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Behavioural Responses to Temporary Separation of a Captive Herd of African Elephants (*Loxodonta africana*)

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Abstract: Elephants are highly intelligent animals with a huge capacity for social cognition, living in large, long-lived, related herds. In captivity, it is extremely difficult to meet all of the species' ecological needs, as well as those required individual by individual, but improvements are continually being made. After identifying impaired welfare, one collection made the decision to relocate four female African Elephants (*Loxodonta africana*) to a different facility. As the worlds' largest land mammal, many safety, welfare, and logistical considerations were undertaken. The elephants travelled in two pairs, a mother–daughter pair and an older unrelated female and a younger unrelated female with a strong social bond. As a result, there was a short gap in between transports, allowing for further habituation to transport crates and the heat of summer. The changes in both social and individual behaviours of the two females remaining when their group was temporarily reduced from four to two were investigated using one-zero sampling. The study determined the daily activities of the elephants comparing 'before transport' to 'after transport' for the two remaining elephants to establish any changes in their behaviours as a result of this disturbance. Post transport, there was an increase in both human-audible vocalisations and temporal gland secretions, and hugely decreased play behaviour was observed. The dynamic between the remaining pair was also altered with more tactile behaviours from mother to daughter seen but more submission from daughter to mother. This led to the conclusion that the elephants, although mostly unrelated and living in an 'unnatural' captive setting, had the same signs of stress and behavioural change as would a highly related group if separated.

Keywords: welfare; social; transport; behaviour; elephants

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1. Introduction

1.1. Elephants in Captivity

Elephants of both extant species (*Loxodonta africana* and *Elephas maximus*) live in matriarchal fission–fusion herds of varying size in situ [1] Their complex social structures and highly related herds have been studied extensively. Populations of both species of elephant are in consistent decline due to poaching and other human–animal conflicts, as well as habitat loss and compartmentalisation of their home ranges [2–4]. In situ, elephants display an incredibly complex range of behaviours, showing their intelligence and social bonds which help maintain the herd dominance hierarchy required to live in such large groups. Kin recognition and recognition of other elephants they have crossed paths with possibly decades earlier, grieving behaviours, and complex play and social learning behaviours have all been well described [5,6]. Long-term (lifelong, following several generations) studies such as those conducted in Amboseli National Park [7] have provided huge insight into the behavioural repertoire of elephants, their communication, and how these behaviours and resulting highly related herds could be affected by anthropogenic change. Ex situ, modern captive settings strive to provide an environment which can not only provide the species' basic ecological needs, but also takes individual needs and preferences into account, being enriching and dynamic enough to work towards the highest

possible welfare through opportunities for natural behavioural expression [8]. Many of the behaviours observed in situ have been reported ex situ despite being housed in an unnatural environment, sometimes with very few or no related individuals. However, captive elephants are known to develop stereotypic behaviours, well documented due to being housed in potentially inappropriate captive environments and the resulting change in psychological state [9].

The captive population of elephants in zoological collections is closely monitored through UK-specific, ongoing, welfare reviews and European-based breeding programmes [10,11]. Elephants are seen as a flagship species in any zoological collection due to their incredible intelligence and similarities to humans in terms of cognition and empathy [12,13]. The organisations housing them have a responsibility to ensure that their husbandry allows physical and mental welfare standards to be met, as well as making an overall contribution to protecting wild populations directly or indirectly [9,14]. In 2010 a study was conducted on all captive elephants of both species within UK collections, collecting independent data regarding mental welfare, physical health, and housing suitability [9]. Results led to UK collections being given a number of requirements to implement within a given time frame to be able to meet new guidelines and continue holding elephants. Subsequently, husbandry guidelines and group composition recommendations were updated [9,10,15], and many collections chose to independently modernise their approach to elephant keeping [16,17].

