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# Behavioural Changes in Zoo Animals during the COVID-19 Pandemic: A Long-Term, Multi Species Comparison

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**Abstract:** Visitors are a prominent feature of the zoo environment and lives of zoo animals. The COVID-19 pandemic led to repeated and extended closure periods for zoos worldwide. This unique period in zoological history enabled the opportunity to investigate the consistency of behavioural responses of zoo animals to closures and subsequent reopenings. Bennett's wallabies (*Notamacropus rufogriseus*), meerkats (*Suricata suricatta*), macaws (red and green: *Ara chloropterus*; blue and yellow: *Ara ararauna*; military: *Ara militaris*) and rabbits (*Oryctolagus cuniculus domesticus*) held at four zoological collections in the United Kingdom were studied during COVID-19 closures and subsequent reopening periods. Facilities were closed for three time periods during 2020 and 2021: March–June/July 2020; November–December 2020; January–April/May 2021. Behavioural data were captured during closures (maximum $n = 3$) and reopening periods (maximum $n = 3$) during five-min scans using instantaneous scan sampling with a one-minute inter-scan interval. General linear models (GLMs) and general linear mixed models (GLMMs) were used to investigate the relationship between observed behaviours and open/closed periods. Changes were observed in behaviour between open and closure periods in all species, and in some instances changes were also observed over time, with animals responding differently to different closure and reopening periods. However, no overt positive or negative impacts of the closures or reopening periods were identified for these species. The study species may have different relationships with zoo visitors, but no clear differences were seen across the species studied. The unique opportunity to study animals over a long period of time during repeated closure periods enabled a greater understanding of the impact of zoo visitors on animals. As with other work in this sphere, these data support the adaptability of zoo animals to zoo visitors. This work contributes to the growing field of research undertaken during the COVID-19 periods and enhances our understanding of the impact that these zoological closures had on a wider body of species in a number of facilities.

**Keywords:** COVID-19; zoo; behaviour; multi-species; welfare; visitor–animal interactions

## 1. Introduction

With millions of people visiting zoos annually around the world, visitors are a prominent feature in the lives of zoo animals [1]. Visitor behaviour is variable and characteristics of visitor presence such as noise, crowd density, activity, behaviour, and proximity to zoo animals, have resulted in behavioural and physiological changes in some zoo species [2–5]. Visitors can have negative, neutral, or positive influences on zoo animal welfare [6]; being a stressor for some animals [7,8] or a form of enrichment for others [9]. The presence of visitors has been identified as a stable background noise for animals [10,11], acting as a noise buffer from other sounds in the zoo [12]. Response to zoo visitors varies between species and individuals [13]. There are a plethora of reasons for this variation, including differences in enclosure design, species characteristics, individual temperament, or previous experiences with humans [13].

Zoo animals which are continuously exposed to visitors may habituate to their presence [13,14]. The COVID-19 pandemic in 2020 led to the temporary closures of zoological facilities across the globe. Within the UK the initial closure period (March to June/July 2020) was followed by a further two closures (November to December 2020; January to April/May 2021). Whilst some facilities may close temporarily to the public throughout different periods of the year outside of the pandemic (e.g., over winter or school terms during winter) [14], the lack of visitors during the summer period in UK zoos was unusual.

There has been now a large body of research assessing the impact of these closures on a range of animals, predominantly through investigation of behavioural change but also through measures of enclosure usage and physiological parameters. Whilst various responses have been reported (positive, negative or neutral), to date no studies have highlighted significant positive or negative implications of the closures or subsequent reopening periods. Anecdotally, keepers and reports on social media highlighted positive, negative and neutral impacts of zoo closures and reopening periods [12].

Positive impacts included closer proximity to visitors, increased engagement with enrichment and positive human–animal interactions (HAIs), with researchers suggesting returning visitors were a positive stimulus. Eastern black-and-white colobus monkeys (*Colobus guereza*), Allen's swamp monkeys (*Allenopithecus nigroviridis*), DeBrazza's monkeys (*Cercopithecus neglectus*), Bolivian grey titi monkeys (*Callicebus donacophilus*), crowned lemurs (*Eulemur coronatus*), polar bears (*Ursus maritimus*) and banteng (*Bos javanicus*) spent more time closer to visitor viewing windows during open periods [15,16]. Olive baboons (*Papio anubis*) approached visitor cars more frequently when the facility was open to the public than they did the ranger's vehicle during closures, and chimpanzees (*Pan troglodytes*) engaged in more feeding and interaction with enrichment when the zoo was open [17]. Meerkats (*Suricata suricatta*) showed increased positive social interactions, positive HAIs and alert behaviours, with the authors suggesting that meerkats were 'looking for' humans [18]. Japanese macaques (*Macaca fuscata*) engaging in cognitive trials did not change participation rates or task accuracy but they did show a preference for the testing booth side closest to visitors during open periods, and response latency was quicker when the zoo was open [19].

Most of the studies undertaken during the COVID-19 pandemic indicated no or negligible behavioural changes, highlighting the adaptability of zoo species to their ever-changing environments. Swamp wallaby (*Wallabia bicolor*), Rothschild giraffe (*Giraffa camelopardalis rothschildi*), nyala (*Tragelaphus angasii*), Chapman's zebra (*Equus quagga chapmani*), snow leopard (*Panthera uncia*), amur leopard (*Panthera pardus orientalis*), Palawan binturong (*Arctictis binturon whitei*), African penguins (*Spheniscus demersus*), greater flamingo (*Phoenicopterus roseus*), brown bears (*Ursus arctos*) and western lowland gorillas (*Gorilla gorilla gorilla*) showed no behavioural changes between open and closure periods [2,14,20–23]. Chimpanzee wounding rates were also unaffected by zoo closures [24]. Some species showed behavioural changes, but these were considered to be attributed to environmental factors rather than the presence or absence of visitors. Changes in Chilean flamingo (*Phoenicopterus chilensis*) behaviour were believed to be influenced by temperature [22], and Nile crocodile (*Crocodylus niloticus*) behaviour was affected by time of day, temperature, and month with greater magnitude than visitor presence [25]. Assessments of glucocorticoids in a range of species have not indicated physiological changes during the closures [16,17].

For some species, the behavioural response to the return of visitors indicated that animals may have been using behaviour to manage stressors caused by the return of visitors, and there was some evidence of variable rehabituation periods. Tokay geckos (*Gekko gecko*), European glass lizards (*Pseudopus apodus*) and Sonoran spiny-tailed iguana (*Ctenosaura macrolopha*) were more visible during zoo closures than when visitors were present [26,27]. Beaded lizards (*Heloderma horridum*) engaged in less social behaviour, Catalina Island rattlesnakes (*Crotalus catalinensis*) increased investigation and Dwarf caimans (*Paleosuchus palpebrosus*) were more active when facilities reopened [27]. Gorillas also rested less when facilities were reopened [17]. Red kangaroos (*Macropus rufus*) housed in a walk-through exhibit spent more time in social proximity with conspecifics after zoos re-opened, as well as greater inactivity, reduced feeding and more restricted space use [28]. Common frog (*Rana temporaria*), pool frog (*Pelophylax lessonae*), golden mantella (*Mantella aurantiaca*), and golden poison dart frog (*Phyllobates terribilis*) were less visible when the facility reopened, however this hiding behaviour waned over time, with species returning to behaviour observed during closures over time [29]. Edes et al. [16] also found that gorillas spent less time close to visitors immediately after reopening but this effect diminished over time.

The majority of the studies investigating behavioural changes in animals as a result of the COVID-19 pandemic focused on behavioural changes during the initial COVID-19 closures and then the reopening periods immediately following (i.e., closure 1 March 2020 with reopening occurring in June 2020 for the majority of zoological institutions). This research sought to build on these short-term studies, by investigating the consistency of responses in zoo animals across these three closure and reopening periods, to determine whether behavioural responses to closures and subsequent reopening changed over time. Specifically we investigated: (i) if there was a difference between open and closure periods; (ii) whether there were any differences between behaviour during the first closure period (March 2020–June/July 2020), the second closure period (November–December 2020) and the third closure period (January–April/May 2021); (iii) whether there were any differences in behaviour during the post-closure reopening periods (post closure one, post closure two and post closure three); (iv) if there were any changes in relation to the number of weeks since the facility reopened. Previous research into the impacts of the COVID-19 closures on zoo animals suggested that some animals may take longer to re-habituate to zoo visitors than others, so it was anticipated there may be variation in behaviour as animals became used to the closure and reopening of the zoo, and that behaviours would change as the weeks from when the zoo reopened increased. We predicted a reduced response to visitors over time, with reduced responses by the third closure period and a return to 'during closure' behaviour levels over time as animals re-habituated to the presence of zoo visitors. We did, however, expect to still see some behavioural changes between open and closure periods, as has been reported in previous work.

## 2. Materials and Methods

### *2.1. Subjects and Study Sites*

Bennett's wallabies (*Notamacropus rufogriseus*), meerkats, macaws (red and green: *Ara chloropterus*; blue and yellow: *Ara ararauna*; military: *Ara militaris*) and rabbits (*Oryctolagus cuniculus domesticus*) held at four zoological collections in the United Kingdom were studied during COVID-19 closures and subsequent reopening periods. Facilities were closed for three time periods during 2020 and 2021: four to five months from mid-March to mid-June 2020 (White Post Farm, Knowsley Safari and Dartmoor Zoo) and mid-March to mid July 2020 (Plantasia); one month from early November to early December 2020; and four to five months from late December to mid-April 2021 (White Post Farm, Knowsley Safari and Dartmoor Zoo) and late December to mid-May 2021 (Plantasia). Data were opportunistically collected by members of zoo staff during some or all of these closure and corresponding reopening periods. Table 1 provides an overview of the demographics of the study individuals and periods of data collection at each site, and Table 2 provides an overview of enrichment activities and human–animal interaction opportunities before and after the COVID-19 facility closures.

**Table 1.** An overview of study individuals and periods of data collection. Observation days reflect number of days animals were observed within the three closure and following reopening periods.

| Study Site | Species (Number of Individuals) | Period of Data Collection | Data Points | Number of Days | Number of Observation Periods |
|---|---|---|---|---|---|
| White Post Farm | Bennet's wallabies ($n$ = 4, 4 M) | 31 August 2020–1 June 2021 | Open vs. closed (all data combined) | Open: 71<br>Closed: 29 | Open: 184<br>Closed: 86 |
| | | | Open period comparisons | Post closure 1: 38<br>Post closure 2: 6<br>Post closure 3: 27 | Post closure 1: 113<br>Post closure 2: 15<br>Post closure 3: 53 |
| | | | Closed period comparisons | Closure 2: 9<br>Closure 3: 20 | Closure 2: 27<br>Closure 3: 59 |
| | Rabbits ($n$ = 3, 1 M, 2 F) | 24 August 2020–20 February 2021 | Open vs. closed | Open: 43<br>Closed: 27 | Open: 121<br>Closed: 78 |
| | | | Closed period comparisons | Closure 2: 9<br>Closure 3: 18 | Closure 2: 27<br>Closure 3: 51 |
| | | | Open period comparisons | Post closure 1: 38<br>Post closure 2: 5 | Post closure 1: 107<br>Post closure 2: 14 |
| | Military macaw ($n$ = 1, 1 M)<br>Blue and yellow macaw ($n$ = 1, 1 F) | 24 August 2020–22 December 2021 | Open vs. closed (Closure period 3) | Open: 34<br>Closed: 14 | Open: 46<br>Closed: 33 |
| | | | Open period comparisons | Post closure 1: 34<br>Post closure 2: 10<br>Post closure 3: 50 | Post closure 1: 97<br>Post closure 2: 22<br>Post closure 3: 92 |
| | Meerkat ($n$ = 4, 4 M) | 24 August 2020–24 June 2021 | Open vs. closed | Open: 37<br>Closed: 29 | Open: 79<br>Closed: 73 |
| | | | Closed period comparisons | Closure 2: 21<br>Closure 3: 8 | Closure 2: 59<br>Closure 3: 14 |
| | | | Open period comparisons | Post closure 1: 10<br>Post closure 3: 25 | Post closure 1: 28<br>Post closure 3: 48 |
| Plantasia | Red and green macaw ($n$ = 1, 1 F) | 8 June 2020–31 August 2020 | Open vs. closed | Open: 47<br>Closed: 29 | Open: 135<br>Closed: 86 |
| | | | Open period comparisons | Post closure 1: 47<br>Post closure 2: 63 | Post closure 1: 135<br>Post closure 2: 180 |
| | Meerkat ($n$ = 2, 1 M, 1 F) | 8 June 2020–31 August 2020 | Open vs. closed (Closure 1) | Open: 46<br>Closed: 29 | Open: 131<br>Closed: 86 |
| | | | Open period comparisons | Post closure 1: 46<br>Post closure 2: 63 | Post closure 1: 131<br>Post closure 2: 183 |
| Dartmoor Zoo | Meerkat ($n$ = 3, 2 M, 1 F) * | 24 August 2020–15 June 2021 | Open period comparisons | Post closure 1: 14<br>Post closure 3: 12 | Post closure 1: 123<br>Post closure 3: 46 |
| Knowsley Safari | Meerkat ($n$ = 7, 4 M, 3 F) | 11 June 2020–26 November 2020 | Open vs. closed | Open: 51<br>Closed: 7 | Open: 107<br>Closed: 17 |
| | | | Closure period comparisons | Closure period 1: 4<br>Closure period 2: 3 | Closure period 1: 12<br>Closure period 2: 5 |

* During the period of the study, the female meerkat was euthanised. Data collected after 19 April 2021 are based on $n$ = 2 meerkats.

