Title: Principal Component Analysis as a Novel Method for the Assessment of the Enclosure Use Patterns of Captive Livingstone's Fruit Bats (*Pteropus livingstonii*)

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Abstract:

The Spread of Participation Index (SPI) is a standard tool for assessing the suitability of enclosure design by measuring how captive animals access space. This metric, however, lacks the precision to quantify individual-level space utilization or to determine how the distribution of resources and physical features within an enclosure might influence space use. Here we demonstrate how Principal Component Analysis (PCA) can be employed to address these aims and to therefore facilitate both individual-level welfare assessment and the fine-scale evaluation of enclosure design across a range of captive settings. We illustrate the application of this methodology by investigating enclosure use patterns of the Livingstone's fruit bat (*Pteropus livingstonii*) population housed at Jersey Zoo. Focal sampling was used to estimate the time each of 44 individuals in the first data collection period and 50 individuals in the second period spent in each of 42 theoretical enclosure sections. PCA was then applied to reduce the 42 sections to five and seven ecologically relevant "enclosure dimensions" for the first and second data collection periods respectively. Individuals were then assigned to the dimension that most accurately represented their enclosure use patterns based on their highest dimensional eigenvalue. This assigned dimension is hereafter referred to as the individual's Enclosure Use Style (EUS). Sex was found to be significantly correlated with an individual's EUS in the second period, whilst age was found to significantly influence individual fidelity to assigned EUS. When assessing the effect of resource location on group-level preference for certain sections, the presence of feeders and proximity to public viewing areas in period one, and feeders and heaters in period two, were positively correlated with space use. Finally, individual EUS remained consistent between both data collection periods. We interpret these results for this species in the context of its observed behavioural ecology in the wild and evaluate the degree to which the current captive enclosure for this population allows for optimal individual welfare through the facilitation of spatial choice. We then explore how these methods could be applied to safeguard captive animal welfare across a range of other scenarios.

Keywords: Spread of Participation Index, Principal Component Analysis, critically endangered, zoo management, enclosure design, fruit bats

Research Highlights:

- Principal Component Analysis can complement traditional enclosure use analysis.
- PCA produces fine-scale information on individual enclosure use.
- Enclosure use analysis can improve our understanding of individual welfare.
- Age and sex affect Livingstone's fruit bats consistency in enclosure use style.
- Heaters and feeders can predict Livingstone's fruit bat enclosure use.

1 Introduction

In the wild, animals typically have scope to move away from aversive exogenous stimuli. However, captive animals housed in all settings, including agricultural, zoological, and laboratory based systems, have largely limited choice surrounding their freedom of movement (Morgan & Tromborg, 2007). Some of the earliest studies of abnormal and stereotypic animal behaviour linked spatial restrictions to decreased welfare (Levy, 1944). However, the functioning of many integral systems to modern society, such as food production, scientific advancement, captive breeding for conservation purposes, etc., require animals to be housed in captivity. Hence the need arises to safeguard the welfare of the animals housed in these systems through careful assessment of optimal design and management of their enclosures (Broom, 1991; F. A. W. Council, 2009; Dawkins, 2012). Through analysing how captive spaces are used by their resident species, we can seek to minimize exposure to unduly stressful stimuli and maximize individual spatial choice (Dawkins, 2004; Morgan & Tromborg, 2007; Wickins-Dražilová, 2006).

To assess how animals utilize space in the captive environment, several metrics have been proposed (Brereton, 2020). Most frequently in zoo-based research, captive population use of an enclosure has been assessed through the calculation of the traditional or modified Spread of Participation Index (SPI) (Dickens, 1955; Hedeen, 1982; Plowman, 2003). The SPI, ranging from 0 (indicating maximal enclosure use) to 1 (indicating minimal enclosure use), indicates how evenly artificially demarcated sections are utilized by a population (Plowman, 2003). The modified version of the SPI allows for sections that are uneven in shape and size (Plowman, 2003) and has been used to assess enclosure use in a number of zoo-housed species (e.g. five Phoenicopteriform species (Rose, Brereton, & Croft, 2018), California sea lions (*Zalophus californianus*) (de Vere, 2018), sitatunga (*Tragelaphus spekii*) (Rose & Robert, 2013), chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla gorilla*) (Ross, Calcutt, Schapiro, & Hau, 2011)). Though widely implemented in zoo-based studies, the SPI does not appear to have been implemented as a measure of spatial occupation in animal agricultural and seldom applied to analyse laboratory animal housing, despite the strong suggestion that space use should be an important component of welfare assessment in these systems (Baumans & Van Loo, 2013; N. R. Council, 2010; Croney, Muir, Ni, Widmar, & Varner, 2018; D'Silva, 2006).

Despite its historic implementation, the SPI has short-comings. Perhaps the most problematic assumption of the SPI, is that "evenness" of enclosure use is often viewed as indicative of positive welfare (a critique that is further elucidated by (Brereton, 2020)). This assumption results in the calculation of the SPI being based solely on how evenly the entire resident population accesses the space overall (Melfi, Bowkett, Plowman, & Pullen, 2005). It does not indicate which regions are important to particular individuals or groups. In zoo-based systems in particular, space is often highly limited. Maximizing the utility of the available space would appear to be a logical course of action. However, if certain sections within an enclosure are not occupied as frequently as others, they may still facilitate critical species-specific ecological or welfare related functions and behaviours (Hughes & Duncan, 1988). It may even be the case that the less population dense regions of an enclosure are entirely necessary for reducing aggression (Videan & Fritz, 2007), safeguarding subordinate individuals and their access to resources (Leighty, Soltis, & Savage, 2010), or for the facilitation of specific welfare-related behaviours (Neal Webb, Hau, & Schapiro, 2018). Therefore, "even use of all sections" alone may not be a useful indicator of appropriate enclosure design.

In this study, we demonstrate how these issues may be overcome through the implementation of Principal Component Analysis (PCA). PCA uses simple observational data to minimize the number of input variables (i.e. artificially demarcated enclosure sections) by grouping them into "dimensions" that most accurately represent the data contained within each variable (Tharwat, 2016). In the same way that PCA produces "personality types" in animal personality analysis (Weiss, Adams, Widdig, & Gerald, 2011), this methodology similarly produces ecological dimensions, referred to hereafter as "Enclosure Use Styles" (EUS). The EUS that most accurately reflects the enclosure use pattern displayed by an individual will be that which has the largest corresponding eigenvalue. For example, if Dimension X is defined as containing only section A, an individual that only accesses section A will have the largest eigenvalue for Dimension X (out of a set of Dimensions X-n) and will subsequently be assigned Dimension X as their enclosure use style.

This methodology can easily be paired with traditional enclosure use assessment to explore possible ecologically driven explanations, as opposed to poor enclosure design, for a particularly high SPI. As suggested by (Estevez, Andersen, & Nævdal, 2007) and (Petherick, 2007), it may be that when animals from artificially assigned groups (as is the case in most animal management systems) are in close proximity to one another there may be a significant increase in aggression and injury. Given the opportunity, individuals preferentially interact with specific social partners, creating subgroups both socially and physically within the larger population (Gutmann, Špinka, & Winckler, 2015). This preference for known social partners would ultimately produce an SPI closer to one than zero, indicating non-even enclosure usage by the group, but would nonetheless be necessary for positive welfare. Hence, further analysis is required before an enclosure design with a high SPI can be deemed inappropriate for its resident population.

By analysing the resource composition of the sections within each EUS, we can also assess what resources are available to individuals with different space use patterns. This analysis is valuable, as some high value resources such as feeding stations and heated indoor spaces may be actively guarded by dominant individuals, and therefore inaccessible to most of the population (Estevez et al., 2007; Oldfield, 2011). By repositioning feeding stations so that there is at least one present in the sections represented by each EUS, management teams may implement more appropriate resource layouts that maximize availability to all individuals. Structuring of environmental changes to maintain individual preference, whilst creating opportunities for choice, may further optimize the captive environment for the group overall (Einarsson et al., 2014; Hemsworth, Mellor, Cronin, & Tilbrook, 2015; Ritter, Beaver, & von Keyserlingk, 2019).

We illustrate the application of PCA as a complement to SPI calculation by examining the enclosure use patterns of the Livingstone's fruit bat (*Pteropus livingstonii*) population housed at Jersey Zoo. Enclosure design for this and other critically endangered fruit bat species is of particular conservation importance, as captive breeding colonies have become increasingly critical components of their IUCN prescribed species action plans (Sewall et al., 2007, 2016). This study sought first to understand how specific individuals utilize their environment through the fine-scale quantification of ecological dimensions and subsequent assignment of enclosure use styles (EUS). The effect (if any) of individual demographic variables, such as sex and age, on which EUS individuals were assigned as well as on their degree of fidelity to their assigned EUS were then assessed to explore demographic determinants of spatial preference. Lastly, the effect of the current resource composition on overall population use of the enclosure was assessed to inform how these features, and more specifically, individual *P. livingstonii*'s ability to access them, should be considered in future enclosure modification.

2 Materials and Methods

2.1 Ethical Approval

Ethical approval for this study was granted by the University of Chester's Faculty of Medicine, Dentistry and Life Sciences Research Ethics Committee on 27/3/19, reference number 1535/19/MW/BS. Access to the enclosure and permission to study the population of *P. livingstonii* housed at Jersey Zoo, Channel Islands was granted in writing by the Durrell Wildlife Conservation Trust on 12/03/19. All health and safety guidelines put in place by Jersey Zoo regarding entry into the enclosure and non-contact with animals were followed throughout.

