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JZAR Review article

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Research article

Current directions in animal enclosure use studies

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Keywords:
enclosure use, exhibit design, Electivity Index, Spread of Participation Index

Article history:
Received: 10 Sep 2017
Accepted: 5 Sep 2019
Published online: 31 Jan 2020

Abstract

Post Occupancy Evaluation is a powerful assessment tool for zoo and aquarium enclosure design, which incorporates animal enclosure use as a key component. Many authors suggest that naturalistic enclosures are valuable for animals, but objective analysis is required to support this statement. Studies of animal enclosure use have become prevalent in published literature, and these studies are often used to quantify the effects of enrichment, enclosure modifications and changes in animal social grouping. Several assessment techniques are available, including zone occupancy, traditional and modified Spread of Participation Index (SPI) and Electivity Index. Many studies also incorporate measures of behavioural diversity and stereotypy prevalence to support enclosure use findings. Given the variety of methods accessible to researchers, there is a need to evaluate which indices are most appropriate for different exhibit types and species. This review revealed a bias toward mammals as subjects for enclosure use studies, though studies have also been initiated for birds and fish. Traditional SPI and zone usage are well represented in published studies as measures of enclosure suitability. By contrast, fewer published studies have used modified SPI, or Electivity Index, which allows enclosures to be analysed based on their biological resources. Several influential studies combined behavioural analyses with SPI measurements to best understand animal enclosure use. Future directions in enclosure use may include the evaluation of thermal or ultra-violet zones for herptiles, depth-based zones for aquatic species, and effects of visitors on zone use.

Introduction

Post Occupancy Evaluations (POE) were originally designed to assess the functionality and use of industrial buildings, but their application to zoos and aquariums is now widely recognised (Kelling and Gaalema 2011). In zoos, these evaluations are used to determine the value of existing enclosures for all stakeholders (Lukas and Ross 2014). As such, the typical POE is comprised of an evaluation of visitor opinions and dwell time (Wilson 2003), functionality for staff, and animal perspectives (Lukas and Ross 2014). A vital component of POE in the zoo, therefore, is assessment of animal behaviour and enclosure use.

Enclosure use studies have been prevalent in zoo research for at least 30 years (Hedeen 1982; Traylor-Holzer and Fritz 1985; Shepherdson et al. 1993; de Vere 2018). In their broadest sense, these studies assess an animal's use of exhibit zones and resources (Mountadouin et al. 2005; Rose and Robert 2013), the effect of enclosure modifications (Lyons et al. 1997), enclosure rotations (White et al. 2003), or inclusion of enrichment (Clark and Melfi 2012). Studies investigating exhibit use in zoo animals have allowed for informed evidence-based management decisions to be made, helping keepers to redevelop areas avoided by animals (Rendle et al. 2018). Given the level of interest and diversity of zoo animal enclosures across the globe, a range of enclosure use measures have been developed (Plowman 2003; Ross et al. 2013). Some methods of enclosure assessment are highly applicable to specific taxa and enclosure types, and recent advances have allowed researchers to better understand the use of different biological resources by animals (Plowman 2003). Given the diversity of species, enclosure types and methods of evaluation that are now available in published literature, a review of enclosure use assessment techniques is timely and relevant.

To identify published literature on enclosure use, the archives for Zoo Biology, Applied Animal Behaviour Science, Der Zoologische Garten, International Zoo Yearbook and the Journal of Zoo and Aquarium Research were reviewed. These journals regularly publish zoo- and aquarium-based research. Papers investigating zoo and aquarium enclosure use were identified through use of the search terms: Enclosure use, Space use and the specific terms Spread of Participation Index and Electivity Index. Papers were excluded if there was no mention of enclosure use assessment in their title, key words or abstract. The archives were searched from 1960 to 2019.

History of enclosure use studies

The interaction between a captive animal and its environment has long been an area of interest for zoo professionals. Discussion of enclosure design and its implications for zoo animals date back to the work of Hediger (1964), who discussed the relevance of naturalistic enclosures. There is consensus among researchers and keepers that zoo enclosures should provide opportunities for species to express natural behaviours (Rose and Robert 2013; Mallapur et al. 2005).

Newly constructed enclosures must satisfy not only the needs of animals, but also requirements for health and safety, zoo staff access, marketing and education (White et al. 2005). Exhibits are often built with a view to educating or perhaps even inspiring visitors, as Conway (1968) discusses in his seminal paper on exhibiting bullfrogs. Naturalistic enclosures, aiming to replicate aspects of a species' wild habitat, are becoming more prevalent in zoos worldwide (Stempell et al. 2007). However, it is important to determine whether animals make use of the resources that are provided to them (Tan et al. 2013). A naturalistic enclosure may be of limited use if the inhabitants cannot engage in species-specific behaviour, or if the animals actively avoid much of the exhibit (Hediger 1964; Blount and Taylor 2000).