**Table 2.** An overview of enrichment activities and human–animal interaction opportunities at the study sites prior to and following the COVID-19 closures.

| | Species | Approximate Enclosure Size | Description of Enrichment Practices | HAI Opportunities Pre-COVID | HAI Opportunities Post-COVID |
|---|---|---|---|---|---|
| White Post Farm | Meerkats | 36 $m^2$ | Scatter fed at each of the three mealtimes. Food also sometimes hidden in objects | Visitors scatter feed in the same way keepers do | No visitor interactions during COVID-19 closures |
| | Bennet's wallabies | 900 $m^2$ | Browse and vegetables scattered, moveable objects filled with food and placed around the enclosure | Walkthrough enclosure but no physical interactions are permitted | Walkthrough enclosure but no physical interactions are permitted |
| | Rabbits | 16 $m^2$ | Food placed in objects to facilitate foraging. Browse and substrates to allow digging | None | None |
| | Military and Blue and yellow macaws | 240 $m^3$ | Seeds placed in alternate feeders, browse provided. Food hidden in objects | None | None |
| Plantasia | Meerkats | 25 $m^2$ | Daily scatter feeds, treats hidden around the enclosure and in puzzle feeders. Occasional changes to enclosure furnishings | None | None |
| | Red and green macaw | 80 $m^3$ | Randomised provision of parrot toys, treats frozen in ice blocks and tactile/puzzle feeders | Zoo keeper experience and birthday parties feed the macaw from outside the enclosure | Zoo keeper experience and birthday parties feed the macaw from outside the enclosure |
| Knowsley Safari | Meerkats | 258 $m^2$ | Food hidden in objects, new enclosure furniture, olfactory enrichment occasionally provided | Public talks and encounters | Encounters but no public talks |
| Dartmoor Zoo | Meerkats | 36 $m^2$ | Food hidden in objects to facilitate foraging | Public talks and encounters (meet the meerkat and feed the meerkat experiences) | Between the first and third closures public talks were exchanged for virtual talks (accessible via QR codes). Public talks commenced after closure 3. Feed the meerkat expe-riences [a] |

[a] 'Feed the meerkat' experiences are undertaken from outside of the meerkat enclosure whereas 'meet the meerkat' involves visitors going into the meerkat enclosure. Visitors were still not entering the meerkat enclosure by the end of the study period.

### 2.2. Behavioural Observations

Methods follow those detailed in Williams et al. [14,18], however, for clarity they have been briefly described here. Behavioural observations were undertaken by zoo staff during periods when the facilities were closed to zoo visitors (closure periods) and reopened to zoo visitors (open periods), according to staff availability. Each observation period lasted five minutes, and behavioural data were captured using instantaneous scan sampling with a one-minute inter-scan interval. Observations started at 0 min which resulted in six behavioural observations per observation period. Observations were not undertaken when keepers were engaging directly with the animals. All observers were experienced with the study species and with the data collection protocol. Observers were kept consistent within facilities. Behaviours were recorded according to a pre-defined ethogram (Table 3).

**Table 3.** Ethogram of behaviours for study animals during the study period [14,18].

| Behaviour | Description |
|---|---|
| Alert | Showing an awareness of/interest in their environment (including looking around/looking at visitors) |
| Positive human–animal interactions (HAIs) | Moving towards or seeking interaction from humans |
| Negative human–animal interactions (HAIs) | Avoiding, moving away from, or showing fear of humans. Behaviour performed in response to the presence of humans. |
| Foraging/feeding | Locating and consuming foodstuffs |
| Comfort [a] | Any self-maintenance or self-grooming behaviour |
| Social (positive) | Engaging in positive social behaviours (e.g., social play, grooming) |
| Social (negative) | Engaging in negative social behaviour (e.g., fighting, displaying) |
| Locomotion | Moving around the enclosure in a non-repetitive pattern. For birds this included climbing around the enclosure/up enclosure bars. |
| Interaction with the environment | Investigating or interacting with things in the environment (other than food). For meerkats this also included digging behaviour. |
| Resting | Animal is inactive. Sitting/perching or lying motionless with eyes open or closed. No other behaviour is being performed. |
| Preening [b] | Using beak to peck, stroke, or comb feathers in any region of the body |
| Abnormal repetitive behaviour (ARBs) | Repetitive behaviour with no obvious function or purpose |
| Other | Any other behaviour not detailed in the ethogram |
| Out of sight (OOS) [c] | Animal out of sight of observer |

[a] This behaviour was only recorded for non-bird species. For bird species comfort behaviour was recorded as preening; [b] Only recorded in the macaws; [c] OOS was captured as a means of understanding whether or not the animals were in public view.

### 2.3. Data Analysis

General linear models (GLMs) and general linear mixed models (GLMMs) were used to investigate the relationship between observed behaviour and the variables of interest: all open vs. closed periods (all of the data when the facility was closed compared to all of the open periods) or open vs. closed periods within a closure period (data from closure 1 compared to post closure 1 etc.); closure period comparisons (maximum of three time separate facility closure points); open period comparisons (maximum of three separate facility reopening periods); weeks since reopening (number of weeks since reopening following the preceding closure). For each behaviour, total frequency of observations was calculated per day. The number of observation periods per day was fitted as an offset variable to control for variation in the total number of separate observations per day. Where data were collected on an individual level (i.e., individuals were identifiable and kept consistent throughout the period of the study), 'individual' was added as a random effect to control for repeated measures. Probability of incorrectly rejecting the null hypothesis was set at 5% for all models. GLMs were used when data were collected at a group level, with individuals not identified (White Post Farm: meerkat; Dartmoor Zoo: meerkat; Plantasia: macaw and meerkat; Knowsley Safari: meerkat). GLMMs were used when data were collected at an individual level and each individual was treated as a separate study animal (White Post Farm: wallabies, rabbits, macaw). Data collected at Plantasia and Knowsley Safari were calculated as presence/absence within the group, and a behaviour was recorded once per scan if it occurred within the group (i.e., the maximum frequency of behaviour per observation period was $n = 6$). At Dartmoor Zoo and White Post Farm each meerkat was treated separately but they were not uniquely identified for the period of the study. Data were therefore pooled to calculate a total number of behaviour frequencies per scan point for the whole group (i.e., the maximum frequency of behaviours per observation was 6 times the number of individuals in the group).

Separate models were created for each behaviour for each animal group to control for variations between zoological collections. An overview of behaviours recorded per species and inferential statistics performed is provided in Table 4. Analyses were undertaken using R (Version 4.0.3) [30] using package "MASS" [31]. Model results are reported as model estimate (ß)±SE. Appropriateness of models was assessed using visual assessment of residuals in a residual by predictor plot and histogram of residuals, and through calculation of the dispersion parameter. Outliers were identified using a Cook's plot and removed if appropriate. Where required, final models were confirmed using AIC values. Confidence intervals were computed using the profiling method. Graphs were produced using the package "ggplot2" [32] and the "melt" function in package "reshape2" [33]. Plots were arranged using "ggarrange" using package "ggpubr" [34]. Model outputs for statistically significant results are presented in the text. Model outputs for all results including model AIC values and confidence intervals are presented in Table S1 in Supplementary Materials.

**Table 4.** An overview of behaviours recorded per species and inferential statistics performed.

| Species | Zoo | Observation Periods * | Behaviours Modelled | Behaviours Not Modelled Due to Low or No Occurrence in Some or All Observation Conditions |
|---|---|---|---|---|
| Bennet's wallabies | White Post Farm | Open vs. closed (closure periods two and three; post closure periods one, two and three) | Alert, comfort, feeding, locomotion, resting, positive HAIs and time spent OOS modelled using negative binomial GLMMs<br>Positive social interactions modelled using a gaussian GLMM | Environmental interactions, negative HAIs and ARBs |
| | | Closed period comparisons (closure periods two and three) | Alert, feeding, comfort, resting, locomotion and time spent OOS modelled using negative binomial GLMMs | Environmental interactions, positive and negative social interactions, positive and negative HAIs, ARBs |
| | | Open period comparisons (post closure one, two and three) | Alert, feeding, resting, locomotion, time spent OOS modelled using negative binomial GLMMs<br>Comfort modelled using a gaussian GLMM | ARBs, environmental interactions, positive and negative social interactions and positive and negative HAIs |
| | | Weeks since reopening (post closure one, two and three) | Alert, feeding, resting and time spent OOS modelled using NB GLMMs<br>Comfort and locomotion modelled using gaussian GLMMs | |

**Table 4.** *Cont.*

| Species | Zoo | Observation Periods * | Behaviours Modelled | Behaviours Not Modelled Due to Low or No Occurrence in Some or All Observation Conditions |
|---|---|---|---|---|
| Rabbits | White Post Farm | Open vs. closed periods (closure periods two and three; post closure one and two) | Alert, feeding, resting, positive HAIs, comfort, positive social interactions, environmental interactions, locomotion and time spent OOS modelled using negative binomial GLMMs | Negative social interactions, negative HAIs and ARBs |
| | | Closed period comparisons (closure period two and three) | Alert, positive HAIs, feeding, comfort, positive social interactions, locomotion, resting and time spent OOS modelled using negative binomial GLMMs<br>Environmental interactions modelled using a gaussian GLMM | ARBs, negative social interactions and negative HAIs |
| | | Open period comparisons (post closure one and two) | Positive HAIs, feeding, comfort, resting and time spent OOS modelled using negative binomial GLMMs<br>Positive social interactions, locomotion and Alert modelled using gaussian GLMMs | Negative social, ARBs, environmental interactions and negative HAIs |
| | | Weeks since reopening (post closure one and two) | | |
| Macaws | White Post Farm | Open vs. closed (closure three; post closure three) | Alert, environmental interactions, positive HAIs, feeding, preening, positive social interactions and resting modelled using negative binomial GLMMs<br>Locomotion modelled using a gaussian GLMM<br>Environmental interactions had one influential outlier removed + | Time spent OOS, ARBs, negative social interactions and negative HAIs |
| | | Open period comparisons (post closure one, two and three) | Alert, feeding, comfort, positive social interactions, locomotion, environmental interactions and resting modelled using negative binomial GLMMs<br>Positive HAIs modelled using a gaussian GLMM<br>Environmental interactions had one influential outlier removed + | |
| | | Weeks since reopening (post closure one, two and three) | | |
| | Plantasia | Open vs. closed periods (closure one; post closure one) | Alert, positive HAIs, environmental interactions, feeding, preening, locomotion, resting and ARBs modelled using negative binomial GLMMs | Positive and negative social interactions, vocalising and time spent OOS |
| | | Open period comparisons (post closure one and two) | Alert, positive HAIs, environmental interactions, feeding, preening, vocalising, locomotion, resting and ARBs modelled using negative binomial GLMMs | Positive and negative social interactions and time spent OOS |
| | | Weeks since reopening (post closure one and two) | Alert, positive HAIs, environmental interactions, feeding, preening, locomotion, resting and ARBs modelled using negative binomial GLMMs<br>Vocalisation assessed using a gaussian GLMM | |

