused by other dolphins scraping their teeth against one another) on the body was scored, since this has been previously been used as an indicator of aggression and social stress in dolphins (Waples and Gales, 2002; Scott et al., 2005; Marley et al., 2013). Lastly, a quantitative measure of the percentage of fish eaten out of the total offered was applied. This was included because a decrease in appetite, even if not severe anorexia, is a common indicator of poor animal welfare (Johnson, 2002; Millman, 2007; Sneddon et al., 2014), and has been correlated with social stress (Waples and Gales, 2002) and poor health (Johnson et al., 2009; Schmitt and Sur, 2012) in bottlenose dolphins specifically.

Our first hypothesis was that we would find correlations between some or all of the chosen four measures, supporting their use as indicators of welfare state, where poorer welfare would be reflected by lower willingness to participate in training sessions, poorer health status, higher occurrence of new rake marks, and a lower percentage of daily food eaten. Our second hypothesis was that *WtP* would predict the early changes in the Health score. This was supported by anecdotal evidence from a previous study where the dolphins participated less and less in training sessions shortly before health conditions were even diagnosed (Waples and Gales, 2002), and the fact that decreased motivation to work for rewards is correlated with decreased health and welfare in other mammal species (Larson, 2002; Pedersen et al., 2002; Rygula et al., 2005; De La Garza, 2005; Kleen et al., 2006), including humans (Yirmiya, 1997; Danna and Griffin, 1999; Fernet, 2013). We expected that the new rake mark occurrence and percentage of daily food eaten would correlate with the Health score due to the potential for links with social stress and sickness behaviour respectively. We did not expect that they would predict early changes in the Health score since in previous dolphin studies that looked at the link between these measures and the animal's health, correlations have only been reported where health problems are severe (Dierauf and Gulland, 2001; Waples and Gales, 2002; Johnson et al., 2009).

MATERIALS AND METHODS

Sample Population and Participating Facilities

Four dolphin facilities from four European countries participated in the project (Parc Astérix, France, $n_{\text{dolphins}} = 7$; Boudewijn Seapark, Belgium, $n_{\text{dolphins}} = 8$; Attica Park, Greece, $n_{\text{dolphins}} = 8$; and Dolfinarium Harderwijk, Netherlands, $n_{\text{dolphins}} = 28$), with a fifth facility aiding in the study's early development stages (Planète Sauvage, France). This resulted in data being collected from a total of 51 bottlenose dolphins (25 males and 26 females, age range of 1–55 years, **Table 1**) over the year long study. The large sample size and long study period was necessary to capture a sufficient number of occurrences where the Health scores varied. At all four facilities, the dolphins were fed a variety of fish and squid species daily during multiple training sessions, with the total amount per day for each dolphin ranging between 1 (for the very young animals) and 12 kg. There were between 5 and 10 training sessions each day at all facilities, excluding the 'free feed' first and last sessions of the day where the dolphins were fed their full ration without any conditioned behaviours being asked. All participating facilities are accredited by the European Association for Aquatic Mammals (EAAM) and follow their standard guidelines (European Association of Aquatic Mammals, 2019), using exclusively Positive Reinforcement Training (PRT) where the dolphins received fish and/or secondary reinforcers (e.g., rubs, attention, toys) after performing conditioned behaviours, and where no punishment or negative outcome for their leaving the trainer's presence (Laule et al., 2003). Training sessions could include training for public presentations, medical training, play sessions and research sessions, and on days when the facilities were open to the public there were between two and three public presentations. All these types of sessions and presentations were considered under the umbrella of 'training session' for our methods and analysis.

The seven dolphins at Parc Astérix (Plailly, France) were housed in an outdoor pool conjoined to two indoor pools

TABLE 1 | Age and sex characteristics of bottlenose dolphin study population.

Facility	Group	N_{total}	N [juvenile:adult]		Age range [years]		Origin
			Females	**Males**	**Females**	**Males**	($n_{wildcaught}$:$n_{captiveborn}$)
Parc Astérix	Parc Astérix	7	1:4	0:2	1–44	32–35	3:4
Boudewijn Seapark	Boudewijn	8	1:5	1:1	1–51	1–11	3:5
Attica Park	Attica	8	0:1	2:5	39–39	5–32	1:7
Dolfinarium Harderwijk	Dome	10	–	0:10	–	12–43	1:9
Dolfinarium Harderwijk	Delta 1	12	2:5	3:2	3–55	4–25	3:9
Dolfinarium Harderwijk	Delta 2	6	2:4	–	2–34	–	1:5
	TOTAL	51	6:19	6:20	1–51	1–43	12:39

Juveniles: ≤10 years old; Adults: 11 years old or more. Ages presented are those taken approximately midway through the study (1st January 2017).

with a total volume of 3,790 m^3 of water, where there was always free access to all pools. At Dolfinarium Harderwijk (Harderwijk, Netherlands), there were three groups of dolphins in two locations: the first location contained the 'Dome' group of 10 dolphins, kept in a network of seven artificial indoor and outdoor pools interconnected by gates and sluice channels, with a total water volume of 2,743 m^3. The second location was called the "Delta" and was a set of natural seawater lagoons, with a total water volume of 11,380 m^3. At the time of the study, the Delta contained two groups of dolphins, 'Delta 1' and 'Delta 2.' Delta 1 consisted of four interconnected pools (free access) with a total volume of 9,467 m^3, and housed 12 dolphins. Delta 2 was made up of two connected pools with a total volume of 1,913 m^3 and had six dolphins living there. At Boudewijn Seapark (Bruges, Belgium), the eight dolphins were housed in an indoor facility made up of a show pool and two smaller side pools, with in total volume of 2,050 m^3 of water. In addition, a channel connected the front pool with the back pool, which had a total volume of 900 m^3 and which was always available to the dolphins when training sessions were not taking place. At Attica Park (Athens, Greece), the outdoor pool system had a total volume of 4,600 m^3 and consisted of four interconnected pools (1 large and 3 smaller holding pools) which were always open to the eight dolphins.

Study Duration and Dataset

The study was carried out over a full year from September 2016 to October 2017. During this period, one dolphin was born (not included in analysis), and two dolphins of 55 and 32 years died (52 and 57 days of data were collected from these individuals before their death). Data was collected every day, multiple times daily, where the number of consecutive days of data taken for each dolphin varied between 272 and 365 days due to the study starting at different points at each facility (mean: 317 days; excluding two dolphins that died during study). This translates to a total of 15,635 days of data, with approximately 99,600 separate scores conducted on the dolphins' *WtP* during training sessions.

Behavioural and Health-Related Animal-Based Measures

The aim of the study was to collect multidisciplinary daily information to establish a large dataset of welfare-related data from a variety of dolphin facilities. The facilities were located in four different countries, where the animal care staff who would collect the information had a range of zero to moderate previous experience with scientific data collection. For this reason, the data collection methods had to be simple and able to be standardised across the international facilities. Therefore, qualitative scoring scales were used for three of the measures, with a fourth measure (Kg of fish eaten as a percentage of total offered) established as a quantitative measure since there was little room for error when recording these data (unlike attempting to quantify the animals' behaviour).

Willingness to Participate, *WtP*

Animals' motivation to work for rewards has been closely linked to their emotional, welfare and health state (Spruijt et al., 2001; De La Garza, 2005; Rygula et al., 2005), but had not yet been investigated in dolphins. Given that dolphins' lives in captivity involve multiple daily sessions where the animals are conditioned to complete certain behaviours for rewards, we used this context to measure their motivation levels. We designed a measure to assess their Willingness to Participate (*WtP*) in sessions, with the aim of investigating whether it might be related to their general health and welfare. Qualitative scoring was the ideal method for measuring *WtP* during training sessions, where knowledgeable trainers could use a 'whole-animal' approach to assess the animal's inclination to complete tasks for rewards, and record it easily multiple times per day. This is a similar approach to QBAs, which have been found to successfully measure the emotional state and welfare of terrestrial animals using qualitative approaches (Stockman et al., 2011; Rutherford et al., 2012; Fleming et al., 2013); however, there is a slight difference in that this study measured one aspect of the animal's demeanour (i.e., its "willingness" or "eagerness") as opposed to traditional QBAs which aim to assess the animal's emotional expressivity as a whole (Wemelsfelder and Lawrence, 2001).

The *WtP* score used in this study was a focal animal 5-point Likert scale, with the integers representing incremental grades of the dolphin's motivation and enthusiasm during training sessions (**Figure 1**). The dolphin trainer who conducted the session with the animal assigned a score (or if multiple trainers, the person who spent the majority of the time with it), which had to be an integer and not a half score. Trainers were allowed to discuss their score choice with other caretakers, since the aim of the

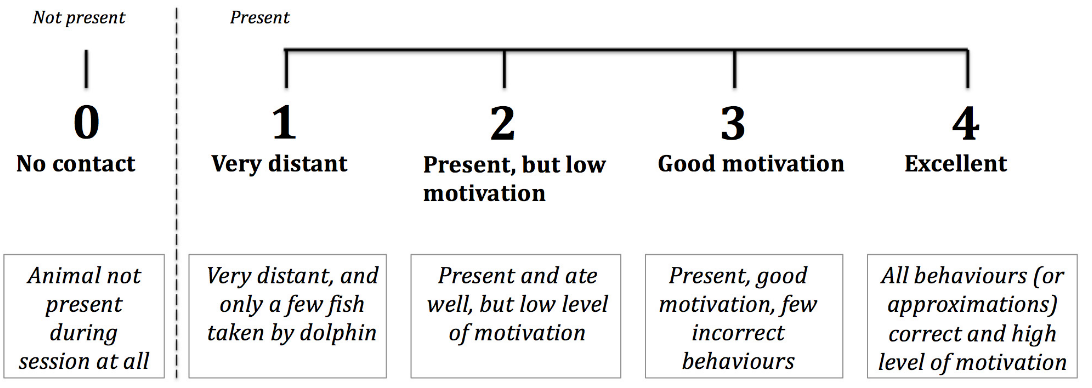

FIGURE 1 | 5-point Likert scale used by trainers in four facilities to score each dolphin's Willingness to Participate (*WtP*) in multiple daily sessions over the year-long study.

study was not to test individual trainer's perceptions of the animals' behaviour.

Before data collection started, an in-person meeting took place at each facility between the lead author (IC), the facility's management, and the trainers who would be taking the scores. Reference videos were presented of each score on the scale, showing examples of indicative behaviours and accompanied by written explanations. Discussions followed on each of the scores, serving to consolidate the distinction between the scores and the aims of the study.

Health Score

The length of the study and many different participants involved meant that our aim was to standardise the measurement of the animals' health as much as possible. Each facility had an associated veterinarian who performed an in-person health check on all animals each week, and so we sought to simplify and exploit this information for our study. Again, we developed a simple qualitative measure of health, a 3-point Likert scale (**Figure 2**), to maximise the likelihood that all veterinarians would score the animals' condition in the same way. This approach is comparable to other multi-facility studies aiming to measure overall health in the long-term (Robinson et al., 2018). As with the *WtP* score, an in-person meeting between IC and each facility's veterinarian took place before the study started, where the scale was discussed and the scores' meaning agreed upon.

Percentage of Daily Food Eaten

In order to measure the dolphins' appetite for food, a classic measure of health and welfare, we used a quantitative measure of the percentage of fish that each animal ate each day, out of the total offered (recorded in kg). The trainers weighed the amount of fish offered and eaten in each session, and totalled it for the whole day. "Offering" fish meant that over the course of the day the trainer was by the pool with the bucket of fish, giving the animal the opportunity to participate in the behaviours asked of it. An animal that scored <100% had chosen either not to approach the trainer for a proportion of the sessions that day, so that the fish could not be given, or had been present with the trainer and performed behaviours, but refused to eat all fish offered. All facilities conducted "free-feeds" in the morning and evening, and operated on the basis that if the animals chose not to perform behaviours in the training sessions, their full daily fish ration would be offered to them at the end of the day. Therefore, variance in the percentage of daily food eaten was primarily capturing those cases where the animal had refused the fish of its own volition. The total amount of fish offered per day to each dolphin varied with age, sex, facility, season, and on an individual basis, but was designed to maintain a healthy weight and optimum body condition.

Occurrence of Rake Marks

Measuring the presence of new rake marks on individual dolphins was used here as a proxy indicator for real-time changes in the social context of the group. During their daily sessions with the dolphins, the trainers visually scanned the animals' bodies for any new rake marks that were visible. In order to standardise the evaluation of rake marks across facilities, we originally used a Likert scale with three categories: no new marks, a small number of new marks (about the size of one to two human hands), and a large number of new marks (covering the area of three hands or more). However, when the data were collected we had a very low sample size of the large rake mark category, which led us to treat the rake mark score as a binary "occurrence" in order to make it more meaningful. In another step to deal with the low variance in this score's dataset, we transformed the daily rake mark score into a weekly score, where a score for any new marks on any day was treated as an occurrence and assigned a 1, and if not then a 0 was given.

Ethics Statement

The study's protocols were reviewed and approved by the welfare committees of the respective facilities; the data collected were solely observational and thus no specific permits were needed. The human participants' involvement (as data collectors) did not require a permit as per the local legislation at each facility. All participating facilities were accredited and regularly inspected by the European Association for Aquatic Animal (EAAM), adhering

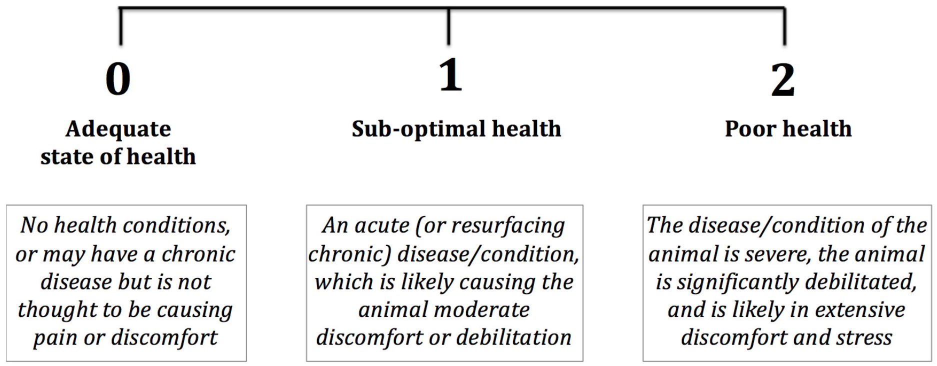

FIGURE 2 | 3-point Likert scale used by veterinarians in four facilities to score each dolphin's health once each week over the year-long study.

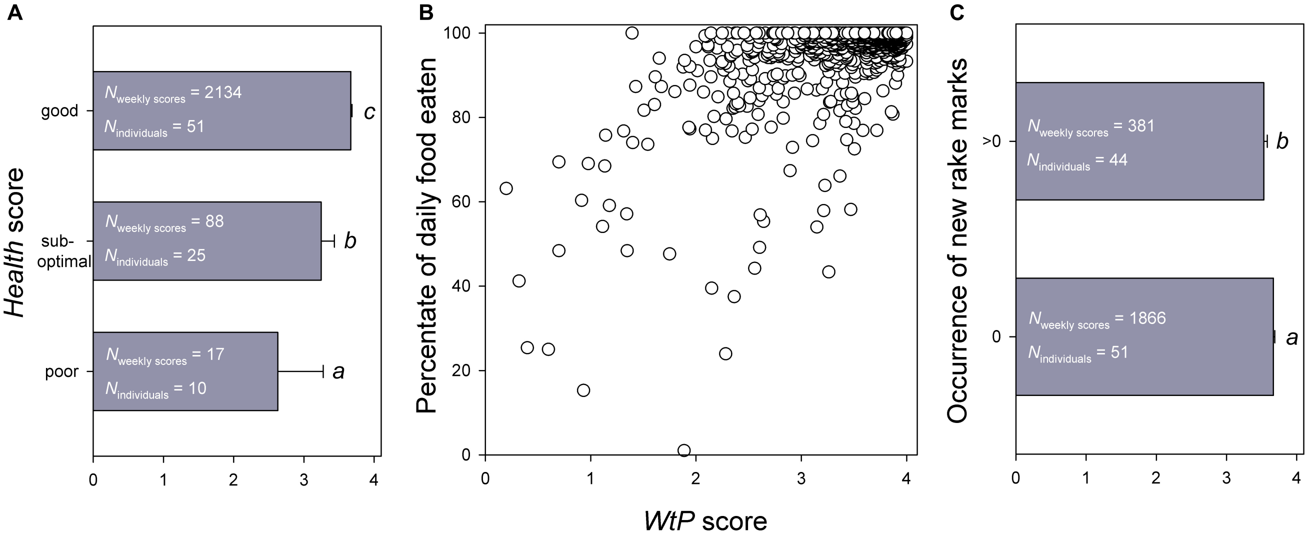

FIGURE 3 | Associations of the average weekly *WtP* score (reflecting the dolphin's willingness to participate in Positive Reinforcement Training) with **(A)** the Health score assigned by the veterinarian during weekly visits, **(B)** the percentage of daily food eaten, and **(C)** the occurrence of new rake marks on the dolphin. All associations were statistically significant, see text for details. Different letters beneath the vertical bars in **(A,C)** highlight significant differences between categories within each figure.

to or exceeding their care and management standards (European Association of Aquatic Mammals, 2019).

Statistical Analysis

Statistical analyses were done with the programme R, version 3.5.2 (R Development Core Team, 2018). Samples used for analyses were repeated measurements of different scores based on 51 bottlenose dolphins living in 6 different groups at 4 different facilities; see details in **Table 1**. For all dolphins, we calculated weekly averages of daily measures of *WtP* scores (ranging from 0 to 4, see **Figure 1**; on a numerical scale due to weekly averages; *total* $n_{\text{weekly values}} = 2{,}247$) and of percentage of daily food eaten (% values; *total* $n_{\text{weekly values}} = 2{,}247$) were averaged weekly. For analysis of the new rake mark score we used a categorisation of '0 = no new rake marks' and '1 = new rake marks' for each week ($n_{\text{weekly values}} = 2{,}247$). Furthermore, a single Health score was available each week (*total* $n_{\text{weekly values}} = 2{,}238$). In some rare cases, when the veterinarian visited the facility for several times per week, we used the weekly median value of the score, and thus the weekly averages remained on an ordinal scale.

In a first step, we analysed associations between the *WtP* score (dependent variable) and either (a) the Health score, (b) the percentage of daily food eaten or (c) the occurrence of new rake marks (dependent variables in separate statistical models. For (a), due to the ordinal structure of the dependent variable, we used a cumulative link mixed-effects model for ordinal data using the *clmm* function provided by the R package *ordinal* (Christensen, 2015). *Post hoc* comparisons (after sequential Bonferroni correction, Holm, 1979), as shown in **Figure 3A**, were done using principally the same model, but based on a subset of the data restricting the analysis only to 2 of the ordinal categories of the dependent variable. For **Figure 3B**, we used a generalised linear mixed-effects model (GLMM) for proportional data, and for **Figure 3C** we used a GLMM for binomial data.

This was done by using *glmer* function of the R package *lme4* (Bates et al., 2017). For all models, we included the identity of the dolphin as a random factor to account for the individual-based repeated measurements across consecutive weeks. We also included the identity of the facility and the identity of the group as further random factors to account for potential effects of the same origin (either facility origin or group origin) of the animals. Furthermore, we tested all remaining, possible associations between the different score variables using the different functions described above (see section Results for details).

In a second step, we analysed whether the three different scores, *WtP*, percentage of daily food eaten and the occurrence of rake marks already showed any apparent changes shortly before the veterinarian determined a 'departure from good health' (DGH) in a dolphin. We considered DGH incidents as where the Health score given by the veterinarian decreased from 0 to 1, or 0 to 2, and no other such case preceded for at least 3 months previously (and therefore cases where scores decreased from 1 to 2 were not included). These criteria were established with the aim of analysing independent health issues, where the previous medical history of the animal was known (i.e., excluding cases where an animal was in decreased health at the start of the study period) and allowing us to set a control period for comparison. Based on these criteria, we included $n = 26$ DGHs from 26 different dolphins (juveniles < 10 years: 3 males, 4 females; adults: 12 males, 7 females) originating from five different groups at all four facilities into this analysis. From these 26 cases, there were 22 cases where the score decreased from 0 to 1 and four cases where the score went from 0 directly to 2. We considered restricting the analysis to only the 22 cases where the Health score decreased from a 0 to 1 to increase standardisation, but we principally found the same significant results, and so decided to keep in all cases of DGHs to maintain a larger sample size. Daily *WtP* scores and the percentage of daily food eaten were averaged over a 3-day period prior to and over a 7-day period following the diagnosis of a DGH by the veterinarian, to test whether these parameters could indicate the onset of DGHs. Furthermore, we assigned a 7-day control period ending 1 week prior to the diagnosis of the departure from good health (see grey bars in **Figures 4A,B**). For the occurrence of new rake marks, we assigned the absence/presence (binomial data structure) during the different periods. For the *WtP* score and the percentage of daily food eaten we ran a linear mixed-effects model LMM, and for the occurrence of new rake marks we ran a generalised linear mixed-effects model GLMM for binomial data, by comparing the three periods using *lmer* and the *glmer* functions of the R package *lme4*, respectively (Bates et al., 2017). In case of significant difference, we calculated pair-wise *post hoc* comparisons between the different periods (after sequential Bonferroni correction, Holm, 1979) using the same kind of model but restricted to subsets of the data. Models always included the identity of the dolphin and the identities of the facility and of the group as random factors. As the distributions of the *WtP* score and the percentage of daily food eaten were different from normal, we calculated *P*-values by parametric bootstrapping, a resampling technique which does not have any specific requirements about the distribution of the data. This was done using the R package *afex* (Halekoh and Højsgaard, 2014). For all models, we tested for potential effects of age class (juvenile vs. adult) and sex, and the interactions of these two factors with period (factor with 3 levels).

RESULTS

Associations Between *WtP* and Health Scores, Percentage of Food Eaten, and Occurrences of New Rake Marks

Higher *WtP* were significantly and positively associated with the veterinary Health score (Cumulative mixed model for ordinal data: $\chi^2_1 = 108.550$, $\beta_{\mathrm{poor/sub-optimal}} = 5.215 \pm 0.876$ SE, $\beta_{\mathrm{sub-optimal/good}} = 7.780 \pm 0.943$ SE, $P < 0.001$; *post hoc* comparisons in **Figure 3A**) and with the percentage of daily food eaten (GLMM for proportional data: $\chi^2_1 = 63.619$, $\beta = 1.094 \pm 0.137$ SE, $P < 0.001$; **Figure 3B**), and were significantly and negatively associated with the occurrence of new rake marks (GLMM for binomial data: $\chi^2_1 = 13.527$, $\beta = -0.328 \pm 0.089$ SE, $P < 0.001$; **Figure 3C**). That is, animals with a higher *WtP* score were in a significantly better health status, took a significantly higher percentage of the food they were offered, and had a significantly lower probability of carrying new rake marks.

Furthermore, animals with a higher Health score also showed a significantly higher percentage of daily food eaten (Cumulative mixed model for ordinal data: $\chi^2_1 = 127.080$, $\beta_{\mathrm{poor/sub-optimal}} = 4.367 \pm 0.469$ SE, $\beta_{\mathrm{sub-optimal/good}} = 7.180 \pm 0.591$ SE, $P < 0.001$). However, there were no significant associations of the animals' Health score (GLMM for binomial data: $\chi^2_1 = 0.742$, $\beta = -0.070 \pm 0.081$ SE, $P = 0.389$) or the percentage of daily food eaten ($\chi^2_1 = 1.728$, $\beta = -0.091 \pm 0.069$ SE, $P = 0.189$) with the occurrence of new rake marks.

Changes in Different Measures Related to the Occurrence of a Diagnosis of a 'Departure From Good Health,' DGH

For analysis, we averaged the daily *WtP* scores, percentage of daily food eaten, and occurrence of new rake marks to be able to compare two periods: a 3-day period prior to, and a 7-day period following, the diagnosis of a 'departure from good health' (DGH) by the veterinarian. Furthermore, we assigned a 7-day control period ending 1 week prior to the diagnosis of the DGH (see grey bars in **Figures 3A–C**).

There were significant differences between the three periods assigned with respect to the *WtP* score (LMM with parametric bootstrapping: $P = 0.004$; **Figure 4A**). *Post hoc* comparisons (given in **Figure 4A**) revealed that *WtP* scores during the control period were significantly higher than during the period prior and during the period after the diagnosis of a departure from good health ('DGH' in **Figure 4**) by the veterinarian. In other words, a significant decrease in the *WtP* score had already occurred prior to the veterinarian's visit during which decreased health was detected.