While many aspects of zoo enclosure design were well developed by the mid twentieth century (Morris 1960), there were limited tools available to determine whether the animals used their exhibits well. In modern collections, there are now several objective methods for measuring both behaviour and enclosure utilisation. These allow researchers to measure the impact of changes to husbandry routine (Ross et al. 2009), or the effectiveness of enrichment (Pochon 1998; Breton and Barrot 2014).

Many recent studies have indirectly measured the suitability of animal exhibits by measuring the prevalence of stereotypy (Montaudouin and Le Pape 2005; Clubb and Mason 2007) and behavioural diversity indices (Troxell-Smith and Miller 2005). These measures, when in combination with measurements of enclosure use, have allowed researchers to further evaluate exhibit relevance and animal welfare between facilities or enclosures (Ross et al. 2011).

Melfi's (2009) study on zoo research output identified that some taxonomic groups such as big cats, primates and elephants have received greater publication focus. Conversely, taxa such as birds and fish are well represented in zoo collections, yet publications on these animals are comparatively fewer (Briek et al. 2018; Rose et al. 2018a). To the author's knowledge, there is no current review available on enclosure use techniques for zoo animals. The purpose of this review is twofold. First, the most common techniques used in enclosure use studies are to be evaluated, and their relevance for a range of studies will be discussed. Second, the paper aims to quantify which taxa are most commonly included in enclosure use studies in zoological collections.

Methods of measuring enclosure use

Zone Occupancy

Zone occupancy or zone use is the most commonly used technique in enclosure use studies; it is also the study method with the greatest amount of variation (Noguiera 2004; Brien et al. 2016). In order to conduct a zone occupancy study, an animal's enclosure must be categorised into zones. These zones may be of unequal sizes, and the enclosure can be categorised into as many, or as few, zones as the researcher wishes (Schultz and Young 1998). For example, Leeds et al. (2016) categorised their black footed cat (F*elis nigripes*) enclosure into only two zones: off show and on show, whereas Noguiera (2004) separated a capybara (*Hydrochoerus hydrochaeris*) enclosure into several zones including water pool, feeding areas and shelters.

The zone categorisation process can be tailored to the research question. For example, Schultz and Young (1998) investigated the effect of human presence on captive coyote (*Canis latrans*) welfare. In order to determine whether coyotes were avoiding the public, they created zones based on their proximity to the enclosure fence. Briek et al. (2018), in their study of American paddlefish (*Polyodon spathula*) feeding strategies, used water depth to segregate their exhibit into zones.

Once an exhibit has been zoned, observations are undertaken for animal inhabitants. The location of each animal is stated, normally using a standardised method such as instantaneous sampling (Mechkour et al. 2008). For groups of animals where identification of individuals is not possible, a scan sample method may be used (Rose et al. 2018). Historically, observations have been undertaken by an observer (Veado 1997; Young 1998); however, novel approaches have been undertaken in more recent studies (Leighty et al. 2010). For example, Rowell (2014) used a camera footage and a grid overlay system to plot the location of individual Asian elephants (*Elephas maximus*). Furthermore, Leighty et al. (2010) used Global Positioning Service (GPS) data from trackers on African elephants (*Loxodonto africana*) to identify their zone location, and Blowers et al. (2012) used Arcview to map the position of individual hippos (*Hippopotamus amphibius*) in a large exhibit. Both camera footage and tracker data could be practical for future studies (Kreeger et al. 1996); trackers specifically could allow researchers to evaluate the distance travelled per animal per day (Leighty et al. 2010).

Once enclosure use data have been collected for animals, analysis may take place (Mechkour et al. 2008). There is considerable variation in previous studies in the analysis of zone occupancy, with some studies demonstrating their results as percentages of time that each animal spent in each zone (Ganslosser and Brunner 1997; Valuska et al. 2013). Other studies have used zone data to determine the effect of enrichment on enclosure use (Gilkison et al. 1997; Blount and Taylor 2000), effect of visitors (Schultz and Young 1998; Learmonth et al. 2018) or effect of mixed-species exhibits (Dalton and Buchanan-Smith 2005). Data from observations before, during and after enrichment may allow the researcher to conduct statistical tests to determine the impact of the enrichment (Clark and Melfi 2012).