In captivity, African elephant herds were historically made up of presumably unrelated individuals that were wild-caught calves taken from Africa after large culls on crop-raiding elephants [18]. This resulted in captive groups of unrelated animals of similar ages consequently supplemented by their captive-born offspring. It is only within the last few decades that captive collections have focused on having herds with high relatability and multiple generations [9,10]. This study focused on a captive herd of four female African elephants (*Loxodonta africana*), housed at Knowsley Safari (KS), Merseyside, UK. At the time of study, KS had made the decision to move their elephants to ZooParc de Beauval, France, in order to offer them higher welfare living conditions. The new environment would offer improved housing and outdoor space, more social options, and potentially opportunities to breed if appropriate. The elephant enclosure at KS was considered to have "sufficient" outdoor space, but it lacked complexity, and the indoor housing was insufficient. Traditionally, elephants are transported through hiring an external company or as an extension to free contact (FC) management. FC relies on the premise that the keeper or trainer is dominant over the animal, allowing them to be in the same space as the elephant, controlling with or carrying an ankus (a short-handled tool with a hook at one end used as a 'guide') [10,19]. Research in Asian elephant transports showed that this can subsequently negatively impact welfare, with faecal cortisol levels and stereotypic behaviour both increasing by nearly 400% [20]. The elephants at KS were managed in protected contact (PC), a husbandry method allowing freedom of choice to the animal, with training conducted through positive reinforcement with keepers never entering the same space as the elephant [10]. PC training was extended to the transportation from KS, with elephants being given access to the transport crates almost daily, without an external company, with familiar keepers training and conducting loading for transport. This training was aimed at desensitising the elephants to the loading process ahead of transport, with the end goal being to reduce stress and improve welfare during and after transportation.

For safety, logistical, and economic reasons, the decision was made to move the elephants in pairs (each in a separate crate), with a time gap in between transports. This allowed the time required to avoid the heat of summer and traffic, reducing discomfort to the elephant and reducing the time on the road, as well as allowing the second pair the extra time they required for desensitisation to the crate.

1.2. Focal Herd

The study herd housed at KS was irregular due to its varied background (Table 1). The two younger individuals born at KS, Nala and Ashanti, shared a father and were considered 'playmates', with keeper observations identifying that they spent a lot of the day together and slept in close proximity to one another. They were housed with two older females, Juba and Tana, with Juba being considered the 'matriarch' of the small group. However, the two older individuals, Tana (Nala's mother) and Juba (unrelated to all) were wild caught around the age of 2 years and brought to the UK and were observed by keeping staff anecdotally to display more behavioural irregularities. Both displayed stereotypic behaviour; Juba would 'sway', and Tana would blow air onto the sulcus of her tusks. Juba and Tana had previously been housed together in a different collection, before their transport to KS together, Therefore, Juba and Tana had been together for around 30 years, 14 of which were with the two younger individuals. The previous knowledge of the relationships among the elephants in the study herd aided in the decision of which elephants to send to the new collection together. Juba and Ashanti were transported first as a pair; although not related, their keepers reported a well-established, strong bond. They were followed by Tana and Nala, the mother–daughter pair. The rationale behind which pair travelled first was dictated by keeper observations of the individual elephants' response to PC training to walk into their transport crates. Ashanti, the most submissive but most playful of the group was extremely confident with keepers and walked into the crate on the first day access was given. This contrasted to Nala's response to the transport crates. Nala was more wary of keepers and took several months to be encouraged over the 'line' between the elephant house she had been housed in all her life and the newly introduced transport crate. Juba and Tana responded well to their training, both habituating to the crates over time. Therefore, Juba and Ashanti were transported as soon as Juba was confident walking into the crate, with Tana and Nala following.

Table 1. Focal herd of elephants (*Loxodonta africana*) at Knowsley Safari (KS) (w. = wild caught orphan, c. = captive born, ~ = estimated, b. = born).

Name	Sex	Origin	Age	Arrival KS	Relatedness	Dominance	Transport
Juba	F	w.1998 Zimbabwe	~31	1993	Unrelated	1	1
Tana	F	w.1988 Zimbabwe	~30	1993	Mother of Nala	2	2
Ashanti	F	c. KS	14	b. 10 January 2003	1/2 sister of Nala	4	1
Nala	F	c. KS	13	b. 5 April 2003	Daughter of Tana	3	2

1.3. Aims

This project aimed to analyse the behaviour of two elephants after the transport of another pair, with whom they had been housed for 14 years, compared to that of their behaviour before, when housed as a four. These analyses were required to determine any changes observed during the short-term separation (positive, neutral, or negative) as although the transport was required on welfare grounds, separating a well-established group of elephants would not be advised for a long period of time, if at all.