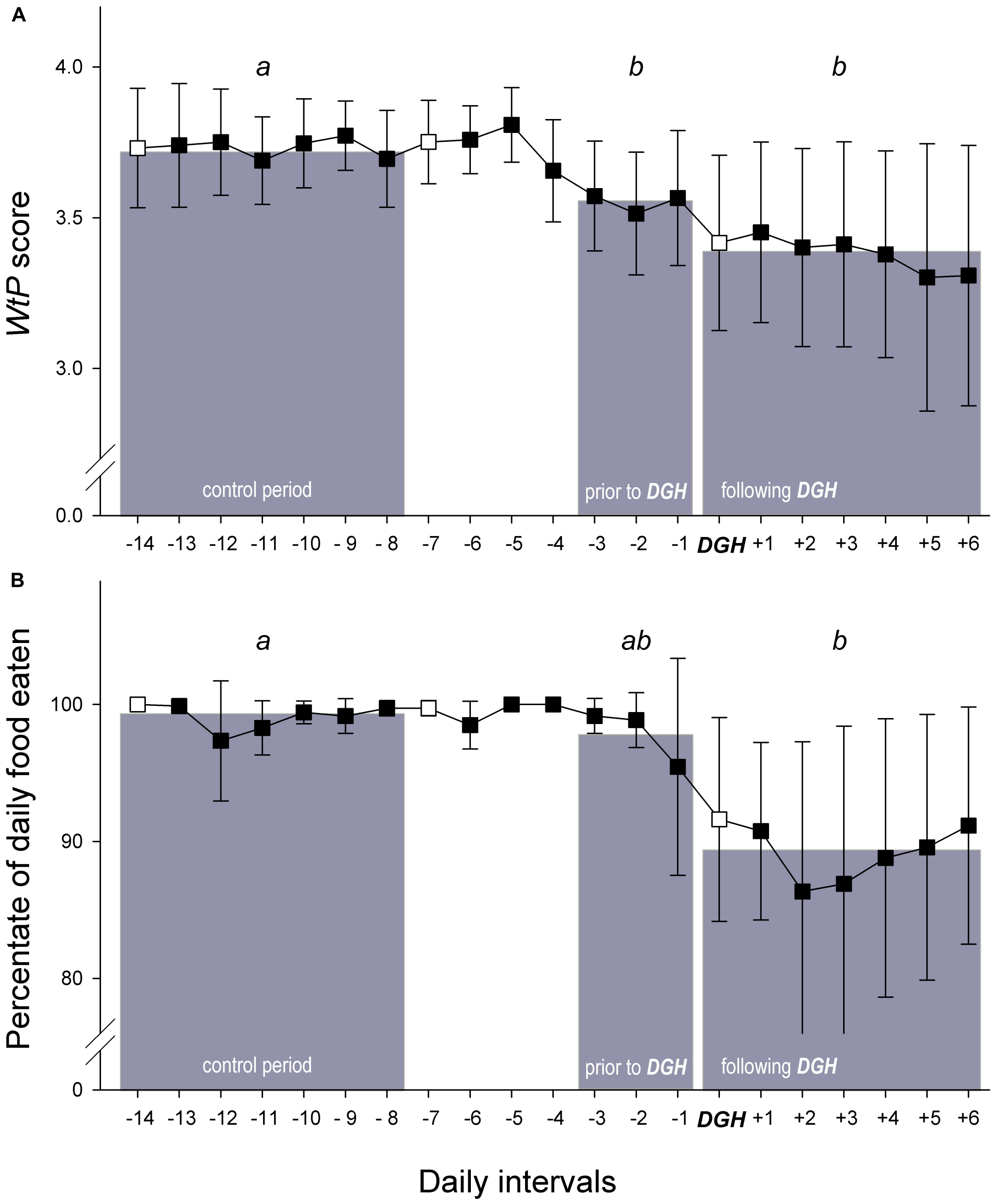

FIGURE 4 | Changes across time in **(A)** the *WtP* score (reflecting the dolphin's willingness to participate in Positive Reinforcement Training) and **(B)** the percentage of daily food eaten before and after a departure from good health ('DGH') in the dolphins (*N* = 26 individuals) was diagnosed during the weekly visit of the facilities' veterinarians, defined as a decrease of the Health score from 0 to 1 (*N* = 22 individuals) or from 0 directly to 2 (*N* = 4 individuals). The days of the veterinarians' weekly visits are indicated by an empty circle. Grey bars in background show the mean values of the different time periods, on which the statistical comparisons were based; see text for details. Statistically significant differences between the three periods are highlighted by different letters (Bonferroni-corrected comparisons *post hoc* to LMM with parametric bootstrapping, see text for details).

In addition, there were some significant differences between the periods with respect to the percentage of daily food eaten (LMM with parametric bootstrapping: $P = 0.007$; **Figure 4B**). As shown by *post hoc* comparisons in **Figure 4A**, the percentage of daily food eaten during the control period was significantly higher than during the period after the diagnosis of a DGH. However, the period prior to detection of decreased health did not differ significantly from the two other periods. That is, there is no significant support by the data that the percentage of daily food eaten was predictive of a DGH during the weekly visit of the veterinarian. Even a comparison between the percentage of food eaten on the last day before the diagnosis of a DGH (day -1) with the control period did not reveal any significant difference (LMM with parametric bootstrapping: $P = 0.356$).

The occurrence of new rake marks did not differ significantly during the control period and the periods prior to or following the detection of a DGH (GLMM for binomial data: $\chi_1^2 = 1.033$, $P = 0.597$).

There were no significant effects of sex and no significant effects of age class (juveniles versus adults) with respect to any of the four scores considered (all $P > 0.10$). Furthermore, there were no significant interactions between sex and period (all $P > 0.10$) or between age class and period (all $P > 0.10$), indicating that there were no sex-specific or age-class specific differences among the three periods considered with respect to any of the four scores.

DISCUSSION

The present study investigated how certain behavioural, health, social and food intake parameters might relate to overall dolphin welfare, through collecting long-term data from multiple dolphin groups and facilities. Firstly, it was found that animals with a higher Willingness to Participate (*WtP)* in training sessions had a significantly better health status, took a higher percentage of the food they were offered, and were less likely to have new rake marks. *WtP* therefore may be a good welfare indicator for captive bottlenose dolphins. In addition, we looked at the above welfare-related parameters around the time period where a departure from good health was recorded by veterinarians, and found that the *WtP* score had already significantly decreased prior to the veterinarian's visit during which decreased health was detected, suggesting its use as an early predictor of health problems.

Correlation of *WtP* With Health Scores, Percentage of Food Eaten, and Occurrence of New Rake Marks

The significant correlation of *WtP* data to the Health score, percentage of food eaten, and occurrence of new rake marks suggests that *WtP* does reflect some type of welfare-related state in dolphins: associations between several multidisciplinary parameters strengthens the power of welfare conclusions (Pritchard et al., 2005; Webster, 2005; Mason and Veasey, 2010). This approach is important because as pointed out in a recent study correlating multidisciplinary parameters of primate health and welfare, there are often complex interactions between individual animal characteristics and how they relate to welfare, which means there are often many alternative explanations for results (Robinson et al., 2018). A few past studies on dolphin welfare correlated two multidisciplinary parameters together to suggest a certain welfare state, but accepted that it remains difficult to conclude the causality or duration of the state (Ugaz et al., 2013; Clegg et al., 2017a). In order to further understand what *WtP* signified in this study, and what it didn't, the correlative results of the other parameters were considered as well as the variation of *WtP* in relation to specific decreased health incidents.

None of the other parameters- Health scores, percentage of food eaten, and occurrence of new rake marks- correlated significantly with all other parameters like *WtP* did. This was surprising, since measures of appetite (i.e., percentage of food eaten) are often used as fundamental measures of welfare (Johnson, 2002; Millman, 2007; Sneddon et al., 2014). Nevertheless, dolphins with a higher Health score also ate a higher percentage of their food, which suggests that appetitive measures are specifically an important correlate of dolphin health, and which has been supported by evidence from previous studies (Johnson et al., 2009; Schmitt and Sur, 2012). The significant correlations of dolphins' *WtP* with other welfare-related parameters suggests parallels to other species, where motivation to 'work for rewards' has been found to decrease with both poor health and welfare (Spruijt et al., 2001; Pedersen et al., 2002; De La Garza, 2005; Rygula et al., 2005). The fact that *WtP* was the only parameter to be correlated to all other measures suggests that it is closer to measuring overall welfare than other, more quantitative parameters such as percentage of food eaten, and its broad scope is more likely to capture a selection of the many animal-based indicators of welfare states. These advantages result from the use of qualitative methods for *WtP* measurement, where trainers rated each animal's *WtP* each session, every day, on a 5-point Likert scale. Qualitative measurement of welfare and other holistic concepts such as animal emotionality are becoming increasingly favoured, in part due to the discovery that they are accurate and reliable but also because they have practical benefits (Wemelsfelder et al., 2000; Rutherford et al., 2012; Fleming et al., 2013). Qualitative measures such as those used in this study allows the harnessing of holistic knowledge from those caretakers who know the animals' behaviour and welfare the best (Whitham and Wielebnowski, 2009; Phillips et al., 2017), and up until now has not yet been exploited in dolphin research, despite the many hours of daily close physical contact spent between animal and caretaker. Such a tool, which is simple to execute accurately, generates meaningful data and facilitates daily monitoring of the animals, would be very valuable to captive dolphin management (Clegg et al., 2015, 2017b).

A dolphin's "Willingness to Participate" in training sessions could indeed be influenced by many variables, and it is likely that for some of the days and data points during our study, we might not have been measuring welfare but instead an individual variation in satiety, or perhaps a time when other events in the pool where far more rewarding than training sessions. However, this is where the importance of the sample size and study duration comes into play, in conjunction with the choice of parameters: firstly, the measures were chosen as they represent elements fundamental to any welfare state (i.e., health, social behaviour, appetite), which meant that explaining any trends should be more straightforward. For example, it is easy to comprehend that a dolphin who has poorer health, *and* is eating less of its food, *and* has more new rake marks is less willing to participate in training sessions because it is in a negative affective state. On the other hand, it would be counter-intuitive to conclude that the animals showing these same results were less willing to participate in training sessions because they were simply satiated. Secondly, the suggestion of *WtP* as a welfare indicator is supported by the large sample size ($n_{\text{dolphins}} = 51$) and the sheer number of data points (almost 100,000 for the *WtP* score) which means that even if there are some false positives, any trends would be a result of the more logical explanations, corroborated by the caretakers' expert opinions.

It is important to highlight here that the occurrence of new rake marks on its own may not signify poorer welfare states. Dolphins can receive rake marks in multiple types of 'intense' social activity: during agonistic interactions, but also during sexual behaviour and rough play (Scott et al., 2005; Marley et al., 2013). However, in line with discussions on this question in other studies (Scott et al., 2005; Marley et al., 2013), rake marks are much more likely to occur during behaviours involving aggression (which could also include coercive sexual behaviour, or play that turns aggressive) since more actual bites have been witnessed together with such activity (MacLeod, 1998; Parsons et al., 2003; Silva-Jr et al., 2005), and as a result, rake mark prevalence has been used in the literature as an indirect measure of aggression (Scott et al., 2005; Martin and Da Silva, 2006; Marley et al., 2013; Cords and Mann, 2014; Orbach et al., 2015). An original objective of this study was to measure the extent of new rake marks, which can reveal much about the associated social behaviour (MacLeod, 1998; Marley et al., 2013), but unfortunately we had a low occurrence of extensive new rake marks (score 2), and thus decided to analyse these data as simply a presence/absence measure. Although our results showed that *WtP* was significantly lower when there was an occurrence of new rake marks, the effect size was low (i.e., the difference of the mean values, see **Figure 3C**), and coupled with the aforementioned ambiguity regarding the link between rake marks and negative affect, we recommend that more work is conducted on this measure before it is used as a welfare indicator.

WtP as an Early Indicator of Departure From Good Health (DGH)

Decreased health has long been used as a context for validating welfare parameters due to its relatively simple measurement and tangible implications (Dawkins, 1980; Broom, 1991; Fraser et al., 1997). Here, we took instances where the veterinarians has diagnosed the dolphins as showing a departure from good health (DGH, as defined in this study either a change in Health score from 0 to 1, or 0 to 2, where no other such case preceded for at least 3 months previously; **Figure 2**), and investigated how *WtP*, new rake mark occurrence and percentage of food eaten varied in the time prior to and following the DGH, and in comparison to a control period. We found that among these parameters, *WtP* was the only variable to significantly differ between the time prior to the DGH and the control period: it was significantly lower in the days prior to the DGH as compared to the control (where the animal was assumed to still be in good health, since one of our criteria for analysing DGHs was that the animals had not had a previous health issue for at least 3 months previously). This suggests that *WtP* can be used an early indicator of a DGH, since the animals started participated less in the sessions around the same time that the veterinarian made an official diagnosis of decreased health (we cannot conclude which one is more sensitive since *WtP* was measured daily, and the Health scores weekly). In addition, *WtP* was found to be significantly lower following DGH diagnosis than the period prior to it.

We also looked at how the other parameters varied in relation to the DGH: percentage of daily food eaten during the control period was significantly higher than in the period *after* DGH diagnosis, but levels just prior to the DGH did not differ significantly from the other two periods. Therefore, while the dolphins indeed ate significantly less in the week after the vet diagnosed them with a DGH, their appetite did not change significantly in the early stages of decreased health. This agrees with other studies showing that dolphins' food consumption seems to decrease only when there is a serious health or social problem (Waples and Gales, 2002; Johnson et al., 2009; Schmitt and Sur, 2012). Our results suggest that the dolphins' food consumption was not as sensitive to affective state change as *WtP*, which was already significantly decreased in the days prior to DGH diagnosis. Lastly, the occurrence of new rake marks did not differ between the control, prior-DGH and post-DGH periods, indicating that in the study population, new rake marks and therefore high arousal social interactions (e.g., aggression, sexual or rough play behaviour) were generally not a meaningful contributor or correlate to DGHs.

Poor health is notoriously difficult to diagnose in cetaceans since they are known to adaptively mask symptoms of pain and illness until the condition is severe and welfare is poor (Castellote and Fossa, 2006; Clegg and Delfour, 2018). However, small but significant changes in behaviour often occur as a health challenge establishes itself and animals enter what some call a 'pre-pathological state' (Moberg, 1985): it has been said that any measures of this subtle state may be the "most appropriate indicators of impaired well-being in that they identify (at an early stage) conditions that threaten tangible harm to the normal functioning of animals" [p197, 103]. Based on our results, we suggest *WtP* in training sessions as one of those indicators at least of decreased welfare due to impaired health, but possibly also for other negative affective states, e.g., linked to social issues.

A principal aim of our study was to gather a large amount of data in multiple facilities over a full year, to allow us to test enough repeats of different states. While the large sample size and long-term nature of the data allowed us to draw the conclusions above more confidently, the approach and especially the remote data collection element inevitably allowed for some risk of non-independence, which merits discussion. One source of non-independence may have been the fact that the veterinarians' health diagnosis was influenced by the trainers telling them about the behaviour of the dolphins in the prior days, i.e., their *WtP*. This may have led to some DGHs diagnoses which would not have occurred if the veterinarian had not spoken to the trainers. This was unavoidable: in general this type of information-sharing is encouraged and necessary in dolphin facilities to ensure the best management of the animals. While this may have meant that strictly some of the prior decrease in *WtP* actually influenced the DGH diagnosis, it would not have changed the underlying reality of the situation which was that the veterinarian indeed believed a DGH was occurring and diagnosed it as such. That is, the non-independence may have increased the likelihood of

DGH diagnoses but not increased false positive results, nor false negatives. The risk of non-independence in the other direction, i.e., veterinarians' sharing views about the dolphins' health state with the trainers which may have influenced their daily *WtP* scores, was likely to be very reduced since the veterinarians saw the dolphins much less regularly (once a week) than the trainers. Non-independence between health and the occurrence of rake marks would have been very unlikely since new marks would be considered a social group consideration to be managed by the training team and the veterinarian would not normally be told unless a period of sustained and excessive new marks occurred (personal communication). Similar to the *WtP* non-independence risk, trainers may have shared information about the percentage of food eaten with the veterinarian, but this would have only increased the likelihood of a correct DGH (or lack of) diagnosis, as opposed to increasing the chances of falsely diagnosing an animal as being in poor or good health.

Significance for Dolphin Welfare Evaluation

Since cetacean species often mask symptoms of poor health until they are considerably compromised, it is all the more important to identify early predictors of any 'pre-pathological states' (Moberg, 1985; Fraser et al., 1997) that occur in order to ensure effective management and good welfare in captivity. From our results, *WtP* in training sessions significantly decreased in the 3 days prior to a DGH being diagnosed, suggesting that it could be used as an early indicator of decreased health, where in most facilities it may not be feasible for veterinarians to physically examine the animals every day. *WtP* was more sensitive indicator of decreased health than monitoring the animals' daily food consumption, which is also often considered a failsafe measure of welfare (Johnson, 2002; Millman, 2007; Sneddon et al., 2014). The *WtP* measure designed in this study was simple, practical and non-invasive for the dolphins and trainers: if such scores (or similar) are taken already, we suggest their integration into the daily management routine. However, it is worth highlighting that to exploit the *WtP* scoring method and data fully, it is almost essential to take formal records of the scores and review the data regularly, i.e., at least calculating daily averages. The significantly different *WtP* scores in the pre-DGH, post-DGH and control periods only varied by an average of 0.2 (**Figure 4A**), which is not likely to be perceptible by a trainer, veterinarian or manager who simply glances over a set of scores (which had to be integers in this study) recorded each day. In addition, the approach and scores used here could be adapted for other animals in similar contexts of regular reward-based interactions, such a working dogs or riding horses.

Our results also showed that animals with higher *WtP* in sessions had significantly better health, took a higher percentage of the food they were offered, and had fewer new rake marks. *WtP* was the only parameter from the set of four used in this study to correlate to all the others, which suggests it is measuring an overall state that manifests through several multidisciplinary indicators. It is likely that dolphins' *WtP* in training sessions is impacted by their health, appetite as well as their social environment, and these factors probably also interact in many ways both inter- and intra-individually: while this study does not determine the cause of the changing welfare states, the variance in dolphins' *WtP* seems to effectively encompass these different welfare-related elements. Nevertheless, more research is certainly needed into why their *WtP* varies in relation to these factors, so that thresholds can start to be established and used to enhance management. While it has previously been advised to correlate several potential welfare measures to increase validity (Pritchard et al., 2005; Boissy et al., 2007), the complex inter-correlation of welfare-related variables means that future studies should even aim to use more than four measures to fully investigate the variance associated with health and welfare states (Robinson et al., 2018).

CONCLUSION

This year-long, multi-facility study investigated the inter-correlations between four parameters related to dolphins' behaviour, health and appetite which were designed to collectively measure their welfare. Firstly, we found that qualitatively measuring their Willingness to Participate (*WtP*) in training sessions seemed to reflect overall welfare state since it was the only one to vary with all other welfare-related measures, and was therefore a potential welfare indicator for captive dolphins. Further investigations in relation to incidents where the veterinarians' had diagnosed a "departure from good health" (DGH) revealed that *WtP* in training sessions significantly decreased in the days prior to the veterinarians' DGH diagnosis, suggesting it reflects early decreases in health. Furthermore, *WtP* was a more sensitive indicator of this 'pre-pathological state' than the change in percentage of food eaten. *WtP* and the other qualitative measures used in this study were shown to be not only meaningful and non-invasive, but also feasible for the animal caretakers to conduct on a daily basis. These results collectively suggest that measuring *WtP* by knowledgeable professionals in training sessions represents an accurate and comprehensive measure of dolphin welfare and may be useful to these animals' management in captivity, although further work is still needed into the causal relationship between the contributing factors.

DATA AVAILABILITY

The datasets generated for this study will not be made publicly available. The data is owned by the owners of the animals, but would be available with their permission.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because only observational data was taken, with no changes whatsoever to the animals' environment or management. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

IC, HR, and FD contributed to the conception and structure of the manuscript. BM, SH, TS, PL, RG, MZ, EV, JB, and PB carried out and oversaw the data collection. IC and HR carried out the data analysis. IC wrote the manuscript. HR and FD edited the manuscript.

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Motion Illusions as Environmental Enrichment for Zoo Animals: A Preliminary Investigation on Lions (*Panthera leo*)

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Investigating perceptual and cognitive abilities of zoo animals might help to improve their husbandry and enrich their daily life with new stimuli. Developing new environmental enrichment programs and devices is hence necessary to promote species-specific behaviors that need to be maintained in controlled environments. As far as we are aware, no study has ever tested the potential benefits of motion illusions as visual enrichment for zoo animals. Starting from a recent study showing that domestic cats are spontaneously attracted by a well-known motion illusion, the Rotating Snake (RS) illusion, we studied whether this illusion could be used as a visual enrichment for big cats. We observed the spontaneous behavior of three lionesses when three different visual stimuli were placed in their environment: the RS illusion and two control stimuli. The study involved two different periods: the baseline and the RS period, in which the visual stimuli were provided to the lionesses. To assess whether the lionesses were specifically attracted by the RS illusion, we collected data on the number of interactions with the stimuli, as well as on the total time spent interacting with them. To investigate the effect of the illusion on the animals' welfare, individual and social behaviors were studied, and compared between the two periods. The results showed that two lionesses out of three interacted more with the RS stimulus than with the two control stimuli. The fact that the lionesses seemed to be more inclined to interact with the RS stimulus indirectly suggests the intriguing possibility that they were attracted by the illusory motion. Moreover, behavioral changes between the two periods were reported for one of the lionesses, highlighting a reduction in self-directed behaviors and an increase in attentive behaviors, and suggesting positive welfare implications. Thus, behavioral observations made before and during the presentation of the stimuli showed that our visual enrichment actually provided positive effects in lionesses. These results call for the development of future studies on the use of visual illusions in the enrichment programs of zoo animals.

Keywords: visual illusions, environmental enrichment, zoo animals, Rotating Snake illusion, animal welfare

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INTRODUCTION

The perception of the psychophysiological needs of zoo animals has widely changed in the last decades. The increasing number of stimulations and techniques used to provide "environmental enrichment" indeed reflects our higher sensitivity to these perceived needs (Carlstead and Shepherdson, 2000; Makecha and Highfill, 2018). Providing an exhaustive definition of "environmental enrichment" is difficult. To date, nine different types of enrichments can be found in the literature (reviewed by Maple and Perdue, 2013): feeding (e.g., manipulation of food), tactile (e.g., including a water pool to provide tactile stimulation), structural (e.g., changes in the environment, such as introducing a new platform in the enclosure), auditory (e.g., presenting conspecifics' vocalization in the enclosure), olfactory (e.g., introducing odor from conspecifics or non-conspecifics), visual (e.g., colored objects in the enclosure), social (introducing social companions or individuals of different species), human-animal (e.g., interacting with keepers during feeding time), and cognitive enrichment (e.g., problem-solving tasks to stimulate higher cognitive functions). All of these enrichments are supposed to increase the physical, social, and cognitive complexity of captive environments.

Among visual stimuli, dynamic objects probably represent the most powerful stimuli because motion is known to attract most animals and elicit predator-searching behavior. Unfortunately, setting up artificial contexts in which dynamic objects are presented in the animal enclosure is difficult and costly because it requires installation of some sort of track along which those objects should move repeatedly. Furthermore, if objects move according to a fixed route, they might result in the emergence of stereotypic behaviors of the animals that might start to move forward and backward in the proximity of the area in which the objects are presented. An alternative way to present dynamic objects consists of presenting videotapes to animal zoos. Video presentations were found to be effective in enrichment for chimpanzees (Bloomsmith et al., 1990; Bloomsmith and Lambeth, 2000) and captive macaques (Platt and Novak, 1997). Similarly, videos showing natural landscapes were partially effective in reducing stereotypic behaviors of European starlings kept in captivity (Coulon et al., 2014). Videotapes, however, require the use of monitors and associated electric equipment that must be safely implemented in the naturalistic enclosure, a condition that might represent a problem in natural parks with a limited budget. In this sense, even though dynamic objects seem to present a powerful tool for visual enrichment of zoo animals, for practical reasons, this type of enrichment cannot be easily implemented in natural parks.

With respect to this issue, motion illusions might play an important role. Motion illusions are a sub-category of visual illusions characterized by the perception of motion that is absent in the physical stimulation. Recently it was demonstrated that non-human animals are susceptible to motion illusions: for instance, rhesus monkeys (Agrillo et al., 2015), guppies, and zebrafish (Gori et al., 2014) were shown to perceive the Rotating Snake (RS) illusion. Despite the name, the perception of snakes is limited if not absent. Rather, it is a peripheral drift illusion consisting of the perception of rotational motion for concentric circles in a constant direction. This visual pattern is made by a regular arrangement of colored local elements (**Figure 2A**): even though the traditional version of the illusion is colored, the illusion is based on a specific achromatic sequence (Kitaoka, 2014): black, dark gray, white, and light gray. In the colored version of the illusion, this gray pattern is hidden in the following sequence: black, blue, white, yellow. The presentation of local information arranged in this order is misperceived in the visual system, leading to a perception of dynamic objects. This seems to be due to the integration of local motion-signal elements in the lateral part of the occipital cortex called the MT complex (Kuriki et al., 2008). Fixational eye movements also seem to be important in eliciting illusory motion. Murakami et al. (2006) and Beer et al. (2008) suggested fixational drifts as the main fixational eye movements underlying illusory motion, whereas Otero-Millan et al. (2012) highlighted the role of transient oculomotor events in initiating illusory motion perception. Billino et al. (2009) found that 84% of human observers experience rotational motion of concentric circles, thus making it one of the most powerful motion illusions in the literature.