2.2 Study Population

This study was conducted on the population of *P. livingstonii* housed in the "Island Bat Roost" enclosure at Jersey Zoo over two distinct data collection periods, totalling five months of observation. The first data collection period took place over 83 days between June and September 2019 and the second took place over 46 days (cut short due to Covid-19 restrictions) between February and March 2020. The study population consisted of 44 individuals (24 female and 20 male) during the first observation period and 50 individuals (28 female and 22 male) during the second observation period. Of the aforementioned 44 and 50 sample sizes, 42 individuals were observed during both observation periods. Each individual had previously been fitted with a Passive Transponder Tag (PIT) for identification purposes as part of routine veterinary checks, at approximately eight months of age. Reading these PIT tags with a Radio-Frequency Identification Device (RFID reader), along with the observation of unique ear notches and back pattern coloration, allowed the observer (MJE) to identify all individuals. Only individuals that were independent from their dams and were old enough (i.e. approximately eight months of age) for PIT tags to be fitted were included in the previously stated sample sizes. All individuals' sex and age in years were known before the commencement of this study.

The heated agricultural polytunnel housing the *P. livingstonii* population throughout the study had the following dimensions: 38m long x 7m wide x 4m high (Bell, Price, Balthes, Cordon, & Wormell, 2019). The northern end of the enclosure included a shed for temporary isolation (e.g. veterinary intervention) and a maternity roost separated from the main tunnel by a wall of mesh. Additionally, a hospital roost (also separated from the main tunnel by mesh) along the eastern wall housed older and injured individuals (Figure 1). The shed, maternity roost, and hospital roost were not included in the spatial analysis presented in this study, as they were only accessible sporadically to a small number of individuals. Individuals housed in these areas during the observation periods were also not included in this study. The *P. livingstonii* shared their enclosure with twelve Rodrigues fruit bats (*Pteropus rodricensis*). Hetero-specific locational data were not recorded due to time constraints.

The main enclosure tunnel foliage consisted of soft *Ficus* sp. and *Tradescantia* sp. along the lower embankment and floor to maintain the safety of the bats during accidental collisions or falls. Artificial turf covered the keeper walkways along the western and eastern walls, as well as along the "island", a raised section in the centre of the enclosure encircled by a 1.5m trench, designed to allow for greater aerial manoeuvrability. The ceiling and walls of the enclosure were covered with a network of medium density mesh and rope for bi/quadrupedal locomotion (Bell et al., 2019). Temperature within the tunnel fluctuated throughout the year, but efforts were made via the implementation of industrial fans, a biomass heating system, sprinklers/misters, and extensive rammed-earth insulation to maintain a minimum of 18ºC and a maximum of 32ºC. Humidity varied within the enclosure from 65% to 95% during both periods.

The bats were fed twice daily, at approximately 11:00 and 16:30. During period one, these feeds consisted of Mazuri leaf-eater primate diet (Mazuri Exotic Animal Nutrition, St Louis, MO) soaked in water twice a week with all other feeds consisting of a mixture of chopped fruits and vegetables. During period two, all morning feeds consisted of the Mazuri leaf-eater primate diet and all afternoon feeds consisted of chopped fruits and vegetables. Individuals that had recently undergone medical interventions or were currently nursing dependent offspring were fed an extra portion of banana by hand each morning. Both feeds were distributed between 65 dispenser cups suspended from the ceiling around the perimeter of the enclosure and a series of short lengths of plastic gutter fixed to the western wall.

Previous studies have been conducted to assess certain aspects of how *P. livingstonii* individuals interact with their environment in captivity, such as how the distribution of foraging sites within the fruit bat enclosure at Jersey Zoo influence the frequency of subgroup access (Thorncroft, Wormell, & Price, 2009), as well as the effect of enclosure design on flight frequency and pattern (Bell et al., 2019). Additionally, previous observation of this species in the wild suggest that they exhibit a harem-based mating system, where dominant males guard access to resources and females (Racey & Entwistle, 2000; Will J Trewhella, Reason, Clark, & Garrett, 1998), which, if this occurs in captivity, would greatly influence individual spatial use, as dominant males may preclude subordinates from accessing certain areas. However, research on the social experience of *P. livingstonii* in captivity suggests that dominance structure is not influenced by individual sex, indicating that males may not exhibit the same harem-based behaviours in captivity that we would expect based on observation of wild individuals (Welch et al., 2020).

2.3 Behavioural Observations

Prior to the commencement of this study, ten days were spent learning to independently identify individuals. This period also allowed the bats to become habituated to the presence of the researcher (MJE) within the enclosure. Keepers entered the enclosure on a routine basis for management purposes, so the presence of the researcher was not deemed to cause any additional stress in the study individuals. A minimum distance of two meters was maintained between the observer and the bats throughout behavioural observations.

The study population was observed for approximately six hours a day between 9:00 and 17:00, over five randomly allocated days a week during each study period. This rotation included all days of the week evenly to account for variation in numbers of visitors. Before the commencement of the study, the enclosure was divided into a hypothetical 14x3 grid of 42 approximately equally sized sections (Figure 1). A central 'island' separated the east and west wings, creating three distinct 'columns'. The 14 'rows' were demarcated by pre-existing pillars within the enclosure. These divisions were selected to naturally follow the layout of the enclosure in order to aid in efficient data collection. The assignment of sections in this way, though ideal for the implementation of the traditional SPI (which requires that zones be the same size and produces more accurate results when these zones are numerous and small), is just one example of how enclosure use data can be collected and does not necessarily represent required data collection parameters for the implementation of PCA, which can function with data from zones of unequal size and shape.

A starting section was randomly chosen before the start of each study period. Each *P. livingstonii* individual within a section, starting with the individual at the far North of the section, was sequentially the subject of a ten-minute instantaneous focal observation (Altmann, 1974), where their location was recorded as a row number (1-14) and column letter (A-C) each minute using the Animal Observer iPad application (Caillaud, 2016). Individuals were followed throughout the enclosure, their location being recorded each minute, for the duration of the ten-minute period. The next individual to be observed was then selected from the original section regardless if the previous focal individual had changed location. This continued until all individuals within a section had been the subject of focal sampling before moving to the next section in a clockwise manner. Individuals that had previously been sampled that day were not sampled again within the same 24-hour period. Sampling continued during both feeding times to record individual locational preferences while foraging. The last section reached each day was noted and used to demarcate the starting section on the subsequent day of data collection.

Though spatial analysis typically employs scan sampling in which the location of all individuals within the enclosure is recorded at once, this methodology would not have been feasible in this case as individuals at the opposite end of the enclosure to the researcher were not identifiable. Focal sampling was therefore selected as the optimal method of data collection for this species.

The presence of relevant resources within enclosure sections was recorded prior to both observation periods, including feeding stations, heaters (period two only) and proximity to zoo visitors. Visitors were able to walk along the southern and part of the eastern walls of the enclosure to view the animals throughout the data collection periods. Though the visitors were often audible, dense foliage often precluded them from being fully seen by individuals within the enclosure (personal observation, MJE).

2.4 Data Analysis

2.4.1 Spread of Participation Index

Enclosure use analysis frequently involves the calculation of the Spread of Participation Index (SPI), a metric based on how often and how evenly hypothetical sections within an enclosure are occupied by the entire housed population (Hedeen, 1982). The SPI can vary from 0, where all sections are used maximally, to 1, where all sections are used as unevenly or minimally as possible. A modified version of the SPI allows for this calculation to be applied to data where enclosure sections are unequal in size and shape (Plowman, 2003). However, as enclosure sections demarcated in this study were approximately equal in size, for simplicity we employed the traditional SPI calculation method.

By opting for the traditional SPI as opposed to the modified version of the calculation, which accounts for the effect of valued resources on zone occupancy, we avoid the potential for bias in defining the bounds of the sections within our analysis. Though the modified SPI is often implemented in zoo settings, as it allows for zones (i.e. sections) to be defined by their resource compositions (Plowman, 2003), and is therefore often easier for researchers to monitor, this methodology can result in biased data. It can be difficult for humans to approximate, especially in the case of cryptic and less studied species, which regions within an enclosure facilitate behaviour and which groups of regions are used by animals for the same function (Melfi et al., 2005). For these reasons, we calculated the SPI based on the traditional formulation (Hedeen, 1982). PCA and further post-hoc analysis will be implemented in later sections to explore the influence of resource composition on how individuals accessed regions within the enclosure. This methodology therefore eliminates unintended bias in choosing what counts as a valued resource before data is collected and illuminates, based on the ecology of the study species, which regions together facilitate behaviour.

We calculated the SPI for each data collection period using the following formula:

$$SPI = (M(Nb-Na)+(Fa-Fb))/2(N-M)$$

where M is the mean number of total observations recorded per section, Nb is the number of sections where the total number of observations recorded was less than M, Na is the number of sections were the total number of observations recorded was greater than M, Fa is the total number of observations in all Nb sections, Fb is the total number of observations in all Na sections, and N is the total number of observations in all sections (Plowman, 2003).

2.4.2 Enclosure Use Over Time

To assess whether enclosure section usage was consistent over time, a Quadratic Assignment Procedural test (QAP) was implemented in the R (version 4.0.3) statistical package “sna” (version 2.6) with 1000 replications (Butts, 2016; Simpson, 2001). This test determines the ability of one matrix to predict another (Simpson, 2001) and is frequently used in social network analysis to identify correlations between association matrices. If the proportion of observations of each individual in each section during the first data collection period could predict the proportion of observations that they were recorded in the same section during the second data collection period, it would suggest that spatial use remained consistent between both periods.

The number of observations of each *P. livingstonii* individual in each enclosure section was first divided by the total number of locational records for that individual, creating a section use matrix of the proportion of total observations each individual spent in each section (individuals as rows and sections as columns) for each data collection period. These matrices were then implemented in a QAP test (Simpson,

2001) to determine if enclosure use was consistent between the two periods. The total number of observations recorded in each section for the entire population was also totalled to assess how frequently each section was used by the population as a whole.