**Table 4.** *Cont.*

| Species | Zoo | Observation Periods * | Behaviours Modelled | Behaviours Not Modelled Due to Low or No Occurrence in Some or All Observation Conditions |
|---|---|---|---|---|
| Meerkats | White Post Farm | Open vs. closed periods (closure two and three; post closure one and three) | Alert, positive HAIs, feeding, comfort, locomotion, environmental interactions, resting and time spent OOS modelled using negative binomial GLMs | ARBs, positive and negative social interactions and negative HAIs |
| | | Closure period comparisons (closure two and closure three) | Alert, positive HAIs positive, feeding, locomotion, environmental interactions, resting and time spent OOS modelled using negative binomial GLMs<br>Comfort was modelled using a poisson GLMs<br>Locomotion had one influential outlier removed + | |
| | | Open period comparisons (post closure one and three) | Alert, positive HAIs, feeding, comfort, locomotion, environmental interactions, resting and time spent OOS modelled using negative binomial GLMs<br>ARB was modelled using a poisson GLM | Positive and negative social interactions and negative HAIs |
| | | Weeks since reopening (post closure one and three) | | |
| | Dartmoor | Open period comparisons (post closure one and three) | Alert, feeding, locomotion, resting and environmental interactions were modelled using negative binomial GLMs<br>Time spent OOS was modelled using a poisson GLM | Positive and negative HAIs, positive and negative social interactions, comfort and ARBs |
| | | Weeks since reopening (post closure one and three) | Alert, locomotion, resting, environmental interactions modelled using negative binomial GLMs<br>Locomotion had one influential outlier removed + | Positive and negative social interactions, positive and negative HAIs, ARBs, comfort and feeding |
| | Plantasia | Open vs. closed (closure one; post closure one) | Alert, feeding, comfort, locomotion, resting, ARBs and environmental interactions modelled using negative binomial GLMs | Positive and negative HAIs, positive and negative social interactions and time spent OOS |
| | | Open period comparisons (post closure one and two) | Alert, feeding, comfort, locomotion, environmental interactions, resting, ARBs, positive social interactions modelled using negative binomial GLMs | Positive and negative HAIs, negative social interactions and time spent OOS |
| | | Weeks since reopening (post closure one and two) | | |
| | Knowsley Safari | Open vs. closed (closure one and two; post closure one) | Alert, positive HAIs, feeding, comfort, positive and negative social interactions, locomotion, environmental interactions, resting and time spent OOS were modelled using negative binomial GLMs | Negative HAIs and ARBs |
| | | Closure periods (closure one and two) | Alert, feeding, comfort, positive social interactions, locomotion, environmental interactions, resting and time spent OOS modelled using negative binomial GLMs | Positive and negative HAIs, negative social interactions and ARBs |
| | | Weeks since reopening (post closure one) | Alert, positive HAIs positive, feeding, comfort, positive social interactions, locomotion, environmental interactions and resting modelled using negative binomial GLMs | ARBs |

* Data were not always collected during all three closure periods or the subsequent post-closure reopening periods. Data collection depended upon staff availability. + Influential outliers were identified via Cook's distance.

*2.4. Ethical Review Statement*

All research protocols were reviewed and favourably considered by Nottingham Trent University, School of Animal, Rural and Environmental Sciences School Ethics Group (reference number ARE192042) and meet the ARRIVE guidelines where necessary. Permission to conduct the study was granted by the participating zoological collections prior to commencement of data collection.

## 3. Results

*3.1. Wallabies*

An overview of wallaby activity throughout the closure and reopening periods is provided in Figure 1.

3.1.1. Open vs. Closed Periods (Closure Two and Three; Post Closure One, Two and Three)

Wallabies engaged in more feeding behaviour (0.429 ± 0.105, Z = 4.076, $p < 0.001$), moved around the enclosure more (0.536 ± 0.181, Z = 2.956, $p = 0.003$) and were out of sight more (0.532 ± 0.238, Z = 2.239, $p = 0.03$) when the site was closed (mean frequency of observations per day ± SD, feeding: 6.5 ± 4.1; locomotion: 1.2 ± 1.5; time spent OOS: 2.9 ± 3.7) than when it was open (feeding: 3.8 ± 3.6; locomotion: 0.6 ± 1.2; time spent OOS: 1.5 ± 2.7). Resting behaviour was higher when the site was open (7.2 ± 4.6) than when it was closed (4.3 ± 3.9) (−0.646 ± 0.097, Z = −6.654, $p < 0.001$). Although generally low, positive HAIs were also higher when the site was open (0.2 ± 0.9) to the public than when it was closed (0.1 ± 0.4; −0.219 ± 0.085, Z = −2.544, $p = 0.01$), as were positive social interactions (open: 0.3 ± 0.8; closed: 0.2 ± 0.7; −0.208 ± 0.079, t = −2.634, $p = 0.009$). There was no significant difference in frequency of alert or comfort behaviours between open and closed periods ($p > 0.05$).

3.1.2. Closed Period Comparisons (Closure Period Two and Three)

Data were analysed to investigate whether behaviour differed between the second and third closure periods. Feeding was significantly higher during the third closure period (7.2 ± 3.9) than the second closure period (5.1 ± 4.2; 0.433 ± 0.145, Z = 2.998, $p = 0.003$). None of the other modelled behaviours were significantly different during closure period two and closure period three ($p > 0.05$).

3.1.3. Open Period Comparisons (Post Closure One, Two and Three)

Wallabies did not show any difference across the three open periods for alert, feeding, comfort or time spent out of sight ($p > 0.05$). Rest differed across opening periods (0.076 ± 0.024, Z = 3.206, $p = 0.001$). Rest during period 3 (7.1 ± 4.1) was significantly greater than reopening period two (2.7 ± 2.7; −1.414 ± 0.194, Z = −7.299, $p < 0.001$). Rest was also significantly greater during reopening period one (7.8 ± 4.8) than reopening period two (1.091 ± 0.191, Z = 5.728, $p < 0.001$). Locomotion differed across opening periods (−0.219 ± 0.072, Z = −3.051, $p = 0.002$). Post-hoc tests revealed locomotory behaviour was significantly lower following the third closure (0.2 ± 0.5) than the first (0.8 ± 1.3; 1.021 ± 0.295, Z = 3.459, $p = 0.0016$) and second closures (1.3 ± 1.8; 1.458 ± 0.438, Z = 3.329, $p = 0.0025$). There was no difference in frequency of locomotion in post closure one and post closure two (−0.436 ± 0.383, Z = −1.139, $p = 0.49$).

There was no impact of weeks since reopening on feeding, comfort, resting, locomotion, or number of observations where animals were out of sight each observation day ($p > 0.05$). Negative binomial GLMMs indicated a reduction in alert in weeks since reopening (−0.038 ± 0.017, Z = −2.204, $p = 0.028$). No overall clear reduction over time was observed (Figure 2).

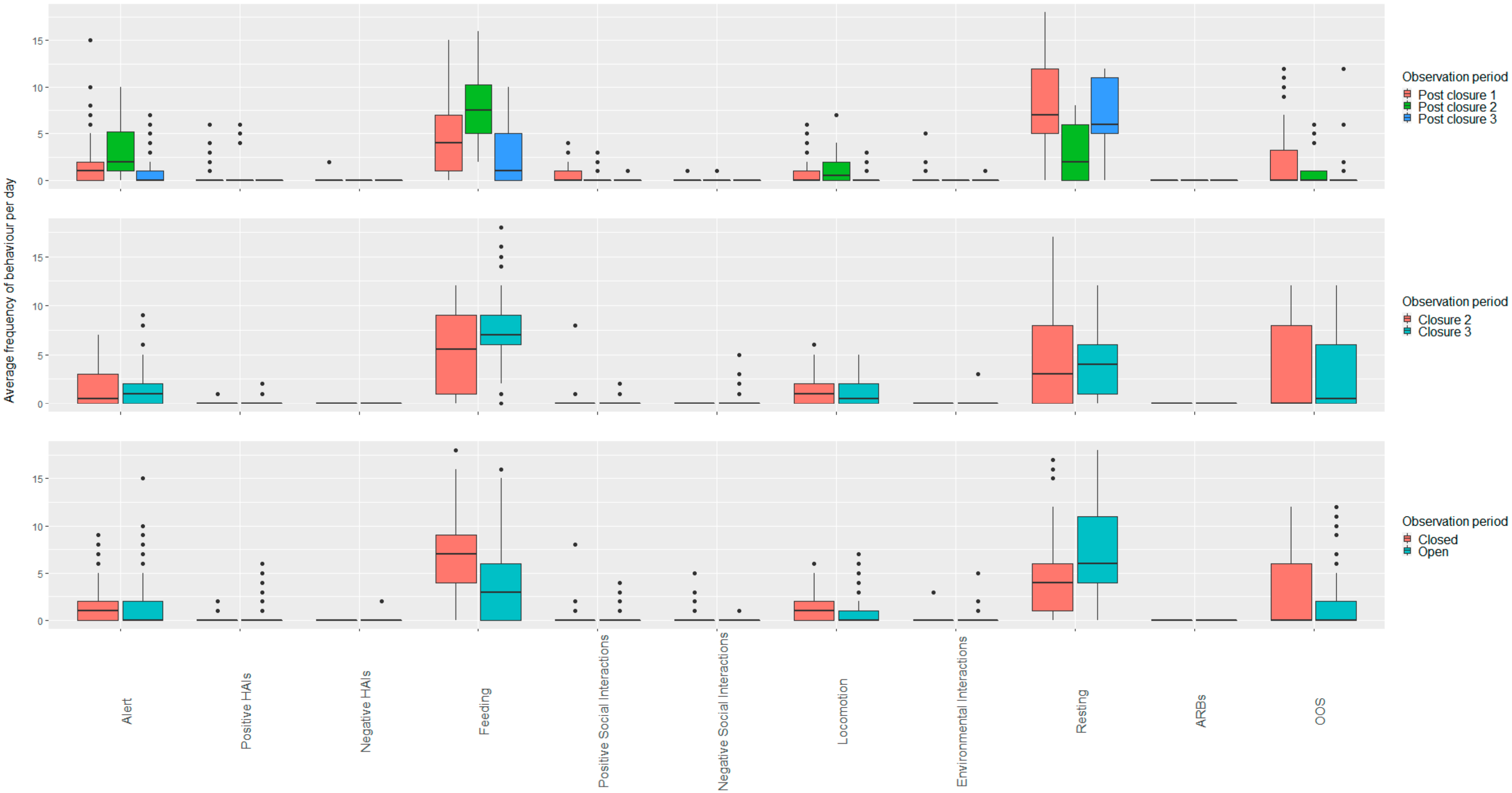


**Figure 1.** An overview of activity in the Bennet's wallabies housed at White Post Farm during COVID-19 closures and reopening periods.