A recent online survey suggested that cats might be susceptible to motion illusion, too. In this study, Baath et al. (2014) asked pet owners to present the RS illusion to their cats and then report whether pets showed some sort of behavior that might suggest a perception of motion (for instance, "attacking" the illusory pattern as they were perceiving a living organism in movement): nineteen out of sixty-six respondents declared that their pet reacted to the illusory pattern. Of course, this study was not an empirical laboratory study; animals were observed in non-controlled conditions. Also, data were directly collected by pet owners with their own subjective judgments and feelings that might have interfered with data collection. Above all, even assuming that these data reflect a spontaneous preference of cats to engage in some activities with the RS pattern, it does not necessarily mean that cats do perceive illusory motion *per se*; rather, they might be simply interested in complex visual patterns. That said, this survey study showed that some cats are particularly attracted by the RS pattern, which aligns with the well-known knowledge according to which felines are attracted by moving objects. If cats appear to be interested in interacting with the RS illusion, the possibility exists that motion illusions could represent another type of visual enrichment for big cats kept in captivity. Visual patterns that elicit motion illusions would be less expensive than the equipment necessary to present true dynamic objects and could be easily placed in multiple areas of the enclosure. As far as we are aware, no study has tested the potential benefits of motion illusions in the environment enrichment of zoo animals.

Animal welfare has been defined as "the state of an animal as regards its attempts to cope with its environment" (Broom, 1986; Hill and Broom, 2009) and can be assessed scientifically by investigating how animals try and achieve to do so (Hill and Broom, 2009). Welfare can vary on a continuum from very good to very poor (Broom, 1988). On the contrary, the presence of species-specific behaviors in zoo animals has been considered a valuable measure of psychological and physiological well-being, with behavioral similarities between captive and wild animals indicating a positive welfare state (Hill and Broom, 2009; Hosey et al., 2013). On the other hand, abnormal and stress-related behaviors such as over-grooming might indicate poor welfare conditions and high individual stress levels (Dawkins, 1990; Lutz et al., 2003; Jacobson et al., 2016). Carnivores in controlled environments are known to be inactive and prone to exhibit abnormal behaviors (Powell, 1995). However, different types of environmental enrichments have been found to increase activity levels, promote functional and natural behaviors, and reduce abnormal behaviors in different species of felids (*e.g.*, *Panthera tigris* and *Panthera leo*: Powell, 1995; Bashaw et al., 2003; Van Metter et al., 2008; *Leopardus geoffroyi, L. tigrinus* and *L. wiedii*: Resende et al., 2009).

In the present study, we investigated the effects of motion illusions as a visual enrichment for big cats. In many respects, human and feline vision are comparable. These similarities encompass stereopsis (Fox and Blake, 1971), rod/cone discontinuity during dark adaptation, the Purkinje shift (La Motte and Brown, 1970), a 5-octave range of spatial frequencies (Blake et al., 1974), and a trade-off in sensitivity between spatial and temporal resolution (Blake and Camisa, 1977). Concerning color discrimination, there is a debate as to whether primates and felines experience a comparable color perception. It has been argued that felines have a dichromatic spectral sensitivity that closely resembles red-green color-blindness in humans (Clark and Clark, 2016). However, the three-cone cat retina described by Ring et al. (1977) resembles the extramacular retina found in macaques, suggesting thricromatic vision in felines too.

To achieve our goal, we presented the RS illusion (physically static stimulus that appears to be dynamic to human observers) and two control stimuli (physically static stimuli that also appear to be static) to three adult lionesses. Because the illusory motion elicited by this pattern is not related to color but to a specific gray sequence, any potential difference in color perception between primates and felines is not expected to alter the perception of motion in lionesses. To assess whether lionesses are naturally attracted by the stimulus associated with illusory motion, we recorded the number of times they approached the stimuli and the time spent interacting with the three stimuli. To ensure that such interaction led to concrete positive benefits in the animal welfare, individual and social behaviors of the lionesses were observed before and during the presentation of our stimuli using a continuous focal animal sampling method.

MATERIALS AND METHODS

Subjects

The study was carried out with three lionesses (Safia, Kianga, and Lubaya) housed at the Parco Natura Viva, a zoological garden in Bussolengo (VR), Italy. The lionesses had been living together in the zoo for 9 years. Safia, the dominant female, was a white lioness (ssp. *Panthera leo krugeri*) and was 10 years old, whereas Kianga and Lubaya were sisters and were 9 years old. The lionesses' enclosure consisted of an outdoor and an indoor area. The outdoor area was 4,359.54 m^2 and was a grassy exhibit containing vegetation and naturalistic furnishing. The indoor area of the enclosure was composed of different rooms connecting with each other through guillotine doors and was separated from the outdoor area through three guillotine doors, although the lionesses used the same door to move between different areas (**Figure 1**). The lionesses were fed once a day (6 days a week, with one fasting day) in the indoor area of the enclosure, and no food was provided in the outdoor area. Water was available *ad libitum*. The lionesses were not used to directly interacting with zookeepers and humans in general, as human-animal direct interaction was strictly forbidden in the zoo.

The stimuli of the experimental period were provided to the lionesses as environmental enrichments, and the study subjects were free to decide whether or not to interact with them. The study did not involve any invasive or stressful techniques and was conducted in accordance with the EU Directive 2010/63/EU and the Italian legislative decree 26/2014 for Animal Research.

Apparatus and Stimuli

The stimuli used in the current study consisted of triplets of wooden panels with illusory and control patterns. In particular, the illusory pattern (RS illusion) (**Figure 2A**) and two control patterns (C1 and C2) (**Figures 2B,C**) were printed on PVC sheets (A1, the same size as the panel) and fixed to each wooden panel with screws. Each panel had one PVC sheet, and each triplet of panels contained one RS, one Control 1 and one Control 2. The patterns on the three PVC sheets within each triplet were:

The Rotating Snake (RS)

The Rotating Snake was the illusory pattern used in this study (**Figure 2A**). The alternation of black, blue, white, and yellow segments causes an illusory sense of movement in human observers.

Control 1 (C1)

This stimulus, previously adopted in studies on human (Kuriki et al., 2008), and non-human animals (Gori et al., 2014; Agrillo

FIGURE 1 | Arrangement of the three triplets of stimuli in the outdoor area of the enclosure. The three triplets were arranged in a semicircle around the guillotine door through which the lionesses had access to the outdoor area (indicated by the arrow).

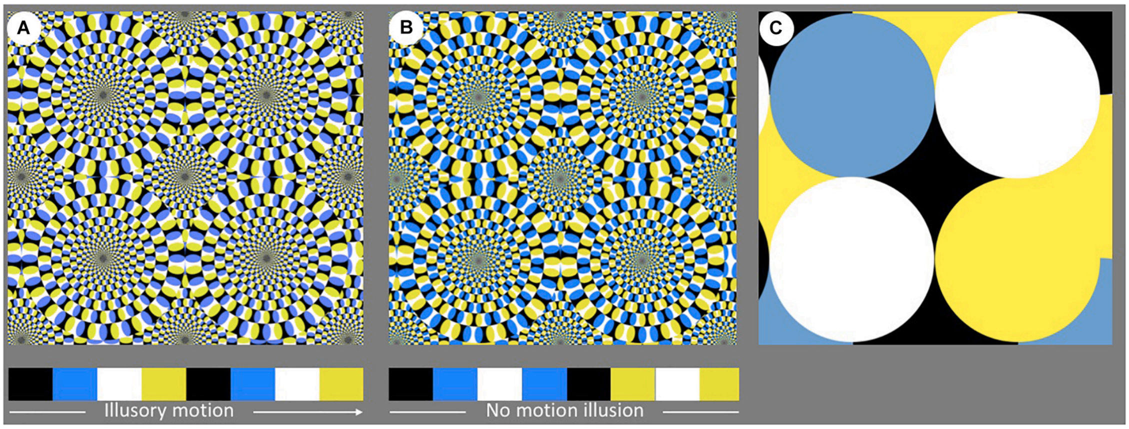

FIGURE 2 | Visual pattern presented within each stimulus: **(A)** Rotating Snake (RS), **(B)** Control 1, and **(C)** Control 2. Stimulus **(A,B)** were identical, with the exception that the sequence of colored segments varied between the two arrays; only the former sequence could elicit the motion illusion in human observers.

et al., 2015), does not evoke any motion perception, even though the overall configuration is identical to that of the illusory pattern (**Figure 2B**). Because the order of the colored segments is reversed between adjacent units, the local motion signal is nulled. This stimulus represents a powerful tool to assess whether lions are attracted by the apparent movement of the RS or simply by a complex visual pattern in which different colors alternated. If the former were true, we would expect a preference for exploring the RS stimulus; if the latter were true, no difference would be reported between the two stimuli.

Control 2 (C2)

This is the control pattern that differs from the first two visual stimuli (**Figure 2C**). It consists of overlapping circles, but the overall stimulus is extremely less complex than RS and C1. In this sense, this stimulus acted as a check to verify whether simple visual stimuli could attract the lions. No illusory motion can be perceived with this pattern by human observers.

Procedure and Data Collection

Assessing the Preference for RS Array

To assess whether the lionesses exhibited a spontaneous preference for interacting with the visual pattern that elicits a vivid perception of motion in human observers, we collected data on the interaction with the PVC panels during the RS period, in which the stimuli were provided. Nine sessions were carried out over approximately 1 month. Within each session, to avoid competition, lionesses were provided with three triplets, each with the RS, C1, and C2. Within each triplet, the three panels were placed approximately 30 cm from each other. The disposition of the visual stimuli varied within triplets and over the study sessions and was defined based on a pseudo-random schedule. The three triplets were placed at approximately 1.5 m (based on the lioness length of head and body, Haas et al., 2005) from each other and were arranged in a semicircle around the guillotine door linking the outdoor and the indoor areas of the enclosure. The radius of the semicircle was approximately 10 m. The stimuli were placed in the outdoor enclosure in the early morning after cleaning and immediately before the lionesses were moved into the area. When the lionesses passed through the guillotine door and entered the outdoor area of the enclosure, they could immediately see the triplets with the stimuli, because the triplets' semicircle was on a gentle rising slope (**Figure 1**).

In the RS period, a GoPro Hero4 camera was positioned at a height of approximately 6 m at the best view from which to video record the interaction of each lioness with the stimuli. The GoPro Hero4 camera was placed every morning before the lionesses entered the outdoor area of the enclosure, where they could find the stimuli. Each video recording started when the lionesses entered the outdoor enclosure (at approximately 9:00 am) and ended when they were called back into the indoor area of the enclosure. On average, each session lasted 5 h. The analysis of the videos allowed us to collect behavioral data of each lioness by using continuous recording with focal animal sampling. For each lioness, the analysis of the videotapes allowed us to collect data on the total number of interactions with RS, C1, and C2 for each subject. Moreover, the duration of each interaction was collected.

Effect of Visual Stimuli on the Lionesses' Behavior

One of the aims of this study was to investigate whether the presence of these visual stimuli affected the behavior and welfare of the study lionesses. To achieve this aim, we collected data on the duration of the individual and social behaviors of the lionesses at baseline, before the provision of the visual stimuli, and during a part of the RS period described above (see section "Assessing the Preference for RS Array"). For each period and each subject, twelve 30-min sessions were done, one in the morning and one in the afternoon, and they were carried out over a 2-week period. Per period, a total of 36 sessions for all lionesses was done, collecting 1,080 min of observation. At baseline, lionesses were observed in the outdoor area of the enclosure using the routine husbandry procedure (sensory enrichment devices impregnated with olfactory stimuli such as spices, perfumes, and herbivore feces). Moreover, in the RS period, the lionesses were observed in the outdoor area of the enclosure where, together with the usual sensory enrichments, the lionesses were provided with the wooden panels with RS, C1, and C2. Durations of the individual and social behaviors of each lioness during the baseline and the RS period were collected using a continuous focal animal sampling method, through the live observation of the subjects. Specifically, data were collected by the same observer, and subjects were observed in a prescribed sequence following a specific design to avoid time-of-day bias. The individual and social behaviors considered in the study are reported in **Table 1** and were defined based on preliminary observation of the study subjects as well as on previous literature on the ethogram of lions and other felid species (Powell, 1995; Stanton et al., 2015). The time spent out of sight (hiding or staying away from the visitor/observer area) by the study subjects was also recorded, because in wild animals this condition might indicate a stressful situation or even be informative of chronic stress (Carlstead et al., 1993; Sellinger and Ha, 2005; Davey, 2006; Morgan and Tromborg, 2007; Hosey, 2013).

TABLE 1 | Behavioral ethogram of the study lionesses.

Inactivity	
Inactivity	Laying or crouching with eyes closed
Activity	
Individual behavior	
Attention	Staring at one area or paying attention to any visual or auditory stimulus
Observing	Looking around calmly
Locomotion	Walking, running or jumping
Maintenance	Yawning, drinking, urinating and defecating
Self-grooming	Licking or scratching of the own body
Scent-marking	Marking substrates or objects in the enclosure by urine-spray (releasing urine backward against a vertical surface or object while standing with tail raised vertically), rolling and rubbing (leaving scents on the substrate or on any object, respectively)
Olfactory exploration	Sniffing the air, an object or the substrate, performing flehmen
Environmental Enrichment	Interacting with an enrichment device by biting, dragging, scratching or carrying it in the mouth
Anticipatory behavior	Moving near the entrance of the indoor area of the enclosure
Social behavior	
Affiliative behavior*	Social play (play-fight, chasing, palying together with an enrichment device), putting the front paw or rubbing on a conspecific, social grooming (licking a conspecific or being licked) and paying attention to conspecifics by observing them with interest
Agonistic behavior*	Dominance mount, threat display, aggression
Interspecific behavior	Paying attention to humans such as visitors and zookeepers
Not observed	
Out of sight	The animal is not visible from the point of observation (visitor window)

**Include actions performed or received by the focal subject. The ethogram was made based on preliminary observation of the study lionesses and based on previous literature on lions' and felids' behavior (Powell, 1995; Stanton et al., 2015).*

Data Analysis

Because not all data were normally distributed, the statistical analyses were done using non-parametric statistic tests. In particular, data obtained from the videos collected in the RS period allowed us to determine the preference for different visual patterns, particularly the RS, whereas data collected through the live observation of the subjects at baseline and in the RS period were used to evaluate the effect of the visual stimuli on the welfare of the lionesses. Significance level was set at $p < 0.05$, and all tests were two tailed. Data from the videotapes (RS period) and from the live observation of the lionesses (baseline vs. RS period) were collected by the same observer.

Assessing the Preference for RS Array

To assess whether in the RS period lionesses spontaneously preferred to interact with the RS stimulus, we used chi-square tests to establish whether the frequency of interactions was different with the three stimuli; Friedman's test was used to assess whether the proportion of time spent interacting with the experimental material was statistically different as a function of the type of stimuli. Finally, to verify whether the interest of the lionesses toward the stimuli remained steady over the RS period, a Spearman correlation was run between the number of sessions (from 1 to 9) and both the duration and frequency of interaction with the PVC panels per session.

Effects of the Visual Stimuli on Lionesses' Behavior

Concerning the investigation of the effects of our visual stimuli on lionesses' behavior, we compared the behavioral data between the baseline and the RS period using a single-case analysis. The Wilcoxon-Mann-Whitney test (software by Marx et al., 2016) was used to compare the durations of individual and social behaviors of each subject between the two periods. In the results, durations are expressed in seconds. For all behavioral categories, medians, interquartile range (IQR), and effect size (r) are reported in the manuscript or in figures and tables.

RESULTS

Assessing the Preference for RS Array

Descriptive data of total interactions and the proportion of time spent near the stimuli are illustrated in **Figure 3**. Lubaya statistically preferred to approach the RS stimulus [$\chi 2(2) = 18.867$, $p < 0.001$, $r = 0.458$]. Friedman's test showed that the subject spent a different proportion of time near the stimuli, with a larger amount of time near the RS [$\chi 2(2) = 8.026$, $p = 0.018$, Kendal's $W = 0.174$]. Safia statistically preferred to approach the RS stimulus [$\chi 2(2) = 9.349$, $p = 0.009$, $r = 0.269$]. However, Friedman's test showed that the subject did not spend a different proportion of time near the three stimuli [$\chi 2(2) = 2.160$, $p = 0.340$, $W = 0.047$]. Kianga statistically preferred to approach Control 1 [$\chi 2(2) = 7.478$, $p = 0.024$, $r = 0.403$]. Friedman's test showed that the subject statistically spent a different proportion of time near the stimuli, with a larger amount of time near Control 1[$\chi 2(2) = 7.682$, $p = 0.021$, $W = 0.295$]. The preference of each lioness did not

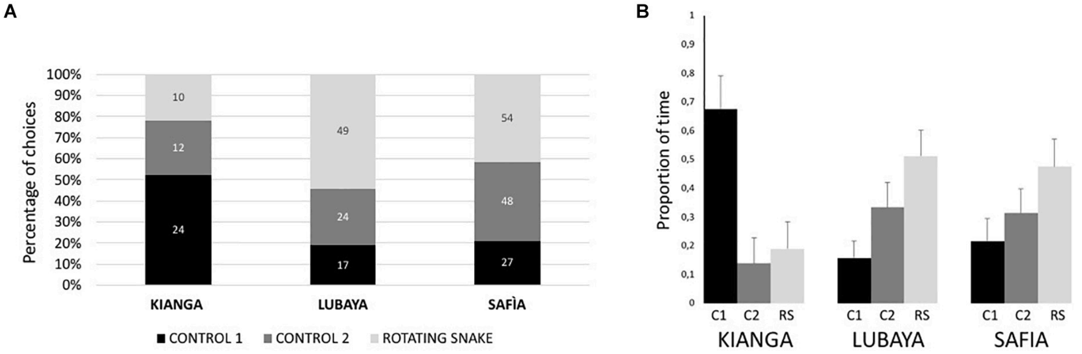

FIGURE 3 | Percentage of times in which lionesses interacted with the three stimuli **(A)** and proportion of time **(B)** spent near the three stimuli (C1, Control 1; C2, Control 2; RS, Rotating Snake). Bars represent the standard error of the mean.

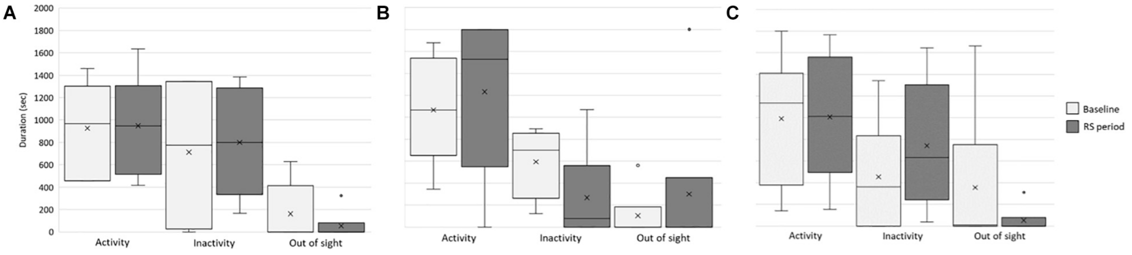

FIGURE 4 | Activity, inactivity, and out-of-sight behavior of the lionesses. Box and whisker plot of the time spent being inactive, active, and out of sight at baseline (light gray) and during the RS period (dark gray) by the study subjects **(A)** Kianga, **(B)** Lubaya, and **(C)** Safia. The horizontal lines within the box indicate the medians; boundaries of the box indicate the first and third quartile. The whiskers extend from the top of the box to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom to the smallest data element that is larger than 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points.

change as a function of time, in terms of both interactions (Spearman's correlation between total interactions in each trial and experimental sessions, for all subjects, $p > 0.070$) and time spent to explore the stimuli (Spearman's correlation between proportion of time near the stimuli and experimental sessions, for all subjects $p > 0.081$).

Effects of the Visual Stimuli on Lionesses' Behavior

To verify whether and how the provision of these visual stimuli impacted the behavior and welfare of the lionesses, we compared activity level and individual and social behaviors between the baseline and RS period. First, we considered whether the stimuli affected the overall activity, inactivity, and out-of-sight condition of each lioness (**Figure 4**). In all the study subjects, no significant differences were found between the two periods in activity (Kianga: $p = 0.253$, $r = -0.163$; Lubaya: $p = 0.065$, $r = -0.336$; Safia: $p = 0.381$, $r = -0.091$), and out-of-sight condition (Kianga: $p = 0.149$, $r = 0.303$; Lubaya: $p = 0.608$, $r = -0.083$; Safia: $p = 0.446$, $r = 0.248$). In the case of inactivity, Lubaya was more inactive at the baseline than in the second period ($p = 0.009$, $r = 0.436$), whereas no significant differences were found for Kianga ($p = 0.608$, $r = -0.073$) and Safia ($p = 0.886$, $r = -0.018$) (**Figure 4**).

To gain a better understanding of the effect of the stimuli on the lionesses' behavior, we considered individual and social behaviors as classes. At baseline, the median (IQR) time spent performing individual behaviors was 708.5 s (438.8) for Kianga, 838 s (883.5) for Lubaya, and 995 s (734) for Safia. In the RS period, the median (IQR) time spent performing individual behaviors was 1343.5 s (798) for Kianga, 1090 s (582.3) for Lubaya, and 1161 s (659.8) for Safia. No significant differences were found for Lubaya ($p = 0.434$, $r = -0.160$) and Safia ($p = 0.310$, $r = -0.128$), whereas Kianga performed more individual behaviors in the RS period than at baseline ($p = 0.033$, $r = -0.544$). On the other hand, at baseline, the median (IQR) time spent performing social behaviors was 548 s (600.3) for Kianga, 192 s (134.8) for Lubaya, and 283 s (372.8) for Safia. In the RS period, the median (IQR) time spent performing social behaviors was 246 s (253.8) for Kianga, 335.5 s (348.8) for Lubaya, and 293 s (406.5) for Safia. Significant differences were found between the two periods. Kianga performed more social behaviors at baseline than in the RS period ($p = 0.017$, $r = 0.480$), and for Lubaya ($p = 0.024$, $r = -0.288$), the opposite pattern was found. No significant difference was reported for Safia ($p = 1$, $r = 0$).

Considering each behavioral category within individual behaviors, we found that Kianga paid significantly more attention and exhibited anticipatory behavior in the RS period than at baseline, whereas the opposite pattern was reported for self-grooming (see **Table 2** for median, IQR, time budgets, and *p*-values). Lubaya performed significantly more maintenance in the RS period than at baseline, whereas no other differences were found (see **Table 2** for median, IQR, time budgets, *p*-values, and effect size). No significant differences were found between the two periods for Safia (see **Table 2** for median, IQR, time budgets, *p*-values, and effect size). Regarding social behaviors, Kianga performed more affiliative behavior in the RS period than at baseline, whereas interspecific behavior was seen significantly more at baseline than in the RS period (see **Table 2** for median, IQR, time budgets, and *p*-values). No significant differences were found in any behavioral category for Lubaya and Safia (see **Table 2** for median, IQR, time budgets, *p*-values, and effect size).

DISCUSSION

Environmental enrichment has been proven to be a relevant strategy to improve zoo animal welfare. However, the effects of environmental enrichment programs on animal behaviors need to be evaluated to ensure that they positively affect the animals' well-being, focusing on the response of each individual (Quirke and O'Riordan, 2011). Here, we tested the hypothesis according to which a visual pattern eliciting illusory motion might serve as a useful tool for environmental enrichment of big cats.

Our data show that two lionesses out of three (67%; Lubaya and Safia) preferred to approach the RS more than the other stimuli. This is partially confirmed by the analysis showing that Lubaya also spent more time in correspondence with the RS. This was not observed with Safia, even though the trend was in the same direction. Although limited, our data align with studies on cats (Baath et al., 2014) and encourage future investigation in this direction. It is important to note that the two types of control stimuli differed regarding the complexity of the visual array (that is, Control 1 presented a more complex visual pattern compared to Control 2). The fact that 2/3 lionesses selected the RS more than both control stimuli ensured us that their choice was not based on the mere complexity of the illusory array presented.

Finally, when focusing on the interaction with the visual stimuli by the study lionesses in the RS period, we reported a lack of correlation between the number of sessions of the RS period and the number of interactions or the time spent by the lionesses dealing with the stimuli. These findings suggest that the interest of the study subjects toward the new enrichment devices remained stable over the experimental sessions. Thus, providing this kind of stimulation for nine sessions over approximately 1 month seems to be appropriate to keep the lionesses interested in the stimuli.