2.4.3 Principal Component Analysis

We then implemented PCA (Wold, Esbensen, & Geladi, 1987) to explore *P. livingstonii* space use and preference in an ecologically relevant manner. Essentially, PCA minimizes a large set of variables into a number of groups that can accurately account for the variance contained within the original data set. In this case, the initial 42 artificially demarcated sections were minimized into a smaller number of ecological dimensions that each contained a set of the initial 42, which we refer to as enclosure use styles (EUS), for each data collection period. The sections that composed each dimension were grouped into EUS based on similar locational patterns exhibited by members of the *P. livingstonii* population. In this way, certain groups of sections that may be necessary for some ecological functions, or that may provide some additional benefit to certain subgroups of individuals, may be identified. Further, by assigning EUS to individuals based on their particular locational patterns, individual space use and the ability of individuals to access critical resources can be more clearly illuminated.

To begin, the input variables (i.e. the proportion of observations each individual was recorded as being located in each section) were standardized to eliminate sampling bias, using the R statistical package “stats” (version 4.0.3) (Kassambara & Mundt, 2017), through the following equation:

$$X = (X_1 - X_M)/X_{SD}$$

where X is the standardized variable, X_1 is the percent of observations an individual was recorded as being in the section of interest before standardization, X_M is the mean percent of observations that the entire population spent in the section of interest, and X_{SD} is the standard deviation of the percent of observations that the entire population spent in the section of interest. This formula was applied to each cell of the section usage matrix for each data collection period separately, producing two covariance matrices.

PCA was then applied to the covariance matrices from each data collection period using the R statistical package "stats" (version 4.0.3) (R Core Team Worldwide) to reduce the number of sections from 42 to a lower number of more ecologically relevant enclosure dimensions. To assess what number of dimensions was appropriate for each data collection period, the percent of cumulative variance within the data that was accounted for by grouping the enclosure sections into additive dimensions (up to 42) was calculated (Kassambara, 2017). Two scree plots with significance lines at alpha = 0.05 were produced to visualize this (Cattell, 1966). The number of dimensions selected for each data collection period was the lowest number that accounted for at least 70% of the cumulative variance (Kanyongo, 2005).

The PCA was then re-ran on each covariance matrix with the number of dimensions fixed by the results of the scree plot analysis of cumulative variance (Kanyongo, 2005). The dimensions were then populated with enclosure sections by reducing the residual values of each enclosure section data set along each dimensional eigenvector using the R statistical packages "factoextra" (version 1.0.7) (Kassambara & Mundt, 2017) and "MASS" (version 7.3-53) (Ripley et al., 2013). The dimension each particular section was assigned to was that which had the largest corresponding eigenvector magnitude, or eigenvalue (Jolliffe & Cadima, 2016). These new groupings of sections represented the EUS present within the population during each data collection period. This process is commonly used in animal personality research, where individual "traits" are assigned to the personality "type" that they contribute to most (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). Hence in this study, we assigned enclosure sections to ecologically relevant EUS.

Similarly, a table of eigenvalues (Jolliffe & Cadima, 2016), was produced for all individuals using the R statistical packages "factoextra" (version 1.0.7) and "MASS" (version 7.3-53). This showed how accurately each of the newly defined EUS represented each *P. livingstonii*'s individual enclosure use pattern. Thus, the EUS that best represented the individual's particular pattern of spatial utilization (i.e. the style for which they had the largest eigenvalue) and their fidelity to that particular pattern of spatial utilization (i.e. the corresponding eigenvalue) could be identified. Instead of simply assessing the amount of time that each individual spent in each enclosure section, this method of analysis assigns an EUS, similar to a personality type (Carter et al., 2013), to each individual that holistically describes their particular pattern of space use over time. This information can then be applied to inform possible ecological underpinnings of the SPI calculated for the same data collection period. The R code for performing this analysis is available for readers to implement (Supplementary Material).

2.4.4 Resource and Variable Effects on Enclosure Use

To further illustrate how the results of both SPI calculation and PCA can be used to elucidate spatial patterns and preferences of both groups and individuals, we applied our findings to the assessment of the effects of demographic variables (sex and age) on individual EUS and their fidelity to that EUS, as well as the effect of resource distribution on how often the population as a whole accessed each section within the enclosure.

Firstly, to explore the effects of resource presence on enclosure section use, we implemented a generalized linear model. We assigned each of the 42 initial sections binary scores for each data collection period to denote which resources were present within each section; these indicated whether of not the section contained a feeder, a heater, or whether it bordered the viewing platform and therefore allowed for visitor presence along the outside of the mesh (see Figure 1). Heaters were not turned on during the first data collection period, so were subsequently not included in the model for period one. They were however, included in the model for period two, as the heaters remained on for the duration of the second data collection period to maintain temperatures within a suitable range for *P. livingstonii.* The number of visitors present in the viewing area was not recorded, as the observer (MJE) remained within the enclosure for all data collection; we simply included a binary measure of whether or not each section bordered the viewing area. Two generalized linear models, one for each data collection period (with Gaussian error structure and identity link function (Faraway, 2016)) were then implemented using the R statistical package “lme4” (version 1.1-26) (Bates, Mächler, Bolker, & Walker, 2014) to assess the effect of the binary variables feeders, heaters, and visitor presence on the total number of individuals recorded in each section.

Akaike Information Criterion (AIC) values were used to select the best fitting model (i.e. had the lowest AIC score that also differed by at least two from all other models) (Richards, Whittingham, & Stephens, 2011). If two or more models had AICs that were within two of each other, they were both assessed. The goodness-of-fit of the 'best fitting' model was then examined using residual vs. fixed effect plots and null vs. residual deviance values (Zuur, Ieno, & Elphick, 2010). If the relationship between residual and predicted values appeared to be random upon visual inspection, and the residual deviance was significantly lower than the null deviance, the model was determined to fit the data appropriately (Sakate & Kashid, 2014). Co-linearity between significant variables was also examined using variance inflation factors (VIF) in the R statistical package "olsrr" (version 0.5.3) (Hebbali & Hebbali, 2017; Thompson, Kim, Aloe, & Becker, 2017). If two or more variables were found to be co-linear, the one that most greatly increased the difference between null and residual deviance upon removal was not included in the final model (Dormann et al., 2013).

To explore correlations between individual demographics and assigned EUS, two Chi-squared tests of independence were conducted for each data collection period (Zibran, 2007), one to examine the relationship between sex and EUS, and the other to examine the relationship between age and EUS. If either test produced a significant result, the contribution of each variable to the Chi-square score was calculated via the following equation:

$$(100*A^2)/\text{Chi-Squared Score}$$

where A is the residual of each variable (Sharpe, 2015). The nature of the dependency was also visualized by creating a balloon plot of residuals using the R statistical package "ggpubr" (version 0.4.0) (Kassambara & Kassambara, 2020). Chi-squared tests were conducted separately for each data collection period.

The possible effect of sex, age, and EUS on degree of fidelity to each individual's assigned EUS (i.e. the corresponding eigenvalue) was then also assessed using two generalized linear models (with Gaussian error structure and identity link function) (Faraway, 2016). The best fitting model was determined as described above, using AIC values (Richards et al., 2011). Each best fitting model was then re-run to determine effect size estimates, significance levels, and the standard error of each variable it contained. The goodness-of-fit of these models were again examined visually using residual vs. fixed effect plots and null vs. residual deviance values, as explained previously (Sakate & Kashid, 2014; Zuur et al., 2010). Co-linearity between significant variables was examined using VIFs (Thompson et al., 2017).

3 Results

3.1 Traditional Enclosure Use Assessment

A total of 645 focals were conducted during the first data collection period, with a mean of 162.7 and a standard deviation of 10.48 locational observations per individual. During the second data collection period 383 focals were conducted, with a mean of 82.6 and a standard deviation of 6.82 locational observations per individual. The second data collection period was curtailed due to restrictions imposed by the Covid-19 pandemic.

The SPI for the first and second data collection periods were calculated as 0.252 and 0.293 respectively. These results indicate non-maximal and non-even usage of the enclosure over both observation periods (Figure 2). A QAP test was implemented to test for consistency in enclosure use over time. The results of this test ($r=0.359$, $p<0.05$) suggest that individual enclosure use remained relatively consistent between both data collection periods, as the two matrices of frequency of presence of each individual (rows) within each enclosure section (columns) were significantly correlated.

3.2 Principal Component Analysis

Scree plots illustrated how the cumulative addition of enclosure dimensions (up to 42) accounted for additional variance within the data (Appendix A). For the first data collection period, the 42 enclosure sections were reduced to five unique ecological dimensions, which accounted for 71.33% of the total variance present within the data set. As is standard for data minimization techniques, the first and second dimensions accounted for the majority of the variance (22.3% and 17% respectively) (Abdi & Williams, 2010). For the second data collection period, seven unique dimensions were found to cumulatively account for 74.11% of the total variance present. The first and second dimensions accounted for 20.1% and 13.2% of variance for this period.

After re-running the PCA with the number of dimensions fixed for each data collection period based on the findings of the scree plots (five and seven respectively), the EUS were created by populating dimensions with their corresponding enclosure sections. Sections were assigned to the EUS for which they had the largest corresponding magnitude of dimensional eigenvector (Appendix B). In other words, when the data for each enclosure section was plotted, the eigenvector that minimized residuals most effectively belonged to the EUS which that section was then assigned to. Eigenvalues for each EUS were then calculated for each individual (Appendix C). The EUS for which an individual had the highest eigenvalue was taken to indicate that individual's most representative grouping of sections (Table 1, Figure 3).