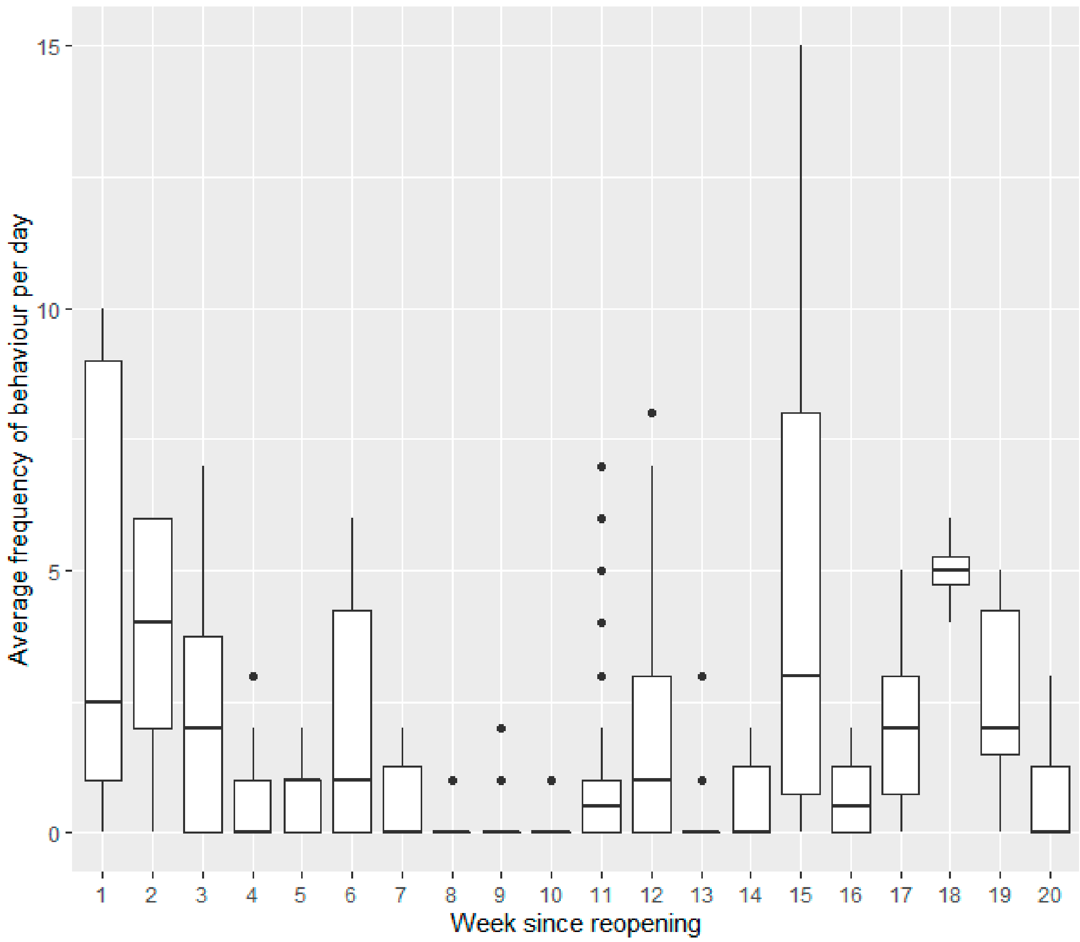


**Figure 2.** Average frequency of alert behaviour recorded in the Bennet's wallabies at White Post Farm per day in the weeks since the facility reopened to the public. Dots represent outliers.

### 3.2. *Rabbits*

An overview of rabbit activity throughout the closure and reopening periods is provided in Figure 3.

#### 3.2.1. Open vs. Closed Periods (Closure Periods Two and Three; Post Closure One and Two)

Alert (−1.003 ± 0.215, Z = −4.675, $p < 0.001$) and positive social interactions (−0.513 ± 0.261, Z = −2.041, $p = 0.041$) were higher when closed (alert: 1.5 ± 1.8; social positive: 0.7 ± 1.1) than when open (alert: 0.5 ± 1.0, social positive: 0.4 ± 0.9) whilst resting was higher when open (8.4 ± 4.6) than closed (6.1 ± 4.4; 0.357 ± 0.098, Z = 3.646, $p < 0.001$). There were no significant differences in feeding, positive HAIs, comfort, locomotion, environmental interactions or number of observations where animals were OOS ($p > 0.05$).

#### 3.2.2. Closed Period Comparisons (Closure Period Two and Three)

There was no difference between the closure periods for alert, positive HAIs, feeding, comfort, positive social interactions, locomotion, environmental interaction or resting between closure period two and closure period three ($p > 0.05$). Frequency of observations out of sight was higher during closure period three (3.0 ± 3.9) than closure period two (0.9 ± 1.9; 1.2469 ± 0.4842, Z = 2.575, $p = 0.01$).

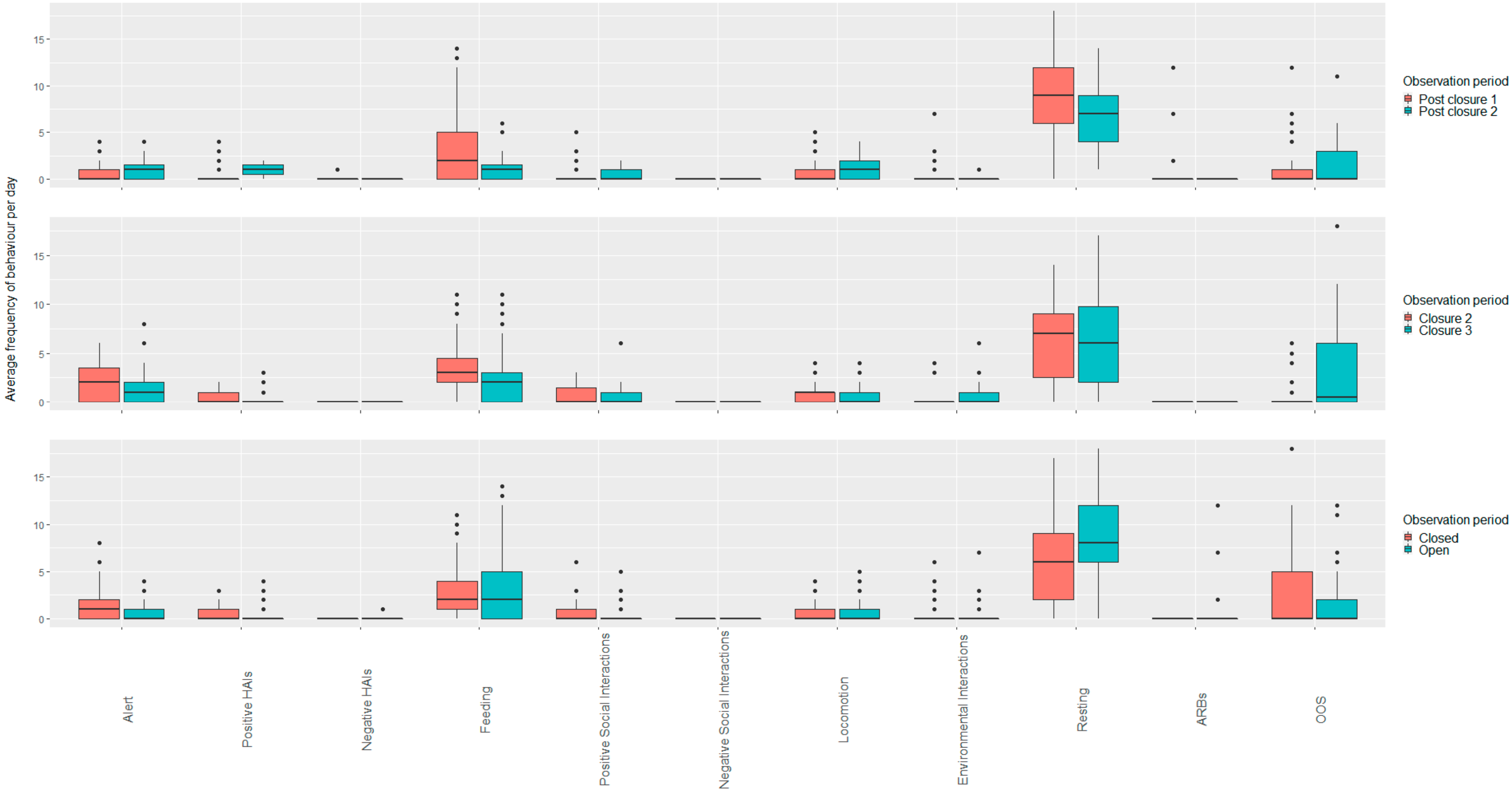


**Figure 3.** An overview of activity of rabbits housed at White Post Farm throughout the closure and reopening periods. Dots represent outliers.

3.2.3. Open Period Comparisons (Post Closure One and Two)

Alert (0.675 ± 0.092, t = −6.101, $p < 0.001$), locomotion (0.596 ± 0.290, t = 2.057, $p = 0.042$) and positive HAIs (1.259 ± 0.386, Z = 3.265, $p = 0.001$) were higher after the second closure period than the first (post closure 1: alert 0.5 ± 0.9, locomotion 0.5 ± 1.0, positive HAIs 0.3 ± 0.7; post closure 2: alert 1.1 ± 1.5, locomotion 1.1 ± 1.4; positive HAIs 1 ± 0.8). There was no difference in feeding, comfort, positive social interactions, resting or time spent out of sight. NB GLMMs indicated that positive HAIs reduced in relation to weeks since reopening (−0.099 ± 0.030, t = −3.269, $p = 0.001$) whereas feeding increased (0.064 ± 0.028, Z = 2.272, $p = 0.023$). Post-hoc, week by week comparisons, did not reveal any significant differences between specific weeks ($p > 0.05$). There was no effect of the number of weeks since reopening on alert, comfort, social positive, locomotion, resting or number of observations when animals were OOS ($p > 0.05$).

*3.3. Macaws*

3.3.1. White Post Farm

An overview of activity throughout the closure and reopening periods for macaws housed at White Post Farm is provided in Figure 4.

Open vs. Closed Periods (Closure Three)

Macaws at White Post Farm were only observed during the final closure period, therefore analyses of whether behaviour differed between open and closure periods focused on during and after the third COVID-19 closure. There was no difference in alert, locomotion, environmental interactions or positive HAIs ($p > 0.05$) during open and closure periods. Feeding was lower when the zoo was open (1.0 ± 1.8) than when it was closed (3.0 ± 2.4; −0.9003 ± 0.3378, Z = −2.666, $p = 0.008$). Preening (0.866 ± 0.349, Z = 2.479, $p = 0.013$) and resting (0.545 ± 0.197, Z = 2.768, $p = 0.006$) were both higher when the zoo was open (preening: 1.0 ± 1.0; resting: 5.3 ± 3.8) than when it was closed (preening: 0.6 ± 1.0; resting: 4.2 ± 4.3).

Open Period Comparisons (Post Closure One, Two and Three)

There was a significant difference in frequency of alert (−0.351 ± 0.041, Z = −8.588, $p < 0.001$), feeding (−0.163 ± 0.075, Z = −2.175, $p = 0.03$), comfort (0.216 ± 0.074, Z = 2.929, $p = 0.003$) and resting (−0.364 ± 0.054, Z = 6.722, $p < 0.001$) across the three post closure periods. Post-hoc analyses revealed alert behaviour was higher during the first post closure period (7.5 ± 4.3) than the third (1.1 ± 1.6; 1.437 ± 0.168, Z = 8.557, $p < 0.0001$), whilst comfort (−0.868 ± 0.029, Z = −3.041, $p = 0.007$) and resting were lower during the first closure period (comfort: 0.7 ± 1.1; resting: 2.0 ± 2.5) than the third (comfort: 1.0 ± 1.1; resting: 5.4 ± 3.7) (−1.470 ± 0.214, Z = −6.869, $p < 0.0001$). Feeding showed only a trend towards a difference between post closure one (3.2 ± 3.9) and post closure three (1.0 ± 1.8), with feeding being higher during post closure one (0.667 ± 0.299, Z = 2.231, $p = 0.07$). There was no difference in frequency of positive HAIs, positive social interactions, locomotion or environmental interaction across the three opening periods ($p > 0.05$). There was no impact of weeks since reopening on alert, positive HAIs, feeding, comfort, positive social interactions, locomotion, environmental interaction or resting ($p > 0.05$).

3.3.2. Plantasia

An overview of activity throughout the closure and reopening periods for macaws housed at Plantasia is provided in Figure 5.