Although we cannot directly draw any conclusion on the neural mechanisms involved in the perception of the RS illusion by lionesses, the possibility that they experience illusory motion raises the intriguing question as to whether motion extrapolation in this species is based on similar mechanisms described in humans. As said, illusory motion seems to be generated by the activity of the MT complex in the occipital

TABLE 2 | Individual and social behaviors performed by the study lionesses.

	Attention	Self-grooming	Env-Enr	Locom.	Mainten.	Scent	Olf expl	Observing	Anticip b.	Affil.	Agon.	Intersp.
Kianga												
Baseline	0 (62.3) 0%	31.5 (98.8) 3%	0 (0) 0%	13 (115.8) 4%	6.5 (16.3), 1%	0 (0) 0%	0 (0) 0%	391 (404.3) 30%	0 (0) 0%	6 (44.8) 1%	0 (0) 0%	467 (604.3) 26%
RS period	119 (119) 7%	0 (10.5) 0%	0 (19.5) 1%	49 (148.3) 5%	8.5 (17) 1%	0 (0) 0%	0 (0) 0%	612 (570.8) 34%	26 (206.3) 16%	75.5 (153.8) 5%	0 (0) 0%	78 (177) 7%
p-value	0.005**	0.008**	0.109	0.722	0.919	1	0.739	0.580	0.014*	0.041*	0.478	0.010*
r	−0.433	0.496	−0.327	−0.091	0.027	−0.204	0.109	−0.128	0.449	−0.320	0.274	0.528
Lubaya												
Baseline	29 (111.3) 4%	0 (0) 0%	0 (0) 0%	17.5 (186.5) 8%	2 (11) 0%	0 (4.5) 0%	0 (0) 2%	495.5 (605.8) 35%	0 (0) 2%	0 (87.3) 2%	0 (0) 0%	164 (199.3) 12%
RS period	58 (239.3) 8%	0 (30) 1%	0 (3) 0%	58.5 (77.8) 3%	13 (22) 1%	0 (0) 0%	0 (0) 0%	733.5 (570.5) 36%	0 (298.8) 9%	125.5 (221.8) 7%	0 (0) 0%	244.5 (342.8) 15%
p-value	0.260	0.590	0.109	0.541	0.036*	0.342	0.739	0.755	0.284	0.053	1	0.542
r	−0.281	−0.138	−0.327	0.096	−0.390	0.263	0.109	−0.064	−0.248	−0.381	−0.204	−0.128
Safia												
Baseline	0 (68) 2%	0 (39.8) 2%	0 (0) 0%	56.5 (190.3) 5%	2 (20.8) 2%	0 (3.8) 0%	14 (82.8) 4%	576.5 (626.8) 34%	0 (0) 0%	27 (64) 3%	0 (0) 0%	199 (357) 15%
RS period	67.5 (231) 6%	0 (89) 3%	50 (260.8) 8%	82 (195.8) 6%	36 (78.3) 2%	2.5 (34.3) 1%	0 (9) 1%	442 (530.3)25%	0 (34.5) 4%	58 (196.5)9%	0 (0) 0%	102 (225)10%
p-value	0.069	0.672	0.017*	0.447	0.121	0.138	0.175	0.410	0.217	0.126	1	0.272
r	−0.351	−0.104	−0.449	−0.127	−0.286	−0.300	0.345	0.368	−0.327	−0.218	–	0.304

*Per subject and per period (baseline and RS period with the visual stimuli), the table reports medians (interquartile range), and mean% time (in seconds) spent performing all the behavioral categories considered in the study (Env-Enr, environmental enrichment; Locom., locomotion; Mainten., maintenance; Scent, scent marking; Olf expl., olfactory exploration; Anticip b., anticipatory behavior; Affil., affiliative behaviors; Agon., agonistic behaviors; Intersp., interspecific behaviors). For each subject, below medians and IQR of the two periods is reported the p-value (Wilcoxon-Mann-Whitney test) resulting from the comparison between the baseline and the RS period and the effect size (r). *Significant difference* $p < 0.05$. ****$p < 0.01$.

cortex (Kuriki et al., 2008), as well as the results of fixational eye (Murakami et al., 2006; Beer et al., 2008; Otero-Millan et al., 2012). In the absence of neurophysiological investigation in this field with felines, we must be open to the possibility that either neural mechanism (if not both) is also involved in the lionesses' perception of illusory motion.

We then asked what the benefits of this type of visual material are to lionesses' behavior. First of all, the lionesses under investigation repeatedly interacted with the PVC sheets by biting them, holding them in the mouth, and dragging them around the enclosure, and they revisited them several times during the observation sessions. Thus, the PVC sheets stimulated the performance of species-specific behaviors related to hunting and prey subjugation (Kruuk and Turner, 1967; Schaller, 1972; Lindburg, 1988).

Considering the activity of the lionesses, the visual stimuli seemed to reduce the inactivity of Lubaya. Carnivores tend to be inactive in a controlled environment and in the presence of visitors (Shepherdson et al., 1993; Mellen et al., 1998), and zoo lions have been found to be particularly difficult in terms of increasing activity level (Powell, 1995). Thus, this finding seems to underlie a positive welfare implication, promoting active behavior in species that tend to be inactive in controlled environments. Moreover, when focusing on the time spent in individual behaviors, the visual stimuli seemed to influence the behavior of all subjects. In particular, they had some positive effects in the case of Kianga. Indeed, Kianga performed more self-grooming at baseline than in the RS period. Self-directed behavior, particularly self-grooming, is normal in cats because it is used to clean the fur and maintain insulation properties (Eckstein and Hart, 2000; Virga, 2005). However, this behavior might also indicate a stressful or conflict situation, highlighting possible welfare issues (Powell, 1995; Virga, 2005). Therefore, the decrease in self-grooming in Kianga during the RS period might underline a welfare improvement, although in both periods, Kianga exhibited low levels of self-grooming. The reduction in this behavior in the presence of the visual stimuli might indicate that the study lioness spent more time showing other relevant species-specific behaviors. In particular, this female showed more attentive behavior in the RS period than at baseline. The reported increase in attentive behavior might therefore indicate a positive welfare implication, because in the presence of the visual stimuli, Kianga became more vigilant, and reactive. This finding aligns with previous research on the effect of environmental enrichment in African lions, reporting that the presence of novel objects as enrichment devices increased activity and alertness in this species (Powell, 1995; Van Metter et al., 2008). Similar findings have been reported in other felids, such as black-footed cats (Wells and Egli, 2004) and tigers (Van Metter et al., 2008). On the other hand, in the RS period, Kianga performed more anticipatory behavior than at baseline. During the RS period, the zoo closing time was earlier than at baseline. Thus, it is possible that the lionesses expected to enter the indoor area, in which the daily amount of food was provided, and performed anticipatory behavior before the end of the data collection session. This behavior has been described as a potential welfare indicator (Ward et al., 2018), but it seems not to be related to the presence of the visual stimuli, as it is directed toward the indoor area of the enclosure during a specific period of the day.

Within individual behaviors, Lubaya exhibited more maintenance in the RS period than at baseline. This result might be linked to the decrease in inactive behavior observed in Lubaya during the RS period, suggesting that in the presence of the novel stimuli, this subject performed more species-specific behaviors.

Regarding Safia, we reported an increase in the interaction with the environmental enrichment stimuli and therefore the performance of species-specific behaviors such as play and hunting-related activities, suggesting a positive welfare implication for this lioness (Powell, 1995; Baker, 1997; Hosey et al., 2013).

The visual stimuli also impacted the social behaviors of Kianga and Lubaya, particularly affiliative behaviors. Indeed, Kianga exhibited significantly more affiliative behaviors in the RS period, whereas a trend toward significance ($p = 0.05$) was reported for Lubaya. Thus, the novel stimuli seemed to improve positive social interactions among lionesses, as previously reported in other studies describing the benefits of environmental enrichment for African lions in zoos (Powell, 1995; Baker, 1997). Moreover, Kianga performed more interspecific social behavior, intended as attention toward humans such as visitors and zookeepers, at baseline than in the RS period. Zookeepers and other human factors have been found to be major determinants of animal welfare and could be, in some cases, stressful for the animals, leading to negative reactions toward the public as well as to the development of abnormal behaviors (Hosey, 2000, 2008, 2013; Davey, 2007; Fernandez et al., 2009; Cole and Fraser, 2018). The reduction of interspecific social behavior of Kianga seems therefore to be positive for the welfare of the subject, as the decrease in time spent interacting with humans might indicate an increase in the performance of other desirable species-specific behaviors, underlining improvements in the animal's psychological well-being (Cole and Fraser, 2018).

The materials used in the current study are convenient, because the PVC sheets can be printed quickly and cheaply in any print shop. However, to avoid competition between subjects, more than one stimulus per subject is needed because they can generate great interest in the subjects. Moreover, although resistant to water and bad weather conditions, the PVC sheets can easily and potentially be destroyed by the lions and are

FIGURE 5 | Example of remains of the stimuli after an experimental session.

not always long-lasting or reusable (**Figure 5**). Instead of PVC sheets, environmentally friendly cloths can be used. Based on our experience, the visual stimuli can be provided to the animals on non-consecutive days to be more efficient (e.g., once a week) and can be left in the lions' enclosure for the whole day, because each individual of the current study played with the PVC sheets and their remains at more times during the day. We suggest that visual stimuli such as motion illusions could be included in the environmental enrichment schedule of lions and possibly other carnivore species in zoos but should be alternated with other types of stimulations (e.g., olfactory, manipulative, and food-related devices) to promote the widest array of species-specific behaviors related to positive welfare.

We are aware that the small sample size – unfortunately, a methodological flaw shared with many studies involving zoo animals (Perdue et al., 2012; Vonk and Beran, 2012; Fuller et al., 2018) – prevents drawing any firm conclusions on the real preference of lionesses for interacting with the RS illusion and the potential impact of such a stimulation in their environment. However, the data included in this study are promising and call for a larger investigation on the use of motion illusions as visual environmental enrichment in natural parks. The illusory pattern seems to have been explored more than other stimuli with a similar configuration, where the perception of motion is absent. Overall, this type of material seems to provide some benefits in the expression of species-specific behaviors of big cats. We hope that in the near future, this hypothesis could be tested on a larger range of individuals and species.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the study was carried out through the behavioral observation of the lionesses, using non-invasive techniques. The study procedure was in accordance with the EU Directive 2010/63/EU and the Italian legislative decree 26/2014 for Animal Research. No special permission to use animals in the current ethological non-invasive study is required, as zoological gardens in Italy are expected to carry out behavioral observations of the individuals in their care, in order to guarantee the animal welfare (D. Lgs.73/2005).

AUTHOR CONTRIBUTIONS

MM, CS, and CA developed the study concept. BR, AR, and GO collected the data. BR, AR, CS, and CA analyzed the data. BR, MM, CS, and CA wrote the manuscript.

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The Effect of Regulating Zoo Visitor-Penguin Interactions on Zoo Visitor Attitudes

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Understanding visitor attitudes toward zoo animals can inform the way zoos manage visitor-animal interactions by identifying the factors that may influence visitors and the way visitors interact with animals. Consequently, we investigated the relationship between visitor attitudes and penguin behavior and the effects of regulating visitor-penguin interactions on visitor attitudes and experience. Visitor attitudes toward little penguins (*Eudyptula minor*), their welfare, enclosure, visitor effects, enclosure manipulations and visitor experience at an Australian zoo were assessed. A 2 × 2 fully randomized factorial design was used to examine potential factors that may influence visitor attitudes: (1) Viewing proximity of visitors to the enclosure: "Normal viewing distance" and "Increased viewing distance" (using a physical barrier set up 2 m from the enclosure) and (2) Intensity of visitor behaviors: "Unregulated visitor behavior" and "Regulated visitor behavior" (using signage and researcher in zoo uniform). Visitor attitudes were assessed using an anonymous attitude questionnaire. Visitors were approached after they had finished viewing the penguins and were given two options to complete the questionnaire, either on an iPad on site during their zoo visit or online (URL sent via email) after their zoo visit. A total of 495 surveys (48% during zoo visit, 52% after zoo visit) were completed. Majority of respondents were non-zoo members, females and aged between 26 and 35 years old. Results revealed a significant relationship ($p < 0.05$) between little penguin behavior and visitor attitudes where the more visible, active and close penguins were to the visitor viewing area, the more positive several visitor attitude scales were. In contrast, there were only a few treatment effects of regulating visitor viewing proximity and behavior on visitor attitudes in which attitudes toward "Positive penguin characteristics" ($p = 0.024$), "Neutral visitor effects" ($p = 0.0023$) and "Physical barriers" ($p = 0.013$) were affected. This suggests that physical barriers and/or signage are factors that influence visitor attitudes. However, it is unclear if the treatment effects influenced visitor attitudes directly, or if it was the changes in penguin behavior as a consequence of the treatments that were associated with visitor attitudes. These findings have increased our understanding of the multifaceted nature of visitor attitudes and have identified some influencing factors on attitudes that can be used to inform the way zoos manage visitor-penguin interactions, but clearly further research is required.

Keywords: visitor attitudes, visitor-animal interactions, zoos, little penguins, penguin behavior, exhibit manipulations

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INTRODUCTION

Understanding zoo visitor perceptions and attitudes has been of growing importance because of the varying effects zoo visitors can have on the behavior and welfare of zoo animals (Hosey, 2013; Sherwen and Hemsworth, 2019). In particular, understanding visitor attitudes toward zoo animals can inform the way zoos manage visitor-animal interactions by identifying the factors that may influence visitors and the way they interact with animals. However, this has yet to be established and thoroughly investigated within zoos (Fernandez et al., 2009; Hosey, 2013; Sherwen and Hemsworth, 2019). Before proceeding further, it is important to define what we mean by "perceptions" and "attitudes" as these two terms are often used interchangeably. On the one hand, while closely related to attitudes, perceptions refer to an individual's interpretation of specific situations, stimuli or objects into something meaningful to them based on past experiences (Pickens, 2005). On the other hand, attitudes refers to the "mindset or tendency to act in a certain way" where we are trying to understand or explain an individual's behavior (Pickens, 2005). Therefore, attitudes are reflective of a positive or negative assessment of a given object which are derived from beliefs (Ajzen, 1991; Eagly and Chaiken, 1993) and are a strong determinant of behavior (Ballantyne and Parker, 2005).

Research on zoo visitors has shown that there are a variety of factors that influence visitor perceptions of zoos, zoo animals, visitor experience, viewing times and interests including exhibit design and animal characteristics such as animal size, color, activity and rarity (Rhoads and Goldsworthy, 1979; Bitgood et al., 1988; Finlay et al., 1988; Reade and Waran, 1996; Nakamichi, 2007; Margulis and Westhus, 2008; Kutska, 2009; Whitworth, 2012; Mun et al., 2013). However, despite this growing research and evidence of visitor effects on zoo animals, we have limited understanding of visitor attitudes toward specific zoo species, what influences these attitudes and how these attitudes affect visitor behavior and the way visitors interact with zoo animals (Fernandez et al., 2009; Hosey, 2013; Sherwen and Hemsworth, 2019). Understanding visitor attitudes toward specific zoo species and the factors, such as animal behavior, that may influence these attitudes, are important because of the potential implications they can have on the way zoos manage visitor-animal interactions. Research on zoo visitor-animal interactions has shown that these interactions can affect both zoo animal welfare and visitor experience and thus, visitor perceptions of zoos and zoo animals (Sherwen and Hemsworth, 2019). Negative visitor perceptions can adversely impact the mission of zoos of providing high standards of animal welfare and positive visitor experiences to support zoos as zoo-based conservation organizations (Ward and Sherwen, 2018; Sherwen and Hemsworth, 2019). Consequently, it is vital for zoos to not only understand how visitors affect zoo animals but also visitor attitudes toward specific zoo species and how potential factors such as zoo animal behavior may affect visitor attitudes. Through this understanding, zoos can then target these attitudes to potentially modify visitor behavior toward zoo animals to better manage visitor-animal interactions. However, limited research has been conducted to understand this relationship between visitor attitudes and zoo animal behavior.

Godinez et al. (2013) is one of the few studies that has investigated the influence of zoo animal behavior on both visitor behavior and visitor perceptions of the animal. They found that crowd size and visitor length of stay increased when jaguars were visible regardless of whether animals were active (e.g., eating, walking), inactive (sitting or lying down) or engaged in stereotypic behaviors (e.g., pacing and circling) compared to when "out of sight" (Godinez et al., 2013). However, visitor perceptions of the jaguars' wellbeing were reduced when the jaguars were displaying stereotypic behaviors (Godinez et al., 2013). This study highlights how animal behavior can influence visitor perceptions, but it remains unclear whether animal behavior influences visitor behaviors as no comparisons were made between active, inactive and stereotypic behaviors on visitor dwell time. Also, Miller (2012) found that after viewing a short video of a tiger engaged in pacing behavior compared to a tiger resting, people's perception of the level of care for the tigers at the facility decreased as did their interest in supporting zoos. It is evident from these studies, that there is a need for more robust research investigating how animal behavior affects visitor attitudes toward zoo animals and subsequently visitor behaviors. Ideally, an experimental approach should be taken whereby the interactions between visitors and animals are manipulated. Doing so, allows for causal conclusions to be drawn which enables rigorous interpretation of the effects of manipulating visitor-animal interactions on visitors and zoo animals (Cochran and Cox, 1957). Only a handful of studies thus far have applied this type of experimental approach to study zoo visitor-animal interactions (e.g., Sherwen et al., 2014, 2015a,b; Learmonth et al., 2018; Chiew et al., 2019). For example, Saiyed et al. (2019) found that zoo-housed African penguins (*Spheniscus demersus*) entering a close encounter with visitors in their enclosure in which visitors were instructed to sit quietly on a bench, showed no subsequent changes in affiliative and aggressive behaviors in comparison to no close encounter. While Sherwen et al. (2015b) and Chiew et al. (2019) found that close visitor contact markedly affected huddling, vigilance, pool use, proximity to the visitor viewing area and preening behavior of little penguins (*Eudyptula minor*) which suggests that visitors looming over penguins rather than sitting may be more fear-provoking. This type of research can help inform the way zoos manage visitor-animal interactions and may require, for example, alterations in exhibit design or the development of interventions to optimize both animal welfare and visitor attitudes and experience. Consequently, it is also important to evaluate the effects of interventions or management strategies that may be used to manage these interactions on visitors and animals.

Some studies have found that modification of zoo visitor-animal interactions using interventions or manipulations in the exhibit area such as visual or physical barriers, may affect visitor experience and potentially visitor attitudes despite the improvement in animal welfare. For example, the presence of a one-way visual screen that reduced the visibility of visitors resulted in reductions in intragroup aggression and fecal glucocorticoid concentrations in black-capped capuchins

(*Sapajus apella*) (Sherwen et al., 2015a). This indicated an improvement in capuchin welfare, but was found to reduce visitor numbers at the exhibit, perhaps because of the reduced interaction with the capuchins and in turn potentially reduced visitor experience and interest in the exhibit (Sherwen et al., 2015a). Also, Chiew et al. (2019) found that regulating visitor viewing proximity and the intensity of visitor behaviors by using a physical barrier to increase visitor viewing distance by 2 m away from the enclosure, reduced little penguin fear responses toward visitors. This was indicated by a reduction in the frequency of potentially threatening visitor behaviors such as banging on enclosure features, looming over the pool and sudden movement which reduced the proportion of penguins huddling and vigilant and increased the proportion of penguin close to the visitor viewing area, surface swimming and preening in the water when the physical barrier was in place (Chiew et al., 2019). However, the physical barrier was found to reduce visitor numbers, similar to that of Sherwen et al. (2015a). In contrast, Blaney and Wells (2004) found that when camouflage netting was installed to the viewing area of a gorilla exhibit that reduced the visibility of visitors, it not only improved gorilla welfare but also improved visitor perceptions of the gorillas. Consequently, assessing visitor attitudes toward such interventions and management strategies is important so that zoos can balance animal welfare and visitor experience and feasibly manage visitor-animal interactions.

Our present study was conducted in conjunction with that of Chiew et al. (2019). Our aims were to examine the relationships between visitor attitudes and experience and penguin behavior and determine the effects of regulating visitor viewing proximity and behavior on visitor attitudes and experience.

METHODOLOGY

Visitor attitudes toward little penguins were studied in conjunction with our study that investigated the effects of regulating visitor viewing proximity and the intensity of visitor behaviors on little penguin behavior and stress physiology (Chiew et al., 2019). Thus, this present study was conducted using the same methodology as Chiew et al. (2019) at the Melbourne Zoo little penguin (*Eudyptula minor*) exhibit (Zoos Victoria, Australia) which housed a breeding group of 15 little penguins in an outdoor, naturalistic 330 m^2 enclosure consisting of sand and vegetation areas, and a large swimming pool that went up to 3 m in depth (**Figure 1**). The enclosure walls were 1.2 m in height and the visitor path ran along three sides of the enclosure in which the main penguin viewing positions were along the length of the pool, side A, but opportunities to view penguins also occurred on the short ledge of the pool, side B (**Figure 1**). The penguins were fed twice a day (9:00 and 15:30 h) and husbandry followed normal routines and remained consistent throughout the course of the study (Chiew et al., 2019).

Design and Treatments

A 2 × 2 factorial treatment arrangement was used to examine the combined effects of regulating both visitor viewing proximity and intensity of visitor behavior on penguins (Chiew et al., 2019) and visitor attitudes and experience. The factors that were examined were as follows (Chiew et al., 2019):

1. **Viewing proximity of visitors to enclosure** at 2 levels:
   - (a) "*Increased viewing distance*" – a barrier was set up 2 m from the enclosure to increase the distance between visitors and the enclosure. This allowed unrestricted viewing of the enclosure but was a strong impediment to visitors physically interacting with the glass windows at the pool, pool water and other enclosure features.
   - (b) "*Normal viewing distance*" – no barrier was in place and visitors could approach to the edge of the pool (i.e., visitors could approach within 2 m of the enclosure).
2. **Intensity of visitor behaviors** at 2 levels:
   - (a) "*Unregulated visitor behavior*" – visitor behaviors were uncontrolled.
   - (b) "*Regulated visitor behavior*" – the objective of this treatment was to attempt to reduce the intensity of visitor behavior using signs requesting visitors to be quiet, move slowly in the exhibit area and avoid physically interacting with the penguins. Also, for this treatment, the researcher was dressed in zoo uniform.

Thus, there were four treatments in a factorial design as described in **Table 1**. For further details and description of the design and treatments imposed refer to Chiew et al. (2019).

Using a fully-randomized factorial design, treatments were randomly imposed for 2-day periods, two treatments per week with one day break in between (Mon-Tues and Thurs-Fri) and three replicates of each treatment (total of 24 study days). The study was conducted from the end of February to May 2016 (Summer/Autumn) over 9 weeks and was only conducted on school working days, to avoid the normal systematic variation in visitor numbers that occurs on weekends and during school holiday periods (Chiew et al., 2019). Two out of the 9 weeks had treatments with no day break in between which was due to public holidays occurring on the Monday one week and Friday the other week (Chiew et al., 2019).

The main penguin behavior measurements used from Chiew et al. (2019) for the present study were the behavioral states of the penguins including the proportion of penguins visible, huddling, distance from the visitor viewing area (sides A and B; **Figure 1**), resting, idle, locomoting on land, vigilant, surface swimming and diving. For further information on the behavioral sampling procedure refer to Chiew et al. (2019).

Visitor Questionnaires

This study received Human Ethics approval from the Veterinary and Agricultural Sciences Human Ethics Advisory Group (Ethics Application 1545739.1). Questionnaires were developed and refined based on focus groups discussions with visitors at Melbourne Zoo (Melbourne, Australia) and Taronga Zoo (Sydney, Australia).