3.3 Demographic Variable and Resource Effects

3.3.1 Resource Presence Effects

The total number of observations of bats per section was used to visualize whole population use of enclosure sections, as well as determine the effects (if any) of resource distribution (Figure 2). A generalized linear model was implemented to analyse the effect of feeders, heaters, and proximity to visitors within sections (Figure 2) on how *P. livingstonii* accessed their enclosure during each data collection period. Heaters were not active during the first data collection period, so were therefore only included as a variable in the second model. The best fitting model for the first period contained both feeder presence and proximity to visitors. Both variables had a significantly positive effect on the number of observations of bats recorded per section (Feeders: $p < 0.001$; Visitors: $p = 0.02$) (Table 2). The best fitting model for the second period contained both feeder and heater presence. Both variables were found to have a significantly positive influence on the total number of observations of bats recorded per enclosure section (Feeders: $p < 0.001$; Heaters: $p = 0.031$), with feeders having the largest overall effect for both data collection periods (Table 2).

Co-linearity between feeder and visitor presence (period one) and feeder and heater presence (period two) was assessed using the R statistical package "olsrr" (version 0.5.3) (Hebbali & Hebbali, 2017). As the variance inflation factor (VIF) was below two for all variables tested, the models they were included within were determined to not be influenced by co-linearity within the data (Thompson et al., 2017).

3.3.2 Individual Demographic Effects

To examine the relationship between sex and assigned EUS, two Chi-squared tests of independence were conducted, one for each data collection period. No correlation was detected for the first period, but the Chi-squared score was significant for the second data collection period ($X^2 = 13.34$, $p = 0.038$). EUS one and six were found to contribute most highly to the overall Chi-squared score (25.73% and 31.47% respectively), suggesting that these EUS were assigned to more females than males than would be expected (Appendix D). The relationship between age and assigned EUS was then examined in a similar way, by conducting two Chi-squared tests of independence. However, neither test produced significant Chi-squared scores.

Two generalized linear models were constructed to determine to what extent the degree of fidelity to an individual's assigned EUS (as represented by their corresponding eigenvalue) was influenced by individual sex, age, or the assigned EUS itself. The best fitting model for the first data collection period contained sex and age. Males and individuals aged six, nine, ten, and twelve years (exclusively) were found to have significantly higher fidelity to their EUS (Table 3). For the second data collection period, sex did not have a significant effect on fidelity. However, individuals aged seven, eight, nine, eleven, and twelve (exclusively) all had significantly higher fidelity to their assigned EUS (Table 3).

4 Discussion

4.1 Evaluation of Methods

This study has provided an example of how Principal Component Analysis can be used to complement traditional methods of enclosure use analysis, providing more detailed information on individual differences in space use in captivity. The application of this methodology is no more time or resource consuming than the calculation of the SPI and the R code is available here (Supplementary material). Additionally, this methodology, like the modified SPI calculation (Plowman, 2003), can account for differences in size and shape of enclosure sections, making it applicable to enclosure use assessment in a number of different captive situations in which large groups of animals are housed, including but not limited to zoos and safari parks, agricultural and industrial farms, and laboratory animal housing.

However, because PCA is essentially a data minimization tool, the dataset to which this method can be applied must necessarily contain information on a sufficiently large sample size of individuals or have a sufficiently high ratio of variables to sample size (Gorsuch, 1997; MacCallum, Widaman, Zhang, & Hong, 1999). In enclosures containing a small number of individuals, any variance that is not accounted for by the defined dimensions (up to 30% of the total variance in some cases) is discarded in the final analysis. This may produce critical gaps in information on how specific individuals utilize their enclosure. However, this effect is minimized as sample size (or variable ratio) increases. Therefore, where the enclosure contains only a small number of individuals (e.g. fewer than ten), individual activity budget construction coupled with variable effect modelling may provide sufficient information on the appropriateness of the design of the enclosure in question and its concomitant resource distribution. We recommend this PCA-based method only be applied to enclosures housing larger groups of animals.

In the future, to truly evaluate the utility of PCA methodology to the application of enclosure use assessment, it must be applied to the study of space use of species with different ecological requirements housed in a wide variety of husbandry systems. To help facilitate the implementation of PCA methodology to independent data sets in this way, we have included complete annotated R code as a supplementary data file.

4.2 Interpretation of Results for P. livingstonii

Our results produce a notable example of how the SPI can benefit from supplementary analysis that provides context to its interpretation. The calculated SPI values for both the first (0.252) and second (0.293) data collection periods were relatively similar, suggesting that the enclosure was used to the same extent in both periods. However, different sections were grouped within each EUS during each period, suggesting that the pattern of resource use for individuals, and the population overall, differed between the two periods. The second data collection period took place during *P. livingstonii*'s mating season in captivity, with peak mating occurring from January-March. Average ambient temperatures were also slightly lower during this time (by approximately 5°C). The physiological, behavioural, and social requirements of mating, as well as the external seasonal changes in the environment, could shape individual needs, potentially explaining these differences in space use patterns.

Table 1 lists the sectional composition of each EUS (as defined by the results of the PCA), and indicates which *P. livingstonii* individuals were assigned to each EUS. From a practical standpoint, this data can be used by zoo keepers to minimize their impact on the population when searching for an individual to be caught for veterinary intervention and routine checks. This table, when combined with Figure 3, functions as a map of locations that each individual is more likely to be found, saving keepers' time and lowering the number of candidate individuals to be scanned (with an RFID reader) when searching for a particular individual.

Several sections along the eastern wall were not accessed at all by *P. livingstonii* during one or both of the data collection periods. This may be due to a lack of positive resources, such as feeders and heaters, or could be caused by the increased presence of heterospecifics (*P. rodricensis*), which are dominant over *P. livingstonii* (personal observation, MJE). It is important to note that these unused sections were not among those with high proximity to visitors, meaning visitor effects are unlikely to explain the lack of use of these sections. These regions should be the subject of further investigation to examine the exact cause of this lack of use.

The presence of feeders (both periods), heaters (period two only), and visitor proximity (period one only) were found to positively affect the overall use of enclosure sections by the entire *P. livingstonii* population (Figure 2, Table 2). In the first data collection period, every EUS, besides style two, contained at least one section with a feeder. In the second data collection period, EUS one, two, and five did not contain sections with feeders and EUS one, two, four, and five did not contain sections with heaters. To access these critical resources, individuals whose EUS did not provide these features may have to venture through sections not contained within their EUS. The effect of this on individual welfare is unknown. Physically, moving through more of the enclosure would mimic more closely the vast distances travelled by wild individuals (Mandl et al., 2021) and would reduce the risk of obesity in captivity. However, there may be social reasons that individuals have certain EUS that may also preclude access to resources. For example, more dominant individuals may be monopolizing feeding locations (Thorncroft et al., 2009).

In response to our suggestion that, instead of adding additional foraging resources, which could heighten the risk of obesity, the existing resources (both feeders and heaters) should be distributed throughout the enclosure more evenly, Jersey Zoo has since moved half of the feeders within the bat enclosure to the opposite side and installed more heating units. This will provide for greater individual choice, whilst still encouraging movement throughout the enclosure. Subsequent PCA may be necessary to assess how these changes in resource distribution could have potentially impacted upon individual access and the composition of EUS.

The varying impacts of visitor presence on the welfare of zoo housed individuals are of particular importance and relevance to enclosure design (Birke, 2002; Sherwen & Hemsworth, 2019). The results of this study suggest that visitors to the “Island Bat Roost” enclosure at Jersey Zoo had a small positive effect on how *P. livingstonii* utilized their enclosure in the first data collection period. Perhaps the dense vegetation planted between the visitor hallway and the internal part of the enclosure sufficiently blocked any potentially negative influence of the visitors while simultaneously attracting bats. Additionally, the presence of the foliage may be somehow influencing the behaviour of visitors to the exhibit to be quieter (Fernandez, Tamborski, Pickens, & Timberlake, 2009). For example, research on the effect of camouflage netting installed between zoo visitors and a gorilla exhibit suggested that, as well as decreasing the rate of stereotypic and aggressive behaviours displayed by the gorillas, the more naturalistic setting produced a quieter crowd of visitors (Blaney & Wells, 2004).

This analysis also identified a significant relationship between the age of an individual and their degree of fidelity to their EUS during both data collection periods. Individuals aged six, nine, ten, and twelve years of age during the first data collection period, and individuals aged seven, eight, nine, eleven, and twelve years of age during the second data collection period, all displayed a higher degree of fidelity compared to individuals of other ages. *P. livingstonii* reach sexual maturity at four years of age, perhaps creating a greater need for territory establishment and maintenance in mature individuals (Trewhella, Rodriguez-Clark, Davies, Reason, & Wray, 2001). As enclosure use was found to be consistent between the two data collection periods, it may also be the case that individuals retain their degree of preference for certain spaces as they age. When choosing individuals for institutional translocation, individuals that have not yet reached sexual maturity may be more appropriate, as they display less fidelity for particular regions within their enclosure, suggesting they may be more adaptable to changes in the physical environment.

Additionally, sex (specifically being male) was found to positively influence EUS fidelity in the first data collection period. Previous research on this species suggests that, because of harem-structured mating systems observed in the wild (Courts, 1997), males in captivity would also be expected to display a higher degree of fidelity for the space they occupy, as control of locational resources is directly linked to their reproductive potential. During the second data collection period, EUS one and EUS six contained significantly more females than males. As this data collection period took place during the mating season for this species in captivity, perhaps this sex-based spatial disbursement is somehow linked to the ecological requirements of mating behaviours. This interpretation is further supported by the observation that many other *Pteropus* species females form “maternity” roosts away from males once they have mated to take advantage of more favourable resources while pregnant (Eby, 1991; Gumal, 2004). More research on the effect of sex on space use differences displayed by *P. livingstonii* in captivity is necessary to understand how artificial environments and their design may be further optimised for the ecological requirements of this species.