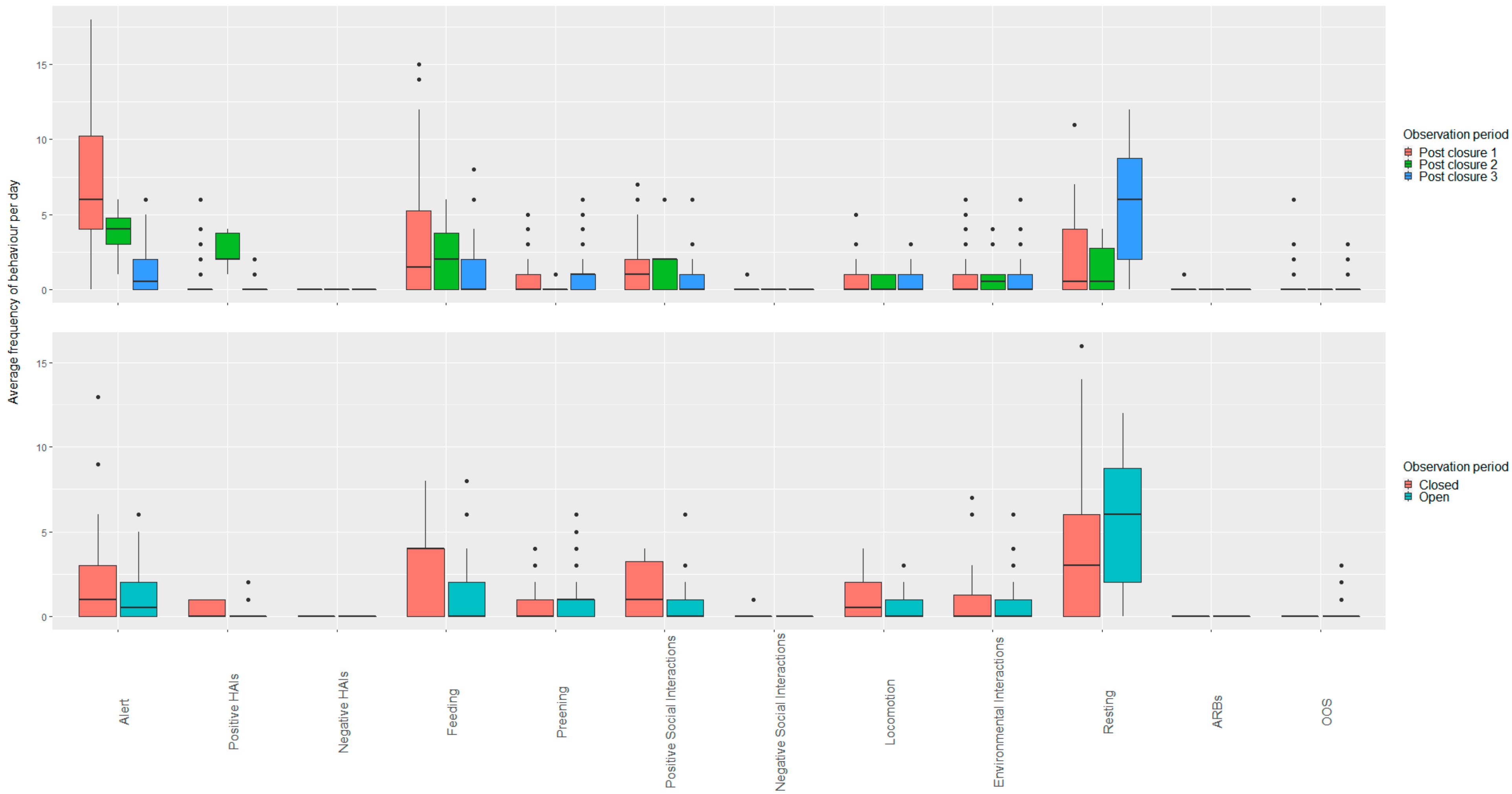


**Figure 4.** An overview of activity throughout the closure and reopening periods for the military macaw and blue and yellow macaw housed at White Post Farm. Dots represent outliers.

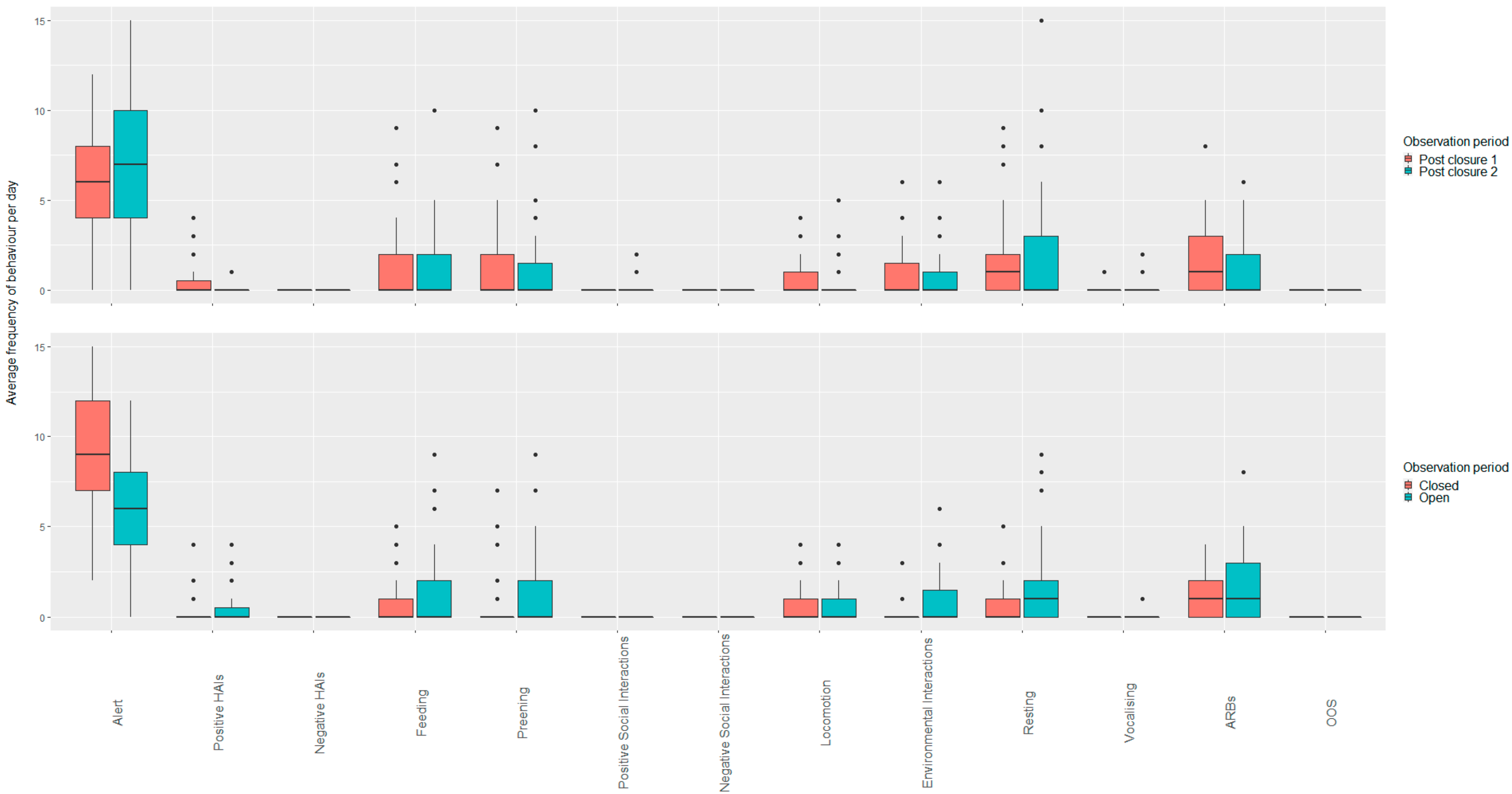


**Figure 5.** An overview of activity throughout the closure and reopening periods for the red and green macaw housed at Plantasia. Dots represent outliers.

Open vs. Closed Periods (Closure One)

Alert behaviour was higher when the facility was closed (9.3 ± 3.2) than when the site reopened following the first closure (5.9 ± 3.2; −0.435 ± 0.100, Z = −4.332, $p < 0.001$). Environmental interactions were higher when the facility had reopened to the public (1.1 ± 1.6) than when it was closed (0.4 ± 0.8; 1.062 ± 0.445, Z = 2.386, $p = 0.017$). There was no difference in positive HAIs, eating, preening, locomotion around the enclosure, resting or ARBs ($p > 0.05$).

Open Period Comparisons (Post Closure One and Two)

The majority of recorded behaviours did not differ between the observation periods following the zoo closures. There was no difference in alert, environmental interactions, feeding, preening, locomotion, resting or ARBs. Positive HAIs were lower post closure two (0.05 ± 0.2) than post closure one (0.4 ± 0.8; −2.046 ± 0.666, Z = −3.073, $p = 0.002$). Vocalisations were rare; however, it was the opposite of positive HAIs, and was significantly higher post closure two (0.3 ± 0.6) than post closure one (0.09 ± 0.3; 1.216 ± 0.553, Z = 2.201, $p = 0.028$). None of the analysed behaviours were impacted by the number of weeks since reopening ($p > 0.05$).

### *3.4. Meerkats*

#### 3.4.1. White Post Farm

An overview of activity throughout the closure and reopening periods for meerkats housed at White Post Farm is provided in Figure 6.

Open vs. Closed Periods (All Open and Closure Periods)

Alert (0.366 ± 0.141, Z = 2.601, $p = 0.009$) and comfort (0.804 ± 0.380, Z = 2.119, $p = 0.034$) were both higher when the site was open (alert: 16.7 ± 8.6; comfort: 1.4 ± 2.2) than when it was closed (alert: 14.8 ± 11.2; comfort: 0.8 ± 1.1). Time spent OOS was lower when the site was open (9.9 ± 11.4) than when it was closed (20.3 ± 13.8; −0.638 ± 0.240, z = −2.662, $p = 0.008$). There was no difference between open and closed periods for positive HAIs, feeding, locomotion, environmental interactions and resting ($p > 0.05$).

Closure Period Comparisons (Closure Two and Three)

Alert (−1.105 ± 0.309, Z = −3.581, $p < 0.001$) and locomotion (−3.225 ± 1.121, Z = −2.876, $p = 0.004$) were lower during the third closure (alert: 4.1 ± 5.2; locomotion: 2 ± 5.3) than the second closure (alert: 18.9 ± 10.2; locomotion: 6.2 ± 5.7). There was no difference in positive HAIs, feeding, environmental interactions, resting, comfort behaviour or frequency of observations spent out of sight of the observer ($p > 0.05$).

Open Period Comparisons (Post Closure One and Three)

Resting was higher when the facility reopened after the third closure (4.7 ± 4.9; 1.358 ± 0.485, Z = 2.798, $p = 0.005$) than after the first closure (1.7 ± 2.4), whilst number of observations spent out of sight was lower following the third closure (post closure one: 17.1 ± 17.5; post closure three: 6.1 ± 5.5; −0.7923 ± 0.3834, Z = −2.067, $p = 0.038$). There was no difference between the opening periods for alert, positive HAIs, feeding, comfort, locomotion, environmental interaction or ARBs ($p > 0.05$). There was no impact of the number of weeks since reopening on alert, positive HAIs, feeding, locomotion, environmental interaction, resting, time spent OOS or ARBs ($p > 0.05$). Comfort behaviour increased in the weeks since reopening (0.248 ± 0.117, Z = 2.124, $p = 0.034$) but post hoc tests indicated there were not significant differences between particular weeks ($p > 0.05$).

#### 3.4.2. Plantasia

An overview of activity throughout the closure and reopening periods for meerkats housed at Plantasia is provided in Figure 7.

