HELSINGIN YLIOPISTO

Visitor effects on red-necked wallaby (*Notamacropus rufogriseus*) behaviour in a walkthrough enclosure

An assessment of the impacts of walkthrough activity on wallaby welfare and visitor experience at Korkeasaari Zoo

Master's Programme in Ecology and Evolutionary Biology
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Abstract:

Walkthrough enclosures allow visitors to more closely engage with zoo animals, which may improve visitor experience and interest towards conservation. However, the presence of visitors may impact animal behaviour and welfare. I investigated how visitor presence within the enclosure, the number of visitors, and noise produced by them impacts the behaviour and space-use of red-necked wallabies (*Notamacropus rufogriseus*) at Korkeasaari Zoo. I utilized the combination of essential behaviours (i.e. resting, foraging/feeding), anxiety-indicative behaviours (i.e. vigilance, retreat, locomotion), and space-use to assess welfare impacts in this population.

I used instantaneous scan sampling to observe the behaviours and location of each wallaby individual as they were exposed to the visitor presence and absence treatments (i.e. walkthrough open or closed), and varying levels of noise and visitor number within the enclosure. Additionally, I conducted a visitor questionnaire to assess visitor experience and interest in wildlife or conservation to examine whether the walkthrough activity at Korkeasaari Zoo improves these visitor variables.

The results indicated that visitor presence, but not number, decreased the use of the visitor path and its immediate surrounding, indicating some avoidance of visitors. The expression of essential behaviours was decreased during visitor presence, and some instances of high visitor number and loud noise, which indicates some level of disturbance. However, the expression of anxiety-indicative behaviours did not increase in a manner which would indicate visitors to be perceived as a source of great danger by the wallabies. Visitor experience was improved by participating in the walkthrough, but interest towards wildlife or conservation did not increase.

Although some potentially negative visitor effects were observed, the welfare impacts are unlikely to be significantly negative in this population. However, the results highlight the importance of adequate space and retreat options, and the moderation of visitor numbers when walkthrough activities are being designed and implemented.

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Läpikulkutarhat tarjoavat kävijöille mahdollisuuden tarkkailla eläimiä läheltä, ja saattavat täten parantaa kävijäkokemusta sekä kiinnostusta luonnonsuojelua kohtaan. Kävijöiden läsnäolo saattaa kuitenkin vaikuttaa eläinten käyttäytymiseen ja hyvinvointiin. Tarkastelin kuinka kävijöiden läsnäolo, lukumäärä, ja tuottama melu vaikuttavat punaniskakenguruiden (*Notamacropus rufogriseus*) käyttäytymiseen ja tilankäyttöön Korkeasaaren eläintarhassa. Hyödynsin kenguruiden olennaista käyttäytymistä (lepääminen, ravinnonhaku/syöminen), ahdistuksesta kielivää käyttäytymistä (varuillaanolo/valppaus, liikkuminen, vetäytyminen) sekä tilankäyttöä arvioidakseni hyvinvointivaikutuksia.

Tarkastelin kenguruiden käyttäytymistä ja sijaintia tarhassa ennalta määrätyin aikavälein (eng. instantaneous scan sampling), kun kengurut altistettiin kävijöiden läsnä- tai poissaololle tarhassa (kengurukuja auki ja kiinni), sekä eriasteisille tarhan kävijämäärille ja melulle. Lisäksi keräsin vastauksia kävijäkyselyyn, jonka tarkoituksena oli tutkia kävijäkokemusta sekä kiinnostusta villieläimiä ja luonnonsuojelua kohtaan.

Tuloksena kengurut välttelivät kävijäpolkua ja sen lähialuetta kävijöiden läsnä ollessa, mutta kävijöiden määrä ei lisännyt tätä välttelyä. Olennaisten käyttäytymisten ilmaisu väheni kävijöiden läsnä ollessa, sekä toisinaan korkean kävijämäärän tai melutason seurauksena, mikä osoittaa kävijöiden aiheuttavan jonkin tasoita häiriötä. Ahdistuksesta kielivä käyttäytyminen ei kuitenkaan lisääntynyt tavalla, joka osoittaisi, että kengurut tulkitsisivat kävijät vakavaksi vaaraksi. Kengurukujaan osallistuneilla kävijöillä kävijäkokemus oli parempi, mutta kiinnostus villieläimiä tai luonnonsuojelua kohtaan ei lisääntynyt. Tulosten perusteella kävijät tuskin aiheuttavat merkittäviä hyvinvointivaikutuksia kenguruille, vaikka joitakin negatiivisia kävijävaikutuksia oli havaittavissa. Tulokset kuitenkin korostavat eläinten tilantarvetta ja vetäytymismahdollisuuksien sekä kävijämäärien valvonnan tärkeyttä läpikulkutarhojen suunnittelussa ja toteutuksessa.

Table of Contents

1 Introduction

1.1 Zoo enclosure design and visitor benefits

Zoos around the world, including Korkeasaari Zoo where the present study was conducted, strive to balance conservation, animal welfare, visitor education and experience (Korkeasaari Zoo, n.d.; EAZA, n.d.). Visitor experience, engagement, attitudes, and education can be influenced through immersive exhibits emulating the animals' natural habitats (Smart et al., 2021), demonstrations such as feedings or training sessions (Lyon et al., 2024; Woolway & Goodenough, 2017) and activities such as walkthroughs, which allow visitors inside the animal enclosure (Moss & Pavitt, 2019). Participating in walkthroughs has been suggested to improve not only visitor engagement and attitudes toward conservation (Moss & Pavitt, 2019), but both psychological (mood) and physiological (salivary cortisol) parameters as well (Sumner & Goodenough, 2020).

Although demonstrations and activities may be associated with benefits to the visitors and improved inspiration towards conservation, their impact on the animals must also be considered. Visitor effects, meaning the influence of visitors on zoo-housed animals, may be positive, neutral, or negative, and will affect animal welfare accordingly (Hosey, 2000). The prioritization of visitor experience in zoo design has received criticism, as by ignoring visitor effects, the animals' needs and welfare may consequently be neglected (Melfi et al., 2005). The research on visitor effects and their implications on welfare is crucial in order to implement activities such as walkthroughs whilst ensuring adequate animal welfare and a balanced experience benefitting both the animals, visitors, and zoos.

1.2 Visitor effects on zoo-housed animals

Historically, the majority of visitor effect research has been conducted on mammals, with a heavy focus on primates (Davey, 2007; Sherwen & Hemsworth, 2019; Williams et al., 2023), although more studies focusing on reptiles, amphibians, and birds have begun to emerge in the recent decade (Williams et al., 2023). Visitor effects are usually examined by observing either behavioural (exhibition of certain behaviours, activity budget, space-use), physiological (faecal cortisol, heart rate), or physical variables (bodyweight) of the animals, sometimes combining multiple types of variables (Williams et al., 2023).

Previous literature on the subject suggests that the presence and number of visitors, as well as noise produced by visitors influence these variables in many animals. In Mexican wolves

(*Canis lupus baileyi*), increased visitor numbers have resulted in decreased eating and lying accompanied by an increase in faecal cortisol (Pifarré et al., 2012), which is a physiological indicator of stress. This result could be interpreted to suggest that a decrease in essential behaviours such as eating and lying/resting are indicative of disturbance, since those behavioural changes are accompanied by a physiological stress indicator. In addition to observing resting and eating, other behaviours such as retreating and vigilance are often utilized in behavioural studies to indicate potential disturbance or anxiety. For example, an increase of vigilance is often interpreted negatively due to its evolutionary history as anti-predator behaviour in prey animals such as wallabies (Meade et al., 2021). Vigilance has been observed to increase in response to both high number of nearby visitors and loud noise in koalas, although its association with physiological consequences such as increased faecal cortisol was not determined in the study (Larsen et al., 2014). However, comparison of studies conducted on different species shows that behaviours are often subject to species-specific differences. For example, retreating increased in Western lowland gorillas (*Gorilla gorilla gorilla*) during high visitor attendance (Kuhar, 2008), whereas it decreased in Sumatran orangutans (*Pongo abelii*), following the reintroduction of visitors after COVID-19 lockdowns (Gading et al., 2025).

In addition to the species-specific differences, interpreting and inferring welfare implications from singular variables may be difficult. Behaviour is in this instance notably challenging, as certain behaviours could be interpreted in both positive and negative manner (Sherwen & Hemsworth, 2019). Due to the ambivalent interpretation of behaviours alone, researchers have suggested and utilized physiological indicators in addition to behaviours to aid in their interpretation (Pifarré et al., 2012; Sherwen & Hemsworth, 2019). As an alternative to combining behavioural and physiological variables, some studies have utilized multiple forms of behavioural variables together, such as behaviour and space-use, to assess visitor effects and animal welfare without physiological variables (Beaudin-Judd et al., 2019; Jones et al., 2021).

1.3 Visitor effects on macropods

The study species of the present thesis, *Notamacropus rufogriseus,* is a macropod commonly known as the red-necked wallaby or Bennett's wallaby. *N. rufogriseus* is native to Australia; it is found in Tasmania and south-eastern parts of the mainland (McKenzie et al., 2016). They have also been introduced to countries such as the United Kingdom

(English & Caravaggi, 2020) and New Zealand where they are an invasive species (Latham et al., 2023). *N. rufogriseus* are nocturnal to crepuscular and usually solitary, although they may graze in groups, primarily feeding on grasses and broad-leaf forbs (Wilson & Mittermeier, 2015). The effects of visitors and walkthrough enclosures on the behaviours and enclosure space-use of *N. rufogriseus* and other macropods has previously been studied at zoos in Australia (Meade et al., 2021; Sherwen et al., 2015), the United States and Canada (Beaudin-Judd et al., 2019), as well as the United Kingdom (Williams et al., 2021).

The results from studies on visitor effects on the behaviour of *N. rufogriseus* and other macropods have been somewhat ambivalent. Behaviours such as fleeing (locomotion) and vigilance could be considered antipredator responses in macropods and have been utilized as behaviours of interest in the study of human disturbance in both wild and captive populations (Austin & Ramp, 2019; Meade et al., 2021). Locomotion has been observed to consistently increase with increasing visitor density (Beaudin-Judd et al., 2019) and increasing visitor number (Sherwen et al., 2015), whilst behaviours such as vigilance and resting have had more mixed results. Higher visitor numbers have been linked to increased vigilance in *N. rufogriseus* and other macropod species (Meade et al., 2021; Sherwen et al., 2015), but the vigilance of *N. rufogriseus* did not significantly differ between walkthrough and non-walkthrough exhibit design or by visitor density (Beaudin-Judd et al., 2019), leading to uncertainty whether the mere presence of visitors or their number is more significant. Resting has had similar, fluctuating results, increasing in response to higher visitor density or visitor presence in some studies (Beaudin-Judd et al., 2019; Frost et al., 2022), whilst decreasing in response to visitor number in others (Meade et al., 2021; Sherwen et al., 2015). In addition to the fluctuating results, the interpretation of decreased resting behaviour in macropods and its implications on welfare has been ambiguous, as it has been observed to occur rarely even in the absence of visitors (Meade et al., 2021). Furthermore, a decrease in resting was not accompanied by an increase in faecal glucocorticoid metabolites (FGMs) in other macropod species (Sherwen et al., 2015), which could suggest that a decrease in resting may not – at least alone, function as a proxy indicator of physiological stress in macropods.

In addition to changes in exhibited behaviours, space-use has been observed to differ in response to visitors in *N. rufogriseus*. Some populations have been observed to spend more time in retreat zones during high visitor presence compared to visitor absence in a walkthrough enclosure (Beaudin-Judd et al., 2019), whilst other populations have shown no increase in retreat when exposed to higher visitor numbers (Meade et al., 2021). Additionally, retreat behaviour has not been observed to increase in response to visitor number in other macropod species such as red kangaroos (*Macropus rufus*) or swamp wallabies (*Wallabia bicolor*) (Meade et al., 2021), indicating a potentially species- or population specific response to visitors in macropods. Furthermore, as *N. rufogriseus* populations in both walkthrough and non-walkthrough enclosures appear to prefer retreat areas furthest from the visitors (Beaudin-Judd et al., 2019), the walkthrough activity may not significantly increase spatial avoidance of visitors. Walkthroughs may even be enriching, as *N. rufogriseu*s housed in a walkthrough enclosure have occasionally been observed to engage more in human-animal interactions, including approaching visitors, during visitor presence (Frost et al., 2022).