4.3 Research Addendums to PCA

PCA, as we have illustrated, can provide a more detailed map of how individuals use space in captivity. Examining the influence of individual variables and extraneous factors (both biological and anthropogenic) is the logical next step to truly understanding what drives differences in enclosure use (Rose, Badman-King, Hurn, & Rice, 2021). This extra analysis is also necessary to unpack the potential welfare implications of certain space use patterns. Individuals within a group can have varied ecological and physiological requirements based on their age, reproductive status, dominance, social connectivity, *etc*. that may impact upon how they use the space available to them. We have demonstrated briefly how addendum analysis can be useful to understanding the map produced by PCA by assessing the impact of age, sex, feeders, heaters, and visitors upon the space use of *P. livingstonii*. There are however, countless variables that could influence how animals use their enclosures. Therefore, which of these variables are relevant to each captive environment should be carefully considered.

5 Conclusion

The degree to which animals in captivity utilize the space available to them to exhibit the necessary range of behaviours to maintain positive welfare states has been extensively examined (Brereton, 2020; Rose & Robert, 2013). Assessment methodologies of the suitability of specific enclosure designs have employed metrics that do not account for how different regions can be important to specific individuals or groups. Previous researchers have instead evaluated how evenly the space is utilized by the entire population (Dickens, 1955; Plowman, 2003). The PCA-based method implemented here addresses this issue by re-framing the enclosure into groupings of sections (termed Enclosure Use Styles here) that are ecologically relevant to the species. The EUS to which each individual is assigned, and their degree of fidelity to that style, can then be used to determine how individual enclosure use varies, and which factors can influence space use. By focusing on the individual, the ecological requirements of subordinate animals or groups within a population will not be overlooked when applying this method. Additionally, this methodology can identify resource layouts that allow for ease of access to all individuals, hence providing an insight into how captive enclosures might be better managed to safeguard individual welfare. By applying these techniques to the study of *P. livingstonii,* we have provided an extended example of how PCA may be implemented as a more detailed complement to traditional enclosure use analysis methodology, with the goal that this work may serve as a template for the application of this methodology to future investigations across a range of captive environments.

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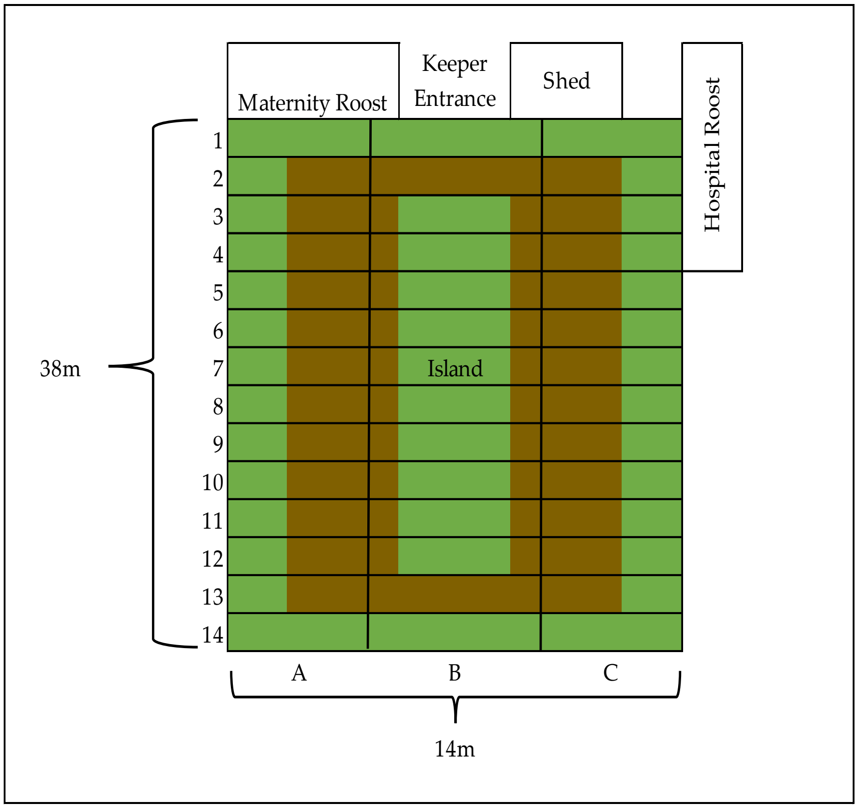
Figures & Tables:

Figure 1: Aerial Enclosure Diagram



<u>Figure 2:</u> Whole Population Enclosure Use by Section

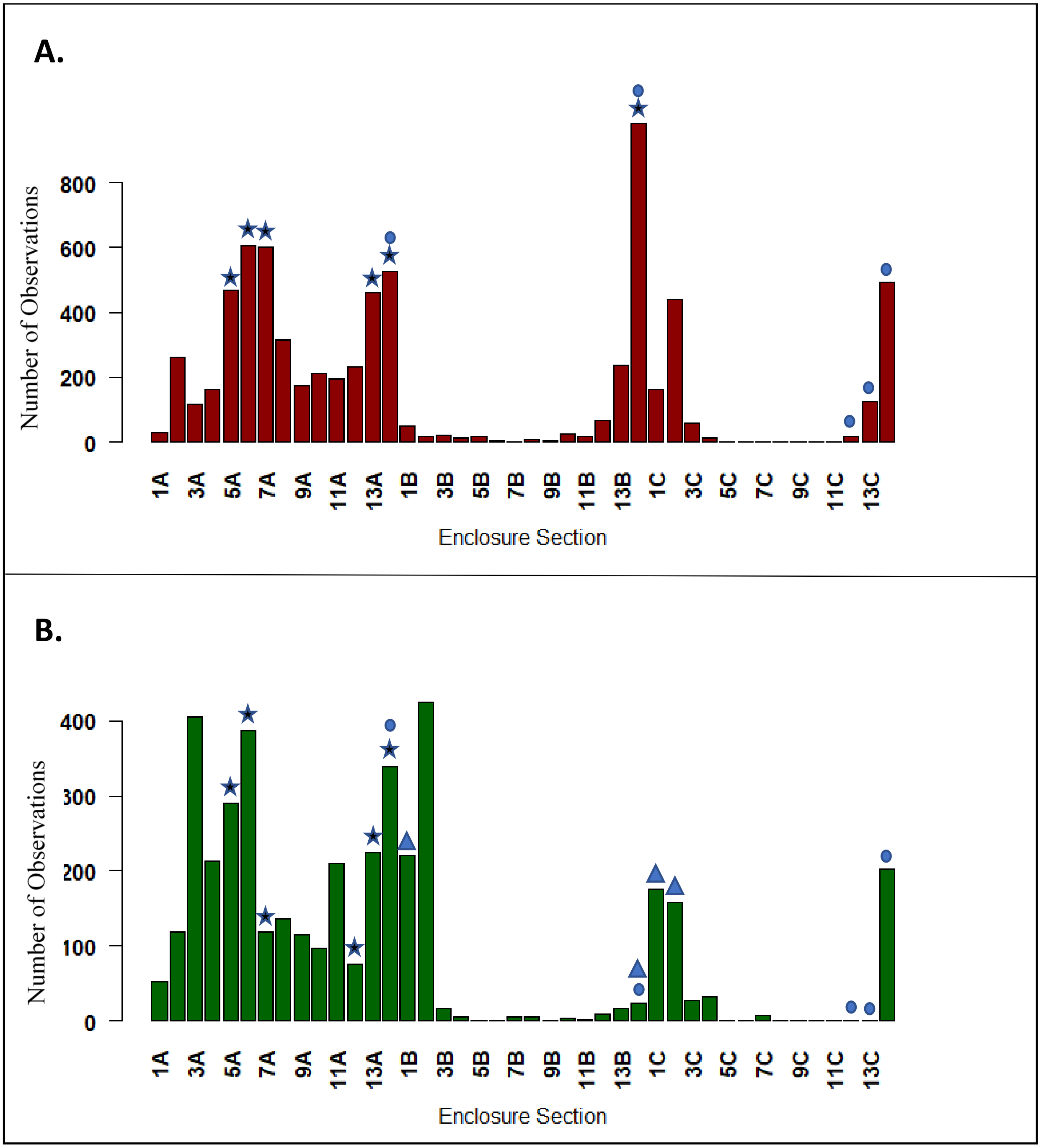


Figure 3: Sections Included in Each Enclosure Use Style in the "Islands Bat Roost"