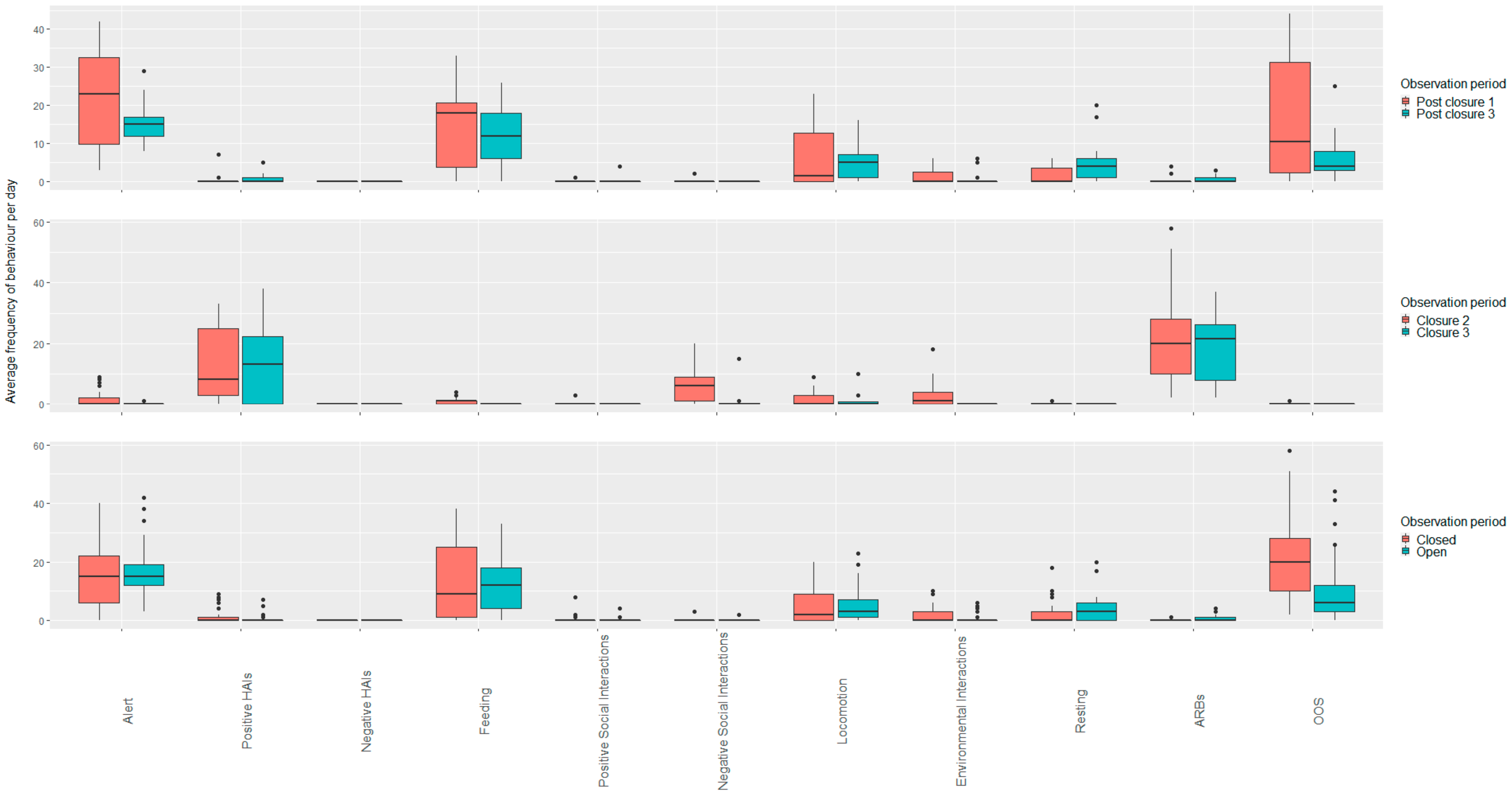


**Figure 6.** An overview of activity throughout the closure and reopening periods for meerkats housed at White Post Farm. Dots represent outliers.

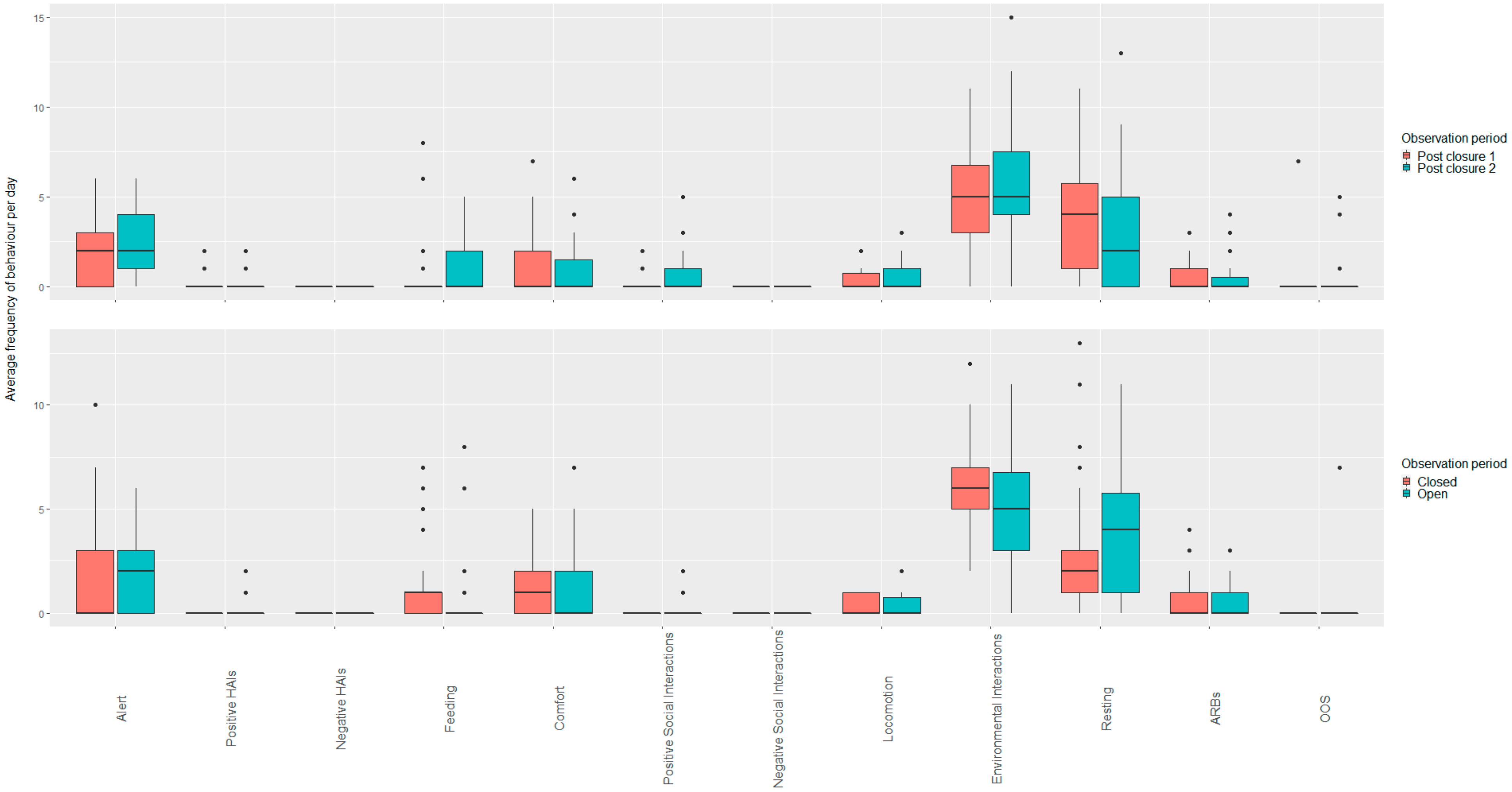


**Figure 7.** An overview of activity throughout the closure and reopening periods for meerkats housed at Plantasia. Dots represent outliers.

Open vs. Closed Periods (Closure One)

Alert, feeding, comfort, locomotion, resting and ARBs did not differ between open and closed periods ($p > 0.05$). Environmental interactions were lower when the zoo was open (6.4 ± 2.0) than when closed (5.0 ± 2.8; −0.213 ± 0.101, Z = −2.12, $p = 0.034$).

Open Period Comparisons (Post Closure One and Two)

There was no difference in alert, feeding, comfort, locomotion or interaction with the environment between post closure one and two ($p > 0.05$). There was a trend towards difference in resting, with less rest seen following closure two (−0.372 ± 0.195, Z = −1.902, $p = 0.06$) (post closure one: 3.8 ± 2.8; post closure two: 2.6 ± 2.9). Alert reduced as the weeks since reopening increased (−0.059 ± 0.030, Z = −2.005, $p = 0.04$), however post hoc tests did not reveal specific differences between weeks ($p > 0.05$). There was no impact of weeks since reopening on frequency of feeding, comfort, locomotion, interacting with the environment or resting ($p > 0.05$).

3.4.3. Knowsley Safari

An overview of activity throughout the closure and reopening periods for meerkats housed at Knowsley Safari is provided in Figure 8.

Open vs. Closed Periods (Closure One and Two; Post Closure One)

None of the modelled behaviours showed significant differences in frequency between the two conditions ($p > 0.05$).

Closure Period Comparisons (Closure One and Two)

There was no difference in alert, comfort, positive social interactions, locomotion, environmental interaction, resting or time spent OOS ($p > 0.05$) during the two closure periods. Feeding was significantly lower during closure period two (3.7 ± 3.2) than closure period one (14.3 ± 4.9; −0.770 ± 0.329, Z = −2.337, $p = 0.019$).

Weeks since Reopening (Post Closure One)

There was an effect of weeks since reopening for frequency of positive HAIs (−0.240 ± 0.061, Z = −3.908, $p < 0.001$), feeding (−0.026 ± 0.012, Z = −2.2, $p = 0.028$), negative social interactions (−0.242 ± 0.060, Z = −4.016, $p < 0.001$), locomotion (−0.051 ± 0.016, Z = −3.114, $p = 0.002$) and environmental interactions (−0.047 ± 0.022, Z = −2.107, $p = 0.035$), with all behaviours showing a reduction over time. However, week by week post-hoc analyses did not reveal significant differences between each week ($p > 0.05$). There was no difference in behavioural frequency per observation day across the weeks since reopening for alert, comfort, positive social interactions, resting or time spent OOS.

3.4.4. Dartmoor Zoo

An overview of activity throughout the closure and reopening periods for meerkats housed at Dartmoor Zoo is provided in Figure 9.

Open Period Comparisons (Post Closure One and Three)

There was no difference between frequency of alert, environmental interactions or time spent OOS during post closure one and three ($p > 0.05$). Feeding (−2.603 ± 0.705, Z = −3.694, $p < 0.001$) was lower following closure three (0.3 ± 0.7) than closure one (10.4 ± 10.5). Resting was higher post closure three (4.3 ± 3.8) than post closure one (3.1 ± 4.3; 1.227 ± 0.412, Z = 2.979, $p = 0.003$). There was no impact of the number of weeks since reopening on alert, resting or time spent OOS ($p > 0.05$). Locomotion increased with weeks since reopening (−0.735 ± 0.028, Z = 2.597, $p = 0.009$), however post hoc tests did not indicate any specific differences between observation weeks. Environmental interactions decreased with weeks since reopening (−0.176 ± 0.053, Z = −3.299, $p < 0.001$). Post hoc tests revealed there were differences between some weeks but no consistent decrease over the weeks (Figure 10).