Visitors were randomly approached by student volunteers and interns (from the Animal Welfare Science Centre, University

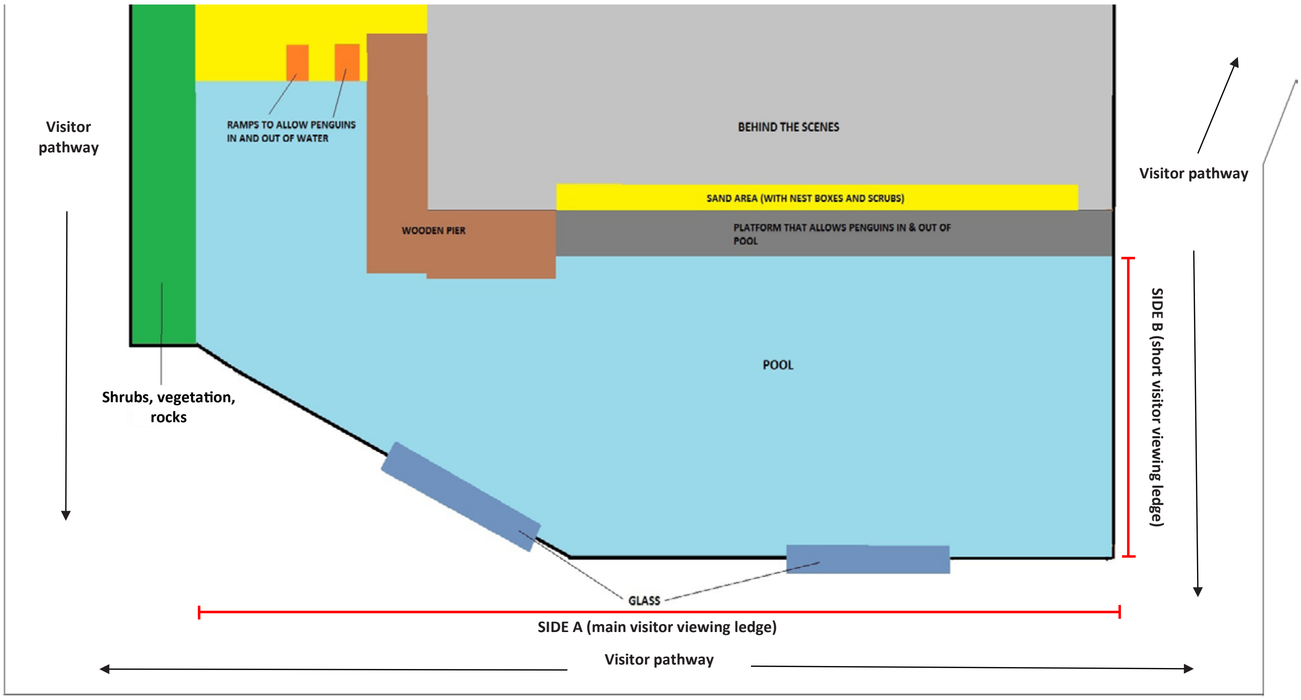

FIGURE 1 | Diagram of Melbourne Zoo penguin exhibit obtained from Chiew et al. (2019).

of Melbourne) during seven 30 min blocks between 09:30 and 15:15 h, after they had finished viewing the penguins and had exited the exhibit area. Visitors were asked to complete an anonymous questionnaire which assessed their attitudes toward the welfare of little penguins, the quality of their exhibit, exhibit manipulations and visitor experience. Visitors were given two options to complete the questionnaire, either on an iPad (on site during their zoo visit) or online (URL sent via email, after their zoo visit). Questionnaires were conducted on all study days.

Questionnaires took no longer than 10 min to complete and were divided into five sections: Section 1 collected information on the participants' demographics; Section 2 collected information on the participants' attitudes toward the little penguins and included questions such as "Do you think the little penguins are aggressive?," "Do you think the penguins are happy?" and "On a scale from 1 to 10, how would you rate the welfare of the little penguins"; Section 3 collected information on the participants' attitudes toward the little penguin enclosure and included questions such as "Do you think the penguin enclosure is well maintained?" and "On a scale from 1 to 10, how would you rate the little penguin enclosure?"; Section 4: collected information on the participants' experience where for example, questions in this section included "It was exciting to see the little penguins." and "On a scale from 1 to 10, how would you rate your experience at the penguin enclosure?"; and the final section assessed the participants' attitudes toward manipulations to the little penguin enclosure which included questions such as "Having one-way visual barriers where penguins cannot see visitors but visitors can see penguins improves penguin welfare." For attitude questions, a 5-point Likert scale was used which consisted of the following options: (1) Strongly disagree, (2) Disagree, (3) Neither agree nor disagree, (4) Agree, and (5) Strongly agree. The responses were scored so that disagreement with a statement had lower scores and agreements had higher scores. For rating questions, visitors were asked to rate, out of 10, the welfare of the little penguins, the little penguin enclosure and visitor experience at the enclosure where 1 was very poor and 10 was excellent.

A plain language statement was also visible at the enclosure and areas in which student volunteers and interns were located. The purpose of the plain language statement, which is a

TABLE 1 | The 2 × 2 factorial treatment arrangement used to examine the combined effects of visitor viewing proximity (using a physical barrier to push visitors 2 m back from the enclosure) and the intensity of visitor behavior (using signage to attempt to regulate visitor behavior) on penguins and visitor attitudes and experience.

FACTORS		**Intensity of visitor behaviors**	
		Unregulated visitor behavior	*Regulated visitor behavior*
Visitor viewing Proximity	*Normal viewing distance*	No physical barrier and no signs (Control)	No physical barrier but signs present (Signs)
	Increased viewing distance	Physical barrier present but no signs (Physical barrier)	Physical barrier and signs present (Physical barrier and Signs)

requirement for human ethics approval by the university, was to provide visitors with details and the purpose of the survey.

Data Analysis

Statistical analyses of questionnaire responses comprised frequency distributions of demographic factors across response categories and principal component analyses (PCAs) on attitudinal data using SPSS version 25. PCAs were conducted on the attitudinal data from the questionnaire to reduce the large number of attitude variables to a relatively small number of components, where the components reflected commonalties amongst those individual variables that correlated highly with each other. Subjective labeling of each component based on semantic content of the items was performed. Cronbach's alphas (α) were performed to measure the internal consistency of the items/questions within each component extracted from PCA (i.e., how closely related a set of items were as a group) as a measure of scale reliability. Scale mean scores for each component were calculated so that the averages were on the same scale as the original items/questions i.e., Likert scale from 1 to 5. Scale mean scores were then used as dependent variables for subsequent statistical analyses including one-way analysis of variance (ANOVA) to identify differences between treatments on scale mean scores. Prior to these ANOVAs, Levene's test statistic was used to test for homogeneity of variance.

The data on the effects of regulating visitor viewing proximity and behavior on penguin behavior from Chiew et al. (2019), were obtained at the same time as questionnaire responses were collected. Pearson correlations were used to examine the relationship between visitor attitudes and penguin behavior where scale mean scores for each day for visitor attitudes and the angular transformed data per day for penguin behavior were used i.e., the proportion of penguins performing each behavior per day (%). This transformation was used so that the residual variation was similar in all treatments and average scale mean scores were calculated per day as penguin behavior was averaged per day. It should be noted that the penguin behavior in Chiew et al. (2019) was averaged across the 2-day period for each treatment whereas single day averages were used in the present study because different visitors were surveyed each day.

RESULTS

Demographics and Percentage of Respondents

A total of 495 visitors completed the questionnaire and 639 visitors refused to complete the questionnaire; 238 were completed onsite (48%) during their zoo visit while 257 were completed online after their zoo visit (52%). Most participants were visitors living in Australia, non-zoo members and primarily females (**Table 2**). Also, majority of respondents were pet owners or had previously owned a pet and were aged between 26 and 35 years old (**Table 2**). Furthermore, most participants' highest level of education was a university or higher education institution degree (**Table 2**). There was a fairly even spread of participants across the four main study treatments, however the "Physical barrier" treatment which increased visitor viewing distance from the penguin enclosure by 2 m to regulate visitor viewing proximity, had the highest percentage of surveys completed on those days (**Table 2**).

Principal Component Analyses (PCA)

There were 46 attitudinal statements that were subjected to PCA (**Table 3**). Scale reliabilities were measured using Cronbach's α coefficients with an $\alpha \geq 0.70$ as the criterion for acceptable reliability (Pallant, 2007). Items were included in a scale if their loading on the relevant component exceeded 0.33 (Pallant, 2007; Tabachnick and Fidell, 2007) and if, based on face validity and semantic content, they could be summarized by just one construct. Varimax or oblimin rotations were performed on component solutions of more than one factor to provide the best simple structure and to simplify interpretation (Pallant, 2007). Selection of a varimax or oblimin rotation was also determined by examining the "component correlation matrix." If the correlations between components in this matrix were greater than 0.30, which indicates there is more than 10% overlap in variance between the components and therefore suggests they are correlated (Pallant, 2007; Brown, 2009), an oblimin rotation was used. If the correlations in the "component correlation matrix" did not exceed 0.30, then a varimax rotation was performed.

The greater the loading, the more the variables are a pure measure of the factor/component; loadings above 0.70 are considered strong/excellent (Tabachnick and Fidell, 2007). **Table 3** provides the extracted attitude components, the questions that loaded on each component and the scale mean scores for each component where the higher the mean score, the more agreement and therefore more positive the attitude. Cronbach's α coefficients are also presented in **Table 3**.

Attitudes Toward Little Penguin

A total of seven attitude questions were subjected to PCA. The Kaiser-Meyer-Olkin value was 0.86 and Bartlett's test of sphericity was significant ($p < 0.05$). No rotation was performed as only a single component was extracted with eigenvalues exceeding 1. The component explained a total of 53.3% of the variance. Based on an inspection of the loadings, the component was labeled as "*Positive penguin characteristics*" (**Table 3**). Single questions related to little penguin aggressiveness and timidness were analyzed separately as they were found to not reliably measure the same underlying construct when subjected to PCA.

Attitudes Toward Little Penguin Welfare

A total of 12 attitude questions were subjected to PCA. The Kaiser-Meyer-Olkin value was 0.88 and Bartlett's test of sphericity was significant ($p < 0.05$). The PCA extracted two main components with eigenvalues exceeding 1. The two components explained a total of 54.0% of the variance; component 1 explained 42.0% and component 2 explained 12.0% of the variance. An oblimin rotation was used and the two components had a correlation of −0.49. Based on an inspection of the loadings observed in the Pattern matrix, component 1 was labeled "*Negative penguin welfare*" and component 2 labeled "*Positive penguin welfare*" (**Table 3**). Also, the question where

TABLE 2 | Demographic information on visitors who completed the questionnaire.

Demographic Factor	Control (standard zoo conditions)	Physical barrier	Signs	Physical barrier and Signs	Total
Number of participants	114 (23.0%)	167 (33.7%)	91 (18.4%)	123 (24.8%)	495
Residence					
Living in Australia	87	127	82	96	392 (80.0%)
Overseas	26	38	9	25	98 (20.0%)
Type of visitor					
Zoo member	54	77	42	48	221 (44.6%)
Non-zoo member	60	90	49	75	274 (55.4%)
Gender					
Male	30	51	29	39	149 (30.0%)
Female	84	116	61	84	345 (69.8%)
Previously owned/Currently own a pet					
Yes	104	157	85	117	463 (93.5%)
No	10	10	6	6	32 (6.5%)
Age					
18–25	30	40	14	35	119 (24.2%)
26–35	29	51	31	33	144 (29.3%)
36–45	30	45	23	27	125 (25.4%)
46–55	6	9	7	9	31 (6.3%)
55+	19	21	15	18	73 (14.8%)
Highest Level of Education					
No formal schooling	0	0	0	0	0 (0%)
Primary school	0	0	1	0	1 (0.2%)
Secondary school	19	27	17	27	90 (18.2%)
Technical or further education institution (including TAFE College)	21	32	19	18	90 (18.2%)
University or other higher education institution	74	108	53	74	309 (62.4%)
Other educational institution	0	0	1	4	5 (1.0%)

visitors were asked to rate the welfare of the little penguins (out of 10) was analyzed separately as it was on a different rating scale to the attitudinal statements. Overall, visitors rated little penguin welfare on average as 7.60 out of 10 (minimum = 3, maximum = 10).

Attitudes Toward the Visitor Effect

A total of five attitude questions were subjected to PCA. The Kaiser-Meyer-Olkin value was 0.60 and Bartlett's test of sphericity was significant ($p < 0.05$). The PCA extracted only two main components with eigenvalues exceeding 1. A varimax rotation was used. The two components explained a total of 70.5% of the variance; component 1 explained 43.5% and component 2 explained 27.0% of the variance.

Based on an inspection of the loadings, component 1 was labeled "*Positive visitor effects*" and component 2 was labeled "*Neutral visitor effects*" (**Table 3**). Cronbach's α for "*Neutral visitor effects*" was 0.59 which was below the criterion of 0.70 (**Table 3**). This was influenced by only two items loading on this component but the Cronbach's α was deemed adequate based on the item loadings being above 0.70 and this component explained 27.0% of the variance.

Attitudes Toward the Little Penguin Enclosure

A total of nine attitude questions were subjected to PCA. The Kaiser-Meyer-Olkin value was 0.89 and Bartlett's test of sphericity was significant ($p < 0.05$). The PCA extracted two main components with eigenvalues exceeding 1. An oblimin rotation was used in which the components had a correlation of −0.55. The two components explained a total of 67.8% of the variance; component 1 explained 56.1% and component 2 explained 11.7% of the variance. Based on an inspection of the loadings, component 1 was labeled "*Positive enclosure features*" and component 2 "*Negative enclosure features*" (**Table 3**). Also, a question where visitors were asked to rate the little penguin enclosure (out of 10) was analyzed separately as it was on a different rating scale to the attitudinal statements. Overall, visitors rated the little penguin enclosure on average as 6.91 out of 10 (minimum = 1, maximum = 10).

Attitudes Toward Visitor Experience

A total of nine attitude questions were subjected to PCA. The Kaiser-Meyer-Olkin value was 0.78 and Bartlett's test of sphericity was significant ($p < 0.05$). The PCA extracted three components with eigenvalues exceeding 1. A varimax rotation was used. The three components explained a total of 71.4% of the variance; component 1 explained 38.8% and components 2 and 3 explained 20.9 and 11.8% of the variance, respectively.

Based on an inspection of the loadings, component 1 was labeled "*Learning*," component 2 "*Experience*" and component 3 "*Interests*" (**Table 3**). Cronbach's α for "*Interests*" was 0.45

TABLE 3 | Extracted attitude components from performing PCAs with the corresponding survey questions that loaded on each component, their loadings and scale mean scores (±standard error of mean, SEM) based on a 5-point Likert scale (1 = strongly disagree to 5 = strongly agree).

Extracted attitude components	Items	Loadings	Scale mean scores ± SEM
Positive little penguin characteristics (Cronbach's α = 0.85)	Do you think little penguins are Playful?	0.80	3.71 ± 0.03 (*n* = 473)
	Do you think little penguins are Curious?	0.78	
	Do you think little penguins are Intelligent?	0.75	
	Do you think little penguins are Interactive?	0.75	
	Do you think little penguins are Proactive?	0.71	
	Do you think little penguins are Friendly?	0.70	
	Do you think little penguins are Social?	0.60	
Negative penguin welfare (Cronbach's α = 0.84)	Do you think the penguins are Frightened?	0.88	2.66 ± 0.03 (*n* = 467)
	Do you think the penguins are Stressed?	0.85	
	Do you think the penguins are Frustrated?	0.73	
	Do you think the penguins are Anxious?	0.68	
	Do you think the penguins are Subdued?	0.66	
	Do you think the penguins are Bored?	0.56	
	Do you think the penguins are Under-stimulated?	0.47	
Positive penguin welfare (Cronbach's α = 0.78)	Do you think the penguins are Alert?	0.89	3.70 ± 0.03 (*n* = 466)
	Do you think the penguins are Healthy?	0.82	
	Do you think the penguins are Happy?	0.74	
	Do you think the penguins are Expressing natural behaviors?	0.62	
	Do you think the little penguins are Calm?	0.40	
Positive visitor effects (Cronbach's α = 0.78)	Do you think penguins find visitors entertaining?	0.89	2.82 ± 0.03 (*n* = 474)
	Do you think penguins find visitors interesting?	0.88	
	Do you think penguins find visitors novel?	0.72	
Neutral visitor effects (Cronbach's α = 0.59)	Do you think penguins find visitors NOT fear-provoking?	0.86	3.21 ± 0.03 (*n* = 472)
	Do you think penguins are unbothered by visitors?	0.82	
Positive enclosure features (Cronbach's α = 0.87)	Do you think the penguin enclosure is interesting to look at?	0.85	3.39 ± 0.03 (*n* = 477)
	Do you think the penguin enclosure is well maintained?	0.84	
	Do you think the penguin enclosure is natural looking?	0.82	
	The exhibit was engaging.	0.68	
	Do you think the penguin enclosure is meeting the needs of penguins?	0.54	
	Do you think the penguin enclosure is NOT bland?	0.43	
Negative enclosure features (Cronbach's α = 0.87)	Do you think the penguin enclosure is small?	0.93	2.92 ± 0.04 (*n* = 481)
	Do you think the penguin enclosure is restrictive?	0.91	
	Do you think the penguin enclosure is NOT spacious?	0.71	
	Do you think the penguin enclosure is bland?	0.45	
	Do you think the penguin enclosure is NOT meeting the needs of penguins?	0.34	
Learning (Cronbach's α = 0.88)	I learnt about a penguin's natural lifestyle.	0.89	2.79 ± 0.04 (*n* = 479)
	I learnt about penguin behavior when I was at the penguin exhibit.	0.88	
	I learnt about conservation issues related to penguins.	0.87	
Experience (Cronbach's α = 0.81)	I like being close to the penguins.	0.81	3.96 ± 0.03 (*n* = 482)
	I like seeing the penguins active and engaging in lots of behaviors.	0.78	
	It was exciting to see the little penguins.	0.77	
	It was entertaining to watch the little penguins.	0.74	
Interests (Cronbach's α = 0.45)	I wish there was more information about the penguins at the exhibit.	0.83	3.77 ± 0.03 (*n* = 477)
	If I could, I would like to do something to help care for little penguins in captivity and in the wild.	0.75	
Visual barriers (Cronbach's α = 0.76)	Having one-way visual barriers where penguins cannot see visitors, but visitors can see penguins improves penguin welfare.	0.90	3.68 ± 0.04 (*n* = 481)
	Having one-way visual barriers where penguins cannot see visitors, but visitors can see penguins improves visitor experience.	0.88	
Physical barriers (Cronbach's α = 0.52)	Having physical barriers that reduce the proximity between visitors and penguins improves visitor experience.	0.92	3.47 ± 0.03 (*n* = 478)
	Having physical barriers that reduce the proximity between visitors and penguins improves penguin welfare.	0.69	

which was below the criterion of 0.70 (**Table 3**). This was influenced by only two items loading on this component but the Cronbach's α was deemed adequate because both item loadings were above 0.70 and this component explained 11.8% of the variance. Also, a question where visitors were asked to rate their experience (out of 10) at the little penguin enclosure was analyzed separately as it was on a different rating scale to the attitudinal statements. Overall, visitors rated their experience at the little penguin enclosure on average as 6.45 out of 10 (minimum = 1, maximum = 10).

Attitudes Toward Exhibit Manipulations

A total of four attitude questions were subjected to PCA. The Kaiser-Meyer-Olkin value was 0.59 and Bartlett's test of sphericity was significant ($p < 0.05$). Although, the scree plot indicated only one eigenvalue exceeding 1, two components with an oblimin rotation provided a more interpretable result. The two components had a correlation of 0.32 and explained a total of 74.9% of the variance; component 1 explained 50.8%, and component 2 explained 24.0%.

Based on an inspection of the loadings, component 1 was labeled "*Visual barriers*" and component 2 was labeled "*Physical barriers*" (**Table 3**). Cronbach's α for "*Physical barriers*" was 0.52 which was below the criterion of 0.70 (**Table 3**). This was influenced by only two items loading on this component but the Cronbach's α was deemed adequate because the item loadings were above 0.70 and the variance explained was 24.0% for this component.

Relationship Between Little Penguin Behavior and Visitor Attitudes

Little penguin behavior was found to be significantly correlated ($p < 0.05$) with all attitude scale mean scores, except for "Perceived Aggressiveness" and "Interests" (**Table 4**). The majority of the correlations fell within the moderate range, 0.40–0.59, with a few in the strong range, 0.60–0.79 (**Table 4**; Evans, 1996).

"Positive penguin characteristics" were positively correlated with penguins close to the visitor viewing area, surface swimming and diving and negatively correlated with penguins idle (**Table 4**). This was also observed for "Experience" (**Table 4**). Similarly, "Positive penguin welfare" was positively correlated with the proportion of penguin visible, surface swimming and diving and negatively correlated with the proportion of penguins idle. This was also found for "Positive enclosure characteristics" which was also negatively correlated with the proportion of penguins locomoting (**Table 4**). In contrast, "Negative penguin welfare" were negatively correlated with proportion of penguins visible, close to the visitor viewing area, surface swimming and diving and positively correlated with penguins locomoting which was also observed for "Negative enclosure characteristics" (**Table 4**). Furthermore, "Physical barriers" was negatively correlated with the proportion of penguins visible and huddling and positively correlated with penguins being close to the visitor viewing area and surface swimming (**Table 4**). When visitors were asked to rate (out of 10) the welfare of the little penguins and their enclosure, both were positively correlated with the proportion of penguins close to the visitor viewing area, surface swimming and diving and negatively correlated with the proportion of penguins idle (**Table 4**).

Treatment Effects on Visitor Attitudes and Rating Questions

Analysis of variance revealed few differences in visitor attitudes (3 out of 17) between the treatment groups (**Table 5**). The treatment groups were: standard zoo conditions (Control), a physical barrier in place to regulate visitor viewing proximity but no signs (Physical barrier), signs present to attempt to regulate the intensity of visitor behaviors but no physical barrier (Signs) and both a physical barrier in place and signs present to regulate both visitor viewing proximity and behavior (Physical barrier and Signs; **Tables 1** and **5**). It was found that the treatment groups only significantly differed ($p < 0.05$) in their attitudes toward "Positive penguin characteristics" ($F_{3,469} = 3.18$, $p = 0.024$), "Neutral visitor effects" ($F_{3,468} = 4.89$, $p = 0.0023$) and "Physical barriers" ($F_{3,474} = 3.64$, $p = 0.013$; **Table 5**).

A "Least Significant Difference" *post hoc* test was performed and found that attitudes toward "Positive penguin characteristics" differed between visitors in the "Physical barrier" and "Signs" treatment groups: visitors exposed to the physical barrier had more positive attitudes compared to visitors only exposed to signs. In other words, visitors exposed to the physical barrier agreed more that the little penguins were playful, curious, intelligent, interactive, proactive, friendly and social compared to visitors exposed to signs (**Table 5**).

For attitudes toward "Neutral visitor effects," differences were found between visitors in the "Control" group and "Signs" treatment group and between visitors in the "Control" and "Physical barrier and Signs" treatment group (**Table 5**). Visitors in the "Control" agreed more that penguins do not find visitors fear-provoking and are unbothered by visitors compared to visitors that were only exposed to signs or both to a physical barrier and signs (**Table 5**). Also, differences were found between visitors in the "Physical barrier" and "Signs" treatment groups where visitors only exposed to a physical barrier agreed more that penguins do not find visitors fear-provoking and are unbothered by visitors compared to visitors exposed only to signs, who on average neither agreed nor disagreed visitors affect penguins (**Table 5**).

Attitudes toward "Physical barriers" differed between visitors in the "Control" and visitors in all other treatment groups (**Table 5**). Visitors in the "Control" had fairly neutral attitudes (i.e., neither agreed nor disagreed) toward physical barriers but visitors exposed to the physical barrier, signage or a combination of both, agreed more that physical barriers improve visitor experience and penguin welfare (**Table 5**). Therefore, visitors in the treatment groups had more positive attitudes toward "Physical barriers" compared to visitors exposed to standard zoo conditions (**Table 5**).

No significant treatment effects were found on any other attitude scales or the questions where visitors rated the welfare of the penguins, the penguin enclosure and their own experience at the exhibit ($p > 0.05$).

TABLE 4 | Pearson correlations between scale mean scores and little penguin behavior.

	Penguins visible	Huddling	<1 m from side A of the visitor viewing area	>1 m from side A of the visitor viewing area	<1 m from side B of the visitor viewing area	>1 m from side B of the visitor viewing area	Resting	Idle	Locomotion	Vigilant	Surface Swimming	Diving
Scale mean scores (Likert scale 1–5: 1 = strongly disagree, 5 = strongly agree)												
Positive penguin characteristics	0.35	−0.21	0.52**	−0.13	0.56**	−0.23	−0.20	−0.43*	−0.28	0.15	0.66**	0.66**
Perceived Aggressiveness	0.11	−0.16	0.08	0.13	0.05	0.11	−0.18	0.02	0.25	0.21	0.13	−0.07
Perceived Timidness	−0.15	0.03	−0.21	−0.22	−0.15	−0.22	−0.59**	0.25	0.26	−0.12	−0.30	−0.19
Negative penguin welfare	−0.48*	0.10	−0.33	0.09	−0.41*	0.22	0.12	0.38	0.45*	−0.20	−0.51*	−0.59*
Positive penguin welfare	0.44*	−0.06	0.30	−0.10	0.37	−0.19	−0.32	−0.42*	−0.34	0.27	0.55**	0.59**
Positive visitor effect	0.19	−0.22	0.27	−0.08	0.35	−0.19	−0.30	−0.31	−0.03	0.05	0.46*	0.47*
Neutral visitor effect	0.54**	0.06	0.20	0.04	0.33	−0.11	−0.20	−0.26	−0.37	0.27	0.41*	0.42*
Positive enclosure characteristics	0.42*	−0.11	0.15	−0.13	0.32	−0.28	−0.22	−0.37	−0.48*	0.18	0.42*	0.44*
Negative enclosure characteristics	−0.13	0.23	−0.28	0.29	−0.41*	0.41*	0.30	0.37	0.32	0.01	−0.45*	−0.44*
Learning	−0.15	−0.28	0.25	−0.42*	0.32	−0.50*	−0.17	−0.29	−0.32	−0.37	0.29	0.39
Experience	0.30	−0.24	0.35	−0.14	0.43*	−0.26	−0.11	−0.47*	−0.32	0.06	0.58**	0.65**
Interests	−0.25	0.16	−0.27	−0.03	−0.18	−0.06	−0.02	0.23	−0.04	−0.33	−0.24	−0.27
Visual barriers	−0.50*	−0.30	0.17	−0.24	0.04	−0.15	0.11	−0.03	0.39	−0.15	−0.02	−0.27
Physical barriers	−0.42*	−0.62**	0.49*	−0.48*	0.44*	−0.48*	−0.45*	−0.23	0.31	−0.29	0.46*	0.31
Rating questions (scale 1–10, 1 = very poor, 10 = excellent)												
Welfare of little penguins	0.08	−0.39	0.42*	−0.34	0.50*	−0.46*	−0.12	−0.58**	−0.33	−0.12	0.61**	0.64**
Little penguin enclosure	0.05	−0.28	0.35	−0.42*	0.48*	−0.55*	−0.22	−0.47*	−0.46*	−0.07	0.48*	0.38
Visitor experience at the little penguin enclosure	0.40	−0.02	0.15	−0.04	0.23	−0.14	0.01	−0.35	−0.42*	0.151	0.36	0.48*

*The angular transformation was used for penguin behavior. *Correlation is significant at the 0.05 level (2-tailed). **Correlation is significant at the 0.01 level (2-tailed).*

TABLE 5 | The effect of the treatments on scale mean scores (±SEM) and rating questions.