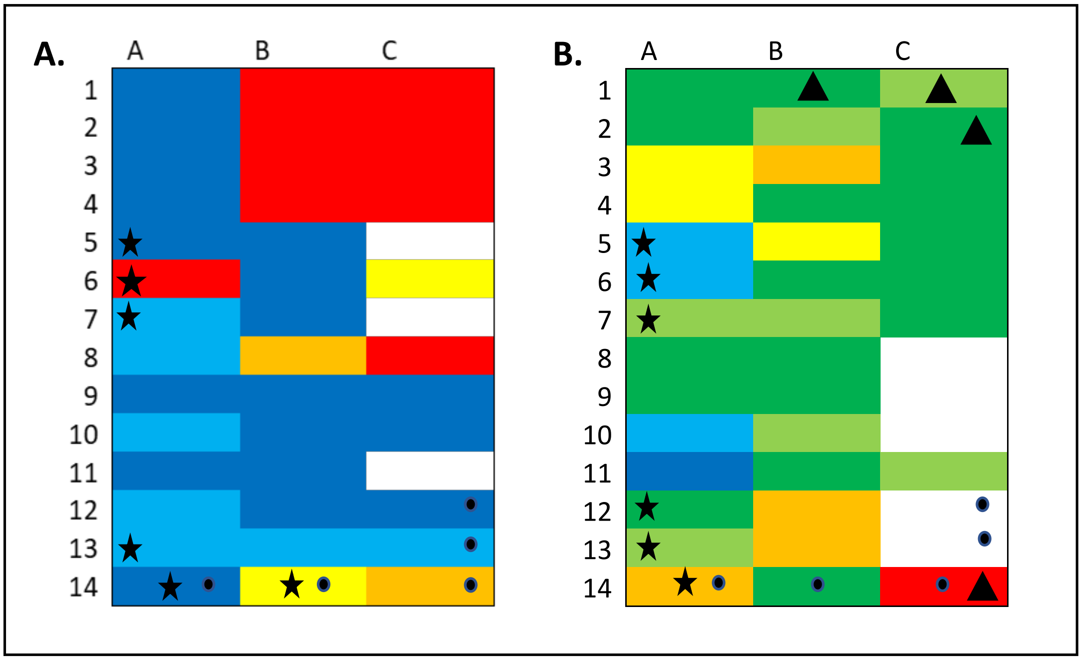


Table 1: Composition of Enclosure Use Styles

Style	Season	Sections	Individuals
1	1	14B, 6C	ACH, ATA*, ECH*, ICA, LOK, MOY*, NZU*
2	1	8B, 14C	NYM*, PAN*, POP, YOR
3	1	6A, 1B, 2B, 3B, 4B, 1C, 2C, 3C, 4C, 8C	ATH*, BAX, CLA*, NAS, NEI*, NER*, NYX*, YME
4	1	7A, 8A, 10A, 12A, 13A, 13B, 13C	CAL*, CER*, CHR*, ERI, HEL, HES, IXI, KID, LIM*, MAR*, SEL*, YEM*
5	1	1A, 2A, 3A, 4A, 5A, 9A, 11A, 14A, 5B, 6B, 7B, 9B, 10B, 11B, 12B, 9C, 10C, 12C	APO, BAL, CLI*, HER, IRI*, KOV, LUN*, MAK*, MET*, MON*, ORL, THO, THR

1	2	3A, 4A, 5B	APO, ATH*, BAZ*, CAL*, ECH*, MAR*, MOY*, NYM*
2	2	14A, 3B, 12B, 13B	BAX, CEP, HEL, LOK, LUN*, NEI*, POP
3	2	14C	PAN*, THR, YOR
4	2	5A, 6A, 10A	ACH, CLI*, HER, ORL
5	2	11A	CLA*, ERI, GAI*, LIP*, NYP, NZU*, YME
6	2	7A, 13A, 2B, 7B, 10B, 1C, 11C	CHR*, IRP*, KOV, LIM*, MAK*, MET*, NER*, SEL*, YEM*
7	2	1A, 2A, 8A, 9A, 12A, 1B, 4B, 6B, 8B, 9B, 11B, 14B, 2C, 3C, 4C, 5C, 6C, 7C	ATA*, BAL, BAP, CER*, HES, ICA, IXI, LIN*, MON*, NAS, NYX*, THO

Table 2: Resource Presence Effects on Whole Population Enclosure Use

Observation Period	Variable	Effect Size Estimate	Standard Error	P value
1	**Feeders**	**471.1**	**59.95**	**<0.001**
	Visitors	**156.94**	**64.78**	**0.02**
2	**Feeders**	**178.83**	**48.05**	**<0.001**
	Heaters	**128.5**	**57.28**	**0.031**

<u>Table 3</u>: Variable Effects on Eigenvalue of Individual Enclosure Use Styles

Period	Variable		Effect size estimate	Standard error	P value
1	Age in Years	2[±]	-1.12	3.68	0.352
		3	5.52	4.4	0.536
		4	11.09	5.62	0.239
		5	7.95	0.552	0.084
		6	**19.03**	**0.606**	**0.007**
		7	11.07	0.960	0.175
		8	-4.9	0.960	0.540
		9	9.02	0.546	0.468
		10	16.23	0.960	0.115
		11	2.48	0.960	0.791
		12	**13.48**	**0.625**	**0.026**
		14	-4.85	0.960	0.552
		15	0.534	0.960	0.574
		18	-3.27	0.724	0.731
		20	4.93	0.960	0.453
	Sex	Male[±±]	5.95	2.62	0.031
2	Age in Years	2[±]	-0.147	2.51	0.954
		3	0.001	2.77	0.999
		4	4.91	3.44	0.162
		5	4.98	3.44	0.157
		6	6.49	3.44	0.068
		7	**22.32**	**3.44**	**<0.001**
		8	**17.65**	**5.33**	**0.002**
		9	**22.42**	**5.33**	**<0.001**
		10	5.97	3.12	0.064
		11	**16.65**	**5.33**	**0.004**
		12	**13.61**	**5.33**	**0.015**
		13	2.48	3.44	0.476
		15	0.381	5.33	0.943
		17	0.012	5.33	0.998
		19	3.99	4.00	0.325
		21	0.081	5.33	0.988

Figure and Table Legends:

Figure 1: This figure depicts an aerial representation of the "Island Bat Roost" at Jersey Zoo, Channel Islands with approximate locations of the maternity roost, shed, and hospital roost labelled. The brown sections show the 1.5m trench surrounding the central island. The 42 artificial sections used for this study are denoted by 14 rows (1-14) and 3 columns (A-C).

Figure 2: Bar charts illustrating the total number of observations made of an individual (across the entire population) being in each artificially demarcated enclosure section in the a) first data collection period and b) the second data collection periods. The corresponding section label is along the x-axis. Stars denote the presence of a feeder within that section, circles denote a section that bordered on visitors' viewing points, and triangles denote heater location. No sections contained active heaters during the first data collection period due to high ambient temperatures. During the second data collection period, no section contained both a heater and a feeder.

Figure 3: This diagram depicts how the sectional composition of each enclosure use style identified by the PCA for the first (A.) and second (B.) data collection periods map onto the enclosure aerially. The colour of each section corresponds to the style in Tables 1 and 2 for which that section contributed most significantly (i.e. had the largest eigenvalue). White sections were not used by any individuals during data collection. Triangles denote the location of heaters, circles denote visitor access, and stars denote the location of feeders as similarly indicated in Figure 2.

Table 1: This table indicates which enclosure sections contributed most strongly to each enclosure use style based on their highest eigenvalue for both data collection periods. It also indicates which style most accurately represented individual enclosure use patterns based on their highest eigenvalue. The colour used to label the styles in column one corresponds with those used to show the sectional composition in Figure 3. Sections 5C, 7C, and 11C were not utilized by the

population during the first period, so were not assigned to a style. Sections 8C, 9C, 10C, 12C, and 13C were not utilized by the population during the second period, so were similarly not assigned to a style.

[*]Denotes a female individual.

Table 2: This table indicates the variables included in the best fitting models for the total number of observations recorded for each enclosure section for both data collection periods. The effect size estimates, standard errors, and p-values of variables are also listed. Data highlighted in bold indicates a statistically significant effect.

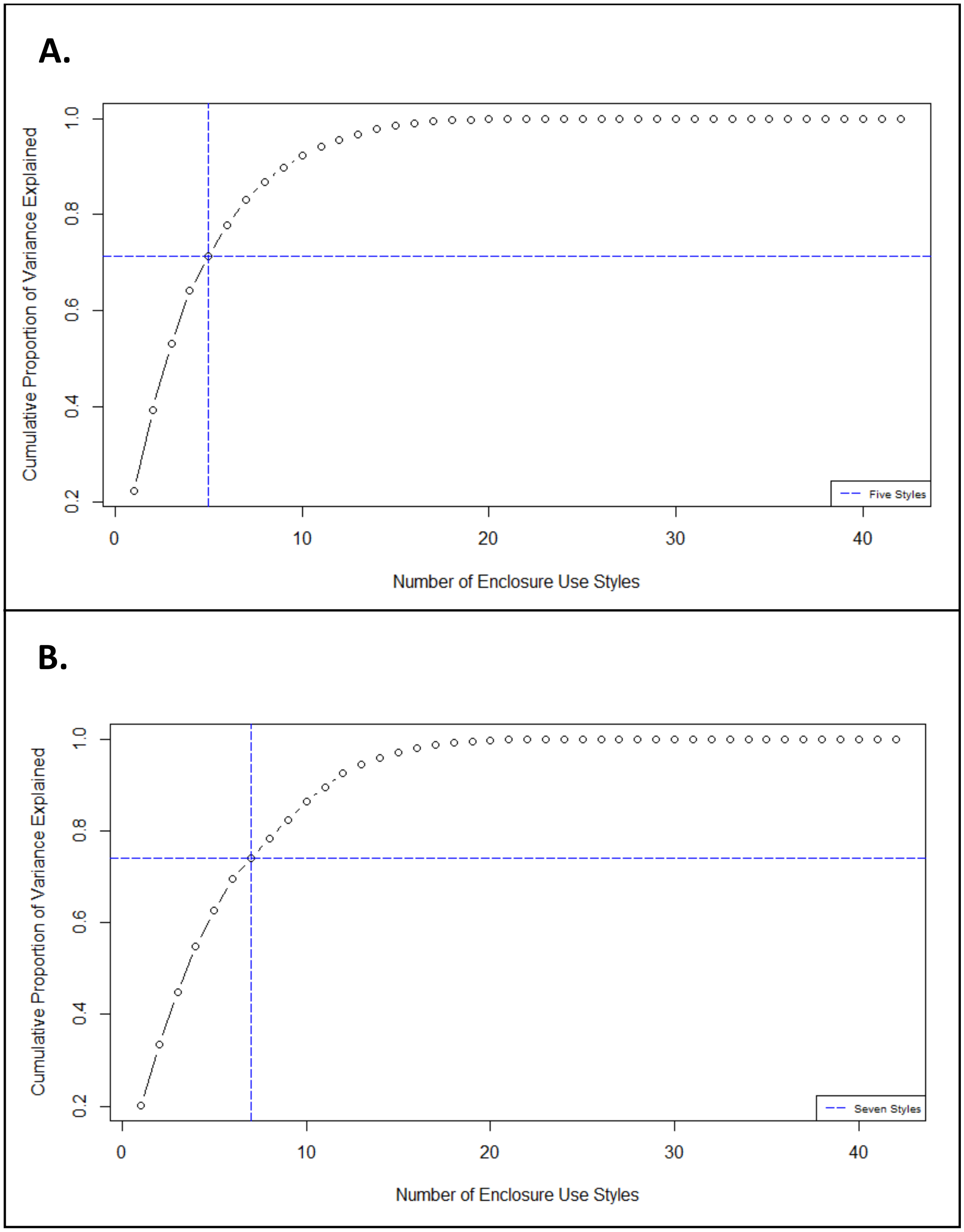
Table 3: This table indicates the variables included in the best fitting model for degree of fidelity to an individual's most representative enclosure use style (based on highest eigenvalue) for both data collection periods. The effect size estimate, standard error, and p-value of variable effects are also listed. Data highlighted in bold indicates a significant effect.