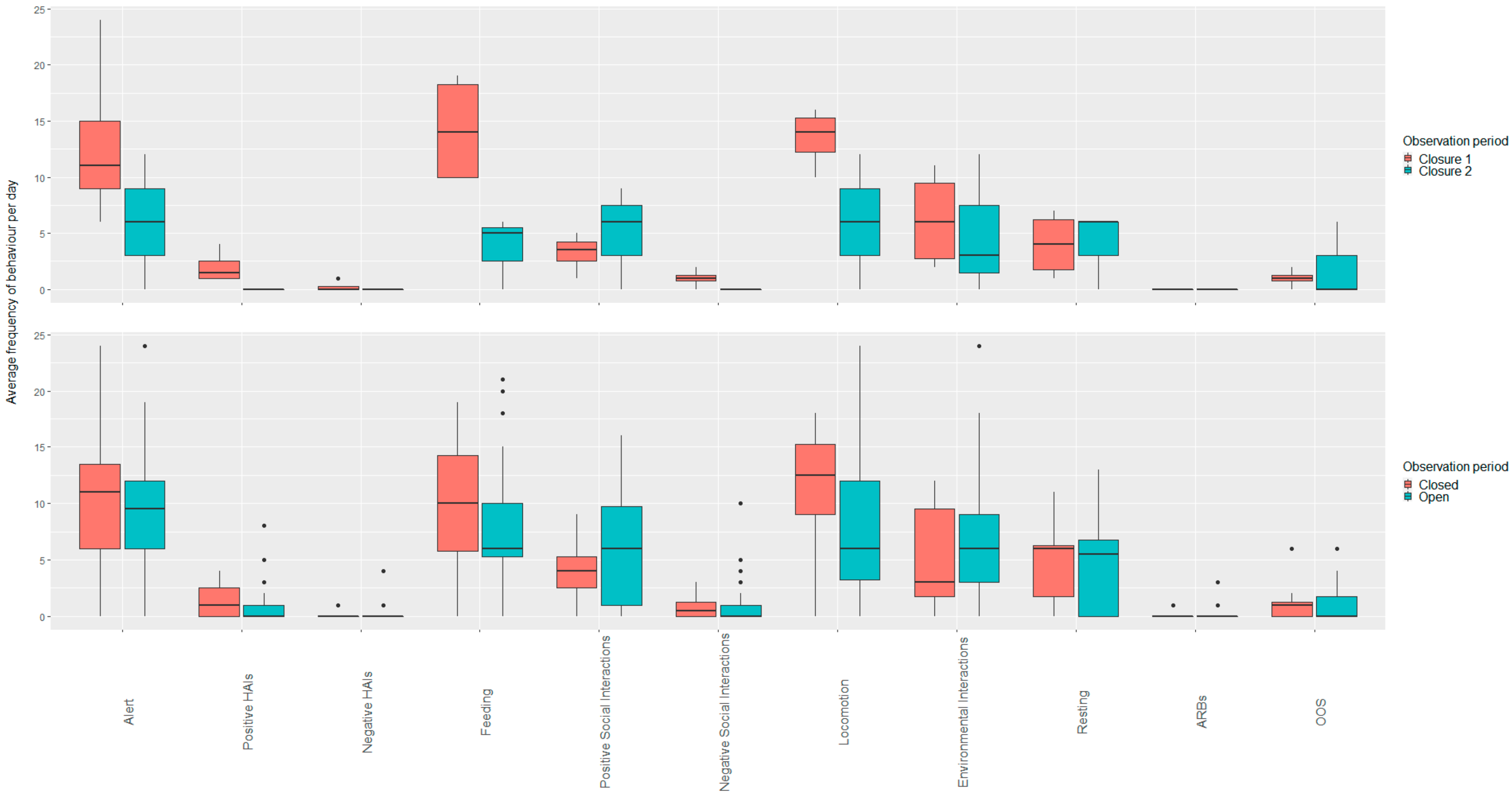


**Figure 8.** An overview of activity throughout the closure and reopening periods for meerkats housed at Knowsley Safari. Dots represent outliers.

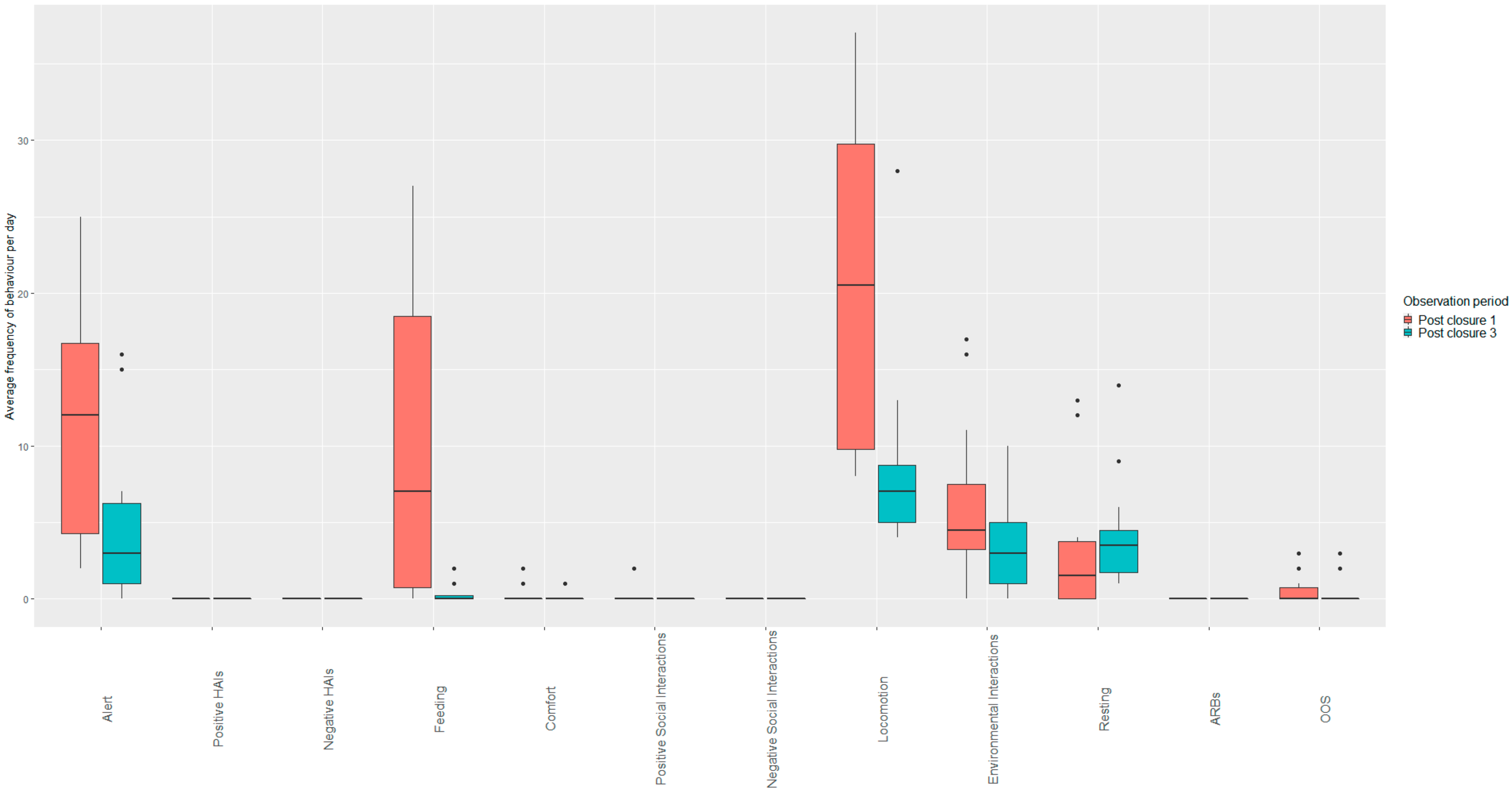


**Figure 9.** An overview of activity throughout the closure and reopening periods for meerkats housed at Dartmoor Zoo. Dots represent outliers.

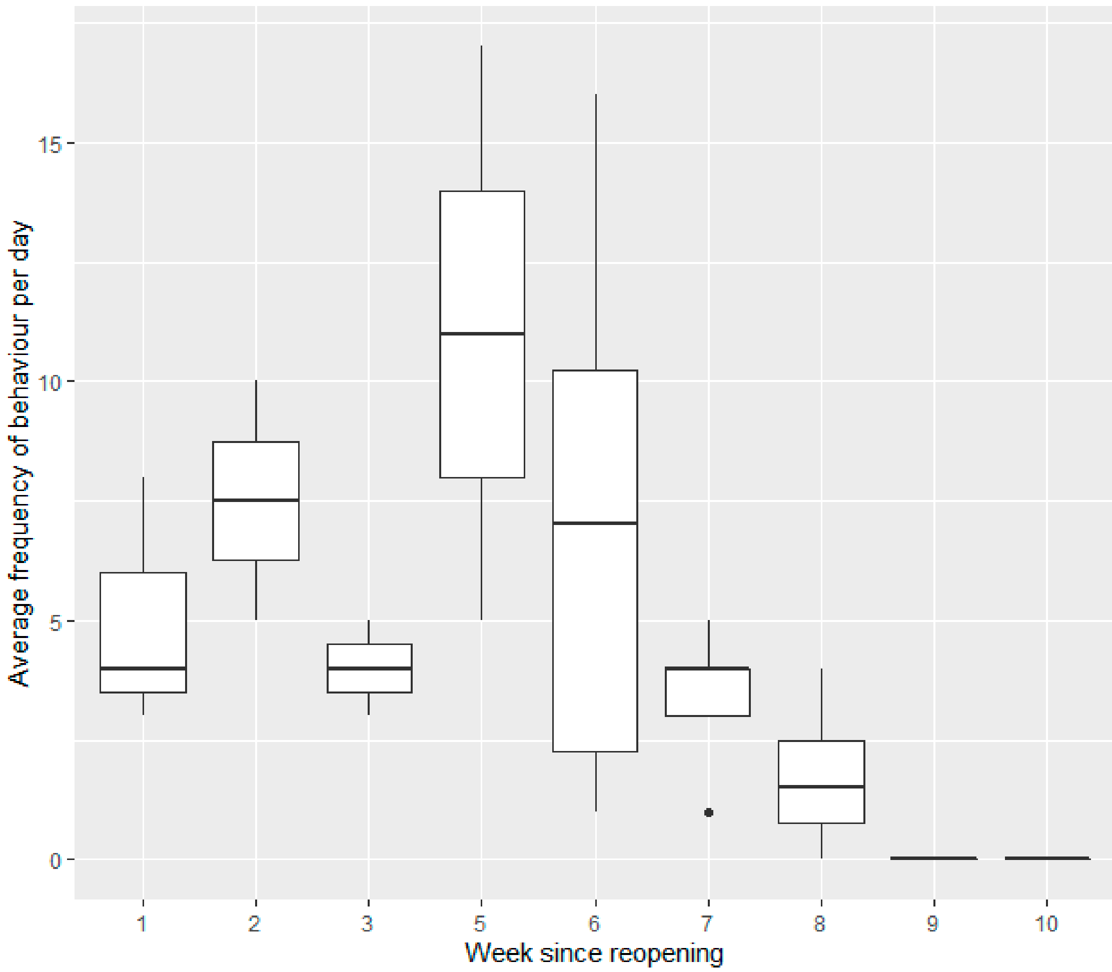


**Figure 10.** Average frequency of environmental interactions recorded in the meerkats at Dartmoor Zoo per day in the weeks since the facility reopened to the public. Dots represent outliers.

## 4. Discussion

Overall, the data highlights variable responses to the closure and reopening periods. Across all species there appeared to be no particular positive or negative impacts of the facility closures. The mixed behavioural responses mirror literature published to date in a range of other species.

### *4.1. Wallabies*

The wallabies at White Post Farm were housed in a walk-through exhibit. When the zoo was open as compared to closed, wallabies showed increased levels of resting behaviour and positive HAIs but they also showed reduced locomotion, feeding and time spent OOS. Behavioural changes were also observed across the three opening periods after the facility closures. The overall increase in positive HAIs, which included approaching humans, suggests the wallabies were engaging with zoo visitors when the facility reopened and that the visitors were a source of positive stimulation for the wallabies; however, these occurrences were low in both settings. The increase in resting behaviour could suggest either a comfort in the environment when the public returned, or conversely, combined with reduced locomotion it could suggest the wallabies were less active when the visitors returned to the zoo. Sherwen et al. [35] and Jones et al. [28] found that red kangaroos fed more when there were no visitors within the habitat, with the behaviour of the kangaroos corresponding to crowd size rather than zoo status. It was beyond the scope of this study to investigate the impact of the number of visitors at the enclosure, but it is possible that either the number of people in the enclosure had reduced following the first closure period (this period corresponded with winter months when the zoo was likely to be quieter) or that the animals had become more used to the return of visitors by that point, as also supported by a reduction in locomotion. Other indicators of the initial reopening period being more stressful for the animals, such as increased social interactions/bunching behaviour, or increased time spent alert, as have been recorded in relation to increased visitor numbers in studies of red kangaroos [28,35] were not observed.

### 4.2. Rabbits

Rabbits are a prey species, and it is thus expected that they would engage in heightened alert behaviour in settings where they felt less comfortable. The increased alert and social behaviour when the site was closed to the public may represent increased discomfort during this time period, with social behaviour acting as a buffer to stress [36]. One potential implication of the lack of visitors in zoos during the COVID-19 pandemic was the lack of 'background' visitor noise acting as a buffer for other noises within the zoo, including general zoo operations (e.g., vehicles, gates opening/closing) and, for prey species, the noises of predators within the environment [37,38]. Indeed, the presence of intermediate levels of humans may lead some species to decrease alert behaviours and show behaviours indicative of being at ease in the environment [39]. Anecdotal reports from a Japanese aquarium highlighted increased fear responses in garden eels during the COVID-19 closures, owing to the lack of visitors within the aquarium [40]. The alert behaviour observed in the rabbits in this study could also thus be a result of heightened noise stress. However, a number of reports also indicated that species were 'looking out' for visitors during the COVID closures [41], and increasing interest in keepers, partially due to the fact that the keepers were spending longer trying to 'entertain' animals [42], but also because there was reduced stimulation from visitors in the environment. Similar reports have been observed in a range of other species including Chapman's zebra, amur leopards and giraffe [14]; Rowden et al. in prep. Whilst the rabbits at White Post Farm were not used as a petting experience before the COVID-19 closures [Vernon, personal communication], the increased positive HAIs when the facility reopened to the public lends support to the theory that the rabbits were looking out for zoo visitors and were responding positively to their return. Although not linear over time, positive HAIs reduced in the weeks since reopening and feeding increased, which is also likely the rabbits adapting to the novelty of visitors returning to zoos, similar to the rehabituation observed in gorillas and amphibians [16,29].