Despite its popularity in published research, zone occupancy has limitations as a measure of enclosure use. For example, zone occupancy does not take into account the size of each respective zone (Horikoshi-Beckett and Schulte 2006). Animals may appear to favour just one enclosure zone, when in fact that zone could be much larger than all other zones (Shepherdson et al. 1993). It is also difficult to determine whether all enclosure zones are being used evenly, or whether some zones are under-utilised (Wheler and Fa 1995). Fortunately, other measures of enclosure use exist, which take into account zone size, or address exhibits at a resource-based level (Ross et al. 2009).

Dickens' (1955) Spread of Participation Index

Spread of Participation Index (SPI) was originally coined by Dickens in 1955 as a method of assessing spatial utilisation of offices for humans (White et al. 2003). Exhibits are broken into zones, and the use of these zones by the animal inhabitants is observed (Ang et al. 2017). The index was first applied to zoo-based studies by Hedeen (1983), who used SPI to assess enclosure use in a group of gorillas (Gorilla gorilla). SPI is routinely used not only within the zoo research sector, but also in labs (Asher et al. 2009; Kistler et al. 2011), and domestic settings (Lindberg and Nicol 1996).

SPI is a measure of an animal's evenness of enclosure use and may be conducted on an individual or colony (Hedeen 1983). In SPI research projects, even use of all enclosure zones is perceived to be a sign of good welfare, as this implies that animals are not actively avoiding any parts of their exhibit (Clark and Melfi 2009). While a common assumption, this may not be true for all species during all seasons. A study on laboratory housing of starlings (*Sturnus vulgaris*) indicated that even enclosure use was associated with impoverished welfare (Asher et al. 2009). In this study, small laboratory enclosures limited starlings in their movement, as the birds with some of the smallest enclosures had little option other than to use all zones.

As a versatile measure of enclosure use, SPI can be used to assess the effects of enclosure modifications or enrichment on zone use (de Vere 2018). For example, Clark and Melfi (2012) used SPI to determine the efficacy of several types of enrichment on sloths (*Choloepus didactylus*), armadillos (*Dasypus novemcinctus*) and bushbabies (*Galago senegalensis*). A trend toward more uniform enclosure use was observed when preferred enrichment devices were provided. In addition, comparisons have been made between enclosure use in empty versus enriched enclosures for zebrafish (*Danio rerio*) and checker barbs (*Puntius oligolepis*) (Kistler et al. 2011). Complementing the findings of previous studies, Kistler et al. (2011) identified that fish used their enclosures more evenly when a diverse, structured enclosure was provided.

Evaluation of rotation exhibit effects on enclosure use have yielded useful implications for zoo animal management (White et al. 2003). Rotation exhibits allow keepers to transfer animals between interconnected enclosures, in order to expose the animals to a changing environment. In a study of five Asian mammal species, White et al. (2003) identified that rotation of animals into different exhibits increased their use of enclosure zones. As animals became accustomed to their new exhibits following a rotation, SPI values became higher and enclosure use became less even.

Several comparative studies have been initiated between related species, such as felids (Lyons et al. 1997). However, care should be taken when comparing differences between species. Animal behaviour change is multifactorial, and effects of enclosure size, husbandry routine, species-specific behaviour and weather must be considered as confounding variables (Ang et al. 2017). With this in mind, carefully designed comparative studies do have the potential to identify suitable enclosure sizes or designs for a range of species.

While SPI has been well established in zoo literature for over 30 years, it is clear that this index still has potential for future studies.

Application of SPI

To conduct a SPI study, animal enclosures should be separated into enclosure zones (Dickens 1955). Enclosure zones may be two dimensional for terrestrial species (measured in square inches, metres or miles), or measured in three dimensions for aquatic species (for examples, cubic metres). When separating an enclosure into zones, it is essential that all zones are of the same size. Separating enclosures into sixths or eighths may therefore be suitable (Hedeen 1983). See Figure 1 for an example enclosure. The formula for Spread of Participation Index is as follows:

$$SPI = (M[nb-na)(Fa-Fb)])/(2(N-M))$$

Here, N is the total number of observations made, M is the average frequency of observations in all zones, and na and nb are the number of zones with frequencies greater or less than M respectively. Similarly, Fa and Fb are the number of observations in zones with frequencies greater than and less than M (Dickens 1955).

Once enclosures have been mapped into zones, observations may take place. These may map the enclosure use of one individual animal, or of a group (Clark and Melfi 2012). When observing animals for SPI studies, repeat observations will need to be taken. For example, observations of enclosure use may take place at one minute intervals for a period of one hour, depending on the species. SPI values may be produced for the summed use of each zone by every animal at the end of each observation period.