	Control (standard zoo conditions)	Physical barrier	Signs	Physical barrier and Signs	*P*-value
Scale mean scores (Likert scale 1–5: 1 = strongly disagree, 5 = strongly agree)					
Positive penguin characteristics	3.71 ± 0.05	3.81 ± 0.05	3.57 ± 0.07	3.67 ± 0.06	**0.024**
Perceived Aggressiveness	1.71 ± 0.08	1.74 ± 0.07	1.95 ± 0.11	1.92 ± 0.08	0.072
Perceived Timidness	3.56 ± 0.09	3.60 ± 0.07	3.57 ± 0.11	3.37 ± 0.08	0.17
Negative penguin welfare	2.56 ± 0.06	2.67 ± 0.05	2.76 ± 0.06	2.66 ± 0.05	0.17
Positive penguin welfare	3.76 ± 0.06	3.74 ± 0.04	3.64 ± 0.06	3.64 ± 0.05	0.24
Positive visitor effect	2.81 ± 0.06	2.82 ± 0.06	2.78 ± 0.07	2.83 ± 0.06	0.96
Neutral visitor effect	3.37 ± 0.07	3.28 ± 0.06	2.99 ± 0.08	3.15 ± 0.07	**0.0023**
Positive enclosure characteristics	3.42 ± 0.08	3.39 ± 0.06	3.31 ± 0.08	3.42 ± 0.06	0.69
Negative enclosure characteristics	2.88 ± 0.08	2.95 ± 0.07	3.04 ± 0.09	2.85 ± 0.07	0.44
Learning	2.71 ± 0.09	2.87 ± 0.07	2.76 ± 0.09	2.76 ± 0.09	0.49
Experience	3.98 ± 0.07	3.93 ± 0.05	3.95 ± 0.06	3.97 ± 0.05	0.88
Interests	3.78 ± 0.06	3.77 ± 0.05	3.77 ± 0.07	3.76 ± 0.06	0.99
Visual barriers	3.50 ± 0.08	3.74 ± 0.06	3.76 ± 0.08	3.70 ± 0.07	0.061
Physical barriers	3.26 ± 0.07	3.52 ± 0.06	3.55 ± 0.09	3.54 ± 0.07	**0.013**
Rating Questions (scale 1–10, 1 = very poor, 10 = excellent)					
Welfare of little penguins	7.52 ± 0.17	7.57 ± 0.14	7.46 ± 0.20	7.81 ± 0.15	0.47
Little penguin enclosure	7.04 ± 0.21	6.78 ± 0.18	6.57 ± 0.25	7.21 ± 0.19	0.16
Visitor experience at the little penguin enclosure	6.65 ± 0.21	6.42 ± 0.18	6.33 ± 0.25	6.38 ± 0.21	0.74

P-values less than 0.05 are in bold.

DISCUSSION

Several visitor attitude scales were found to be correlated with penguin behavior, but it should be noted that due to the large number of statistical tests, only those attitude variables that were consistently correlated with more than one penguin behavior variable are discussed. In contrast, there were only a few treatment effects on these scales. The correlations indicate that the more visible, active and close the penguins were to the visitor viewing area, the more positive visitor attitudes were toward positive little penguin characteristics, penguin welfare, visitor effects, the enclosure, learning, visitor experience and exhibit manipulations. This suggests penguins that display fewer behaviors indicative of fear such as avoidance, huddling and vigilance and more behaviors that are active such as swimming and diving, elicit more positive visitor attitudes toward the penguins, their welfare, enclosure and visitor experience. Our findings are supported by studies that have found zoo animals that engage in active behaviors and increased behavioral diversity, improve visitor perceptions of the animals (Anderson et al., 2003), predict visitors' self-reported positive affective responses (Luebke et al., 2016) and increase conservation intent (Hacker and Miller, 2016). In contrast, other studies have found zoo animals that display stereotypic behaviors such as pacing, reduced visitor perceptions of the animals' welfare and the level of care for the animals and decreased support for zoos (Miller, 2012; Godinez et al., 2013). Thus, the current results, consistent with previous research, provides evidence that zoo animal behavior is an important factor that is associated with zoo visitor attitudes and experience.

It is well understood that human attitudes can be a strong predictor of human behavior as demonstrated by the agricultural research on human-animal relationships (Fishbein and Ajzen, 2010; Hemsworth and Coleman, 2011). Positive attitudes in stockpeople toward animals they work with, have been found to result in increased positive handling toward animals and subsequently, positive effects on animal behavior and welfare which reinforces positive handling and attitudes (Hemsworth and Coleman, 2011). Chiew et al. (2019) found similar results to that of Sherwen et al. (2015b) where the close proximity of visitors which increased intense visitor behaviors such as leaning over the enclosure, sudden movement and tactile contact with the enclosure and pool's water, increased little penguin avoidance behavior and other behaviors indicative of fear but not fecal glucocorticoid metabolite concentrations (Chiew et al., 2019). This suggests that despite the positive visitor attitudes toward little penguins at Melbourne Zoo, visitors still had a negative effect on the penguins which contrasts with the agricultural research on human-animal relationships (Hemsworth and Coleman, 2011). This may be because positive visitor attitudes toward penguins may have increased visitors' desire to interact or be in close contact with penguins, thus engaging in potentially intense and threatening visitor behaviors and resulting in negative effects on the penguins. However, we were not able to directly correlate each visitor's attitudes with their behavior and in the present study we examined the general attitudes of visitors toward little penguins rather than the visitors' attitudes specifically toward the behaviors that they, as visitors, engage in toward little penguins. Consequently, further research is clearly required to understand visitor attitudes toward the behaviors they engage in when viewing zoo animals.

It is also possible that visitors may lack knowledge or awareness of the effect they can have on zoo animals. This is supported by the finding where attitudes toward “Positive visitor effects” and “Neutral visitor effects” were on average neutral (i.e., neither agreed nor disagreed). These results suggest the uncertainty visitors have about whether little penguins find visitors positive, negative or neutral. If visitors are not aware that their behavior may result in negative consequences on penguins, provision of such information may allow visitors to choose to change their behavior that may minimize their negative effect on penguins. Abraham and Denford (2017) argue that the provision of information may be vital in changing people’s behavior when people lack an understanding of their own behavior or its consequences. Thus, visitor education to raise awareness of visitor effects may be required to shift and modify visitor behavior to minimize negative effects on zoo animals. Research in agriculture has demonstrated that stockperson attitudes and their behavior toward animals can be improved through training (Hemsworth et al., 1994; Coleman et al., 2000). Consequently, further research is required to examine visitor attitudes and behavior in conjunction with the examination of visitor effects, identifying what behaviors visitors are performing that may affect zoo animals and attitudes toward those behaviors so that they can be targeted and modified.

Despite the growing research investigating how zoo animal behavior influences visitors’ attitudes, there is still limited research to link this understanding with observations of visitor effects on zoo animals. This is important as it may help with identifying strategies to manage zoo visitor-animal interactions. For example, Blaney and Wells (2004) found that visual contact with visitors resulted in increased intra-group aggression and abnormal behaviors including repetitive teeth clenching and body rocking in gorillas (Blaney and Wells, 2004). However, installation of camouflage netting to the viewing area of the gorilla exhibit to reduce the visibility of visitors, reduced conspecific-directed aggression and stereotypic behaviors in the gorillas but also increased visitor perceptions of gorillas where they were perceived as more exciting and less aggressive (Blaney and Wells, 2004). This demonstrates that the camouflage netting is a highly suitable management strategy to manage zoo visitor-gorilla interactions that has no detrimental impact, and rather positive effect, on the animals and visitors. In contrast, some research has found that modification of zoo visitor-animal interactions using visual or physical barriers, for example, may affect visitor experience and potentially visitor attitudes despite the improvement in animal welfare (Sherwen et al., 2015a; Chiew et al., 2019). This highlights the importance of examining visitor attitudes when investigating the effects of visitors on zoo animals to identify suitable ways to manage visitor-animal interactions. Consequently, the second aim of our present experiment was to address this by determining the effects of regulating visitor-penguin interactions by imposing exhibit manipulations (i.e., treatments: physical barrier and/or signage) to the visitor viewing area on visitor attitudes.

No treatment effects were found on visitor attitudes toward penguin welfare, the exhibit, learning, visitor experience, visitor interests and visual barriers as well as how visitors rated the penguins’ welfare, the enclosure and their own experience at the enclosure. This suggests that there was no detrimental impact of a physical barrier and/or signage on these visitor attitude scales or visitor experience. Interestingly, this contrasts with the few studies that have suggested one-way visual barriers to reduce visual contact with visitors and a physical barrier to regulate visitor viewing proximity and behavior, may negatively affect visitors and their experience due to the reduced visitor numbers and reduced interaction with zoo animals at the exhibit when these barriers are in place (Sherwen et al., 2015a; Chiew et al., 2019). However, there were some differences in visitor attitudes between visitors that were exposed to standard zoo conditions, a physical barrier (set up 2 m from the enclosure), signage or a combination of both a physical barrier and signs for attitudes toward “Positive penguin characteristics,” “Neutral visitor effects” and “Physical barriers.”

Visitors exposed to standard zoo conditions had more positive attitudes that penguins are not affected by visitors compared to visitors exposed to the exhibit manipulations which on average were neutral (i.e., neither agreed nor disagreed). Considering there is evidence indicating penguins can be negatively affected by visitors (Ozella et al., 2014; Sherwen et al., 2015b; Chiew et al., 2019), this result may be a concern for zoos as it suggests that visitors exposed to standard zoo conditions have misconceptions that visitors do not affect penguins. In comparison, visitors exposed to exhibit manipulations may have considered more the potential effects visitors have on penguins because of the presence of the exhibit manipulations. Thus, this suggests that exhibit manipulations may be a positive influence on visitor attitudes toward visitor effects. However, attitudes toward “Positive little penguin characteristics” differed between visitors that were exposed only to either a physical barrier or signage, indicating visitors exposed to a physical barrier had more positive attitudes toward “Positive little penguin characteristics” compared to visitors exposed to signs. This was also found for attitudes toward “Neutral visitor effects” indicating visitors exposed to a physical barrier had slightly more positive attitudes compared to visitors exposed to signs. This suggests that the type of exhibit manipulation or strategy to manage visitor-animal interaction is important where signs may have more of a negative influence on visitor attitudes compared to a physical barrier. This is somewhat consistent with Blaney and Wells (2004) which as previously discussed found camouflage netting (i.e., a physical barrier) installed to the viewing area of the gorilla exhibit, increased positive perceptions of gorillas. However, Meis and Kashima (2017) found that what influences the perceived effectiveness of a sign is the clarity of the signs purpose, especially for unfamiliar signs which in our study were unfamiliar and may not have had a clear purpose for visitors. This could explain why there was a potential negative effect on attitudes when visitors were exposed to signs in the present study compared to visitors that were not, since limited explanation was given to visitors as to why they were requested to be quiet, move slowly and not interact with the animals. However, clearly further research is still required to understand the effectiveness of signs within zoos on visitor attitudes and behavior.

Based on the few treatment effects on visitor attitudes, the results suggest that, if a management strategy were to be implemented to manage visitor-penguin interactions, a physical barrier may be more suitable over the use of signage, having less of a negative influence on visitor attitudes compared to signs. This is also supported by our finding that irrespective of whether it was the visitors exposed to a physical barrier, signage or a combination of both, in comparison to the visitors exposed to standard zoo condition, visitor attitudes toward physical barriers were more positive. In other words, there was more agreement that physical barriers would improve both visitor experience and penguin welfare when visitors were exposed to the exhibit manipulations compared to those that were not. Furthermore, Chiew et al. (2019) found that the physical barrier reduced potentially threatening visitor behaviors such as banging on enclosure features, leaning over the pool, tactile contact with the pool's water and sudden movement while signs had no effect on visitor behavior. This is also supported by Park et al. (2008) that found direct management by using a physical fence, was the most effective strategy to control visitor behavior compared to educational signage at Acadia National Park, United States. Consequently, our findings suggest that a physical barrier could be a suitable management strategy to manage visitor-penguin interactions. However, it should be noted that it is unclear if these few treatment effects on visitor attitudes affected visitor attitudes directly, or was a consequence of the treatment effects on penguin behavior that influenced visitor attitudes. For example, it was likely that the increased positive perceptions of the gorillas by visitors found by Blaney and Wells (2004) was influenced by the presence of the camouflage netting but also the changes in gorilla behavior because of the camouflage netting reducing visual contact with visitors.

We recognize that the methodology used in the present study, does not allow us to disentangle the direct effects on visitor attitudes of regulating visitor viewing proximity and behavior using a physical barrier and/or signage *per se*, from the effects of changes in penguin behavior on attitudes arising from this regulation. Also, the generalizability of our findings to other zoos is limited and the questionnaires completed were biased toward people living in Australia, pet owners and females which are common biases found in survey data (Driscoll, 1992; Kendall et al., 2006). Therefore, the visitors surveyed within our present study may not be representative of the population of visitors to Melbourne Zoo. Furthermore, we recognize that using the average daily penguin behavior and survey data, may have diluted the effects and masked the variation that is possible throughout the day in both penguin behavior and visitor attitudes. However, using daily averages and a randomized factorial design with three replicates of each treatment helps average out chance variation. Despite these limitations, the results gathered in our experiment provides insight on current visitor attitudes at Melbourne Zoo and has identified some influencing factors on visitor attitudes which provides a foundation for further research to build upon.

CONCLUSION

This study is the first study, to our knowledge, that provides information on visitor attitudes specifically toward zoo-housed little penguins, their welfare, enclosure, visitor effects, visitor experience and exhibit manipulations at an Australian zoo. We were able to identify two factors that influence visitor attitudes which were little penguin behavior and exhibit manipulations. The more visible, active and close the penguins were to the visitor viewing area, the more positive visitor attitudes were toward positive little penguin characteristics, penguin welfare, visitor effects, the enclosure, learning, visitor experience and exhibit manipulations. However, there were limited effects of the exhibit manipulations on visitor attitudes and experience. These findings have increased our understanding of the multifaceted nature of visitor attitudes and have identified some influencing factors on attitudes that can be used to inform the way zoos manage visitor-penguin interactions, but clearly further research is required.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

This study, which involved human participants to part take in an anonymous questionnaire, received human ethics approval from the Veterinary and Agricultural Sciences Human Ethics Advisory Group, Faculty of Veterinary and Agricultural Sciences, University of Melbourne, Australia (Ethics Application 1545739.1). The participants provided their written informed consent to participate in the study.

AUTHOR CONTRIBUTIONS

All authors designed the study. SC was responsible for liaising with the Wild Seas keeping team and other staff at Melbourne Zoo (Zoos Victoria, Australia) as well as the staff and student volunteers and interns from the Animal Welfare Science Centre (University of Melbourne, Australia), organized and carried out the data collection with the help of student volunteers and interns from the Animal Welfare Science Centre. SC collated all data and with the aid of GC, performed the statistical analysis of the data and interpretation. SC and GC wrote the manuscript. PH, SS, and VM provided feedback and additions to the manuscript.

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Personality in Zoo-Hatched Blanding's Turtles Affects Behavior and Survival After Reintroduction Into the Wild

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Reintroduction programs in which captive-bred or reared animals are released into natural habitats are considered a key approach for conservation; however, success rates have generally been low. Accounting for factors that enable individual animals to have a greater chance of survival can not only improve overall conservation outcomes but can also impact the welfare of the individual animals involved. One such factor may be individual personality, and personality research is a growing field. We designed a project to ascertain the presence of personality traits in Blanding's turtles (*Emydoidea blandingii*), a species of special concern in the state of Michigan, and to assess potential links between traits and post-release success. As hypothesized, the Blanding's turtles in this study displayed behavioral responses to modified open field tests indicative of distinct personality traits: exploration, boldness, and aggression. Additionally, the personality traits were correlated differently with survival and behavior patterns when the turtles were released into the Shiawassee National Wildlife Refuge. More exploratory turtles had higher survival rates, while neither boldness nor aggression was related to survival. Exploratory turtles were also more likely to travel longer distances after release. The use of muskrat dens was related to increased survival, and both bolder and more exploratory turtles made higher use of this feature. Exploratory and aggressive turtles were found basking outside of water more often, while bold turtles were more likely to be found at the water surface. Both these basking behaviors may increase the risk of predation and may be reflective of a trade-off between the risk and behaviors related to physiological health. Understanding how personality affects behavior and survival post-release can be a critical tool for improving reintroduction success. Zoo animal welfare scientists and practitioners can implement approaches that improve the welfare of individuals within the context of conservation initiatives.

Keywords: personality, reintroduction, Blanding's turtle, conservation, zoo, animal welfare

INTRODUCTION

Reintroduction programs in which captive-bred or reared animals are released into natural habitats are considered a key approach for conservation (Bremner-Harrison et al., 2004). Historically, North American zoological parks have played critical roles in the reintroduction of several species extinct or nearly extinct in the wild, including black-footed ferrets (*Mustela nigripes*), California condors (*Gymnogyps californianus*), and the Wyoming toad (*Bufo baxteri*) [Association of Zoos and Aquariums (AZA), n.d.]. Despite these notable examples, a recent literature analysis showed that from 1974 to 2013, zoos and aquariums contributed captive-bred animals to only about 25% of North American reintroduction programs (Brichieri-Colombi et al., 2019). During this time period, zoos contributed the most to amphibian (42%), terrestrial invertebrate (29%), and mammal (19%) programs, with contributions to reptile reintroductions relatively limited at 15% of North American releases (Brichieri-Colombi et al., 2019). With decades of experience in evidence-based breeding and animal management, as well as institutional shifts emphasizing the importance of *in situ* conservation, zoos are well-positioned to increase their contributions to conservation *via* captive breeding and release programs.

Despite their perceived importance as a wildlife conservation strategy, the success rates of reintroduction programs generally have been low (Stamps and Swaisgood, 2007; Swaisgood, 2010; Ewen et al., 2014), and in some cases, large numbers of released captive-bred animals perish (Teixeira et al., 2007). One reason for this is that released individuals may not be prepared to cope with the various challenges they encounter post-release (Beck, 1995; Bremner-Harrison et al., 2004). Thus, animal reintroduction programs naturally include factors that directly impact the welfare of individual animals. However, relatively little discourse has occurred between animal welfare scientists and conservation practitioners (Fraser, 2010). Animal welfare is also rarely monitored or addressed explicitly in published literature about reintroduction programs (Harrington et al., 2013). Incorporating factors that enable individual animals to have a greater chance of survival is not only a welfare goal but can also improve overall conservation outcomes. One such factor may be the impact of individual personality.

The study of personality in animals is a growing field with species studied ranging broadly. In a 2001 review, Gosling identified 187 studies in 64 species, which included mammals, birds, and fish, as well as reptiles, amphibians, arthropods, and mollusks. Perhaps unsurprisingly, animal personality research has focused largely on mammals, ranging from the African striped mouse (*Rhabdomys dilectus*, Joshi and Pillay, 2016) to brown and sloth bears (*Ursus arctos arctos* and *Melursus ursinus inornatus*, respectively, Pastorino et al., 2017), snow leopards (*Uncia uncia*, Gartner and Powell, 2012), African elephants (*Loxodonta africana*, Horback et al., 2013) and a number of non-human primate species including chimpanzees (Freeman et al., 2013), rhesus macaques (*Macaca mulatta*, Capitanio, 1999), and squirrel monkeys (*Saimiri sciureus*, Polgár et al., 2017). Although fewer studies have been devoted to other taxa, some work has been conducted with a variety of reptile species, including snakes, lizards, and turtles. Waters et al. reviewed the existing literature in 2017 and noted that anti-predator behavior in snakes was found to be consistent over time. Additionally, they provided an overview of personality traits found to exist in lizards, including aggression, boldness, exploration, and sociability (Waters et al., 2017).

In turtles and tortoises, as in other species, personality has been explored using a variety of methods. Germano et al. (2017) used the presentation of threatening stimuli to measure boldness and the effect of novel objects on investigative behaviors to measure exploration in desert tortoises (*Gopherus agassizii*). Latency to move from an initial location in an arena was used to assess exploration in red-eared slider turtles (*Trachemys scripta*, Carter et al., 2016) and eastern Hermann's tortoises (*Eurotestudo boettgeri*, Mafli et al., 2011). Boldness was measured in Spanish terrapins (*Mauremys leprosa*) using the righting response, which is the time it takes an individual to right themselves after being turned over onto their carapace (Ibáñez et al., 2013). A similar method was used to study anti-predator responses in European pond turtles (*Emys orbicularis*, Ibáñez et al., 2018). Kashon and Carlson (2018) measured boldness in eastern box turtles (*Terrapene Carolina*) using the time to emerge from the shell and the time to move after a brief period of confinement. Aggressiveness in eastern Hermann's tortoises was measured by staging fights between two conspecifics and measuring the amount of time to initiate a fight, rates of biting and ramming, as well as the percentage of fights won or given up (Mafli et al., 2011).

Terminology used in this field of research has been inconsistent (David and Dall, 2016) with terms such as temperament and behavioral style also being used and noted by some to be interchangeable (e.g., Réale et al., 2007). Others have noted that care is needed when using the term personality (e.g., Waters et al., 2017). The use of terms other than personality may be due, in part, to avoiding anthropomorphic implications (Gosling, 2008; Weinstein et al., 2008), resulting in a focus on behavioral patterns without further connections to emotion or cognition in animal personality research. Weinstein et al. (2008) argue that using the term personality more consistently has a number of advantages, including being able to connect work across fields. Definitions of personality also differ, and using a consistent term requires careful attention to the definition being used. For the purposes of this paper, we define personality broadly as behavioral variation between individuals (Carter et al., 2013). Differences in behavior should remain constant across measures, context, and time (Briffa and Weiss, 2012).

In wild animal populations, personality traits have been linked to specific factors impacting individual fitness, such as general health, metabolic rates, parasitism, dispersal, predation, reproductive success, and survival (Smith and Blumstein, 2008). Given these overall relationships between personality and fitness, it is not surprising that personality traits have been linked to post-release survival and behavior in a variety of species in reintroduction programs. Many such studies have focused on traits including exploration, boldness, and aggression. An individual's ability to disperse, select suitable habitat, and avoid threats in a new environment may be impacted by their personality (Kelleher et al., 2018), and the tendency to explore has been suggested as a critical trait for reintroduced animals (Berger-Tal and Saltz, 2014). Understanding how the behavior of individuals may affect their survivorship has therefore been suggested as an avenue of research (Harrington et al., 2013).

Additionally, individuals with different personality types likely respond differently physiologically, and behaviorally, to stressors (Carere et al., 2010). Differences in coping with stress can have an impact on how animals respond to reintroductions (Merrick and Koprowski, 2017). Given the importance of maximizing the success of reintroduction programs to advance conservation efforts, consideration should be given to how personality traits impact the survivorship of individual animals.

Although methods used to study personality also vary, two main categories are identified: behavior coding and trait rating. Rating of traits by knowledgeable observers has proven to be reliable and practical (Vazire et al., 2007); however, many studies still rely on direct coding of behaviors to assess personality traits (Gosling, 2001; Vazire et al., 2007). One established paradigm for assessing personality in nonhuman animals is the open field test, which involves measuring the behavior of an animal after entry into an open, novel arena (Perals et al., 2017). The parallels between the open field test and the eventual process of releasing captive-bred individuals into new environments suggest that this approach could be especially informative about how individuals with different behavioral traits might fare after release into wild habitats. As a measure of personality, open field tests are typically thought to capture traits related to exploration (Perals et al., 2017) and/or general activity levels (Carter et al., 2013). Additionally, modified open field tests may be used to assess traits such as aggression and sociality, by using mirrors as a proxy for other individuals (see Réale et al., 2007 for review). Behavior under pressure from predators, including simulated predation threats, has been used to measure the degree of boldness in modified open field tests (see Réale et al., 2007 for review).