### 4.3. Macaws

Macaws varied in their response between the two study zoos that housed them. The HAI literature predominantly focuses on primate species [43], but studies have shown that visitors are usually drawn to more active animals [13,44]. The alert behaviour performed by the macaws at Plantasia could be similar to the 'looking out for people' that was anecdotally reported by a number of facilities during the closure periods [45], and the increased environmental interaction when the facility reopened to the public could be an active behaviour being undertaken by the birds in a bid to gain human attention when the facility reopened. Conversely, the high alert behaviour could be a product of the altered soundscape in the zoo [12]. The difference in the macaws' behaviour between the post closure periods may also suggest a greater interest in and 'missing' of visitors after the longer first closure period than the later post closure periods. There were a number of reports on social media of psittacine species [12], with around 50% of these reports indicating that they were 'missing' zoo visitors (Hunton et al. unpublished data). At White Post Farm, the macaws engaged in increased preening behaviour and vocalisation. The auditory environment can have implications for behaviour of zoo-housed parrot species [46] and recent research has suggested it can impact on the welfare state of birds as a whole [47]. When psittacines were exposed to auditory enrichment they increased the frequency with which they engaged in calm vocalisations and preening behaviour [46].

Bird-focused research within zoos is relatively rare in comparison to studies of their mammalian counterparts [48], and there is limited research in particular on the implications of HAIs on birds [13,47]. However, research that has been published to date indicates visitors can have a positive, negative or neutral impact on bird species, with positive HAIs leading to decreased fear responses and lowered corticosterone [47]. Penguin behaviour has been linked to visitor numbers [49]; however, research of African penguins during the COVID-19 pandemic found no significant differences when the public were back in the zoo as compared to when it was closed [18]. Kidd et al. [22] found similar mixed behavioural responses in two species of flamingos. The changes in vocalisations and public interactions when the zoos reopened could thus be related to the return of visitors and the associated noise and interaction from them. Whilst it is possible there are other factors driving these behavioural changes (e.g., time of year) the behavioural results for the macaws at these two sites largely mirror these anecdotal reports, with the increased attention towards visitors, increased resting and reduced alert behaviour suggesting a positive influence of the return of visitors. It is important to note that vocalisations were classed as positive HAIs at Plantasia if the macaw was 'talking to visitors'. If visitors were not mentioned it was coded as a vocalisation only. It is thus possible that these vocalisations were also an attempt to gain human attention. No behavioural changes were seen on a week-by-week basis at either of the study zoos.

### *4.4. Meerkats*

Meerkats were observed at four facilities in the UK. Behavioural changes were seen between open and closure periods, and also within the different reopening periods, but changes were not consistent across facilities. Meerkats at Plantasia and White Post Farm engaged in more alert behaviour, environmental interactions and comfort behaviour when the facilities were open. Differences were observed over time, with meerkats at White Post Farm displaying less alert and locomotion behaviour during the third closure than the second, meerkats at Knowsley Safari feeding less during the second closure than the first and meerkats at Plantasia and Dartmoor resting more following the second and third closures (respectively) than the first. These findings differ from other studies, which indicated that meerkats spent more time engaged in environmental interactions and reduced alert behaviour during initial COVID-19 closures than the first month post reopening [18]. The engagement with the environment during the COVID-19 closures may have been due to active behaviour by keepers to reduce the impact of the lack of stimulation from visitors, with media reports indicating that keepers were providing novel forms of enrichment [50] and some of the study zoos providing more varied or complex types of enrichment for their meerkats during closure periods owing to having more time to prepare the enrichment items (Vernon, pers. Comm; Cox, pers. Comm). This variable response to visitors has also been reported in the general human–animal interaction literature, with some studies suggesting meerkats are indifferent to visitor behaviour [51] and others reporting changes in physiological parameters [52]. Changes in behaviour over time potentially reflect the speed with which the animals adapted to the third closure period.

### *4.5. Impact of Prior Interactions with Humans*

Historical interactions with people may impact on zoo animal responses to visitors [13]. The species involved in this research had variable interactions with visitors prior to the COVID-19 pandemic. Meerkats at White Post Farm were scatter fed by the public, meerkats at Dartmoor Zoo were involved in 'meet the meerkat' and 'feed the meerkat' experiences, where members of the public had the opportunity to feed the meerkats, and meerkats at Knowsley Safari were used in private encounters and were one of the focal species for public talks. Following the COVID-19 closures the 'feed the meerkat' experiences and encounters were restarted at Dartmoor Zoo and Knowsley Safari, respectively, but the 'meet the meerkats' and public talks were not. The 'meet the meerkats' experience at Dartmoor Zoo involves visitors going inside the meerkat enclosure, whilst the 'feed the meerkats' is from outside of the enclosure. Interactions with the public within the meerkat enclosure had not been restarted during this study, and public talks at Knowsley Safari had not been commenced in order to reduce visitor gathering. The meerkats at Plantasia did not have any specific interactions with the public either before or after the COVID-19 closures. Wallabies at White Post Farm were housed in a walk-through exhibit but no touching was permitted within the exhibit, whilst the rabbits and macaws did not have any interactions with the public. The range of interactions prior to the pandemic closures could have led to the development of differential relationships between the study species and the public; however, descriptively there did not seem to be clear relationships between previous levels of visitor interaction and behavioural response to zoo visitors. Previous research into the impact of the COVID-19 pandemic on zoo housed Rothschild giraffe found that the study animals were engaging in increased positive HAIs during the zoo closures, which the authors attributed to the giraffe 'looking out for' the public and seeking interactions with zoo keepers as a filler for public interactions that they had experienced (via feeding encounters) prior to the COVID-19 closures [14]. The opposite of this was found with the wallabies in this study, who engaged in more positive HAIs when the zoo was open to the public, which may reflect their interest in the public when the facility reopened. Research by Jones et al. [28] indicated no changes in keeper or visitor directed behaviour in red kangaroos as a result of the COVID-19 pandemic, and Sherwen et al. [35] found there was no difference in location to visitors in response to increasing visitor number. Rabbits housed at White Post Farm and macaws housed at Plantasia engaged in more positive HAIs after the second closure than the first closure, although at least for the rabbits it is unclear whether this was an artefact of the sampling protocol (see limitations) or a more reserved response to zoo visitors following the first closure as a result of the animals taking longer to rehabituate to zoo visitors [16,29].

### *4.6. Limitations*

There are limitations when collecting data opportunistically during such unique circumstances. These have been borne in mind during interpretation of the key findings from this research.

#### 4.6.1. Seasonal Impacts on Behaviour

This study focused simply on the status of the zoo, to enable keepers to capture data during discrete periods of time in a fast and repeatable manner. However, other factors, which could not be accounted for in this analysis, could have been impacting the behaviour of the study animals. These principally include, but are not limited to, visitor number and behaviour and weather conditions. Weather can impact on animal behaviour and the closure periods occurred at different times of year; it could thus be that behavioural responses seen during the second and third closure periods (and reopening periods thereafter) were a result of behavioural response to meteorological changes in the enclosures, rather than a direct result of the absence of people in zoos, as was noted by Kidd et al. [22]. Whilst it is not possible to differentiate visitor effects from seasonal effects, there were no extreme weather conditions during the data collection periods and the inclination for species towards HAIs is likely due to the presence of visitors, rather than seasonal effects, as was highlighted by Jones et al. [28].

#### 4.6.2. Data Collection Methods

Zoos and zoo keeping staff were needing to quickly adapt to an ever-changing world when the data collection for this research began. Due to the requirements for staff to undertake the observations to ensure consistency within facilities there was variation in amounts of data collected per week, both during closures and during subsequent reopening periods, and on the starting date for data collection. For example, there may be more data during the initial weeks following the second and third closure periods than the first, which could have led to capturing of data which enabled greater impact of novelty to the new condition during those time periods, rather than once animals were more accustomed to the visitors returning to zoos. There was also a shorter period of time between the second and third closures than between the first and second. The lack of extreme behavioural responses in any of the open or closed periods suggests that, as has been highlighted in previous work during the COVID-19 pandemic, that zoo-housed animals are behaviourally adapted to the presence and absence of zoo visitors [14,20,22] and thus that this limitation, although important, is likely to have had minimal impacts on the data collected. The lack of behavioural change in the weeks since reopening also suggests minimal impact. Finally, there was also a lack of data from during the first closure. Data were only collected during the first closure period for animals housed at Plantasia and Knowsley Safari, and this data collection did not commence until approximately two months after the closure period began. It is likely that this period would have shown the greatest behavioural change, due to the sudden and unexpected change in the situation, and that the delay in capturing these data meant animals had adapted to the closure period and the associated lack of stimulation from visitors. However, this immediate response would likely have been a response to the new and novel setting, rather than more representative of the longer-term impact of the temporary closures.

The data were collected based on 5-min data collection periods, the limitations of which have been detailed in Williams et al. [14,18]. In essence, the data captured provided only a snapshot of animal behaviour. Whilst this is a recognised limitation, it provided a means of looking at how animal behaviour had changed over this prolonged period of time in a repeatable and comparable manner. There were differing numbers of data collection periods per day, again due to staff availability. In recognition that there is not likely to be independence of data within the same day, analysis was undertaken on data which had been pooled to create a total number of observations of behaviour per day, with number of observations per day fitted as an offset variable in statistical models. Although this ensured independence in data points, it did lead to the need to investigate change over time since reopening on a week-by-week basis rather than a day-by-day basis. This may have led to a lack of fine scale data, which could have revealed differences in animal responses to humans during immediate reopening periods. For example, it may be that the animal responses to reopening were greatest during the initial days since reopening, rather than the slightly longer time period of one week. However, this study sought to understand behavioural change over a longer period of time, rather than immediate response to novelty, and thus understanding behavioural change on a week-by-week basis was considered to be of greatest relevance. In order to create simple and repeatable protocols, there was also no opportunity to gather information on visitor numbers or visitor behaviour, which could have affected animals during the observation periods. However, in most instances staff were able to undertake more than one observation per day, so the pooling of these data, consideration on a ‘week-by-week’ scale for longitudinal change and broad ‘closure’ and ‘reopening’ comparisons enabled the effect of potentially varying visitor numbers to be diluted.

Finally, data analysis was undertaken using GLMs and GLMMs in order to undertake simple hypothesis testing rather than predictive modelling. These methods were chosen due to their relative simplicity owing to limitations described in the data set. Model results were interpreted with caution owing to large confidence intervals, and whilst representative of genuine behavioural change as is evidenced descriptively in graphical representation of animal activity, these results could not be directly extrapolated to other species or groups of species. Nevertheless, the data adds to our increased understanding of the impact of COVID-19 zoo closures on animal behaviour.

## 5. Conclusions

The species in this study represented a range of animals that were housed in enclosures that had different levels of visitor access. As has previously been reported in other studies investigating the impact of COVID-19 zoological closures on animals, the animals in this study showed variable responses to the closures and subsequent reopening periods. Changes were observed between open and closure periods, and in some instances, changes were also observed over time, with animals responding differently to each of the closure and reopening periods. However, no overt positive or negative impacts of the closures or reopening periods have been identified for these species. This unique opportunity to study animals over a long period of time during repeated closure periods enabled a greater understanding of the impact of zoo visitors on animals, and, as with other work in this sphere, has highlighted the adaptability of zoo animals to the zoo visitor. This work contributes to the growing field of research undertaken during the COVID-19 periods and enhances our understanding of the impact of these zoological closures on a wider body of species in a number of facilities.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jzbg3040044/s1, Table S1: Summary of model outputs for the four species held at four zoological collections in the UK (HAI: human–animal interactions; OOS: out of sight). Statistically significant differences have been highlighted in bold.

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