SPI generates a score between 1 and 0. A value of 1 refers to highly uneven enclosure use, and 0 suggests perfect proportional use of all enclosure zones (White et al. 2003). Previous studies have compared SPI values between individuals (Lyons et al. 1997), or between species (White et al. 2003). Care should be taken when comparing values between enclosures or species to ensure that methodology remains as similar as possible, and that all factors that may affect enclosure use are considered (Lindberg and Nicol 1996).

Original SPI should be applied to studies in which use of an animal's entire space requires investigating. This index may be used in research in which biological zones are too complex to accurately measure. For example, callitrichids and passerines make use of growing plants and branches in their enclosures; branches and twigs are difficult to measure using other indices (Plowman 2003). Original SPI is also valuable in aquariums, in which tanks could be separated into depths (Kistler et al. 2011).

Plowman's (2003) modified Spread of Participation Index

While Dicken's SPI is used to investigate overall animal enclosure use, it cannot evaluate the use of different biological resources within an enclosure (de Vere 2018). In order to better evaluate the use of individual resources, a new index; SPI, modified for unequal zones, was published by Plowman in 2003.

Modified SPI allows researchers to break enclosures down into biologically unique zones of different sizes, such as ponds, sand or grass substrates. This allows assessment of enclosure resources to take place in addition to overall enclosure use (Pastorino et al. 2017). For example, research by Rose and Robert (2013) identified that in sitatunga (*Tragelaphus spekii*), some individuals used their enclosure unevenly. Further analysis based on zone preference identified that 'river bank' zones containing long grasses and reeds were used more than was expected. This may be linked to *T. spekii*'s wild foraging behaviours; the research may be used to create evidence-based sitatunga enclosures in future.

Further studies have utilised modified SPI to investigate enclosure use for bears (Pastorino et al. 2017), primates (Daoudi et al. 2017) and birds (Rose et al. 2018a, 2018b). There have been advances through the use of SPI to determine individual animal characteristics in enclosure use. A study of bears revealed that some individuals used significantly their enclosures significantly more evenly (Pastorino et al. 2017). Additionally, Rose and Robert's (2013) study revealed that a young male sitatunga used its enclosure less evenly, possibly due to avoidance of conspecifics. Given its ability to determine whether animals