Understanding the way in which different individuals may respond to environmental factors, both physical and social, may help conservationists tailor release conditions to individual needs in ways that may maximize their success, while improving the welfare of animals involved in releases. As organizations that emphasize both the welfare of individual animals and the conservation of wild populations, zoos are uniquely qualified to bridge this gap between welfare and conservation practice. One potential way to do so is to use the skills of zoo animal welfare scientists and behaviorists to develop behavioral profiles that may predict how particular individuals will respond to conditions they encounter upon release.

Blanding's Turtles

Blanding's turtles (*Emydoidea blandingii*) are a species of special concern in the state of Michigan. The species is considered vulnerable due to degradation and destruction of natural habitat, and populations are declining due to a number of challenges, including road-related mortality. Additionally, lengthy maturation time, as adults do not reach sexual maturity until 14–20 years of age, and nest and hatchling predation also contribute to lower population growth. In 2011, the Detroit Zoological Society began a collaboration with the U.S. Fish and Wildlife Service and the University of Michigan-Flint to headstart this species and reintroduce juvenile turtles into the Shiawassee National Wildlife Refuge, an area that is part of their natural range in Michigan, USA. Headstarting involves the captive rearing of animals until such a time as they are considered less prone to environmental dangers. Headstarting is used in many taxa, although less so for freshwater turtles (Spencer et al., 2017). The Blanding's turtles in this conservation program were hatched at the Detroit Zoo and released after reaching a carapace length of at least 10.16 cm or 18 months of age. Prior to release, a number of the turtles were outfitted with radio transmitters to monitor behavior and survival rates, work conducted by University of Michigan-Flint researchers. This monitoring took place between June 2014 and November 2015, encompassing the turtles' first winter hibernation.

Project Aim

Due to previous correlations between personality types and reintroduction outcomes, and the relatively lesser amount of personality research conducted on reptiles, we designed a project to ascertain the presence of personality traits in Blanding's turtles and assess potential links between traits and post-release success. We hypothesized that the turtles would display different personality traits based on performance during a suite of modified open field tests. Furthermore, we hypothesized that turtles rating differently on personality traits would have differential survival, in addition to expressing different behavioral patterns and microhabitat choices, post-release.

MATERIALS AND METHODS

Subjects and Housing

The subjects for this investigation were 23 Blanding's turtles (*Emydoidea blandingii*) from two clutches that were hatched at the Detroit Zoo in Royal Oak, Michigan, USA, as a part of the headstarting program in cooperation with the U.S. Fish and Wildlife Service, Michigan Department of Natural Resources, and the University of Michigan at Flint. In 2012, two gravid females were captured in the Shiawassee National Wildlife Refuge (SNWR) in Saginaw, Michigan (where the headstarted turtles were later released) and brought to the Detroit Zoo to lay eggs. At the zoo, the females were first radiographed to determine the number of eggs and then induced to lay using oxytocin administered at a dose of 10 U/kg intramuscularly.

Turtle eggs were split into two groups to achieve a ratio of 3:10 males (7:10 females) and incubated for 60–75 days at 28.3°C for males and 30.8°C for females. Hatchlings were raised in groups of 5–6 individuals in TurtleTub® enclosures (Zoo Med Laboratories Inc., San Luis Obispo, CA, USA) measuring 99.1 (l) × 53.3 (w) × 40.6 (d) cm. The enclosures (**Figure 1A**) were roughly divided into half land area (including a dry ramp from the water to the land) and half water, which was filled to a depth of 7.6 cm for the turtles' first year of life and 17.8–22.9 cm after that. Water temperature was maintained at 25.5°C, and air temperature ranged from 23.9 to 26.7°C.

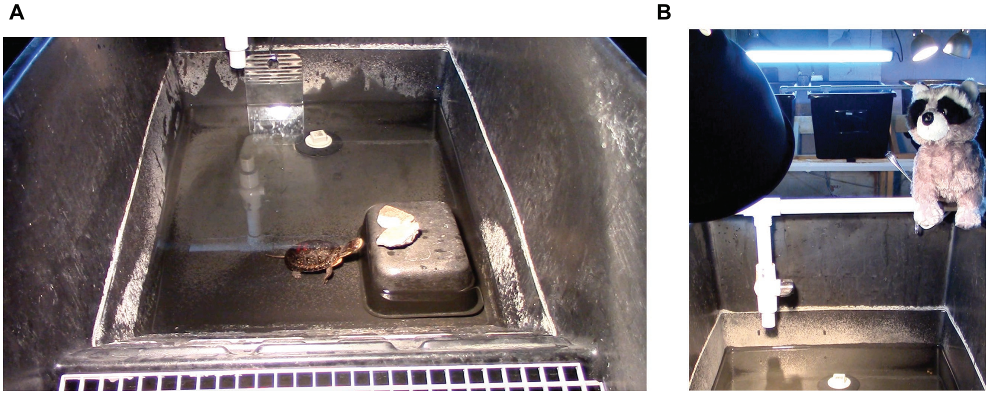

FIGURE 1 | (A,B) Enclosure used for housing turtles and as the arena for the four modified open field tests used to assess Blanding's turtle personality. **(A)** The arena during the second test (mirror test). **(B)** The arena during the fourth test (predator test), with the mock-predator present and other turtle enclosures visible in the background.

The water contained plants for the turtles to climb on and a drain plug, and the tanks were connected through a shared filtration system. UV lights were hung 60 cm above the enclosure. The turtles were maintained on a diet of aquatic turtle pellets, blackworms, and krill. They were fed three times a week, and on these days, they were moved into smaller tubs and left there overnight to consume their food.

Behavior in the Open Field Tests

Behavioral tests were conducted between May 14 and June 10, 2014 when the turtles were 12 months old. To control for time of day, all tests were conducted from 700 to 1,000 h. Turtles were not fed until after testing was completed, which did not require changing their regular feeding time. All tests were conducted in a single experimental arena, a TurtleTub® identical to their home enclosures (**Figure 1A**). The arena was cleaned and filled with fresh water between tests with different turtles to reduce the presence of olfactory cues from previous trials. The arena contained a hide made from an overturned plastic dish with one side cut out to serve as an exit, a drain plug, and a waterspout hanging down the side of the tank on one side. The tank was otherwise empty with the exception of items added during the open field tests.

Each turtle was tested in four variations of an open field test to explore the consistency of their responses in different contexts. The first test (Simple Open Field Test) consisted of a standard open field test, in which the turtle could freely explore the tank with no other stimuli present. For the second test (Mirror Test), a mirror was placed next to the waterspout on the side of the tank opposite the hide (**Figure 1A**). For the third test (Food Test), two small (~1 cm) pieces of mealworms were placed in the tank, one on the side containing the hide and the other on the side with the waterspout. For the fourth test (Predator Test), two pieces of worm were added as in the previous test, and a mock predator (a stuffed toy raccoon, **Figure 1B**) was placed on the top of the outer wall of the tank next to the waterspout.

The following protocol was used for all trials. Each trial lasted 20–23 min and consisted of the four open field tests, each lasting 5 min. The four tests were administered consecutively, in numerical order, to the turtle once it was placed in the arena to minimize turtle handling. Breaks between tests were minimized and consisted only of enough time to add the mirror, raccoon, or worms to the tank. To start a trial, the turtle was removed using gloved hands from its home tank and placed in the arena, and the hide was placed on top of the turtle. The open field test began immediately when the hide covered the turtle. After 5 min, the mirror was placed in the tank and the next test began. After 5 min, the mirror was removed, and the worm pieces were placed in the tank. After five more minutes, two additional worm pieces were added to the tank without removing the pieces from the previous trial, and the raccoon was put in place. The turtle was never removed from the tank or returned to the hide between subsequent tests.

To explore the consistency of the turtles' behavior across time, each turtle completed a full trial (all four open field tests) on 3 separate days, for a total of 12 modified open field tests per turtle. Trials were separated by 1 week. The order the turtles were tested was randomized at the start of the first week and kept consistent in subsequent weeks, so each turtle was always tested on the same day of the week. Each trial was videotaped for later analysis of behavior.

The behavior of the turtles during the trials was recorded from videos using The Observer XT 12 (Noldus, Wageningen, the Netherlands) on a Microsoft Surface Tablet (Redmond, WA, USA). Three observers coded all the videos, and inter-observer reliability was confirmed as >90% based on percent agreement coding a test video. For each test, the behavior of the turtle and its use of the hide (outside the hide, partially in the hide or in the hide) were simultaneously recorded as separate channels using continuous sampling and the ethogram in **Table 1**.

Post-release Tracking and Environmental Assessment

SNWR is a 9,800-acre reserve composed of forested wetland and emergent marsh habitats. Headstarted turtles were released in the SNWR at four different sites in June 2014 when they were 22 months old. The first site consisted of open water habitat; the second was dominated by cattails (*Typha* spp.) and duckweed; the third was dominated by willow (*Salix* spp.) and duckweed; and the fourth was characterized by dense cattail habitat. Detailed methods for field monitoring of released turtles can be found in Starking-Szymanski et al. (2018).

Turtle movements were monitored by radio tracking of transmitters affixed to their carapaces. Between the 2014 and 2015 field seasons, each turtle was located between 23 and 44 times (mean ± standard deviation = 37.3 ± 6.8). Home range sizes were estimated using the minimum convex polygon without including release points. Overall movement patterns were described by summing the distances between each point where turtles were located during subsequent tracking events.

When turtles were located, their behavior was recorded as basking, at the water surface, underwater, swimming, on land, or other. Microhabitat factors were also recorded including vegetation type, water depth and temperature, substrate depth, and air temperature. A total of six microhabitat types were identified using these variables by Starking-Szymanski et al. (2018), and these categories were used for further analyses: cattails, lowland forest, muskrat dens, open water, willows, or other floating vegetation.

TABLE 1 | Ethogram for behavioral data collection in modified open field tests.

Behavior	Behavior type	Operational definition
Strike mirror	Event	Turtle hits mirror with head or nose and then immediately moves or is pushed back away from the mirror
Surface	Event	Turtle moves body so that any part of the head is above the water
Eat worm	State	Capture and consumption (including chewing, swallowing, or holding in the mouth) of a worm
Spit worm out	State	Removes worm from mouth
Retract head	State	Retracts at least head and possibly legs as well
Investigate	State	Nosing (physically touching an object with the nose) or stretching (lengthening the neck so that the nose moves within 1 cm of an object); does not include nosing/stretching at enclosure wall
Climb	State	Movement across an object (plug or hide) or vertical movement on a substrate (climbing the wall); for climbing the wall, at least 2 feet are contacting the wall and the turtle is moving
Move	State	Swimming or walking; turtle may briefly pause movement, surface, or nose/contact the wall during this state
Inactive	State	Turtle is not moving around the enclosure; may be moving head to look around an open area, stretching the neck when not in proximity to objects, or nosing the wall during this state
Other	State	A behavior that does not fit into any of the described categories
Not visible	State	Cannot see body or behavior

DATA ANALYSIS

Exploratory Factor Analysis

For analysis of behavior in the open field tests, the percent of time spent performing all state behaviors and the rates of event behaviors were first calculated for each of the 12 tests. Descriptive statistics were calculated using Microsoft Excel (Redmond, WA, USA).

The analysis used in this study precluded using all the behaviors in the ethogram for personality assignment, so a subset of behavioral variables were selected or calculated (**Table 2**) that were consistent with operational definitions of personality (or temperament) in nonhuman animals as identified in Réale et al.'s (2007) review. Behaviors linked to exploration and general activity included distance covered in an open field test (Réale et al., 2007), which was operationalized here as the percent of time moving (high exploration) and the percent of time spent in the hide (low exploration) in the simple open field test. Latency to approach novel objects near food sources has also been used as a measure of exploration (Réale et al., 2007), and in this study, this was simplified by measuring the percent of food consumed in the food test. In rodent tests, rearing in an open field test has also been considered an exploratory behavior (Réale et al., 2007). Even freshwater turtles with limited ability to utilize aquatic oxygen can dive for 6–31 min, depending on water temperature (Priest and Franklin, 2002), so we considered the possibility that coming to the surface of the tank could represent an exploratory behavior perhaps analogous to rearing in rodents. Blanding's turtles are also known to forage while basking at the water surface (Millar et al., 2012), suggesting that surfacing behavior could play a role in exploring the surroundings for food but could also be related to boldness *via* exposure risk.

To measure boldness, previous studies have examined the latency for an animal to return to a food source after being startled by a predator (Réale et al., 2007). Other studies have presented the predator and food simultaneously; for example, boldness in Hermann's tortoises (*Eurotestudo boettgeri*) was measured by the experimenter presenting a food object by hand to the tortoise and measuring an index of behaviors including retraction into the shell, latency to approach the hand, and time spent eating (Mafli et al., 2011). In this study, the food and predator were presented simultaneously, but behaviors were indexed based on values from the presentation of food alone to control for activity level and motivation to feed (calculated as predator-food test). Because the turtles would be expected to approach and consume the food more quickly when the predator was not present, we subtracted the latency to consume food in the predator test from the latency to consume food in the food test (Food-Predator Test), so a larger value would theoretically represent a bolder individual.

Finally, agonistic displays and attacks have been used to operationalize aggression in prior studies utilizing mirror tests, and this study employed mirror strikes as well as the latency to approach the mirror, which could be related to either aggression or boldness based on previous studies (Réale et al., 2007). The inverse of the latency to strike the mirror was used so that a higher score would correspond to greater aggression. For turtles

TABLE 2 | Results of the exploratory factor analysis based on the behavior of $n = 23$ Blanding's turtles in four modified open field tests.

Behavioral variable	Test type	ICC (3, k)	Communalities (extracted)	Exploration (FAC1)	Boldness (FAC2)	Aggression (FAC3)
Percent of time moving	Simple open field	0.54	0.88	**0.91**	0.05	–0.22
Percent of time spent in hide	Simple open field	0.535	0.67	**–0.79**	0.15	–0.14
Rate of surfacing	Simple open field	0.55	0.56	**0.71**	0.16	0.17
Percent of food consumed	Food test	0.09	0.31	**0.51**	–0.20	–0.10
Difference in percent of time moving	Predator-food test	0.24	0.90	–0.14	**0.94**	–0.02
Difference in rate of surfacing	Predator-food test	0.42	0.54	0.07	**0.72**	–0.14
Difference in latency to consume food	Food – predator test	0.28	0.77	–0.08	**0.87**	–0.001
Rate of striking at mirror	Mirror test	0.30	0.84	0.03	–0.04	**0.91**
Latency to strike conspecific (inverse)	Mirror test	0.10	0.96	–0.03	–0.11	**0.975**

The table shows the rotated factor matrix. Bold scores indicate the component on which the factor loaded.

that did not strike the mirror at all, maximum latencies were assigned as the inverse of 300 s (the length of the test).

Behaviors from the ethogram (**Table 1**) not used in further analysis included spitting out the worm, retracting the head, investigating, and climbing. In some cases (e.g., climbing as a measure of exploration and retracting as a startle response related to boldness), these behaviors were considered but were ultimately dismissed on the basis of their repeatability.

Because repeatability is a central feature of personality (Réale et al., 2007), the repeatability of these behaviors across the three testing days within each turtle was examined using intraclass correlation coefficients (ICCs). The ICC analysis was conducted using a two-way mixed model for consistency, and values for the ICC (3, *k*) are reported in **Table 2**. From the behaviors that had positive ICC values, a subset was then selected that included each of the open field test types while avoiding variables that were highly auto-correlated within each test.

Exploratory factor analysis (EFA) was used to identify turtle personality traits. Historically, many studies of personality have employed principal components analysis (PCA); however, Budaev (2010) argues that EFA is more appropriate for identifying latent, unobservable behavioral constructs such as personality. Although it is commonly believed that very large samples sizes are required for EFA, recommendations for the correct ratio of variables to sample size are not empirically based (Budaev, 2010). In fact, EFA can be appropriate for sample sizes around $n = 25$ when the communalities of the variables are high (Budaev, 2010). Given the current sample size of $n = 23$ turtles, the EFA was conducted with caution, minimizing the number of variables employed. Behavioral variables were chosen that had positive ICC values, relatively high communalities (**Table 2**) and that represented the range of testing conditions.

To perform the EFA, percentages, rates, or latencies of behavioral variables were averaged for each turtle across the three testing days. Preliminary testing confirmed suitability of this dataset for EFA using the Kaiser-Meyer-Olkin Measure of Sampling Adequacy (0.55) and Bartlett's Test of Sphericity ($X^2_{(36)} = 114.33$, $p < 0.001$) (Budaev, 2010). Behaviors were loaded into the EFA using the correlation matrix. Principal axis factoring was used to extract factors, as recommended when the data violate assumptions of normality (Yong and Pearce, 2013). The number of factors was based on the number of eigenvalues >1, and a three-factor solution was confirmed by visual analysis of the scree plot. Final factors are presented using a varimax rotation (**Table 2**). Given the small sample size, we only accepted factors with relatively high loadings (>0.5). Finally, factor scores were calculated for each turtle using the Bartlett method, which produces unbiased scores that can be compared across factors (Yong and Pearce, 2013).

Further Analysis of Personality Factors

We used non-parametric Spearman correlations to examine the relatedness of the factor scores from the EFA analysis. Survival was also compared to the proportion of times the turtles were located in specific microhabitats during tracking, behaviors observed at tracking events, and with average body mass across the 2-year study using Spearman correlations.

The remaining outcome variables were analyzed using generalized linear mixed models. For most models, turtle ID was nested within release group. When applicable, the year (2014 or 2015) was used as a repeated statement. The three factor scores were used as fixed effects for all models. Survival status was modeled using binary regression and a logit link function, and in this case, no repeated statement or offset term was used. Turtle mass was measured twice, once before release and again 1 year later. Mass at the 1-year mark was modeled using a normal distribution with an identity link function and turtle nested by release group; there was no repeated statement or offset term. Mass at release was included as a covariate in the model, and interactions between mass at release and each personality variable were also tested in the model. Home range area (MCP estimate) and straight line distance traveled were modeled using normal distributions and identity link functions, and models were offset by the number of tracking events. Counts of behavior and microhabitat locations observed at each tracking event were summed for each year (2014 and 2015) and modeled using negative binomial distributions and log link functions, with counts offset by the ln(number of tracking events). However, the count of tracking points in lowland forest was analyzed using a Poisson distribution and a log link function because a model would not converge with a negative binomial distribution. We were unable to fit a model for use of other floating vegetation; however, this was not a preferred habitat type (Starking-Szymanski et al., 2018).

Degrees of freedom were calculated for all models using a Satterthwaite Approximation. Model fits were compared using Akaike information criterion (AIC), and the repeated statement was modeled using either an unstructured, variance components, or first-order autoregressive covariance matrix, depending on which produced the lower AIC. Models included a random intercept for release group with an unstructured covariance structure, except for the following variables for which a model could not be fit with a random statement: count of at the water surface, count of lowland forest and count of cattails.

Tests of fixed effects and fixed parameter estimates (followed by 95% confidence intervals in parentheses) are reported for results that were significant ($p < 0.05$) or trended towards significance ($0.05 \leq p < 0.1$). Exponeniated coefficients are presented for binomial and count variables.

RESULTS

Results of the Modified Open Field Tests

The EFA analysis produced three factors that cumulatively explained 71.44% of the variance in turtle behavior, with the first factor (FAC1) accounting for 25.12% of the variance, the second factor (FAC2) accounting for 25.08% of the variance and the third factor (FAC3) accounting for 21.24% of the variance. Based on the categories defined by Réale et al. (2007), we identified FAC1 as exploration, FAC2 as boldness, and FAC3 as aggression.

Boldness scores were correlated with aggression scores (Spearman's $\rho = 0.47$, $p = 0.02$, $n = 23$), but bivariate correlations were not statistically significant between exploration and boldness ($\rho = -0.01$, $p = 0.95$, $n = 23$) or exploration and aggression ($\rho = 0.08$, $p = 0.70$, $n = 23$). For exploration, 10 turtles (43.48%) had positive scores and 13 turtles (56.52%) had negative scores. For boldness, 12 turtles (52.17%) had positive scores and 11 turtles (47.83%) had negative scores. Finally, six turtles (26.09%) had positive scores and 17 turtles (73.91%) had negative scores for aggression. **Figure 2** presents a scatterplot of the factor scores for the 23 turtles.

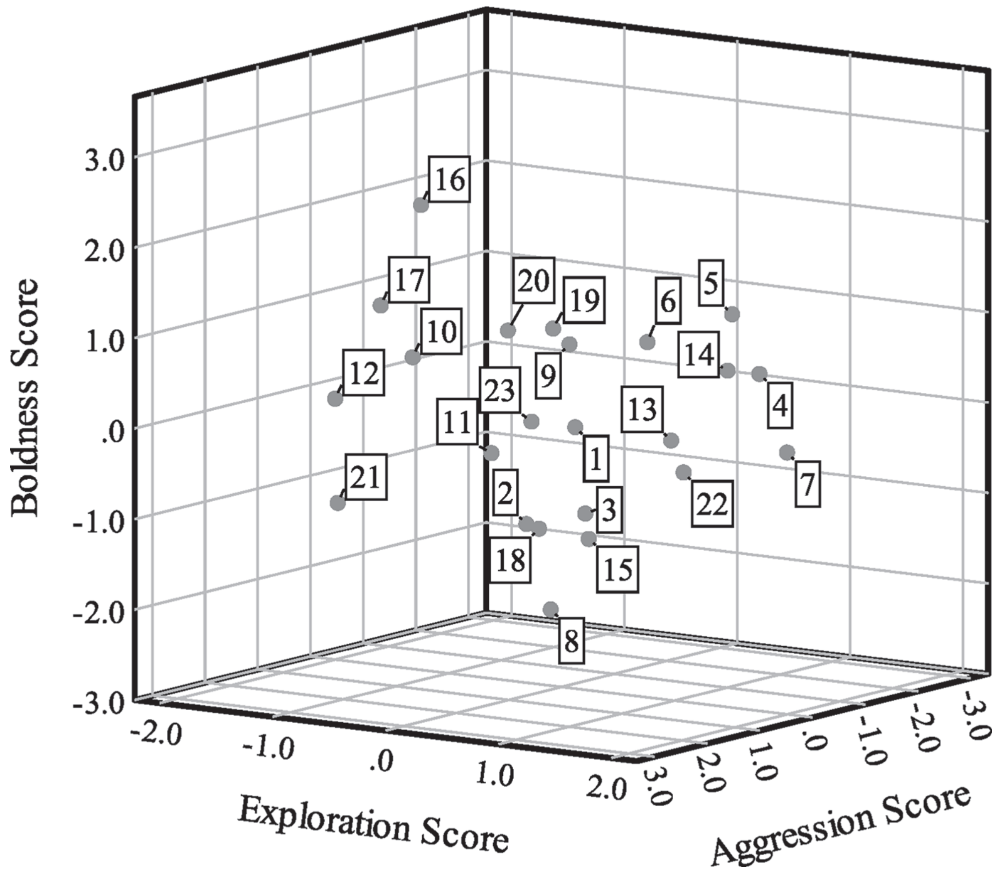

FIGURE 2 | Scatterplot of factor analysis scores showing exploration (factor 1) scores on the x-axis, boldness (factor 2) scores on the y-axis and aggression (factor 3) scores on the z-axis for $n = 23$ Blanding's turtles. Cases are labeled by turtle number.

Personality Type, Post-release Behavior, and Microhabitat Selection

At the end of the tracking period in 2015, 14 turtles were alive and being tracked, while one turtle was confirmed dead and eight individuals were missing or of unknown status. Turtles with lower exploration scores were more likely to be dead or missing (**Figure 3**), but boldness and aggression scores did not predict survival status in the mixed model (**Table 3**). The model predicted that for every unit increase in exploration score, a turtle was about four times more likely to be alive for 2 years after release.

High aggression scores were significantly associated with lower mass 1 year after release (**Table 3**). However, the most significant predictor of mass at the 1-year mark was mass at release [$F_{1,15} = 73.53$, $p < 0.001$; $b = 1.18$ (0.88–1.47)], and turtles that were heavier at release were heavier 1 year later as well. There was no significant interaction between aggression score and body mass at release ($F_{1,5} = 1.08$, $p = 0.345$) or between release mass and the other personality factor scores. Additionally, there was no relationship between average body mass (for both years) and survival status at the end of the study period ($\rho = 0.13$, $p = 0.54$, $n = 23$).