The previous research on walkthrough exhibits and visitor effects on *N. rufogriseus* have either compared separate zoos offering walkthrough and non-walkthrough enclosures (Beaudin-Judd et al., 2019) examined visitor effects in a multi-species walkthrough enclosure (Meade et al., 2021), or examined visitor presence-absence in one single-species walkthrough enclosure without considering visitor number (Frost et al., 2022). To my understanding, visitor effects on *N. rufogriseus* have not been studied in a single-species walkthrough enclosure in one zoo, with visitor presence-absence within the enclosure, numbers, and noise included, which is what my study aims to investigate.

1.4 Research aims, objectives, and hypotheses

1.4.1 Primary aim: Visitor effect on *N. rufogriseus*

The primary aim of my thesis is to comprehensively examine visitor effects on *N. rufogriseus* housed in a walkthrough enclosure. The objective is to examine the effects of visitor presence within the enclosure (walkthrough activity), the number of visitors inside the enclosure, and visitor-derived noise by observing the behaviour and space-use of the wallabies. My hypotheses included a combination of multiple behaviours and space-use as an indicator of welfare, as based on previous literature the interpretation of behaviours such as vigilance or resting alone is extremely challenging. Assuming that the visitor presence during the walkthrough activity, loud noise from the visitors on the walkthrough, and high visitor numbers disturb the wallabies, I hypothesized that:

H1A. The walkthrough path and areas near it would be used less by the wallabies during visitor presence within the enclosure, loud noise, and high visitor numbers, as they avoid visitor contact and visitor-derived noise.

H1B. The wallabies would express more behaviours potentially indicative of anxiety or disturbance, such as vigilance, locomotion, and retreating, and express less essential behaviours such as foraging/feeding and resting during visitor presence within the enclosure, loud noise, and high visitor number.

1.4.2 Secondary aim: Visitor experience

The secondary aim of my thesis is to examine the experiences and interests of visitors, with the intent to assess whether the walkthrough increases visitor experience and interest towards wildlife and conservation. This together with the primary aim will assist Korkeasaari Zoo in evaluating whether their wallaby walkthrough activity is balanced in terms of visitor experience and wallaby welfare. The objective of my secondary aim is to examine the differences between visitor groups in their experience rating and interest in wildlife and conservation by conducting a visitor questionnaire. Assuming that the walkthrough activity improves visitor experience and interest in wildlife and conservation, I hypothesized that:

H2A. The visitors who participated in the walkthrough would rate their experience higher than those who did not participate.

H2B. The visitors who participated in the walkthrough would rate their interest in wildlife and conservation higher than those who did not participate.

2 Materials & methods

2.1 Site and subjects

I conducted my study at Korkeasaari Zoo, located in Helsinki, Finland. Korkeasaari Zoo provides visitors with the opportunity to see the wallabies up close by entering the wallaby enclosure. This “Wallaby Walkthrough” is open for one hour each day in July.

The Korkeasaari Zoo houses 12 *N. rufogriseus* individuals. The individuals followed a stable feeding schedule and diet throughout the study; dry, basic foods (i.e. dry hay, pellets and tree limbs) were always available, and fresh hay was provided at approximately 15:20

daily. During the observations the individuals were housed in an outdoor enclosure with a total area of 1241m^2. The outdoor area consisted of a large, open-top area with a short fence, and a smaller, square-shaped, mesh-topped area with a ceiling-high fence. The wallabies were free to roam between these outdoor areas during study hours. A partitioned hallway providing the wallabies with an area of reduced visibility was located between the outdoor area and indoor housing. The wallabies were free to enter the hallway during the observations. During nighttime, the wallabies had access to both the indoor and outdoor areas. The full study area is visualized in Figure 1.

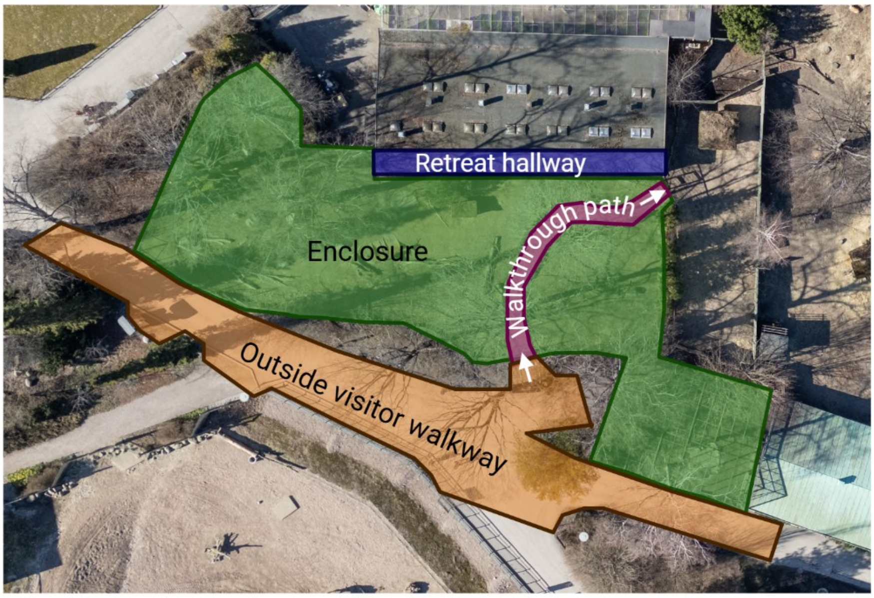

Figure 1. Aerial photograph of the study area. Green = enclosure space. Blue = partitioned retreat hallway. Pink = walkthrough path. Orange = outside visitor walkway. White arrows indicate entry, exit and direction of the walkthrough path. Figure created in Biorender.com

2.2 Data collection and equipment

2.2.1 Behavioural and enclosure space-use data collection

During the study the wallabies were exposed to two treatments: The Closed Walkthrough (CW) treatment with no visitors inside the enclosure, and the Open Walkthrough treatment (OW) with visitors inside the enclosure. The wallabies were also exposed to varying noise levels and visitor numbers as they occurred naturally.

Prior to data collection, I conducted pilot observations in May to familiarize myself with the software and refine my sampling methodology. The observations for the CW treatment were collected during 14 days between 2.6 – 27.6 and 11.8. – 14.8. The observations for the

CW treatment had to be supplemented with the second period of sampling in August, as I discarded any data collected during days when the wallabies' routine differed, an individual was not in the enclosure, or if I noticed that made a significant error during sampling. The observations for the OW treatment were collected during 14 days between 30.6. – 19.7 when the wallaby walkthrough activity was part of the zoo's repertoire.

During observations, I collected behaviour and enclosure space-use data at 3-minute intervals for an hour at 15:30-16:30 with instantaneous scan-sampling using the ZooMonitor-software (Lincoln Park Zoo, 2022). I walked along the visitor walkway outside the enclosure and logged the identity, behaviour and approximate location of each visible individual at the intervals into the software on a tablet. I created an ethogram to be used during behavioural sampling (Table 1). The ethogram consisted of nine behaviours inspired by previous ethograms and observations of macropod behaviours (Beaudin-Judd et al., 2019; Kaufmann, 1974; Russell, 1970; Stirrat, 2000; Watson & Croft, 1993; Williams et al., 2021). Individuals which were not visible were logged as expressing "Out of sight (Retreating)" behaviour, with no location data logged.

Table 1. The ethogram used during the behavioural sampling which consisted of nine behaviours, their descriptions, and any related miscellaneous comments.

Behaviour	Description	Miscellaneous comments
Autogrooming	Individual uses tongue, teeth, fore- or hindlimbs to clean itself.	
Foraging / feeding	Individual reaches for or rips leaves from branches on the ground, eats from feeding troughs and plates, holds food between forelimbs or chews.	If an individual is simultaneously feeding and vigilant, vigilance will be prioritized as the present behaviour
Locomotion	Individual moves around the enclosure either by quick bipedal hopping, or slower quadrupedal movement.	
Negative social behaviour	Individual kicks, strikes, wrestles / spars, or bites other individuals, coupled with agonistic displays.	Agonistic displays include grass-pulling, snorting or growling.
Neutral social behaviour	Individual sniffs or grazes against another individual.	
Positive social behaviour	Individual allogrooms / is allogroomed, playfights.	
Out of sight (Retreat)	Individual is out of sight.	Individuals which are in the retreat hallway but visible from the doorway, are not considered "out of sight / retreating".
Resting	Individual lays down or sits, eyes may be open but the individual is not actively vigilant.	
Vigilance	Individual stands erect or semi-erect, head and ears are up and eyes open. The individual is clearly observing its surroundings.	

Additionally, at each interval I approximated the total number of visitors. During the CW treatment this was the number of visitors outside the enclosure, and during the OW it was the combined number of visitors both inside and outside the enclosure. The noise level within the enclosure was measured with a CESVA SC250 sound level meter (CESVA, n.d.), which was attached to the partitioned wall near the walkthrough path. Two Google Nest Cam (Google, n.d.) cameras were installed to record the enclosure and inside of the partitioned hallway, in case I needed to revise my observations later.

I downloaded data relating to weather such as air temperature, cloud cover, precipitation amount and wind speed from the Finnish Meteorological Institutes website (Finnish Meteorological Institute, 2025). The Kaisaniemi observation station was chosen as the source of weather observations due to its proximity to the Korkeasaari Zoo, thus providing the most accurate weather data.

In the planning stages of my study, a faecal analysis was considered in order to determine physiological indicators of stress in the wallabies, but such analysis was ultimately decided to be outside the scope of this thesis. Furthermore, obtaining threshold values indicative of stress in the study population would have required the wallabies to be exposed to stress prior to the experiment, which my supervisors and I saw as ethically precarious. Without the physiological indicators we cannot be as certain of the physiological welfare implications, but both behaviours and space-use patterns together should be sufficient to indicate whether visitors have a disturbing effect on the wallabies.

2.2.2 Visitor questionnaire data collection

Using signs positioned at the front and back of the wallaby enclosure, visitors were requested to fill in an electronic questionnaire. The questionnaire could be accessed by scanning a QR-code on the sign, which would take the visitor into a Microsoft Forms page. The questionnaire was anonymous and available in both Finnish and English.

In the questionnaire visitors were requested to indicate whether they experienced the walkthrough or not that day, with the intention to divide them into the Walkthrough (W) and No Walkthrough (NW) visitor groups. Additionally, questions on their interest in wildlife and conservation, and their opinions on the impact of the walkthrough activity on visitors and animals were presented. To confirm whether the difference between groups in experience was due to actual experience or imagined experience, I tested them for both

(Q2 and Q3). I decided to do this, because if there was a difference between groups in imagined experience but not actual experience, it may be due to cognitive bias and not because the walkthrough truly improves the experience. Furthermore, included an “I don’t know” option for the impact questions (Q3 and Q6) but not the interest and experience questions (Q2, Q4, & Q5). I chose to do this as I thought that visitors might not have an opinion on a matter they might not feel educated in, such as impact on welfare, but they should be able to evaluate their own experience and interests. The questions and their corresponding answer options can be found in Table 2.

Table 2. Visitor questionnaire questions and their corresponding answer options. The questionnaire consisted of 6 questions, only one of the answer options could be picked in response to each question.

Question	Possible answers				
Q1. Did you participate in the wallaby walkthrough today or did you observe the wallabies from outside the enclosure?	I participated in the wallaby walkthrough.	I observed the wallabies from outside the enclosure.			
Q2. How would you rate your experience of the wallabies today?	Very bad	Bad	Neutral	Good	Very good
Q3. Which do you think would offer a better experience for a visitor: participating in the walkthrough or observing the wallabies from outside the enclosure?	Participating in the walkthrough	Both offer an equal experience	Observing the wallabies from outside the enclosure	I don’t know	
Q4. Rate the following statement according to your personal opinion: My experience of the wallabies today increased my interest in wildlife.	Strongly disagree	Disagree	Neither agree nor disagree	Agree	Strongly agree
Q5. Rate the following statement according to your personal opinion: My experience of the wallabies today increased my interest in conservation.	Strongly disagree	Disagree	Neither agree nor disagree	Agree	Strongly agree
Q6. I think that the visitor’s presence in the wallaby enclosure will impact the wallabies’ welfare…	Negatively	Neutrally	Positively	I don’t know	

2.3 Data refinement

Data refinement was conducted in Rstudio (Posit Team, 2025, v2025.9.0.387) running R (R Core Team, 2025, v4.5.1).