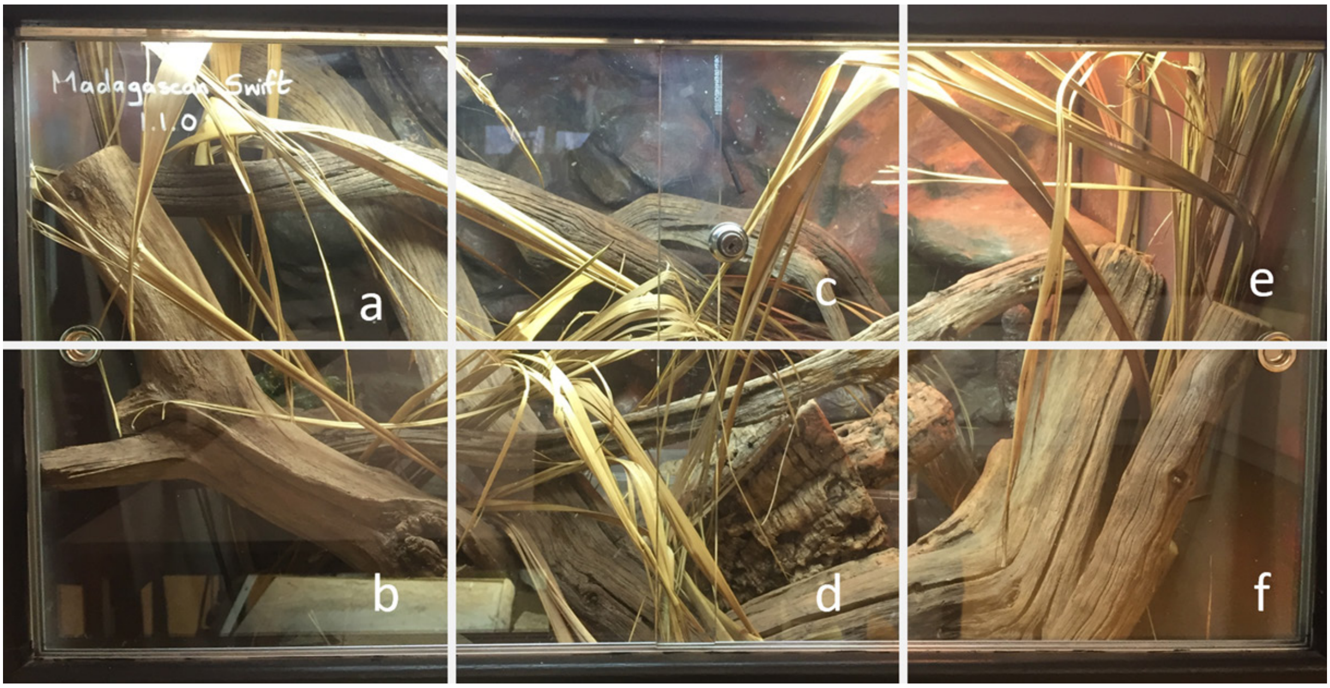

Figure 1. An enclosure for Madagascan swifts (*Oplurus cuvieri*) at Sparsholt College, separated into zones using Dickens' (1955) SPI. All zones should be the same size.

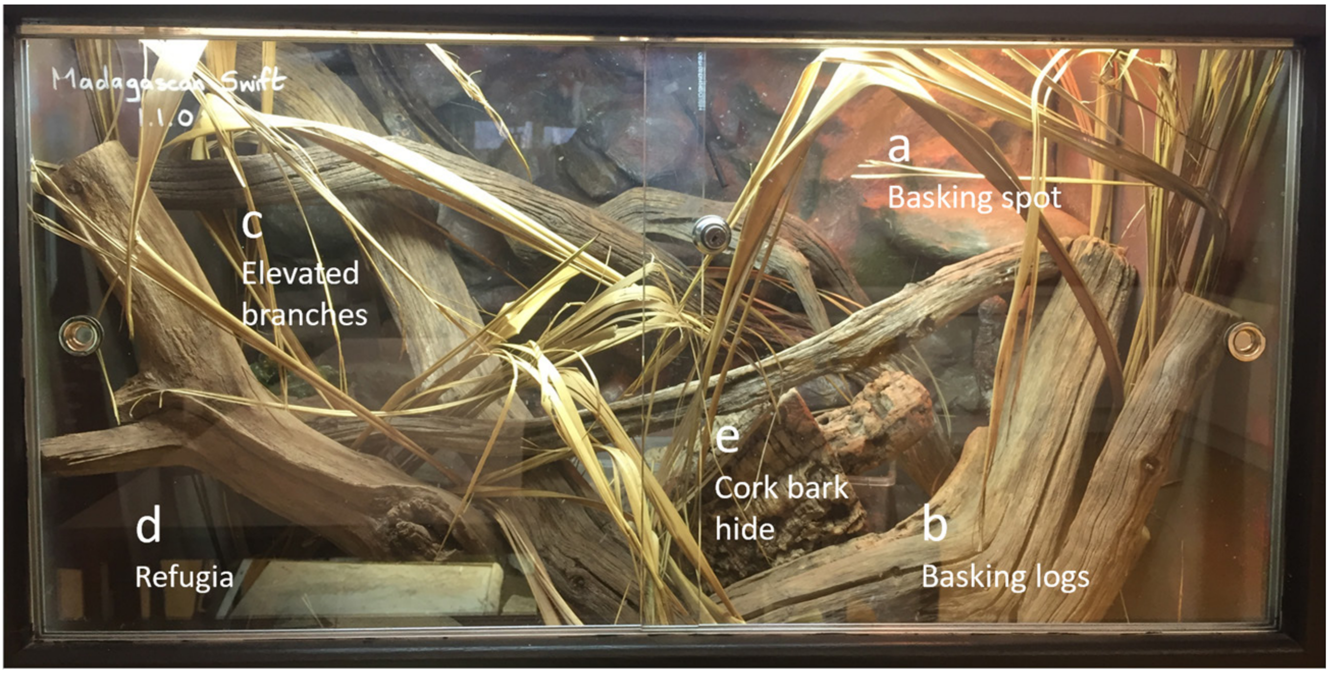

Figure 2. Madagascan swift enclosure categorised into biological zones for modified SPI observations. Zones have different biological functions for the animals. Given that they are different sizes, all zones must be measured as accurately as possible.

actively avoid or prefer specific resources, modified SPI has great potential to identify how use of resources may be improved in future enclosures.

Application of modified SPI

Similar to Dickens' SPI, enclosures must be separated into zones. However, these zones do not have to be of equal size (Plowman 2003). Zones should be categorised based on their biological relevance to the animal. For example, an enclosure might be separated into zones of grass, rocks, water or platforms (Figure 2).