[±]Variable effects measured in relation to an age of one year in 2019 for the first data collection period and an age of one year in 2020 for the second data collection period.

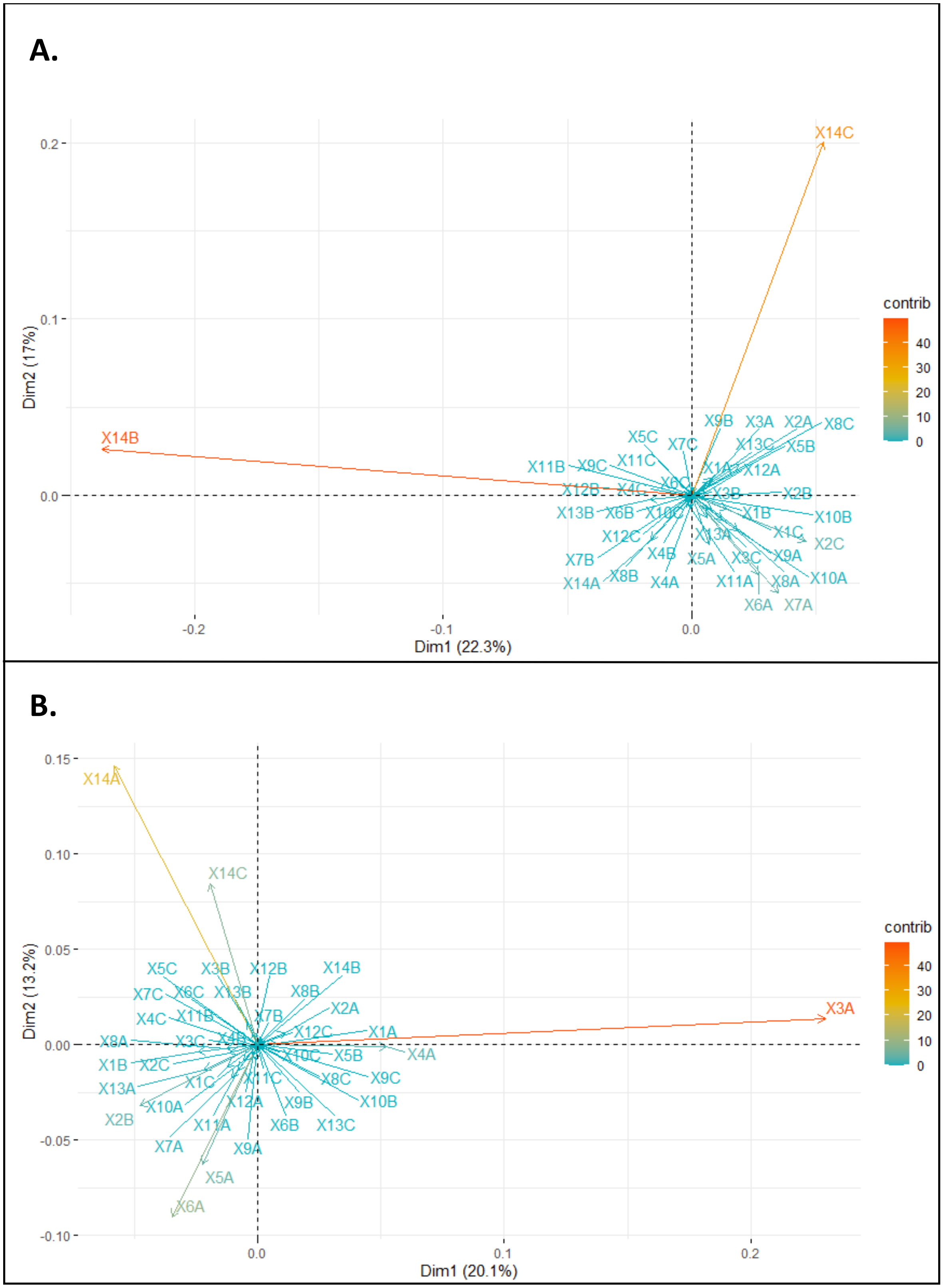
[±±]Variable effects measured in relation to being female.

Appendices:

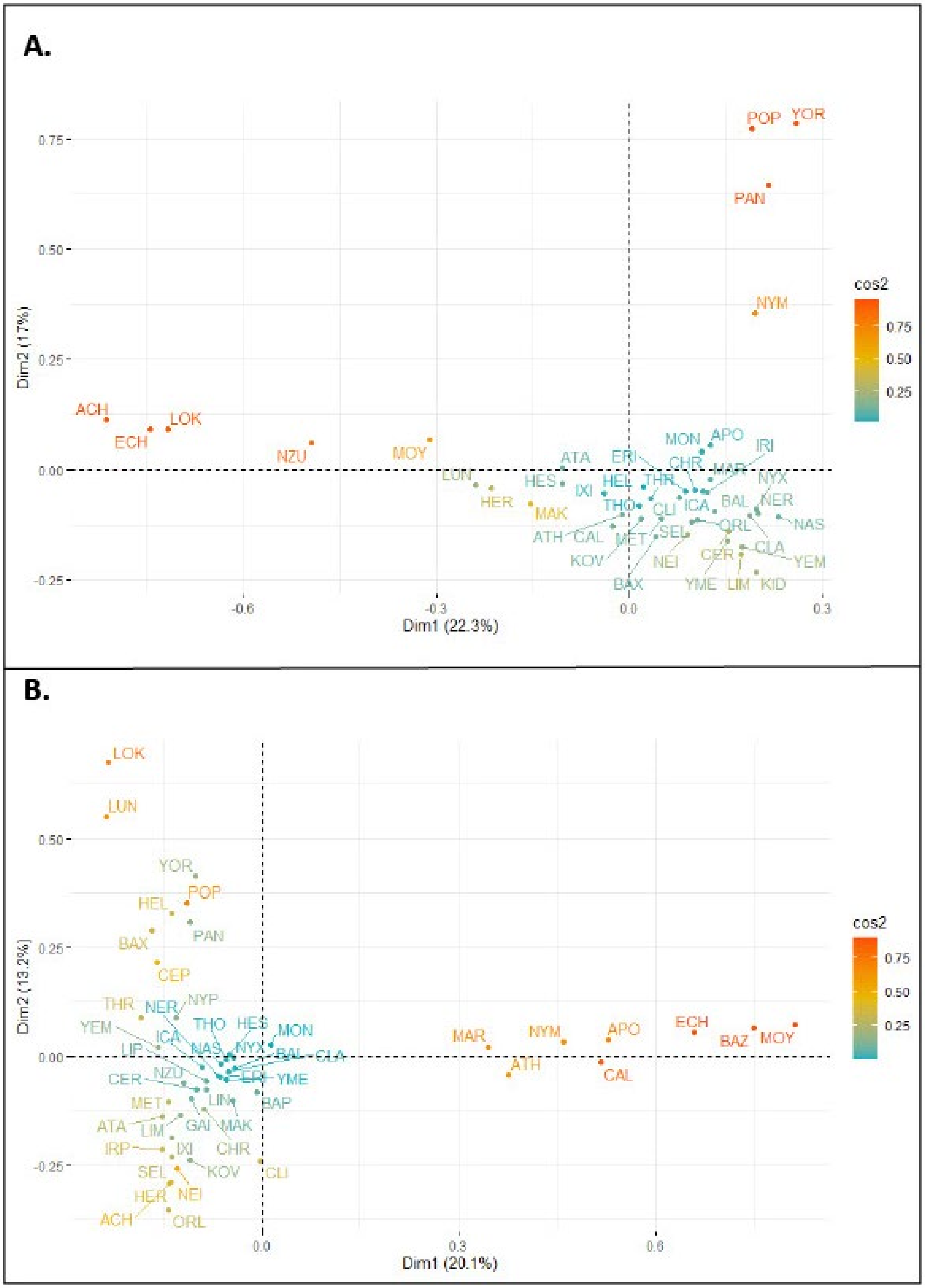
<u>Appendix A:</u>



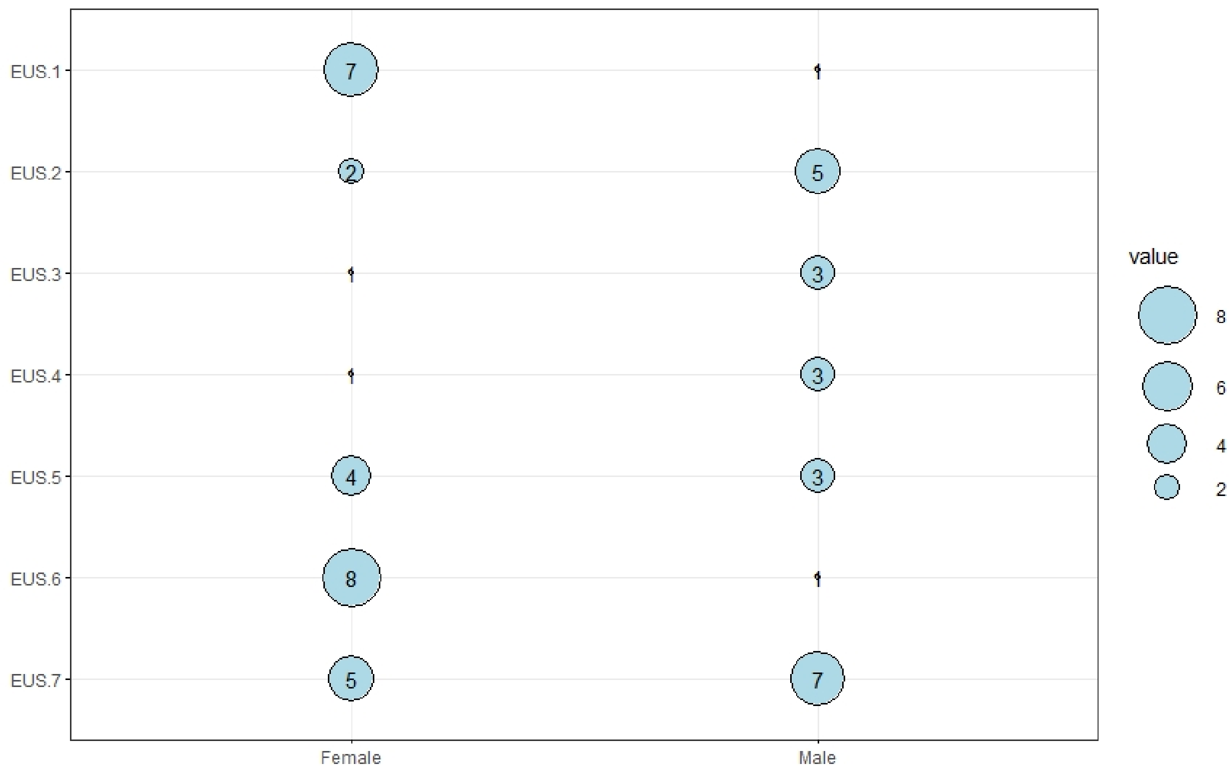
Appendix B:


A.
X14C
X14B
X9B X3A X2A X8C
X5C X7C X13C X5B
X11B X9C X11C X1A X12A
X12B X4C X6C X3B X2B
X13B X6B X10C X1B X10B
X12C X13A X1C X2C
X7B X4B X5A X3C X9A
X14A X8B X4A X11A X8A X10A
X6A X7A
Dim1 (22.3%)
Dim2 (17%)
contrib
B.
X14A
X14C
X5C X3B X12B X14B
X7C X6C X13B X8B
X2A
X4C X11B X7B
X12C X1A
X8A X3C X4B X3A
X10C X5B X4A
X1B X2C
X13A X1C X11C X8C X9C
X10A X12A X9B X10B
X2B X11A X6B X13C
X7A X9A
X5A
X6A
Dim1 (20.1%)
Dim2 (13.2%)
contrib

Appendix C:


A.
POP
YOR
PAN
NYM
ACH
LOK
ECH
NZU
MOY
LUN
HER
MAK
HES
ATA
IXI
ERI
HEL
THR
THO
CLI
ICA
MON
APO
IRI
CHR
MAR
NYX
BAL
NER
NAS
ORL
SEL
MET
ATH
CAL
KOV
BAX
NEI
CEP
CLA
YEM
YME
LIM
KID
Dim2 (17%)
Dim1 (22.3%)
0.75
0.50
0.25
0.00
-0.25
-0.6
-0.3
0.0
0.3
cos2
0.75
0.50
0.25
B.
LOK
LUN
YOR
POP
HEL
PAN
BAX
CEP
THR
NER
NYP
YEM
THO
HES
MON
ICA
LIP
NAS
NYX
BAL
CLA
CER
NZU
ERI
YME
MET
LIN
BAP
ATA
LIM
GAI
MAK
IRP
IXI
CHR
SEL
KOV
CLI
HER
NEI
ACH
ORL
MAR
NYM
APO
ECH
BAZ
MOY
ATH
CAL
Dim2 (13.2%)
Dim1 (20.1%)
0.50
0.25
0.00
-0.25
0.0
0.3
0.6
cos2
0.75
0.50
0.25

Appendix D:



Appendix E:

```
#Load packages
library(factoextra)
library(MASS)

#Load Data Files
EnSu19<-read.csv("EnclUseSu2019.csv", header=TRUE, row.names=1)

#Convert Data to Matrices
EnSu19.m<-as.matrix(EnSu19)

#Principle Component Analysis
```

```
Su19PCA<-princomp(EnSu19.m, cor=TRUE, scores=TRUE)

#Select Number of Components that Explain Significant Variance
##Standard Deviation of each component
std.de.Su19<-Su19PCA$sdev
##Compute Variance Explained by each component
var.Su19<-std.de.Su19^2
##Compute Proportion of variance explained by each component
prop.var.Su19<-var.Su19/sum(var.Su19)

#Get Eigenvalues
##has eigenvalues, percent variance, cumulative percent variance
eig<-get_eig(Su19PCA)

#Scree Plots to Select Number of Components
##Percent of variance in Data
plot(prop.var.Su19, xlab = "Principal Component",
     ylab = "Proportion of Variance Explained",
     type = "b")
abline(h=0.04, col="red", lty=5)

##Cumulative Scree Plot
plot(cumsum(prop.var.Su19), xlab = "Principal Component",
     ylab = "Cumulative Proportion of Variance Explained",
     type = "b")
abline(v = 10, col="blue", lty=5)
```

```
abline(h = 0.7018632, col="blue", lty=5)
legend("bottomright", legend=c("Cut-off @ PC10"),
       col=c("blue"), lty=5, cex=0.6)
cumsum(prop.var.Su19)

#Graph of Individual Scores for Dim1 and Dim2
fviz_pca_ind(Su19PCA,
             axes = c(1,2),
             col.ind = "cos2", # Color by the quality of representation
             gradient.cols = c("#00AFBB", "#E7B800", "#FC4E07"),
             repel = TRUE     # Avoid text overlapping
)

# Results for individuals
res.ind.Su19 <- get_pca_ind(Su19PCA)
res.ind.Su19$coord[,1:10]          # Coordinates
res.ind.Su19$contrib[,1:10]        # Contributions to the PCs (eigenvalues)
res.ind.Su19$cos2[,1:10]           # Quality of representation

#Graph of Variables (i.e. sections) for Dim1 and Dim2
##Correlated Variables are closer together
fviz_pca_var(Su19PCA,
             axes = c(1,2),
             col.var = "contrib", # Color by contributions to the PC
             gradient.cols = c("#00AFBB", "#E7B800", "#FC4E07"),
             repel = TRUE     # Avoid text overlapping
```

```
)

#Results for enclosure sections (i.e. variables)
res.sec.Su19<-get_pca_var(Su19PCA)
res.sec.Su19$contrib[,1:10]        #Contributions to the PCs (eigenvectors)

#Biplot of Individual eigenvalues and Enclosure Section eigenVectors
fviz_pca_biplot(Su19PCA,
        axes = c(1,2),
        repel = TRUE,
        col.var = "#2E9FDF", # Variables color
        col.ind = "#696969"  # Individuals color
)
```

Appendix Legends:

Appendix A: Scree plots illustrating the cumulative proportion explained by the step-wise addition of subsequent principal dimensions (i.e. enclosure use styles), up to the original number of sections (42). The horizontal blue line is drawn at the 70% cumulative variance cut-off, which corresponded to five enclosure use styles for the first period (A.) and seven enclosure use styles for the second period (B.).

Appendix B: These plots depict the eigenvectors of each labelled enclosure section (preceded by an ‘X’) from the first data collection period (A.) and the second data collection period (B.) for enclosure style one along the x-axis and enclosure style two along the y-axis. These styles are depicted here as they cumulatively accounted for the highest amount of variance present within the data. The cumulative percent variance within the data set accounted for by styles one and two are labelled.

The colour of the enclosure sections corresponds to their relative contribution (based on their eigenvalues) to enclosure use styles one and two.

Appendix C: These plots depict the eigenvalues of each individual for enclosure use style one (along the x-axis) and enclosure use style two (along the y-axis) for the first (A.) and second (B.) data collection periods. Individuals whose patterns of enclosure use were similar are grouped closer together. Colour corresponds to the strength of an individual's enclosure use representation based on the magnitude of the eigenvector for these two styles for each data collection period.

Appendix D: This balloon plot illustrates the number of female and male individuals assigned to each enclosure use style during the second data collection period. The size of each circle corresponds to the number of individuals. An examination of the residuals of the associated Chi-squared test of independence indicated that EUS's one and six contributed most strongly to the Chi-squared score and contained significantly more females than males.

Appendix E: R code for PCA.