2.3.1 General data refinement

I discarded precipitation, wind speed and cloud cover from all datasets due to insufficient data and biological irrelevance. The enclosure is located near the center of the zoo, and is mostly surrounded and shaded by trees, which prompted me to conclude cloud cover and wind speed as largely irrelevant. Precipitation data was insufficient for modelling. Thus, I used only air temperature (°C) as the environmental covariate in the analyses.

The correlation between walkthrough treatment type and total visitor number was moderate to strong in space-use data and behavioural data (Pearson's correlation coefficients of 0.72 and 0.69 respectively, obtained using function "cor()" from R base package *stats*), with the highest visitor numbers occurring during the OW treatment. As I was primarily interested in the effect of the visitors inside the enclosure, I subset the visitor data to include only observations from the OW treatment and only the number of visitors inside of the enclosure, instead of total visitor number. I divided the number of visitors inside the enclosure into three categories: Low (<10), Moderate (10-19), and High (≥20) to simplify the models. Instances of >30 visitors were included in the High category to improve model convergence, as only a few instances of visitor numbers at or above 30 were observed.

The correlation between walkthrough treatment type and noise was weak to moderate in both space-use data and behavioural data (Pearson's correlation coefficients of 0.39 and 0.40 respectively). Because noise was not strongly correlated with a walkthrough treatment type, I decided to examine the effect of noise using observations from both treatments. I divided noise into three levels: Low (40-50dB), Moderate (50-60dB), and Loud (≥60dB) to simplify the models. Noise levels over 70dB were included in the Loud category to improve model convergence, as only few instances of noise level at or above 70dB were observed.

2.3.2 Space-use data refinement

I removed any observations with no location data from the space-use dataset. Thus, the space-use data consisted of only visible, identifiable individuals.

For the space-use analysis I divided the enclosure into sections determined by approximate distance to the path and created a figure using Biorender.com (Figure 2). Each section was maximum one square in width, and diagonally the squares followed Chebyshev distance. In the colour-coded figure, each section consists of the same colour squares on both sides of the path. Originally, I attempted to divide the sections based on path side in addition to distance, but some sections did not have sufficient data for the models to converge properly. Any squares with zero observations during both treatments are transparent and not considered as part of the sections in the analyses, even if they are within the enclosure.

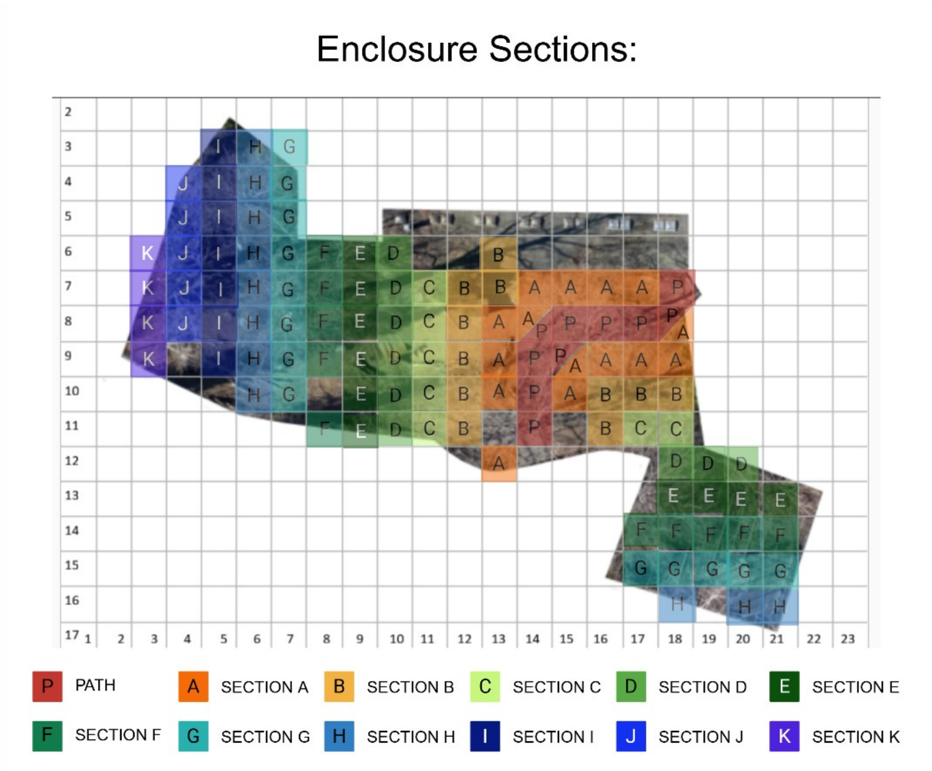

Figure 2. The study enclosure divided into sections to be used in the analysis. Sections extend to both sides of the path, with each section one grid cell further away from the path. SectionB and SectionD include the retreat hallway doorways. Figure created in Biorender.com.

2.3.3 Behavioural data refinement

I removed any observations where the identity of a visible individual could not be confirmed. Additionally, any observations with no behavioural data were discarded from the behavioural dataset, and I considered any non-visible individuals (“Out of sight”) to exhibit retreating behaviour. Thus, the behavioural data consisted of visible and identifiable individuals and any non-visible individuals automatically assumed to be retreating. I combined the original positive-, neutral- and negative social interactions seen in Table 1. into a single "Social behaviour", because the observations of the three separately were rare. The final behavioural dataset thus includes seven behavioural categories: Autogrooming, Foraging/feeding, Locomotion, Retreating, Resting, Social behaviour, and Vigilance.

2.3.4 Questionnaire data refinement

For the analysis of the questionnaire data, I compiled answers from both the Finnish and English questionnaires into one dataset. I removed any filled forms which indicated having participated in the walkthrough activity before the walkthrough was opened in July. For the analysis of the questionnaires, I used the answers to Q1 to divide responders into two visitor groups: those who participated in the walkthrough (W) and those who did not (NW). I created separate datasets for Q2-Q6 and removed any "I don't know" answers from the datasets of Q3 and Q6, as they would not offer the required information.

2.4 Data analysis

All data analyses were conducted in Rstudio (Posit Team, 2025, v2025.9.0.387) running R (R Core Team, 2025, v4.5.1). Additionally, I used packages *dplyr* (Wickham et al., 2023, v1.1.4), *performance* (Lüdecke et al., 2025, v0.15.2), *emmeans* (Lenth et al., 2025, v2.0.0), *DHARMa* (Hartig et al., 2024, v 0.4.7) and *ggplot2* (Wickham et al., 2025, v4.0.0) for data wrangling, model diagnostics, and visualization.

2.4.1 Initial space-use data exploration

To initially investigate the space-use data, I created a heatmap comparing observations between the OW and CW treatments. I started with separate datasets for the treatments, calculating the proportion of observations in a given square to all spatial observations of the treatment (pCW and pOW). I then calculated the ratio of those proportions to determine whether a given square was used proportionally more during the CW or OW treatment (pCW/pOW). Finally, I took the Log2 of this ratio for each square, resulting in positive values when a given square was used more during CW, and negative values when it was used more during OW (Log2(pCW/pOW)). I used Biorender.com to construct a heatmap, in which the red colour indicates positive values and blue indicates negative values. I created a colour-gradient between these colours, with each step indicating a 0.5 change in value. This heatmap can be found as Figure 3. in the results section 3.1.1.

As additional initial investigation I also conducted a Vanderploeg & Scavia's electivity index (Vanderploeg & Scavia, 1979) analysis for the OW and CW treatments, to examine which sections were preferred or avoided during each treatment. The Vanderploeg & Scavia's electivity index returns values between –1 and 1, with 0 indicating random selection, -1 strong avoidance, and 1 strong preference (Vanderploeg & Scavia, 1979). I assumed values of below -0.25 and above 0.25 to indicate significant results (Van Ginderdeuren et al., 2014) and used the function "vs_electivity" from the package *electivity* (Quintains, 2019, v1.0.2) to conduct the analysis. The results of the electivity index analysis can be found in the results section 3.1.1.

2.4.2 Initial behavioural data exploration

To initially explore how behaviours differ between treatments and individuals, I constructed stacked bar-charts of behavioural proportions separated by treatment and by individual. I calculated the proportions by dividing the number of times a given behaviour was observed in a treatment or individual (nBehav) by all observations of that treatment or individual (nBehav/nTotal). The results visualized as stacked bar-charts of behavioural proportions can be found in Figure 7. and Figure 8. in the results section 3.2.1.

2.4.3 Space-use and behavioural models

To examine differences in enclosure space-use and behaviour between the walkthrough treatments (CW, OW), noise level (Quiet, Moderate, Loud), and visitor number inside the enclosure (Low, Moderate, High), while accounting for temperature, individual and daily variation, I analysed section-use counts and behavioural counts using four generalized linear mixed models with the function "glmmTMB" from the package *glmmTMB* (Brooks et al., 2025, v 1.1.12). I used Model1 and Model2 to examine space-use, and Model3 and Model4 to examine behaviour. I subset the datasets for Model2 and Model4 to include only observations from the OW treatment, as they were used to examine the response to visitors inside the enclosure.

I used a truncated Poisson distribution with a log-link in Model1 and Model3, and a regular Poisson distribution with log-link in Model2 and Model4. The purpose of using a truncated Poisson was to address the fact that the sampling method should not introduce zeroes into the spatial or behavioural data, as only observed space-use and behaviour is logged, thus zeroes could be excluded from the distribution (Zuur et al., 2009). However, the visitor number models (Model2 & 4) had difficulties converging with truncation, leading to the utilization of a regular Poisson distribution.

The response variable for both space-use models (Model1 & 2) was the number of times a given section was used (SectCount). The response variable for both behavioural models (Model3 & 4) was the number of times a given behaviour was expressed (BehavCount). Fixed effects included the interaction between walkthrough treatment and sections (Model1 only) or interaction between walkthrough treatment and behaviours (Model3 only), interaction between noise level and sections (Model1 & 2) or interaction between noise level and behaviours (Model3 & 4), interaction between visitor number inside the enclosure and sections (Model2 only) or interaction between visitor number inside the enclosure and behaviours (Model4 only), the interaction between temperature and sections (Model1 & 2) or the interaction between temperature and behaviours (Model3 & 4). I did not include interactions between walkthrough treatment and noise level, walkthrough treatment and temperature, visitor number and noise level, or visitor number and temperature in any of the four models, as I made the simplifying assumption that the noise- and temperature sensitivity of the wallabies would remain constant during both treatments and visitor numbers in all models.

I included an offset of total observations for each individual x day combination (TotalObs) in each model. With this offset I effectively modelled frequency of occurrence per unit of exposure (Zuur et al., 2009). In my models in the biologically relevant sense this is the frequency of use of each section in relation to total daily space-use (Model1 & 2), or frequency of each behaviour in relation to total daily behavioural activity (Model3 & 4). Additionally, in the space-use models (Model1 & 2) I included an offset of section size (SectionArea) to account for the varying section size, as I expected larger areas to be used more through random chance. Furthermore, I included individual identity and days as random effects in all models to account for individual and daily variation. I did not include sex or age of individuals as a fixed effects to simplify the models. Model names, purposes and formulas are summarised in Table 3.

Table 3. The name, purpose, and formula of each GLMM used in the analysis of space-use and behavioural data.

Model:	**Model results utilized in examining:**	**Model formula used in R:**
Model1	Space use in response to walkthrough treatment, noise level, temperature	SectCount ~ Walkthrough*Sections + Temp*Sections + Noise*Sections + (1|Individual) + (1|Day) + offset(log(TotalObs*SectionArea)), family = truncated_poisson()
Model2	Space-use in response to visitor number inside the enclosure	SectCount ~ Visitors*Sections + Temp*Sections + Noise*Sections + (1|Individual) + (1|Day) + offset(log(TotalObs*SectionArea)), family = poisson ()
Model3	Behaviour in response to walkthrough treatment, noise level, temperature	BehavCount ~ Walkthrough*Behaviours + Temp* Behaviours + Noise*Behaviours + (1|Individual) + (1|Day) + offset(log(TotalObs)), family = truncated_poisson()
Model4	Behaviour in response to visitor number inside the enclosure	BehavCount ~ Visitors*Behaviours + Temp*Behaviours + Noise*Behaviours + (1|Individual) + (1|Day) + offset(log(TotalObs)), family = poisson()

The reference level for walkthrough was the CW treatment in Model1 & Model3. For noise level the reference was “Low (40-50dB)” in all models. For Model2 and Model4, the reference level for visitor number was “Low (<10)”. Temperature was centered at the mean of each model’s dataset (Model 1: 19.8 °C, Model2: 22.3 °C, Model3: 19.8 °C and Model4: 22.1 °C), which was used as the reference level.