The formula for Plowman's modified SPI is:

$$SPI = (\mid fo\text{-}fe \mid)/(2\ (N\text{-}femin))$$

Here, fo refers to the number of times an animal was observed in a given zone, fe refers to the expected number of times an animal should be seen in a given zone based on its size, and Femin refers to the expected observation value in the smallest one. N refers to the total number of observations taken (Plowman 2003).

Modified SPI, therefore, generates expected observation values based on the comparative size of each enclosure zone (Plowman 2003). Similarly to Dickens' SPI, modified SPI also provides values between 1 (highly uneven enclosure use) and 0 (perfect, even enclosure use). SPI values of 0.3 and below are usually defined as relatively even enclosure use, whereas values above 0.7 are considered to be uneven enclosure use (Daoudi et al. 2017). While this value only refers to the overall use of all enclosure zones, investigations into the expected versus observed use of each zone can be used to interpret resource utilisation.

Modified SPI should be used for projects in which the use of biological resources is of particular interest. For example, the use of ponds or lakes may be identified (Plowman 2003), or the use of different substrates, such as concrete, grass and sand (Rose et al. 2018b). Given that the size of each zone must be measured, modified SPI should not be used for projects where zone sizes are difficult to measure, or where zones regularly change in size. Many large zoo species are highly suitable for this form of enclosure use research.

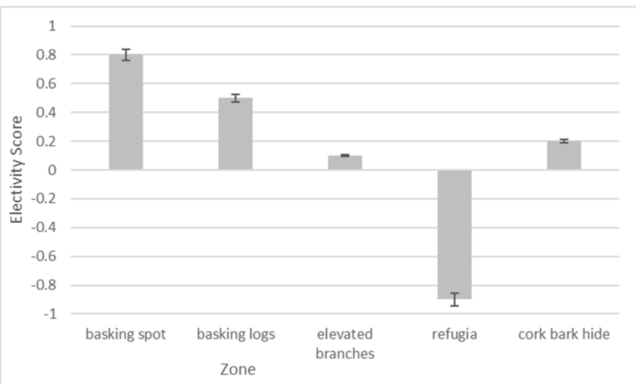

Figure 3. Output from a hypothetical Electivity index study. The graphs shows that the basking spot and basking logs are over-utilised in comparison to their size. The refugia, by contrast, is an underutilised resource, given its electivity score of 0.9. Electivity index takes into account the relative size of each zone, meaning that animals are expected to spend more time in larger zones.

Vanderploeg and Scavia's (1979) Electivity index

Electivity index, as coined by Vanderploeg and Scavia (1979) was originally developed for analysis of resource use by marine organisms. Though commonly applied to a range of wildlife studies, Electivity index has been applied to a handful of zoo studies, including work on Round island skinks (*Leiolopisma telfairi*) (Wheler and Fa 1995), St Lucia parrots (*Amazona versicolor*) (Fa and Cavalheiro 1998), chimpanzees (*Pan troglodytes*) and gorillas (Ross et al. 2009), then later for siamangs (*Symphalangus syndactylus*) (Goh et al. 2017). Electivity measures the over- or under-utilisation of individual zones or resources within an enclosure.

Ross et al.'s (2009) study revealed that chimpanzees under-utilised open spaces, and over-utilised zones containing mesh fences and corners. Similarly, gorillas were shown to significantly under-utilise open space areas. During the study, both gorillas and chimpanzees were moved to a new, more naturalistic facility; the effect on enclosure use was evaluated. Both gorillas and chimpanzees used their new enclosures more evenly following the move. However, avoidance of open spaces was still noted. Ross et al. (2009) hypothesised that this may be related to the natural habitat of the great apes; as animals found commonly in forested regions, open exhibits may have limited biological relevance.

Electivity index was also used to determine use of support structures for siamangs (Goh et al. 2017). The study determined that horizontal, as opposed to vertical, supports were preferred for brachiation. Siamangs were able to brachiate most effectively in enclosure zones where several horizontal, stable support structures were available.

If funds or keeper time is spent in developing new resources, it is important to assess the overall use of these by animals. Electivity index could be used in future studies to evaluate the use of covered zones, wooded areas or hides or shelters prepared for animals (Fa and Cavalheiro 1998).