Turtle movement patterns were impacted weakly by personality variables (**Table 3**). There was a trend for turtles with higher exploration scores to travel greater distances, as measured by the straight line distance between tracking points (**Table 3**). Turtles with high (positive) exploration scores had home range sizes about twice those of turtles with low (negative) exploration scores, with a mean MCP estimate of 15,333.42 ± 8,033.71 (standard error) m^2 for turtles with positive exploration scores and a mean MCP of 7,782.88 ± 2,334.15 m^2 for turtles with negative exploration scores. However, this difference was not significant in the mixed model analysis (**Table 3**).

Turtle behaviors during tracking events varied with factor scores (**Table 3**). Initial analyses showed there was a very strong relationship between aggression score and finding the turtles on land, with more aggressive turtles more often observed on land [$F_{1,19} = 6.24$, $p = 0.02$, exp $(b) = 11.75$ (1.49–92.71)]. However, the high coefficient prompted further inspection of the data, which suggested that one individual (turtle 2), who had the highest individual score for aggression (2.69) and the fourth highest score for the proportion of tracking events on land (0.07), was largely driving this pattern. The relationship between behavior on land and aggression score was no longer statistically significant when this outlier was removed (**Table 3**). There was no relationship between exploration or boldness score and behavior on land, whether or not turtle 2 was included in the model. Interestingly, turtles more often observed on land were less likely to be alive at the end of the tracking period ($\rho = -0.50$, $p = 0.02$, $n = 23$); however, this pattern does not seem to have been driven by turtle 2, which was alive at the end of the tracking period. Additionally, excluding turtle 2 from models did not significantly change the outcomes for any of the other behavior variables, so turtle 2 was retained in these models. More aggressive turtles were more likely to be found basking (**Table 3**), but aggression scores did not predict any other behavioral variables.

Turtles with higher exploration scores were less likely to be observed underwater and more likely to be observed basking compared to those with lower exploration scores (**Table 3**). Turtles with higher boldness scores were much less likely to be found underwater, and there was a trend for more bold turtles to be observed more at the water surface (**Table 3**). There were no significant relationships between any of the factor scores and the frequency of observing turtles swimming.

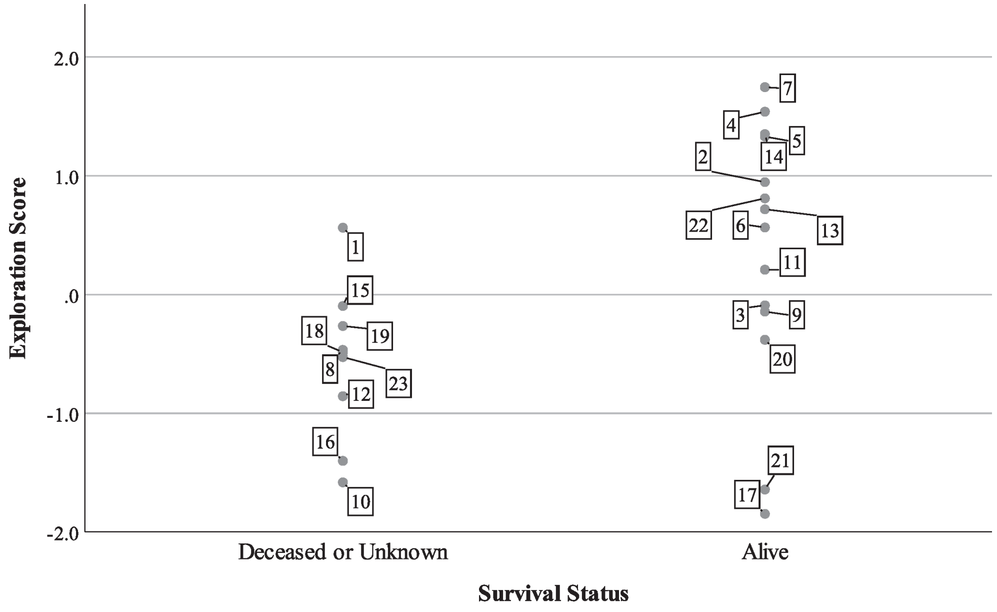

FIGURE 3 | Survival status of $n = 23$ Blanding's turtles 2 years after reintroduction compared to exploration factor scores. Cases are labeled by turtle number.

TABLE 3 | Relationships between personality scores and variables related to post-release condition, behavior, and microhabitat selection.

Outcome variable	Exploration (FAC1)	Boldness (FAC2)	Aggression (FAC3)
Survival status (binary)	$F_{1,19} = 3.67$ $p = 0.07$ exp (b) = 4.14 (0.88–19.57)	$F_{1,19} = 0.27$ $p = 0.61$	$F_{1,19} = 0.15$ $p = 0.71$
Body mass 1 year after release (g)	$F_{1,14} = 0.35$ $p = 0.565$	$F_{1,14} = 0.06$ $p = 0.82$	$F_{1,15} = 5.565$ **$p = 0.03$** $b = -5.39$ (–10.27 - -0.51)
MPC home range area (m^2)	$F_{1,17} = 0.52$ $p = 0.48$	$F_{1,17} = 0.04$ $p = 0.84$	$F_{1,17} = 0.01$ $p = 0.925$
Total straight line distance traveled between tracking points (m)	$F_{1,39} = 3.01$ $p = 0.09$ $b = 78.145$ (–13.00–169.29)	$F_{1,38} = 0.62$ $p = 0.44$	$F_{1,35} = 0.004$ $p = 0.95$
Count of tracking points on land*	$F_{1,14} = 1.13$ $p = 0.31$	$F_{1,15} = 0.29$ $p = 0.60$	$F_{1,18} = 2.49$ $p = 0.13$
Count of tracking points basking	$F_{1,16} = 7.925$ **$p = 0.01$** exp (b) = 1.53 (1.11–2.11)	$F_{1,18} = 2.09$ $p = 0.165$	$F_{1,18} = 5.74$ **$p = 0.03$** exp (b) = 1.44 (1.05–1.99)
Count of tracking points at water surface	$F_{1,19} = 2.71$ $p = 0.12$	$F_{1,19} = 3.78$ $p = 0.07$ exp (b) = 1.22 (0.985–1.515)	$F_{1,19} = 1.91$ $p = 0.18$
Count of tracking points swimming	$F_{1,18} = 1.355$ $p = 0.26$	$F_{1,19} = 1.31$ $p = 0.27$	$F_{1,18} = 0.79$ $p = 0.385$
Count of tracking points underwater	$F_{1,18} = 4.955$ **$p = 0.04$** exp (b) = 0.955 (0.915–1.00)	$F_{1,19} = 10.87$ **$p = 0.004$** exp (b) = 0.93 (0.88–0.97)	$F_{1,18} = 0.002$ $p = 0.96$
Count of tracking points in cattails	$F_{1,19} = 5.08$ **$p = 0.04$** exp (b) = 0.86 (0.75–0.99)	$F_{1,19} = 0.86$ $p = 0.365$	$F_{1,19} = 0.40$ $p = 0.54$
Count of tracking points in lowland forest*	$F_{1,18} = 1.06$ $p = 0.32$	$F_{1,19} = 3.38$ $p = 0.08$ exp (b) = 0.50 (0.23–1.10)	$F_{1,19} = 1.10$ $p = 0.31$
Count of tracking points in muskrat dens	$F_{1,18} = 3.11$ $p = 0.095$ exp (b) = 1.59 (0.915–2.75)	$F_{1,17} = 6.37$ **$p = 0.02$** exp (b) = 2.21 (1.14–4.30)	$F_{1,18} = 1.64$ $p = 0.22$
Count of tracking points in willow	$F_{1,16} = 2.06$ $p = 0.17$	$F_{1,16} = 4.695$ **$p = 0.046$** exp (b) = 1.41 (1.01–1.96)	$F_{1,16} = 0.10$ $p = 0.76$
Count of tracking points in open water	$F_{1,17} = 3.96$ $p = 0.06$ exp (b) = 0.48 (0.22–1.04)	$F_{1,17} = 5.02$ **$p = 0.04$** exp (b) = 2.00 (1.04–3.85)	$F_{1,18} = 0.05$ $p = 0.82$

*Results show tests of fixed effects in generalized liner mixed models. Fixed parameter estimates (followed by 95% confidence intervals in parentheses) are included for results that were significant (in bold, $p < 0.05$) or trended toward significance ($0.05 \leq p < 0.1$). Exponentiated coefficients are presented for binomial and count variables. Body mass at release significantly predicted body mass 1 year after release and was included as a covariate in the body mass model.*Count of tracking points on land (behavior) and in lowland forest (microhabitat) were analyzed with one outlier excluded (turtle 2), who had the highest factor score for aggression. Turtle 2 also had the highest score for use of lowland forest and the fourth highest score for being observed on land.*

Turtle microhabitat usage also showed relationships with personality scores (**Table 3**). As with behavior on land, initial models showed that turtles with high aggression scores were much more likely to be located in lowland forest [$F_{1,18} = 17.61$, $p = 0.001$, exp (b) = 12.0 (3.45–41.67)]. Again, the high coefficient prompted further inspection of the data, which suggested that turtle 2 was having a large impact on this result as well. In this case, turtle 2 not only had the highest aggression score but also the highest proportion of tracking events located in lowland forest (0.75) of all the turtles. Excluding this individual, the model for lowland forest did not show a significant relationship with aggression score (**Table 3**). However, it is worth noting that despite turtle 2's relatively moderate exploration score (0.95), when this turtle was included in the model, the relationship between exploration score and lowland forest use attained statistical significance, showing that turtles with higher exploration scores utilized lowland forest less frequently [$F_{1,17} = 8.17$, $p = 0.01$, exp (b) = 0.24 (0.08–0.69)]. There were no other microhabitat variables that were significantly related to turtle aggression score, whether or not turtle 2 was retained in the models. Retaining turtle 2 in the models also had minimal effects on fixed effects or parameter estimates related to exploration or boldness scores and usage of other microhabitats; therefore, turtle 2 was utilized in analyses for all the other microhabitat types.

Turtles with higher exploration scores were less likely to be found in cattails and showed a trend to use open water less. However, more exploratory turtles were more likely to be found in muskrat dens (**Table 3**). Bolder turtles showed a trend to use lowland forest less. However, they were more likely to be found in open water and areas dominated by willow trees and much more likely to be found in muskrat dens compared to peers with lower boldness scores (**Table 3**).

Microhabitat preferences also showed some relationships with survival (alive or missing/dead) after 2 years. Turtles that were observed in open water a greater proportion of the time were less likely to be alive at the end of the study period ($\rho = -0.54$, $p = 0.01$, $n = 23$). Turtles that spent more time in willow habitat showed a trend towards a decreased likelihood of survival as well ($\rho = -0.36$, $p = 0.095$, $n = 23$). In contrast, there was a positive relationship between the percent of time the turtles were found near muskrat dens and the likelihood of survival ($\rho = 0.47$, $p = 0.02$, $n = 23$).

DISCUSSION

As hypothesized, the Blanding's turtles in this study displayed behavioral responses to modified open field tests indicative of distinct personality traits: exploration, boldness, and aggression. Additionally, the personality traits were correlated differently with survival and behavior patterns when the turtles were released into the Shiawassee National Wildlife Refuge.

Personality Traits

The 23 turtles that underwent behavioral tests were rated on three identified continuums: less to more exploratory, less to more bold, and less to more aggressive. Ten of the turtles showed high exploration, 12 showed high levels of boldness and six showed high aggression. We utilized variations of the open field test to assess these personality traits and selected behaviors for analysis that were reported to reflect these personality traits in previous research (Réale et al., 2007). However, one limitation of our approach was that the number of behaviors we could include in the EFA was constrained by the small sample size. There is a possibility, therefore, that our results could have differed based on the behaviors we selected. For example, we expected that rates of retracting into the shell in the presence of a predator would likely reflect boldness. However, this behavior had a poor ICC value, meaning that individual turtles did not perform it consistently in this context, so we were unable to use it in the factor analysis. The turtles did not obviously direct any behaviors towards the raccoon, so it is possible that they saw the toy raccoon as a novel object rather than a potential predator. If this was the case, the responses in this test could reflect exploration rather than boldness (Réale et al., 2007). However, it is worth noting that the same behaviors (moving percentage, surfacing rate, and percent of food consumed) clustered with exploration when measured in the simple open field and food tests, but the *differences* in these behaviors between the food and predator tests clustered on a different factor—which we identified as boldness. This pattern suggests that the turtles did perceive a meaningful difference between the food and predator tests. The use of multiple measures has been advocated for (Carter et al., 2012), and perhaps future studies could include additional measures to help more definitely identify separate personality traits.

An additional limitation of our experiment is that the four open field tests were always conducted in the same order. For example, turtles that consumed food faster in the predator test (test four) than the food test (test three) may have simply habituated to the experiment, rather than truly showing boldness under threat of a predator attack. We are also unable to account for the habituation and learning processes that would likely occur over the three repetitions of the experiment. We controlled for this by using behaviors with high repeatability in our analysis, but it is possible that order effects and/or habituation could have influenced our results. Despite these limitations, the strong relationships we found between the personality assignments based on the captive tests and the behavior of the turtles after release suggest that the EFA uncovered meaningful individual differences in the turtles' personalities.

Personality and Survival

One year post-release, 14 of the turtles were confirmed to be alive. The turtles' survival was correlated with tendency to explore, with less exploratory turtles more likely to be dead or missing. Similar effects of exploration on survival were found in juvenile desert tortoises (*Gopherus agassizii*, Germano et al., 2017). Neither boldness nor aggression was correlated with survival. Boldness in particular has been found to impact survival positively in other species (e.g., Trinidadian guppies, *Poecilia reticulata*, Smith and Blumstein, 2010; European mink, *Mustela lutreola*, Haage et al., 2017). Contrastingly, boldness was found to decrease survival in reintroduced swift foxes (*Vulpes velox*, Bremner-Harrison et al., 2004), brushtail possums (*Trichosurus vulpecula*, May et al., 2016), and juvenile largemouth bass (*Micropterus salmoides*, Ballew et al., 2017). Carter et al. (2016) found no effect of personality on survival in hatchling red-eared sliders (*Trachemys scripta elegans*). Such findings highlight the need to evaluate the influence of personality at the species level.

More exploratory turtles were also found to have higher body mass, which could be reflective of their ability to locate resources more readily, although in brushtail possums, this was linked to boldness rather than exploration (May et al., 2016). Body mass was not correlated with bold or aggressive traits in this study. Although we found a correlation between exploration and survival as well as body mass, survival and body mass were not correlated. Studies involving other species did find that body mass and survival were linked (Biro and Stamps, 2010; Paterson et al., 2014; Kelleher et al., 2018). This lends support to the impact of personality on survival in these turtles. In other studies, correlations were also found between sex and survival. The sex of the turtles in this study was not determined prior to release, and we therefore cannot make any comparisons based on this factor.

Personality and Movement

Turtles that rated higher in exploration traveled longer distances post-release. These individuals may have therefore moved to safer or more resource-rich areas, increasing their survival rates. Dingemanse et al. (2003) found that great tits (*Parus major*) did the same. Neither boldness nor aggression were predictors of travel distance. Aggression was associated with dispersal tendency in delicate skinks (*Lampropholis delicata*), but exploration was not (Michelangeli et al., 2017). The underlying mechanism for this tendency could include that more aggressive or bold individuals suppress dispersal in others (Michelangeli et al., 2017). More exploratory wild burbot (*Lota lota*) showed higher rates of movement and larger home ranges (Harrison et al., 2014). Larger home ranges may enable an individual animal to exploit more resources, resulting in more successful individuals.

When hatchling red-eared sliders were monitored after being reintroduced, personality was not found to affect dispersal (Carter et al., 2016). Germano et al. (2017) also found no effect of personality on dispersal in juvenile desert tortoises. However, tendency to travel may also result in non-random distributions of animals with particular personality types. The implications for this include biased population trends that could be more susceptible to environmental changes.

Home range size was not found to differ based on personality type. Although this correlation has been seen in other species (wild burbot, Harrison et al., 2014; brushtail possums, May et al., 2016), these Blanding's turtles may have benefitted from the types of resources found within their home range but not adjusted the size of their range based on the quality of those resources. Pressure or competition from neighboring individuals may have impacted some turtles' abilities to expand their home range or move into better habitats.

Personality and Habitat Use

Based on use versus availability, these turtles displayed personality-dependent habitat selection, which was influenced by the inclusion of particular features. These preferences may have, in turn, impacted turtle survival. None of the turtles were more likely to be found in lowland forest areas. This type of habitat was used less than would be predicted based on availability. In a study of hatchling Blanding's turtles, Paterson et al. (2012) found that once the turtles moved from terrestrial to aquatic habitats, they tended to remain there. As these turtles were all reproductively immature, using habitat related to travel and access to nesting sites may be less important. Open water was correlated with decreased survival. Interestingly, turtles that scored higher on the boldness scale before release were more likely to be found in open water than other turtles. Fewer resources are available in open water, and this type of space offers little protection from predators. The greater use of open water by bolder turtles in this case could represent a preference antithetical to survival, which is consistent with the finding in other studies that boldness can inhibit survivorship, as in swift foxes (Bremner-Harrison et al., 2004). Open water was also avoided by Blanding's turtles in a previous study (Millar and Blouin-Demers, 2011) but was actually preferred in another (Ross and Anderson, 1990). Other pressures may affect habitat preferences in different populations.

Cattails were found to be a preferred habitat feature, and as such, all turtles utilized it, showing no differences in personality type. More woody vegetation was also preferred by hatchling Blanding's turtles in the study by Paterson et al. (2012). For these turtles, bolder individuals were more likely to be found in areas with abundant willow, which was also related to lower rates of survival. Starking-Szymanski et al. (2018) found that overall, the released turtles used this type of habitat less than would be predicted based on availability, suggesting that although willow may provide cover, it may not be a beneficial resource in other ways. Hatchling Blanding's turtles were more likely to survive when in more structurally complex habitats, such as swamps and marshes, which contain large amounts of vegetation (Paterson et al., 2014). Bogs and wetlands have been found to be preferred by Blanding's turtles in many cases (for review, see Markle and Chow-Fraser, 2014). It may be that a preference for abundant vegetation overrides selection of more beneficial types of vegetation for some personality types. However, the habitat features/types used to monitor these turtles after reintroduction do not match up perfectly with descriptions used in other studies of Blanding's turtles and therefore, habitat use comparisons may be affected as a result.

Muskrat dens were used more than expected based on availability (Starking-Szymanski et al., 2018), and use of this feature was correlated with increased survivorship, as seen in juvenile desert tortoises using burrows (Germano et al., 2017). Exploratory and bold turtles were more likely to be found in muskrat dens, and they could have been more willing to enter the dens or more efficient at locating them during their movements. The dens may provide protection from predators, leading to higher survival rates for some of these individuals. These data highlight some of the complexities of linking personality to survival; for example, bolder turtles were more likely to use one type of habitat related to increased survival (muskrat dens) but also preferred another habitat type (open water) related to decreased survival.

Personality and Post-release Behavior

There were also differences in behavioral tendencies based on the personality type. Bold turtles were more likely to be found at the water surface, suggesting a willingness to surface more readily. This could also be considered a type of basking behavior (McGinnis, 1968; Moll and Legler, 1971). However, aggressive and exploratory turtles were more likely to be found basking out of water, although bolder turtles were not. This is contrary to bold eastern box turtles (*Terrapene ornata*) that maintained higher body temperatures (Kashon and Carlson, 2018) and bold male Namibian agama lizards (*Agama planiceps*) that basked more (Carter et al., 2010). If bold turtles in this case are basking in the water, as indicated by time spent at the water surface, the findings of this study do fit into previous work and highlight the importance of different habitat types for important thermoregulatory behaviors that may be utilized by different personality types. Basking promotes a number of health parameters in ectotherms. Male Spanish terrapins (*Mauremys leprosa*) infected with *Hepatozoon* were more likely to be found basking (Ibáñez et al., 2015). Basking, however, is a more vulnerable position from a predation standpoint. Kashon and Carlson (2018) also found that eastern box turtles displaying higher body temperatures also tended to have more injuries to their shells. There may, therefore, be a trade-off between risk and other factors affecting physiological health. This could be manifested differently between personality types.

As more exploratory turtles were more likely to be found basking, their exposure to predators may also be higher. Convict cichlids (*Amatitlania nigrofasciata*) that spent more time exploring and searching for food were slower to respond to predators (Jones and Godin, 2010). The trade-off between access to resources and potential for predation is an important aspect of personality traits. Although we cannot predict the predator response of more exploratory turtles based on the results of our study, the fact that they are more likely to put themselves in a vulnerable position may also be linked to predation rates. However, less exploratory voles (*Microtus rossiaemeridionalis*) experienced higher predation after being reintroduced (Banks et al., 2002). Consistent impacts should not be assumed when considering how personality affects reintroduced animals.

Implications for Reintroduction Programs

Understanding how personality affects behavior and survival post-release can be a critical tool for improving reintroduction success. Environmental pressures, including predation, differ between locations, and reintroduced or translocated animals displaying different personality traits may be affected differently. Aggression and boldness are reflective of a proactive coping style (Koolhaas et al., 2007), and these individuals tend to be more successful in stable environments with highly predictable situations (Koolhaas, 2008). Individuals with a more reactive coping style perform better under variable conditions. As individuals differ in their behavioral responses and habitat use, selection of release sites that result in higher likelihoods of survival for a variety of personality types is important. Animals that are less successful in one context may do better in another (Watters and Meehan, 2007). Additionally, individuals display substantial differences in their level of behavioral plasticity (Dingemanse and Wolf, 2013) and thus may not readily adapt to changes in the environment.

One way to safeguard against this type of event would be to release animals representing multiple personality types into all release sites. While this may help at the population level, it will also likely result in negative experiences, including suffering and death, for some of the reintroduced individuals. Acknowledging that not all individuals will fare equally well is also the rationale behind the recommendation to release large numbers of individuals [e.g., Association of Zoos and Aquariums (AZA), 1992; International Union for the Conservation of Nature (IUCN), 2013]. This is a welfare compromise, and the underlying ethical issues still need to be more fully addressed by everyone involved in reintroduction programs. Additionally, especially for species with slower maturation rates or lower reproductive output, each individual has important implications for the success of the species as a whole. If matching individuals with particular personality traits with release sites in which they can be more successful increases survival rates, both the individual animals and the overall populations benefit. Determining personality types present within a conservation breeding population and how those personality traits relate to survivorship should therefore be a consideration within reintroduction programs.

Zoo Animal Welfare Science and Conservation Initiatives

Increasing overall species survival in reintroduction programs necessitates ensuring that individuals being reintroduced have high survival rates. One could consider this a blurring of individual animal welfare and population or species welfare. Animal welfare science focuses on identifying factors that affect individual animals in captive settings, and many of these factors, such as response to stress and environmental change, also impact animals in the wild. Swaisgood (2010) and Harrington et al. (2013), among others, have advocated for better integration between conservation action and welfare science.

A specific area of animal welfare science that has demonstrated potential as a tool for increasing reintroduction program success is the use and evaluation of enrichment in animals designated for release (Watters and Meehan, 2007; Coelho et al., 2012). Enrichment, when properly designed and implemented, can stimulate a variety of species-appropriate behaviors, such as foraging and investigation. It can also provide varying levels of challenge for animals, which may be lacking in some captive settings (Meehan and Mench, 2007) and may help them cope with the conditions they face post-release. This survival skill-building can improve the success of reintroduction programs (Reading et al., 2013).

Additional tools and methods used by animal welfare scientists should be incorporated into reintroduction programs. Handling and housing animals in ways that minimize stress and exposing captive-bred animals to challenges that may prepare them for wild conditions are potential tools (Fraser, 2010). Overall improvements in captive conditions that promote the development of species-appropriate behaviors and reduce stress and disease can also contribute to effective conservation breeding programs (Greggor et al., 2018). It has also been encouraged to make released animals more comfortable in their release sites, based on the natal habitat preference induction phenomenon (Stamps and Swaisgood, 2007).

Linking *in situ* and *ex situ* conservation initiatives is becoming more common (Minteer and Collins, 2013). Captive breeding programs that release animals back into natural habitats are one example and may be the one practical short-term option to combat declining numbers for some species (Conway, 2011). An increase in the contribution of captive-bred animals by zoos to conservation initiatives has been recommended (Brichieri-Colombi et al., 2019). Collaborations between zoos and other entities involved in conservation programs has also been encouraged, including through the One Plan approach (Barongi et al., 2015). This presents zoo animal welfare scientists with the opportunity to contribute to *in situ* conservation efforts. Utilizing approaches that improve the welfare of individual animals within conservation contexts can better achieve goals of both fields. As suggested by Beausoleil et al. (2019), this could result in a more robust and inclusive field of conservation welfare.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the University Committee for the Use and Care of Animals from the University of Michigan-Flint and the Senior Leadership in Animal Welfare and Management Committee from the Detroit Zoological Society.

AUTHOR CONTRIBUTIONS

SA, LT-W, MS, and TY-N contributed to the conception and design of the study. SA, LT-W, and MS collected the data. GF performed the statistical analysis. SA and GF wrote the manuscript. All authors contributed to the manuscript revision, read, and approved the submitted version.

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