2.4.4 Visitor questionnaire analysis

I conducted Mann-Whitney U tests on Q2, Q4, Q5, and Q6 to analyse whether the visitor groups’ responses differ (Chicco et al., 2025) and to test my hypothesis that the NW visitor group would rate their experience and interest lower, and their impact more negatively. I used the function “wilcox_test” from the package *coin* (Hothorn et al., 2023, v1.4.3). In these tests the questionnaire answers were the dependent variable, and the visitor groups the independent variable. I added alternative hypothesis arguments “alternative = less”, to indicate my hypothesis that the NW visitor group should have lower scores than the W group (Hothorn et al., 2023, v1.4.3). As the answer options for Q3 are nominal instead of ordinal, and the Mann-Whitney U requires ordinal data (Chicco et al., 2025), I could not use a Mann-Whitney U test for Q3. I originally planned to use a Chi-Square Test of Independence instead to analyse difference between groups in Q3 (Chicco et al., 2025). However, the expected counts for some cells of the contingency table for Q3 were <5, which lead me to choose the Fisher’s exact test, a commonly suggested option in such a case. Thus, to analyse the difference between the visitor groups' answers to Q3, I conducted a Fisher's exact test using the function "fisher.test" from the R base package *stats,* which allows Fisher's exact tests on contingency tables larger than the standard 2x2.

In addition to analysing differences between groups, I decided to investigate whether the combined visitor groups' responses differed from neutral in order to observe the general opinion of visitors. To examine this, I conducted one-sample Wilcoxon signed-rank tests on Q2, Q4, Q5, and Q6 by using the function "wilcox.test" from the R base package *stats* without grouping answers by visitor group. In these tests, the argument "mu =" was set to the "neutral" response score, which was "2" in Q6 and "3" in Q2, Q4, and Q5. I added the alternative hypothesis arguments "alternative = greater" for Q2, Q4 and Q5, to indicate the hypothesis that on average visitors should rate their experience as positive, and observing the wallabies increases interest in wildlife or conservation. I added the argument "alternative = less" for Q6, to examine whether visitors on average rate their impact on the animals as negative, thus the response scores should be significantly lower than the neutral option. I conducted a Chi-Square Goodness-of-Fit test on Q3, to analyse whether the combined answers from both visitor groups differed from neutral (Chicco et al., 2025). To conduct the Chi-Square GOF test I used function "chisq.test" from the R base package *stats,* without grouping responses by visitor group. In the Chi-square test I set the probability argument to equal 1/3 for each answer option, because assuming the visitors have no preference, each of the three responses should occur equally (Chicco et al., 2025).

2.5 Research ethics

In accordance with 21§ of 497/2013 "Act on the Protection of Animals Used for Scientific or Educational Purposes / Laki tieteellisiin ja opetustarkoituksiin käytettävien eläinten suojelusta", Korkeasaari Zoo has a permit (permit ESAVI/165/04.10.05/2017) to conduct observational studies on vertebrates. The current study did not cause harm to the animals, as it was purely observational and the environment of the animals was not manipulated in an unusual manner.

Responding to the visitor questionnaire was anonymous and voluntary; it was not a prerequisite for participation in the walkthrough. Only individuals above the age of 15 were requested to respond to the questionnaire, and respondents were informed that the answers would be utilized in this thesis.

I did not utilize artificial intelligence to generate or edit the images or text in this thesis. I utilized artificial intelligence (OpenAI GPT-5) to assist in the coding of the data analysis.

3 Results

3.1 Enclosure space-use results

3.1.1 Enclosure space-use initial exploration results

As an initial investigation, I created a heatmap of the space-use data, which can be found in Figure 3. In the heatmap, a clear trend can be observed, where the walkthrough path and its immediate surroundings were used more during the CW treatment than during the OW treatment.

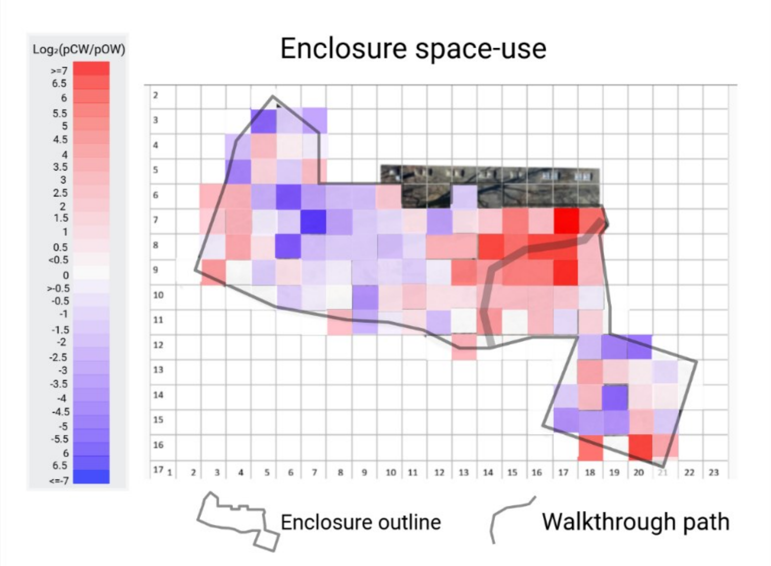

Figure 3. Enclosure space-use data as a heatmap. Red squares = more use during CW. Blue squares = more use during OW. Each step on the colour gradient indicates a 0.5 difference in value (except values between 0 and -0.5 or 0.5). OW: n = 2014, CW: n = 2576. Figure created in Biorender.com

Assuming significant preference at an electivity score above 0.25 and avoidance below -0.25, the Vanderploeg & Scavia's electivity analysis of the OW treatment indicated a preference for SectionB, SectionD and SectionE, and avoidance of Path, SectionA, SectionG, SectionJ, and SectionK (Table 4). Electivity analysis of the CW treatment indicated a preference for SectionA and SectionD, and avoidance of SectionF, SectionG, and SectionI (Table 4). These results appeared to be in unison with the trend I observed in the heatmap, as areas closest to the visitor path were avoided during the OW treatment but not during the CW treatment.

It must be noted that the heatmap and electivity analysis were strictly for initial investigation, as they only present the difference in space-use between the two treatments without accounting for other effects. I addressed the effects of noise, visitor number and temperature, as well as the individual and daily variation in my generalized linear mixed models, which can be found in results sections 3.1.2, 3.1.3, 3.1.4, and 3.1.5.

Table 4. Preference and avoidance of sections during OW and CW treatment according to the Vanderploeg & Scavia's electivity index. Cyan = Avoidance. Orange = Preference. White = Neutral. OW: n = 2014, CW: n = 2576.

Section	OW treatment	CW treatment
Path	-0.877	-0.024
SectionA	-0.669	0.289
SectionB	0.319	0.225
SectionC	0.086	0.035
SectionD	0.544	0.262
SectionE	0.251	-0.137
SectionF	-0.136	-0.503
SectionG	-0.255	-0.429
SectionH	-0.059	-0.100
SectionI	-0.227	-0.400
SectionJ	-0.605	0.010
SectionK	-0.396	0.054

3.1.2 Walkthrough treatment: effect on space-use

I found a significant effect of the OW treatment on enclosure space-use, as the OW treatment was associated with a decreased use of Path, SectionA, SectionG and SectionH (Figure 4, Table A1).

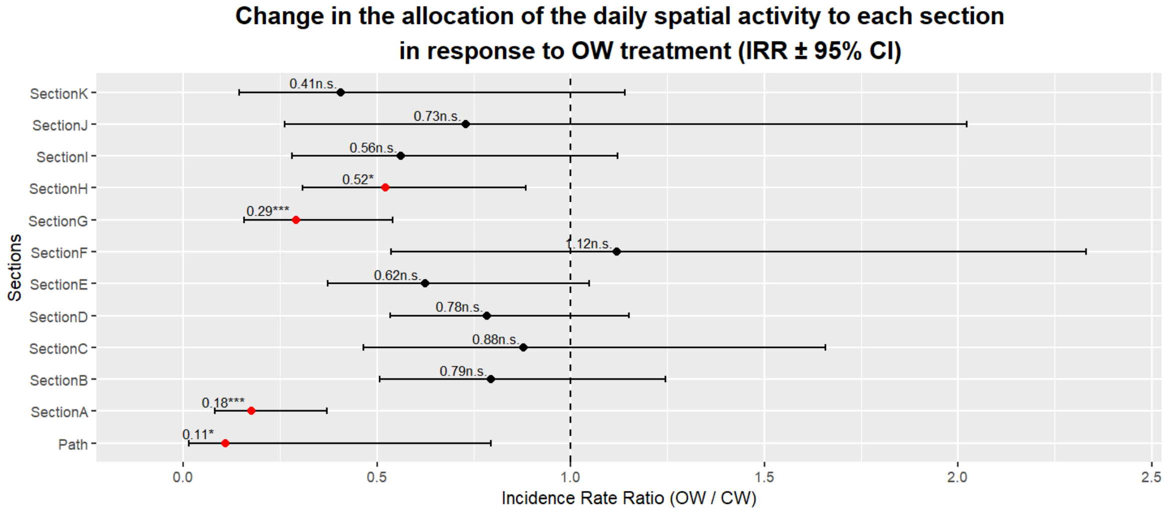

Figure 4. Change in the allocation of the daily spatial activity to each section in response to the OW treatment. Results as the Incidence Rate Ratio (±95 % CI) in section use between the OW and CW treatment. Values < 1 indicate less use of the given section during OW, values > 1 indicate more use of the given section during OW. Red colour indicates significant results, and stars indicate the level of significance (p-values of each star indicator: *<0.05, **<0.01, ***<0.001). OW: n = 2014, CW: n = 2576.

3.1.3 Noise: effect on space-use

I found a significant effect of noise on space-use, as assuming an equal effect of noise in both walkthrough treatments, in comparison to quiet noise, moderate noise was associated with increased use of Path, SectionA, SectionD, SectionG and SectionH (Figure 5, Table A2). Loud noise was not associated with any change in space-use when compared to quiet noise (Figure 5, Table A3). However, loud noise was associated with decreased use of SectionA, SectionD and SectionE when compared to moderate noise (Figure 5, Table A4).

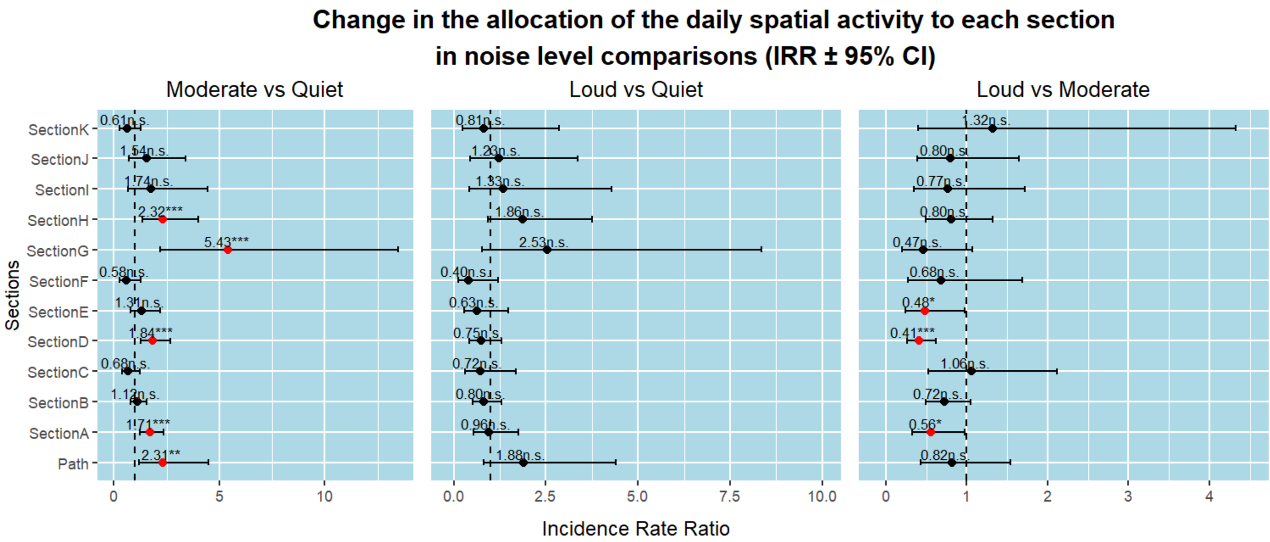

Figure 5. Change in the allocation of the daily spatial activity to each section in response to different noise levels. Results as the Incidence Rate Ratio (±95 % CI) in section use between the noise levels indicated in the title above each facet. Values > 1 indicate more use of the given section during the noise level first in the facet title, values < 1 indicate less use of the given section during the noise level first in the facet title. Red colour indicates significant results, and stars indicate the level of significance (p-values of each star indicator: *<0.05, **<0.01, ***<0.001). Quiet: n = 944, Moderate: n = 3006, Loud n = 640.