Application of Electivity index

While Electivity index rarely appears in zoo animal literature, the method is highly applicable to many captive species. Electivity index generates a value ranging between 1 (over-utilisation) and -1 (under-utilisation) of each zone. These values are generated based on expected observation values for each zone based on its size. Similarly to Plowman's (2003) modified SPI, biological zones should be determined before commencing observations, and all zones must be measured. Zones do not need to be of equal size. The formula for Vanderploeg & Scavia's (1979) electivity index is

$$E^* = (Wi - (1 / n))/(Wi + (1 /n)) \qquad Wi = (ri / pi)/\sum(ri / pi)$$

Here, *ri* refers to the observed use of a resource or zone, and *pi* refers to the expected use of a given resource. The letter n denotes the total number of zones or resources available to the study species.

Electivity index values may be used to compare the utilisation of different zones in an exhibit, accounting for differences in their size (Figure 3). Electivity index has also shown promise in comparing zone use following changes in enclosures (Ross et al. 2009).

Electivity index should be used in projects where a form of enrichment or a particular biological resource are of interest. Electivity index is also valuable for investigations of bespoke enclosure designs. Given its similarity to Plowman's (2003) SPI, Electivity index should be avoided in enclosures where zones cannot be accurately measured.

Behavioural assessments of enclosure use

Many papers that use key words such as Enclosure use and Spread of Participation Index also use behavioural techniques to evaluate

Table 1. Proportion of studies using enclosure use techniques, and taxonomic groups studies. Data were collected from archives for the International Zoo Yearbook, Journal of Zoo and Aquarium Research, Applied Animal Behaviour Science, Der Zoologische Garten and Zoo Biology.

	Zone Occupancy	Spread of Participation Index	Modified Spread of Participation Index	Electivity Index	Total
Mammals	30	11	5	2	48
Birds	4	2	2	1	9
Reptiles	2	0	0	1	3
Amphibians	0	0	0	0	0
Fish	1	1	0	0	2
Total	35	14	7	4	62

the suitability of enclosures (Tan et al. 2013; Mallapur et al. 2005). There are a plethora of behavioural measures available, and a full analysis of all techniques is not possible within this review. However, some of the most common techniques seen in enclosure design papers included behavioural diversity measures (Clark and Melfi 2012) and stereotypy (Clubb and Mason 2007).

Within these studies, activity budget data are often used to support the finds from enclosure use indices (Mountaudouin and Le Pape 2005). Many studies aim to identify the effects of enrichment or exhibit modifications on existing stereotypies (Mallapur et al. 2005; Troxell-Smith and Miller 2016), or to compare levels of stereotypy in animals held in different enclosures (Tan et al. 2013; Breton and Barrot 2014). Previous research has determined that stereotypy is multifactorial (Kroshko et al. 2016); however, investigating the effects of changing one exhibit variable may have some validity.

Kistler et al.'s (2011) studies have revealed that zebrafish exhibit significantly more stereotypical behaviour when placed in a barren environment, in addition to using a smaller proportion of their exhibit. Breton and Barrot (2014) reported similar findings in tigers (*Panthera tigris*) when maintained in smaller enclosures. There are limitations to using stereotypy as an indicator of enclosure relevance, as it is known that levels of stereotypy differ between species and individuals, and the absence of stereotypy does not mean that an animal's welfare is optimal (Clubb and Mason 2007). However, stereotypy may represent an animal's inability to express a specific behaviour (Kroshko et al. 2016); an animal living in an unsuitable enclosure may therefore be more likely to stereotype.

Behavioural diversity measures are also commonly used in zoo studies (Kistler et al. 2011; Clark and Melfi 2012). Theory suggests that animals housed in diverse, complex environments will have the opportunity to exhibit a more diverse array of behaviours (Clark and Melfi 2012). Accordingly, a high behavioural diversity index is indicative of good welfare (Lyons et al. 1997). A range of behavioural diversity measures have been used in prior studies to evaluate the diversity and evenness of behaviours expressed (Clark and Melfi 2012; Lyons et al. 1997).

These behavioural measures are often combined with SPI or zone use techniques (White et al. 2003; Clark and Melfi 2012),

Table 2. Most-studied taxonomic groups for enclosure use studies.

Taxa	Number of citations	Authors
Great apes	11	Hedeen 1983; Traylor-Holzer and Fritz 1985; Bettinger et al. 1994; Goff et al. 1994; Lukas et al. 2003; Ross and Lukas 2006; Ross et al. 2009; Ross et al. 2011; Lukas and Ross 2014; Bloomfield et al. 2015; Yamanashi et al. 2016; Ang et al. 2017.
Felids	7	Shepherdson et al. 1993; Foreman 1997; Gilkison et al. 1997; Lyons et al. 1997; Breton and Barrot 2014; Leeds et al. 2016; Schimmelpfennig et al. 2017.
Bears	3	Forthman and Bakeman 1992; Powell 2006; Pastorino et al. 2017.
Elephants	2	Leighty et ai. 2010; Rowell 2014.

allowing researchers to determine what their animals did, and also where they did it. This combination of techniques may be highly valuable for future studies.