3.1.4 Visitor number: effect on space-use

I found a significant effect of visitor number inside the enclosure on space-use by using only observations from the OW treatment. High and moderate visitor numbers were not associated with an increased or decreased use of any section when compared to low visitor number (Figure 6, Table A5 and Table A6). However, high visitor number was associated with decreased use in SectionB and SectionD when compared to moderate visitor number (Figure 6, Table A7).

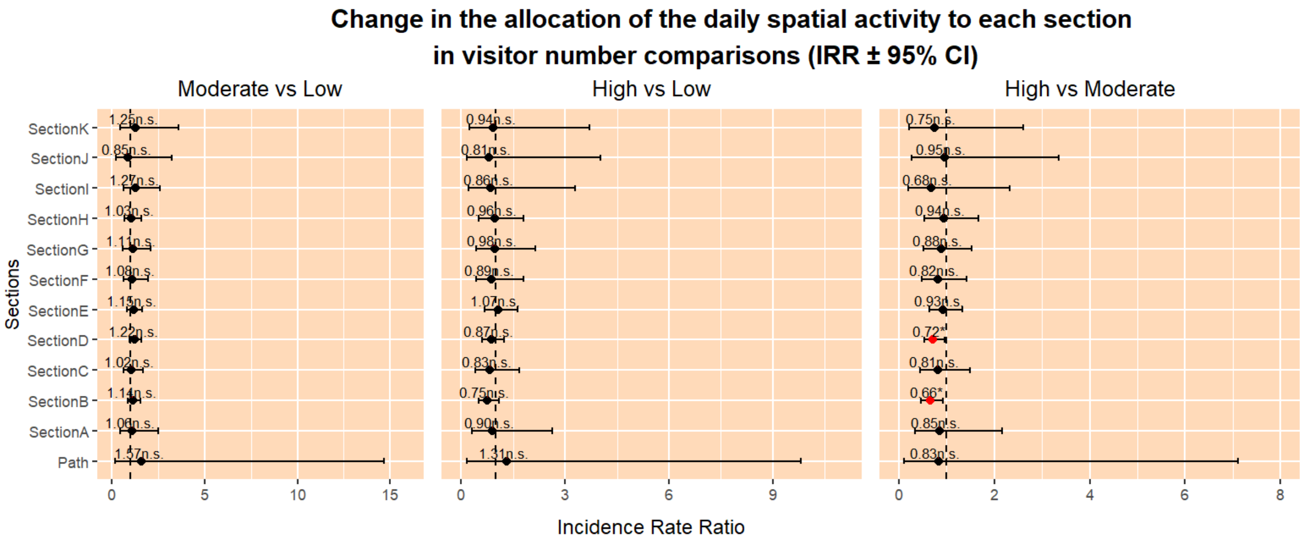

Figure 6. Change in the allocation of the daily spatial activity to each section in response to different visitor number levels. Results as the Incidence Rate Ratio (±95 % CI) in section use between the visitor number levels indicated in the title above each facet. Values > 1 indicate more use of the given section during the visitor number level first in the facet title, values < 1 indicate less use of the given section during the visitor number level first in the facet title. Red colour indicates significant results, and stars indicate the level of significance (p-values of each star indicator: *<0.05, **<0.01, ***<0.001). Low: n = 422, Moderate: n = 1276, High: n = 316.

3.1.5 Temperature: effect on space-use

Although temperature was included in the model as a covariate and not a predictor of interest for welfare assessment, I found a significant effect of temperature on space-use (Table A8). Higher temperatures were associated with increased use of SectionA (p = 0.012), SectionB (p = 0.003), SectionE (p = 0.024), and SectionG (p = 0.039).

3.2 Behavioural results

3.2.1 Behaviour initial exploration

As initial investigation, I created stacked bar charts of behavioural proportions separated by treatment (Figure 7.) and by individuals (Figure 8.). Based on the comparison of behavioural proportions between the CW and OW treatments, it appears that resting and foraging/feeding decrease and retreating increases during OW. There appears to be little to no change in vigilance, autogrooming or locomotion. Based on the comparison of behavioural proportions between individuals, variation in behavioural proportions appears to be present. Both bar-charts indicate that autogrooming, locomotion, and vigilance are expressed rarely across both treatments and all individuals. Most of the behavioural activity appears to be allocated to foraging/feeding, retreating and resting in both treatments.

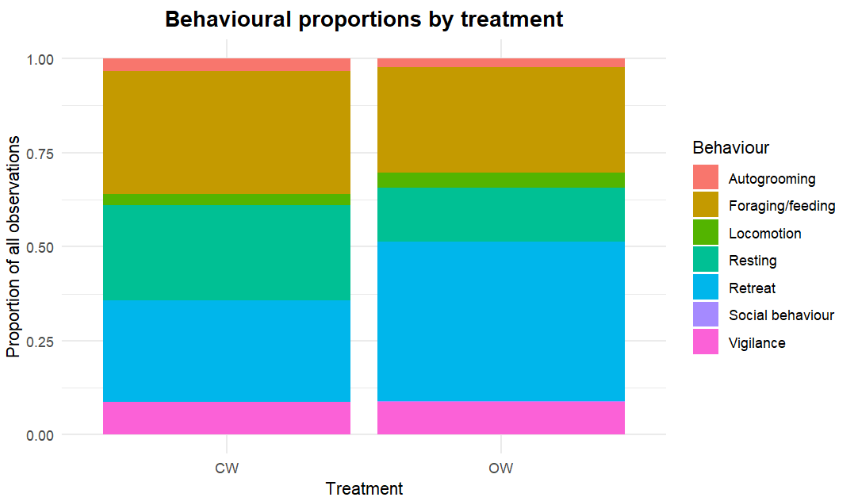

Figure 7. Stacked bar-chart of behavioural proportions in the CW and OW treatment. Each colour band signifies a different behaviour and its proportion out of all observations of a treatment. OW: n = 2014, CW: n = 2576.

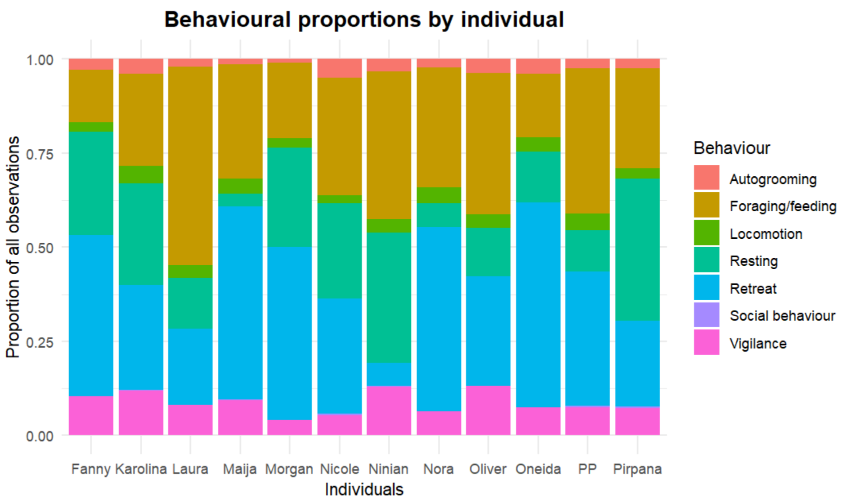

Figure 8. Stacked bar-chart of behavioural proportions of each individual in the study. Each colour band signifies a different behaviour and its proportion out of all observations of a given individual. Fanny: n = 585, Karolina: n = 585, Laura: n = 585, Maija: n = 585, Morgan: n = 585, Nicole: n = 585, Ninian: n = 585, Nora: n = 585, Oliver: n = 585, Oneida: n = 582, PP: n = 585, Pirpana: n = 585.

As was the case with initial space-use investigations, it must be noted that these charts do not take into account other effects such as noise, visitor number, or environmental conditions, which are addressed in the generalized linear mixed models in sections 3.2.2, 3.2.3, 3.2.4, and 3.2.5.

3.2.2 Walkthrough treatment: effect on behaviour

I found a significant effect of the OW treatment on behaviour, as the OW treatment was associated with a decrease of autogrooming, foraging/feeding, retreating, and resting (Figure 9, Table A9).

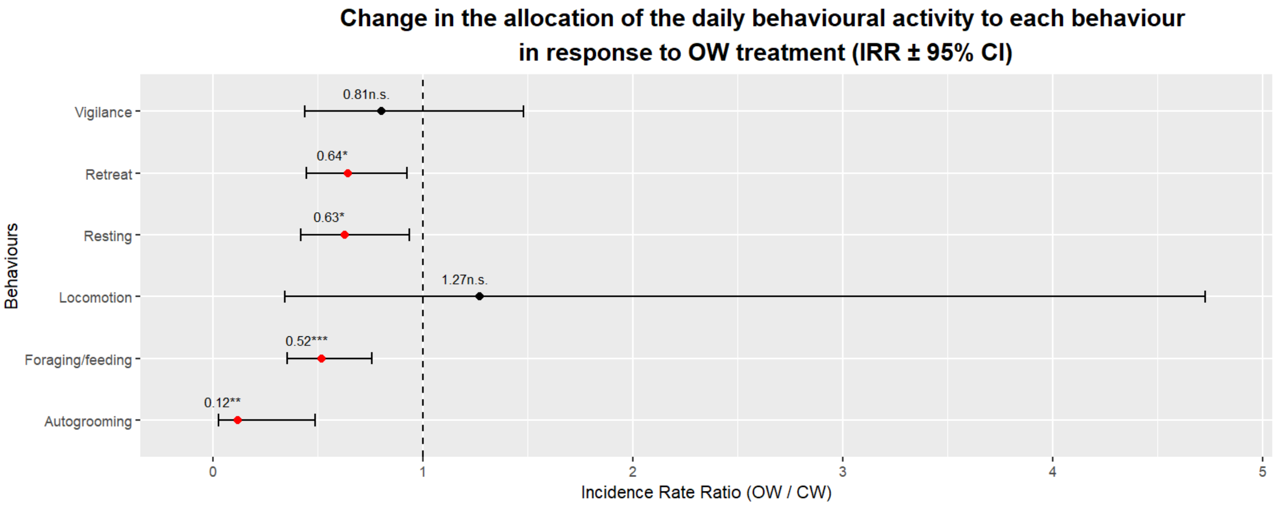

Figure 9. Change in the allocation of the daily behavioural activity to each behaviour in response to the OW treatment. Results for each behaviour as the Incidence Rate Ratio (±95 % CI) in behaviour between the OW and CW treatment. Values < 1 indicate less engagement in a given behaviour during OW, values > 1 indicate more engagement in the given behaviour during OW. Red colour indicates significant results, and stars indicate the level of significance (p-values of each star indicator: *<0.05, **<0.01, ***<0.001). OW: n = 3492, CW: n = 3525. I excluded social behaviour from the figure due to its large 95% CI.