Discussion

Enclosure use studies in previous literature

From the five journals analysed, a total of 62 publications were identified that specifically measured enclosure use. Of these, zone occupancy was the most common assessment method used, with traditional SPI appearing as the second most common enclosure use tool (Table 1) (Kroshko et al. 2016). A bias was identified in taxonomic grouping, with mammals appearing in the majority of studies (Table 1). A significant bias was also identified within taxonomic groups, with 12 of the 62 studies focussing purely on great apes (Table 2).

By contrast, no amphibian enclosure use studies were identified in the literature. While some sit-and-wait amphibians are not good candidates for exhibit use studies, there are many active species such as dart frogs (*Dendrobates spp.*) which could be easily observed (Melfi 2009). The bias identified in study species does not appear to reflect the collection plans of zoological collections; previous research suggests that zoos house a diversity of birds, fish and reptiles, which have not been fully represented in research (Goulart et al. 2009). Further investigation of enclosure use, with a view to further developing enclosure design and husbandry, would be valuable for a range of non-mammalian zoo animals.

Directions for future study

Current enclosure assessment techniques are versatile, and though many studies have already been conducted, there is considerable potential for future studies. Research revealed a considerable bias in favour of carnivore and primate studies. For example, many enclosure use projects have covered tigers (Lyons et al. 1997; White et al. 2003; Breton and Barrot 2014; Schimmelpfennig et al. 2017), whereas enclosure use has been rarely addressed in published literature for zoo-housed amphibians or invertebrates (Kistler et al. 2011).

Focus should be placed on understudied taxa, such as small birds, reptiles, amphibians, fish and invertebrates (Melfi 2009). This will help to apply an evidence base to future enclosure design, and may aid in developing husbandry guidelines. Further potential enclosure use studies include:

Thermal zones, ultra-violet light (UV) gradients and enclosure design. It is well established that herptiles rely on external sources of heat to warm their bodies, but few studies have evaluated heat provision and enclosure design (Rose et al. 2014). Similarly, UV is essential for many zoo-housed animals, but it is often difficult to document how much UV the animals are exposed to. Future studies using Electivity index could segregate enclosures into thermal or UV zones, based on substrate temperatures or UV indices. In turn, this may identify reasons why reptiles and amphibians avoid, or prefer, specific zones.

It is well established that visitor presence may be stressful for many zoo-housed species (Davis et al. 2005; Eltorai and Sussman 2010; Sherwen et al. 2014, 2015). While adrenocorticoid analysis is the gold standard in visitor effect studies, this may be unfeasible on a budget (Ross et al. 2011). However, enclosure use studies, particularly modified SPI and Electivity index, may be used to investigate the use of zones near to the public on busy versus quiet days (Mallapur et al. 2005; Learmonth et al. 2018).

Assessment techniques may also be used in enclosures where animals have access to three dimensions, such as aquariums for aquatic animals (Horikoshi-Beckett and Schulte 2006; Briek et al. 2018). Kistler et al. (2011) have utilised original SPI for fish; further SPI studies may help to further develop enclosure design.

Conclusions

A range of enclosure use assessment methods may be found within current zoo literature, ranging from use of individual zones, to SPI and Electivity index. While all are valid tools, consideration should be paid to the type of study undertaken, and therefore the most appropriate measure to use.

Behavioural tools used to support findings from enclosure use studies include behavioural diversity indices and prevalence of stereotypy. Where possible, both behaviour and enclosure use should be incorporated to develop an understanding of exhibit relevance.

While enclosure use measures are well established, there are still many future avenues for evidence-based research with the potential to improve captive animal husbandry and enclosure design. Key areas for future focus include thermal, UV and depth-based zones for enclosure studies.

The majority of published enclosure use research has focused primarily on carnivores or primates. Future studies on other taxa, such as reptiles, amphibians and fish would provide a stronger foundation for enclosure design theory.

Acknowledgements

The author would like to thank Dr L Riley, Mrs Y Foulds-Davis, Mrs S Brereton, Mr Y Christodoulides, Mr B Livesey and Mr M Myhill for their useful feedback on the manuscript. The author would also like to thank the staff at University Centre Sparsholt for their support during the course of the research.

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