3.2.3 Noise: effect on behaviour

I found a significant effect of noise on behaviour, as assuming equal effect of noise in both walkthrough treatments, moderate noise was associated with increased foraging/feeding, retreating, resting and vigilance when compared to quiet noise (Figure 10, Table A10). Loud noise was associated with increased retreating when compared to quiet noise (Figure 10, Table A11). Loud noise was associated with decreased foraging / feeding, retreating, and resting when compared to moderate noise (Figure 10, Table A12).

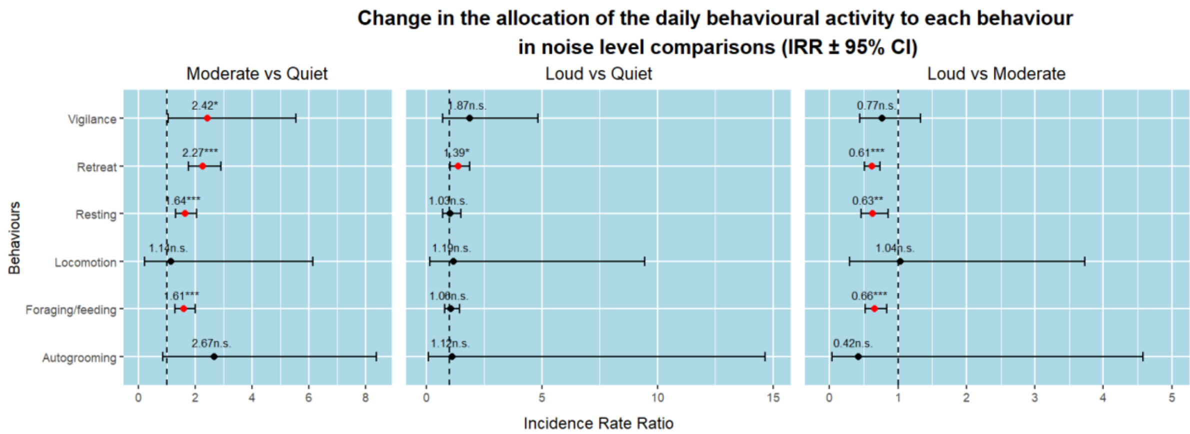

Figure 10. Change in the allocation of the daily behavioural activity to each behaviour in response to different noise levels. Results as the Incidence Rate Ratio (±95 % CI) in behaviour between the noise levels indicated in the title above each facet. Values > 1 indicate more engagement in the given behaviour during the noise level first in the facet title, values < 1 indicate less engagement in the given behaviour during the noise level first in the facet title. Red colour indicates significant results, and stars indicate the level of

significance (p-values of each star indicator: *<0.05, **<0.01, ***<0.001). Quiet: n = 1187, Moderate: n = 4786, Loud: n = 1044. I excluded social behaviour from the figure due to its large 95% CI.

3.2.4 Visitor number: effect on behaviour

I found a significant effect of visitor number inside the enclosure, as by using observations only from the OW treatment, moderate visitor number was associated with increased retreating when compared to low visitor number (Figure 11, Table A13). High visitor number was not associated with a significant change in behaviours when compared to low visitor number (Figure 11, Table A14). However, high visitor number was associated with a decreased foraging / feeding and retreating when compared to moderate visitor number (Figure 11, Table A15).

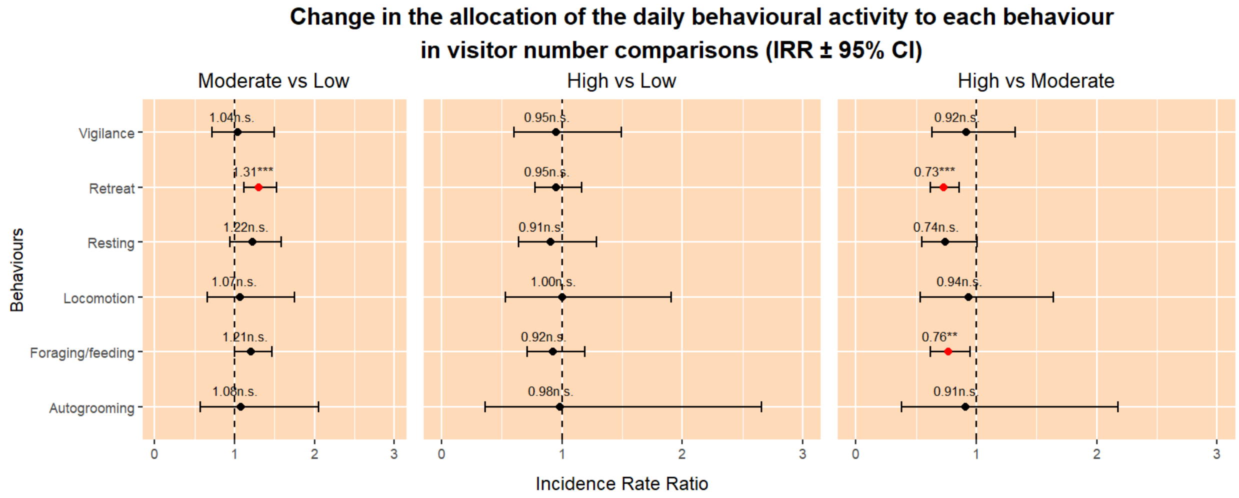

Figure 11. Change in the allocation of the daily behavioural activity to each behaviour in response to different visitor number levels. Results as the Incidence Rate Ratio (±95 % CI) in behaviour between the visitor number levels indicated in the title above each facet. Values > 1 indicate more engagement in the given behaviour during the visitor number level first in the facet title, values < 1 indicate less engagement in the given behaviour during the visitor number level first in the facet title. Red colour indicates significant results, and stars indicate the level of significance (p-values of each star indicator: *<0.05, **<0.01, ***<0.001). Low: n = 732, Moderate: n = 2184, High: n = 576. I excluded social behaviour from the figure due to its large 95% CI.

3.2.5 Temperature: effect on behaviour

Although temperature was mainly included in the model as a covariate and not a predictor of interest for welfare assessment, I found a significant effect of temperature on behaviour (Table A16). Assuming an equal effect of temperature in both walkthrough treatments, higher temperature was associated with increased autogrooming (p = 0.045), foraging/feeding (p = 0.003), retreating (p = 0.015), and resting (p = 0.003). The effect of temperature on locomotion and social behaviour could not be estimated reliably.

3.3 Visitor questionnaire results

3.3.1 Visitor group difference in responses

After conducting the Mann-Whitney U tests and the Fisher's exact test on grouped visitor responses, I found a significant difference between the visitor groups' responses to Q2 and Q6 (Table 5).

Table 5. The results of the Mann-Whitney-U tests on grouped visitor responses. Bold p-values indicate questions where the NW visitor group's responses were significantly lower on the Likert scale compared to those from group W.

Question	N_NW	N_W	Z	r	p-value
Q2	131	58	-4.086	0.297	**< 0.001**
Q4	131	58	-1.353	0.098	0.088
Q5	131	58	0.103	0.008	0.540
Q6	83	36	-1.958	0.179	**0.020**

I found that for Q2, the NW visitor group gave significantly lower Likert scores compared to the W visitor group (Table 5). This result indicates that the visitor who did not participate in the walkthrough rated their experience significantly lower than the visitors who did participate.

I found no significant difference in the visitor groups' answers in the Fisher's exact test on Q3 ($p = 0.209$). This indicates that visitor groups did not significantly differ in their perception of whether the best experience is offered by the walkthrough, no walkthrough, or equally by both.

Additionally, the Mann-Whitney U tests on Q4 and Q5 did not result in significant differences in the responses of the visitor groups (Table 5). This result indicated that there was no significant difference between the visitor groups in terms of interest towards wildlife and conservation after observing the wallabies.

I found that for Q6, the NW visitor group gave significantly lower scores compared to the W group (Table 5). The lower score in this question signified that the impact of visitor presence inside the enclosure was perceived more negatively by those who did not participate in the walkthrough.

3.3.2 General visitor responses

After conducting the one-sample Wilcoxon signed-rank tests on ungrouped visitor responses to Q2, Q4, Q5, and Q6 (Table 6.) and Chi-square test on Q3, I found a significant difference from a neutral answer in the response to Q2, Q3, Q4, and Q5.

Table 6. The results of the one-sample Wilcoxon signed-rank tests on ungrouped visitor responses. Bold p-values indicate questions where answers were significantly different from neutral. (Q2, Q4, Q5 alternative = greater, Q6 alternative = less.)

Question	N_total	N_NotNeutral	Z	r	p-value
Q2	189	161	9.36	0.74	**<0.001**
Q4	189	132	7.81	0.68	**<0.001**
Q5	189	118	7.15	0.66	**<0.001**
Q6	119	72	-0.205	0.024	0.408

I found a significant difference from "Neutral" in the combined visitor groups' responses to Q2, indicating that on average visitors rate their experience significantly higher than neutral (Table 6).

From the Chi-square test on Q3, I found a significant difference from "Neutral" in the combined visitor groups' responses (N = 180, X^2 = 116.4, df = 2, p < 0.001), indicating that on average visitors perceive a significant difference in the experience offered by walkthrough and no walkthrough. The standardized residuals (stdres) for the Chi-square test indicated that the perception of the walkthrough being better occurred more frequently than expected (stdres = 10.436), whilst the perception that the no walkthrough is better or they are equal occurred less frequently than expected (stdres = -7.589 and stdres = -2.846 respectively). This result indicates that on average, visitors perceive the walkthrough to offer a better experience.

From the one-sample Wilcoxon signed-rank test on combined visitor groups' responses to Q4 and Q5, I found a significant difference from "Neither agree nor disagree" in both Q4 and Q5 (Table 6), indicating that on average visitors rated their interest in wildlife and conservation higher than neutral after observing the wallabies. I found no significant difference from a neutral answer in the combined visitor groups' responses to Q6, indicating that on average visitors did not think that the walkthrough would have a negative impact on the wallabies' welfare (Table 6).

4 Discussion

4.1 Behaviour and space-use

The primary aim of this thesis was to examine visitor effects in the form of visitor presence inside the enclosure, number of visitors, and noise level on red-necked wallabies by observing their behaviour and space-use. The results indicate the existence of some visitor effects in *N. rufogriseus*, influencing both their behaviour and space-use, although the observed effects did not conform to the full extent of my original hypotheses. This indicates that whilst the presence of visitors within the enclosure, visitor number and noise has some effects on *N. rufogriseus* and thus implications for their welfare, these effects may be minor enough to mitigate without fully ceasing the walkthrough activity.

Behavioural results indicated that some essential behaviours (resting and foraging/feeding) decreased in response to visitor presence, as less of the daily behavioural activity was allocated towards autogrooming, foraging/feeding, retreating, and resting when visitors were present in the enclosure during the OW treatment. However, as the wallabies have a constant source of dry hay and pellets, the current temporary decrease in feeding during the walkthrough may not cause significant harm to welfare in the form of long-term hunger, but may signify some disturbance. Furthermore, the decrease in essential behaviours was only partially in unison with original hypothesis as it was not accompanied by an increase in vigilance, locomotion, or retreating. This decrease in foraging/feeding, no significant increase in vigilance, and decrease in retreating during the OW treatment supports findings of previous studies on *N. rufogriseus* (Beaudin-Judd et al., 2019; Frost et al., 2022), but the significant decrease in resting in response to the OW treatment in *N. rufogriseus* is novel. Contrary to my hypothesis, retreating decreased during the OW treatment, and as there was no significant increase in vigilance or locomotion, it may suggest that *N. rufogriseus* does not view the presence of visitors inside the enclosure as a serious danger (i.e. a predator) worth continuously observing and immediately fleeing or hiding from.

Regarding space-use, the wallabies used the Path and SectionA less when visitors were present in the enclosure as hypothesized. However, contrary to my hypothesis, visitor number inside the enclosure did not decrease the use of the Path or SectionA, suggesting that mere visitor presence – regardless of number, appears to cause avoidance of the path and its immediate vicinity. The avoidance of the visitor path during OW treatment is contrary to findings from a previous comparison of walkthrough and non-walkthrough enclosure types which found no difference (Beaudin-Judd et al., 2019). The spatial avoidance together with the behavioural changes suggests that whilst the wallabies may not perceive visitors as a source of danger, they likely do not consider visitors as enrichment or positive stimulus worth closely interacting with either, which is contrary to the findings of Frost et al. (2022).

Additionally, I observed an unexpected avoidance of SectionG and SectionH in response to the OW treatment, which indicates that the spatial avoidance is not strictly linear, as both sections close to and further from the path are avoided during visitor presence. The exact reason for the avoidance of SectionG and SectionH in response to visitor presence, and the avoidance of SectionD and SectionE in some instances of high visitor number or loud noise remains unclear. However, I hypothesize that the sections could contain traits influencing their use that I did not consider in the model. As an example, SectionG lacks any small cover structures, and is moderately far away from the entrances to the retreat hallway. This lack of easy retreat options may lead to the decreased utilization of such areas, as wallabies such as the tammar wallaby (*Notamacropus eugenii*) tend to position themselves closer to cover (Blumstein & Daniel, 2002). Curiously, SectionG and SectionH were used more when noise increased from low to moderate. I hypothesize the wallabies may move to these sections when noise increases slightly to gain distance from the visitors, but do not spend significant time there during the entirety of the OW treatment due to their undesirable traits, leading to the observed pattern.

Furthermore, I found only a moderate correlation between walkthrough treatment and noise level, which leads me to believe that visitor presence within the enclosure may not have been the main or only source of noise. No clear avoidance of the path was observed in the quiet to loud noise comparisons. In quiet to moderate comparisons, the use of areas both close to and far away from the path increased, whereas moderate to loud comparison displayed a decrease in the use of SectionA but not of the Path. I believe these unclear patterns may be due to the lack of strong connection between visitor presence and noise level in this study, which complicates the interpretation of noise effects in the manner that my original hypothesis would require. However, I observed behavioural and space-use patterns in response to noise which could be indicative of situational adaptation. Retreating increased when noise increased from quiet to loud and vigilance increased when noise increased from quiet to moderate, which may be tied to the spatial pattern observed for SectionG and SectionH. The wallabies increased their use of these sections located further from the path when noise increased from quiet to moderate, but not when it increased from quiet to high. This pattern indicates that the wallabies may choose to completely retreat in response to sudden high noise, only distance themselves from the path and increase vigilance in response to moderate noise, and completely avoid certain sections during long-term disturbances (OW treatment); suggesting that the wallabies utilize their enclosure space and retreat options differently depending on the level and type of stimulus or disturbance. The increased retreating in response to loud noise suggests that including retreat areas in enclosures is important, as it supports the concept of "choice-and-control": allowing animals agency over their behaviour and contact with visitors (Fernandez et al., 2023; Hosey, 2000). Limiting this agency may lead to the manifestation of behaviours associated with negative welfare (Fernandez et al., 2023). In terms of welfare implications for this population, I hypothesize the option to retreat and avoid visitor areas may impact welfare positively, as the wallabies are allowed to disconnect from potentially disturbing stimulus. This option to self-regulate may contribute to the lack of expression of other anxiety-indicative behaviours during visitor presence, high visitor numbers and loud noise.

In addition to utilizing their space and retreat options differently depending on the type and level of stimulus, I observed other inconsistent behavioural responses between differing levels of visitor numbers and noise. I observed the expected decrease of foraging/feeding in moderate to high visitor number comparison and decrease of foraging/feeding and resting in moderate to high noise comparison. However, I did not observe the same reaction in the low to high visitor number or quiet to loud noise comparisons. Thus, based on my observations, a permanent aversion to all noise and visitors has not developed in the wallabies; the observed pattern is rather an increase in reactivity to a high-level stimulus when first exposed to a moderate, "priming" stimulus. This pattern could be due to a kind of a short-term sensitization effect. Sensitization occurs when the repetition of a moderate level stimulus and presentation of a strong stimulus leads to an augmented response (Byrne, 2008), in this instance amplified behavioural response. Perhaps the presence of a moderate level of visitor number or noise has led to a build-up of anxiety, which is then expressed through decreased feeding and resting when the visitor number or noise level increases from moderate to high. As seen in the low to high visitor number and noise level, when the increase occurs without a moderate period in-between, a response does not arise as frequently. Future studies could examine this pattern in wallabies or other zoo-housed animals by further manipulating visitor numbers and exposure times.

Surprisingly, moderate noise also increased foraging/feeding, resting, vigilance and retreating when compared to quiet level. The combination of more retreating and more feeding during moderate noise appears counterintuitive at first, as I predicted retreating to increase, and feeding and resting to decrease as the noise levels rise. However, explanations for this pattern could include both the individual variation in habituation to noise, and even some level of covert competition over resources.

As two behaviours cannot be expressed simultaneously by the same individual in my study, the increase of feeding, retreating, and resting during moderate noise could be explained by different individuals engaging in different behaviours simultaneously. This could occur due to individual variation in response to disturbances, a phenomenon which has been observed in zoo-housed Bornean orangutans (*Pongo pygmaeus*) (Queiroz et al., 2025). Although the study by Queiroz et al. (2025) tested physiological responses to noise instead of behavioural responses, it shows the potential for individual differences in tolerance to disturbances in a zoo environment. This variation could be present in the red-necked wallabies, with wallabies more or less sensitive to the increase in noise disturbance engaging more or less in retreating respectively. Variation in habituation towards animal caretakers (staff observation) was already present in this population, further supporting the idea.

The pattern could also be tied to covert competition over food, as the less sensitive individuals that are less inclined to retreat may take advantage of the reduction in number of conspecifics. When the number of conspecifics is reduced, the remaining individuals may choose to engage in feeding rather than other behaviours such as autogrooming, in order to maximize their foraging efficiency during decreased competition. An increase in feeding in the absence of conspecifics has been observed in Allenby's gerbils (*Gerbillus andersoni allenbyi*), as individuals visited food patches more frequently and foraged/fed for longer in the absence of conspecifics (Berger-Tal et al., 2015). If a similar phenomenon took place in my study population, the longer feeding times and more frequent feedings would appear as increased foraging/feeding in the data, as is the case. However, I did not observe much overt competition over food in the form of negative social interactions during my sampling, and dry hay and pellets were always available at multiple locations, so it is unlikely that competition over food – covert or overt, rather than individual variation in habituation is the cause of the behavioural pattern in this population.

Interpreting the increase of resting during moderate noise and decrease during the OW treatment or loud noise is also challenging. Contrary to low resting behaviour even in the absence of visitors in Meade et al. (2021), a large part of the daily activity in my population constituted of resting during both treatments (Figure 7.). It must be noted that the observations of Meade et al. (2021) were conducted at an earlier time of day, which may also contribute to the differing baseline frequency of resting in the studies. My observations indicate that resting is a significant part of the routine and its disturbance could have welfare implications. However, as red-necked wallabies are less active during the daytime (Wilson & Mittermeier, 2015), resting could occur before study hours, and the decrease in resting during one hour in the afternoon may not have significant welfare consequences, but may indicate disturbance. Furthermore, the decrease in resting during loud noise or the OW treatment was not accompanied by increase of its opposing, anxiety-indicative behaviours vigilance or locomotion, in addition with a previous study finding that decreased resting was not accompanied by increased physiological stress indicators in macropods (Sherwen et al., 2015). Thus, I could not conclude negative welfare implications from the decrease of resting with absolute certainty.

4.2 Visitor experience

According to my results, combined visitor groups rated their experience positively, but the walkthrough activity significantly increased visitor experience. Visitor imagined and actual experience rating align with one another, as the walkthrough experience is perceived as better both in theory and practice. Although the consensus from both visitor groups was that interest in wildlife and conservation increased after observing the wallabies, the walkthrough experience did not significantly increase interest in either when compared to a traditional enclosure experience. Thus, I found no proof that participating in a walkthrough increases interest in conservation, conversely to what was suggested by Moss & Pavitt (2019). It must be noted that the red-necked wallaby is not considered endangered (McKenzie et al., 2016) and thus its ability to encourage conservation may be innately limited. More naturalistic enclosures and encounters with animals during training or feeding demonstrations have been shown to increase visitor engagement (Lyon et al., 2024; Smart et al., 2021; Woolway & Goodenough, 2017), which could help foster an increased interest towards wildlife and conservation, but the implementation of such demonstrations or a refurbishing of the enclosure would require further research and consideration.

Visitor perception of the impact suggests that visitors who did not experience the walkthrough viewed their potential impact on the wallabies more negatively. However, the consensus from combined visitor groups did not differ significantly from a perceived neutral impact. I did not study whether visitors viewed their impact negatively prior to engaging in the walkthrough activity and positively after engaging in the activity. Studying pre- and post-activity perceptions of the impact could allow to detangle whether initial perceptions are the reason visitors do or do not engage in the activity, or if engaging in the activity may change that initial perception. Further studies on animal-visitor interactions should consider this when designing visitor questionnaires.

4.3 Limitations of the study

Due to the prevalence of GL(M)Ms in previous literature on macropod behaviour (Beaudin-Judd et al., 2019; Meade et al., 2021; Sherwen et al., 2015), and technological constrains, I used a Poisson distribution GLMM as an alternative to a multinomial distribution model, which would have also suited the data present in this thesis and could be utilized as an option in future studies of similar nature (McCullagh, 1989).

The sampling and analysis of this study may have benefitted from a more thorough consideration of the functional traits of the enclosure, such as the small retreat structures which allow partial visual cover, the distance to the retreat hallway, and the presence/absence of food sources in each section. Such traits could be further considered in future studies in order to detangle certain space-use patterns. Additionally, sampling was conducted only by me, which introduced limitations and an increased risk of mistakes during observations.

In my data the walkthrough treatment was not strongly correlated with noise level; it is thus possible that visitors on the path were not the primary source of loud noises, converse to what I hypothesized. This may simply be due to visitors not producing as much noise as hypothesized, or alternatively the sampling method lacking in intricacy. Although the sound recorder was installed near the walkthrough path with the intention to capture noise as close to the path as possible, similarly to Meade et al. (2021) it only recorded ambient sound and the origin of noises could not be indisputably attributed to visitors on the path. Other sources of loud noise during my study could have included visitors outside of the enclosure, zookeeper and maintenance vehicles, or various vocal bird species in the area, which would not cause a reason to avoid the path. The issues in sampling could potentially be mitigated by assigning another observed to be responsible for measuring sounds at the path and noting any unusual occurrences to ensure the most accurate data, or manipulating the noise as suggested by Meade et al. (2021). Furthermore, because ambient, unmanipulated noise was used, the noise levels did not occur at equal frequencies. Although some noise levels had fewer observations than others, which may have increased the size of standard errors, the mixed models should be able to handle data which is unbalanced in this manner (Zuur, et al., 2009). The same phenomenon was present in visitor numbers. The number of visitors allowed into the enclosure was arbitrarily controlled by the zoo staff and not intentionally manipulated for the study. In further studies the unbalanced observations of naturally occurring noise and visitor numbers could be avoided by manipulating them in a controlled manner.

4.4 Practical implications on zoo design

Based on my observations, the practical implications for the walkthrough at Korkeasaari Zoo and for future zoo design to maximize welfare could include the following:

1. For future zoo design, walkthroughs should not be implemented in narrow enclosures, since wallabies need to be able to distance themselves as suggested by the avoidance of the Path and SectionA during OW. Based on the width of SectionA in my study, it appears walkthrough enclosures require at least 3.5 meters of space on both sides of the path. Furthermore, retreat options should be made available, so that animals may self-regulate by fully disconnecting from visitors.

2. Due to some evidence of the high visitor number’s effect on feeding, monitoring the number of people within the enclosure may be beneficial in further mitigating visitor effects. Perhaps a limit on the number of visitors allowed within the enclosure at once should be enforced more strictly, as high visitor number (≥20) caused a decrease in essential behaviours in some instances.

   Understandably the visitor number may be difficult to control in, as hundreds of visitors are queuing for the walkthrough activity with only an hour of time per day.

However, I would not recommend extending the walkthrough activity slot before longer exposure times to visitors have been studied and other mitigation attempts made.

4.5 Conclusions

My study found some evidence for visitor effects in red-necked wallabies, including differences in both behaviour and space-use during the walkthrough activity. The current walkthrough activity does not appear to cause the full range of responses I established as indicative of negative welfare impacts, but the observed avoidance of the walkthrough path and decrease in essential behaviours may be a cause for some concern. The overall space-use and behaviour pattern suggests that whilst the wallabies may not interpret visitors as a source of serious danger, the visitor presence may be somewhat disturbing. Curiously, the behavioural and space-use results may suggest an existence of a short-term form of a sensitization effect, and situational adaptation in space-use and retreat behaviour in captive red-necked wallabies. For the visitors, the walkthrough activity appears enjoyable but not as inspiring as previous literature would suggest.

To combat visitor effects, stricter monitoring of visitor numbers during the walkthrough activity could be implemented. Additionally, the observed spatial avoidance of visitor-heavy areas highlights the importance of adequate space and retreat options, which needs to be considered in future zoo enclosure design and in the implementation of walkthrough activities in existing enclosures. In addition to mitigating potentially negative welfare impacts, the walkthrough activity's influence on visitor interest towards wildlife and conservation could be improved to maximize its benefit to all parties, but the exact method to do so without jeopardising welfare would need to be determined.

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7 Appendices

The following tables include the full results of each generalized linear mixed model used. R package *emmeans* (Lenth et al., 2025, v2.0.0) was used to acquire the summaries. Comparison, source model and sample size is indicated in each table caption.

Table A1. The effects of the OW treatment on space-use when compared to the CW treatment. OW – CW emmeans summary of Model1. OW: n = 2014, CW: n = 2576.

Section	Estimate	SE	z-value	p-value
Path	-2.211	1.010	-2.187	**0.029**
SectionA	-1.742	0.384	-4.537	**<0.001**
SectionB	-0.229	0.229	-1.002	0.317
SectionC	-0.130	0.324	-0.401	0.689
SectionD	-0.243	0.196	-1.241	0.215
SectionE	-0.470	0.263	-1.785	0.074
SectionF	0.112	0.375	0.300	0.764
SectionG	-1.235	0.317	-3.897	**<0.001**
SectionH	-0.649	0.268	-2.418	**0.016**
SectionI	-0.577	0.353	-1.634	0.102
SectionJ	-0.317	0.521	-0.608	0.543
SectionK	-0.900	0.526	-1.712	0.087

Table A2. The effect of moderate noise on the use of each section when compared to quiet noise. Moderate – Quiet emmeans summary of Model1. Quiet: n = 944, Moderate: n = 3006.

Section	Estimate	SE	z-value	p-value
Path	0.835	0.283	2.949	**0.009**
SectionA	0.539	0.133	4.041	**<0.001**
SectionB	0.111	0.136	0.818	0.692
SectionC	-0.386	0.252	-1.530	0.277
SectionD	0.612	0.159	3.840	**<0.001**
SectionE	0.273	0.220	1.244	0.427
SectionF	-0.538	0.331	-1.627	0.234
SectionG	1.691	0.388	4.363	**<0.001**
SectionH	0.841	0.234	3.601	**<0.001**
SectionI	0.554	0.400	1.386	0.348
SectionJ	0.432	0.340	1.272	0.411
SectionK	-0.489	0.318	-1.536	0.274

Table A3. The effect of loud noise on the use of each section when compared to quiet noise. Loud – Quiet emmeans summary of Model1. Quiet: n = 944, Loud: n = 640.

Section	Estimate	SE	z-value	p-value
Path	0.633	0.362	1.749	0.187
SectionA	-0.042	0.258	-0.161	0.986
SectionB	-0.218	0.203	-1.074	0.530
SectionC	-0.329	0.363	-0.906	0.637
SectionD	-0.289	0.236	-1.224	0.439
SectionE	-0.461	0.360	-1.279	0.407
SectionF	-0.925	0.474	-1.951	0.125
SectionG	0.927	0.511	1.816	0.164
SectionH	0.621	0.299	2.074	0.095
SectionI	0.287	0.499	0.574	0.834
SectionJ	0.208	0.428	0.487	0.878
SectionK	-0.214	0.541	-0.396	0.917

Table A4. The effect of loud noise on the use of each section when compared to moderate noise. Loud – Moderate emmeans summary of Model1. Moderate: n = 3006, Loud: n = 640.

Section	Estimate	SE	z-value	p-value
Path	-0.202	0.269	-0.752	0.733
SectionA	-0.580	0.235	-2.473	**0.036**
SectionB	-0.329	0.160	-2.059	0.099
SectionC	0.057	0.296	0.192	0.980
SectionD	-0.901	0.182	-4.949	**<0.001**
SectionE	-0.734	0.302	-2.429	**0.040**
SectionF	-0.387	0.388	-0.998	0.578
SectionG	-0.764	0.354	-2.156	0.079
SectionH	-0.220	0.212	-1.037	0.553
SectionI	-0.267	0.345	-0.775	0.718
SectionJ	-0.224	0.307	-0.729	0.747
SectionK	0.275	0.508	0.541	0.851

Table A5. The effect of moderate visitor number on the use of each section when compared to low visitor number. Moderate – Low emmeans summary of Model2. Low: n = 422, Moderate: n = 1276.

Section	Estimate	SE	z-value	p-value
Path	0.449	0.954	0.471	0.885
SectionA	0.059	0.367	0.159	0.986
SectionB	0.135	0.124	1.090	0.520
SectionC	0.018	0.212	0.087	0.996
SectionD	0.199	0.113	1.767	0.181
SectionE	0.140	0.146	0.962	0.601
SectionF	0.076	0.249	0.306	0.950
SectionG	0.108	0.271	0.399	0.916
SectionH	0.029	0.182	0.162	0.986
SectionI	0.235	0.302	0.779	0.716
SectionJ	-0.159	0.567	-0.280	0.958
SectionK	0.226	0.447	0.506	0.868

Table A6. The effect of high visitor number on the use of each section when compared to low visitor number. High – Low comparison from emmeans summary of Model2. Low: n = 422, High: n = 316.

Section	Estimate	SE	z-value	p-value
Path	0.267	0.861	0.310	0.949
SectionA	-0.105	0.457	-0.229	0.972
SectionB	-0.286	0.165	-1.727	0.195
SectionC	-0.191	0.303	-0.632	0.803
SectionD	-0.136	0.148	-0.919	0.628
SectionE	0.063	0.185	0.343	0.937
SectionF	-0.120	0.302	-0.397	0.917
SectionG	-0.019	0.332	-0.058	0.998
SectionH	-0.036	0.266	-0.136	0.990
SectionI	-0.148	0.571	-0.259	0.964
SectionJ	-0.210	0.684	-0.307	0.950
SectionK	-0.292	0.533	-0.548	0.848

Table A7. The effect of high visitor number on the use of each section when compared to moderate visitor number. High – Moderate emmeans summary of Model2. Moderate: n = 1276, High: n = 316.

Section	Estimate	SE	z-value	p-value
Path	-0.183	0.915	-0.200	0.978
SectionA	-0.163	0.400	-0.408	0.912
SectionB	-0.420	0.146	-2.882	**0.011**
SectionC	-0.210	0.258	-0.812	0.696
SectionD	-0.335	0.122	-2.743	**0.017**
SectionE	-0.077	0.156	-0.494	0.874
SectionF	-0.196	0.232	-0.847	0.674
SectionG	-0.128	0.235	-0.542	0.851
SectionH	-0.066	0.247	-0.266	0.962
SectionI	-0.383	0.525	-0.730	0.745
SectionJ	-0.051	0.537	-0.095	0.995
SectionK	-0.292	0.533	-0.548	0.848

Table A8. The effect of temperature on the use of each section. Results from Model1. n = 4590.

Section	Estimate	SE	z-value	p-value
Path	0.066	0.042	1.570	0.116
SectionA	0.081	0.032	2.51	**0.012**
SectionB	0.092	0.031	3.02	**0.003**
SectionC	0.007	0.046	0.146	0.884
SectionD	0.027	0.027	0.980	0.327
SectionE	0.076	0.034	2.259	**0.024**
SectionF	0.008	0.043	0.193	0.847
SectionG	0.074	0.036	2.061	**0.039**
SectionH	0.023	0.032	0.713	0.476
SectionI	0.084	0.0442	1.896	0.058
SectionJ	-0.037	0.053	-0.703	0.482
SectionK	0.063	0.061	1.035	0.301

Table A9. The effect of the walkthrough treatment on each behaviour. OW – CW emmeans summary of Model3. OW: n = 3492, CW: n = 3525.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	-2.128	0.720	-2.956	**0.003**
Foraging / feeding	-0.654	0.192	-3.413	**<0.001**
Locomotion	0.240	0.670	0.359	0.720
Retreat	-0.440	0.186	-2.372	**0.018**
Resting	-0.465	0.204	-2.284	**0.022**
Social behaviour	-4.347	310e+1	0.000	0.999
Vigilance	-0.217	0.311	-0.696	0.487

Table A10. The effect of moderate noise on each behaviour when compared to quiet noise. Moderate – Quiet emmeans summary of Model3. Quiet: n = 1187, Moderate: n = 4786.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	0.983	0.490	2.013	0.109
Foraging / feeding	0.474	0.090	5.185	**<0.001**
Locomotion	0.135	0.720	0.188	0.981
Retreat	0.820	0.110	7.658	**<0.001**
Resting	0.497	0.090	5.249	**<0.001**
Social behaviour	-6.507	312e+2	0.000	1.000
Vigilance	0.885	0.350	2.498	**0.033**

Table A11. The effect of loud noise on each behaviour when compared to quiet noise. Loud – Quiet emmeans summary of Model3. Quiet: n = 1187, Loud: n = 1044.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	0.117	1.100	0.107	0.994
Foraging / feeding	0.060	0.130	0.464	0.888
Locomotion	0.170	0.890	0.192	0.980
Retreat	0.333	0.130	2.601	**0.025**
Resting	0.032	0.160	0.206	0.977
Social behaviour	-0.604	128e+2	0.000	1.000
Vigilance	0.624	0.410	1.539	0.273

Table A12. The effect of loud noise on each behaviour when compared to moderate noise. Loud - Moderate emmeans summary of Model3. Moderate: n = 4786, Loud: n = 1044.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	-0.865	1.020	-0.849	0.672
Foraging / feeding	-0.414	0.100	-4.194	**<0.001**
Locomotion	0.035	0.550	0.064	0.998
Retreat	-0.487	0.080	-6.278	**<0.001**
Resting	-0.465	0.130	-3.500	**0.001**
Social behaviour	5.903	339e+2	0.000	1.000
Vigilance	-0.262	0.230	-1.120	0.501

Table A13. The effect of moderate visitor number on each behaviour when compared to low visitor number. Moderate – Low emmeans summary of Model4. Low: n = 732, Moderate: n = 2184.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	0.084	0.268	0.312	0.948
Foraging / feeding	0.191	0.082	2.329	**0.052**
Locomotion	0.082	0.207	0.397	0.917
Retreat	0.261	0.067	3.924	**<0.001**
Resting	0.195	0.110	1.783	0.175
Social behaviour	0.285	0.874	0.326	0.943
Vigilance	0.025	0.153	0.163	0.986

Table A14. The effect of high visitor number on each behaviour when compared to low visitor number. High – Low emmeans summary of Model4. Low: n = 732, High: n = 576.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	0.091	0.392	0.231	0.971
Foraging / feeding	-0.076	0.109	-0.694	0.767
Locomotion	0.018	0.272	0.065	0.998
Retreat	-0.057	0.085	-0.673	0.780
Resting	-0.097	0.150	-0.650	0.793
Social behaviour	0.114	0.869	0.131	0.991
Vigilance	-0.058	0.192	-0.304	0.950

Table A15. The effect of high visitor number on each behaviour when compared to moderate visitor number. High– Moderate emmeans summary of Model4. Moderate: n = 2184, High: n = 576.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	0.007	0.346	0.020	0.999
Foraging / feeding	-0.267	0.091	-2.923	**0.010**
Locomotion	-0.064	0.237	-0.272	0.960
Retreat	-0.318	0.071	-4.496	**<0.001**
Resting	-0.292	0.129	2.264	0.061
Social behaviour	-0.171	1.01	-0.170	0.984
Vigilance	-0.083	0.154	-0.541	0.851

Table A16. The effect of temperature on each behaviour. Results from Model3. n = 7017.

Behaviour	Estimate	SE	z-value	p-value
Autogrooming	0.195	0.097	2.004	**0.045**
Foraging / feeding	0.078	0.026	2.987	**0.003**
Locomotion	NA	NA	NA	NA
Retreat	0.061	0.025	2.425	**0.015**
Resting	0.080	2.709	2.962	**0.003**
Social behaviour	-0.153	1.735+e3	0	1
Vigilance	-0.018	0.039	-0.463	0.643