2. Materials and Methods

2.1. Study Site

Knowsley Safari is a privately owned zoological collection situated in a large estate in Merseyside, UK. The focal elephants were housed in the 'Foot Safari' area of the park, in a 26,709 m^2 enclosure comprising of a large grass paddock, smaller sand paddock, concrete hardstand, small outdoor holding pen, and indoor house (Figure 1). The elephants were

observed in the outdoor paddocks during the day, with all areas visible from the keeper side of a public viewing platform overlooking the enclosure (Area 6, Figure 1).

Figure 1. Aerial View of the Elephant enclosure at Knowsley Safari Park, Merseyside. Area 1 = grass paddock. Area 2 = sand paddock. Area 3 = concrete hardstand with pool. Area 4 = outdoor holding pen. Area 5 = indoor housing. Area 6 = viewing platform from which observations were made.

2.2. Data Collection

The focal herd was observed with consistent methods for two study periods, referred to as *before transport*, when the elephants were studied as a four, and after transport, when two elephants remained. Individual elephants were identifiable by differences in size, tusk length, gait, and facial features. On 25 non-consecutive days from 31 January 2017 to 3 April 2017 (before transport) and then again, following the transport of Juba and Ashanti on 5 July 2017, from 6 July 2017 until 27 August 2017 (after transport), 30 min observations between 10:30 a.m. 4:00 p.m. were recorded. These study periods gave 12.5 h of observations before transport and 12.5 h after transport. The time of day at which recordings were taken was randomised throughout to ensure no bias was created by keeper presence or anticipation of feed. The first study period, before transport, gave a random sample of the herd's hierarchy and social interactions as a group of four: Juba, Ashanti, Tana, and Nala. The second study period, after transport, focused on the two remaining individuals, started the day after the transportation of Juba and Ashanti.

As elephants are highly social, social interactions and their occurrence were investigated, as well as individual behaviours which can either be linked to their physiology, communication, stress, and/or excitement. All elephants present were studied simultaneously for 30 min each observation session using 1 min one-zero sampling [21]. This offered Hansen's frequency as opposed to true frequency. Due to time restrictions related to the lead author's role as a keeper, focal sampling of an appropriate length could not be undertaken, giving less reliability to the results. The duration (in seconds) of some behaviours (proximity, stereotypy, sleep, and rest) were also recorded through continuous sampling and analysed separately, as well as for occurrence. All recordings were taken by hand, for both study periods. Social and individual behaviours were recorded

simultaneously. As behaviour is difficult to quantify and all animals are individuals with a huge range of potentially observable behaviours, the categories 'unusual' and 'other' were included in the ethograms to allow for any behaviours not specifically described. Although some individual behaviours can interact with or follow social behaviours, due to the data collection methods, it was not possible to conclusively prove that one led to the other; hence, for the purpose of analysis, the two were treated separately. Therefore, only anecdotal conclusions could be drawn about interconnections.

2.2.1. Social Behaviour

Table 2 details the ethogram used to identify social behaviours shown by the study herd, compiled from several sources, as well as the authors' personal observations [22–25]. The data for *before transport* and *after transport* were compared using the Mann–Whitney U test, as a Shapiro–Wilk normality test showed the data were non-normally distributed ($p < 0.001$) and data for *before* and *after* transport were not paired. Each group of behaviours was compared as one, according to their assigned category: proximity, affiliative/associative, investigatory, dominance/aggression, submission, and other. 'Proximity', in addition to being recorded in terms of expression during each minute interval (one or zero), was recorded in time (seconds).

Table 2. Social behaviours ethogram giving a brief description of each behaviour alongside its potential function within the social structure of the herd.

Behaviour	Description	Function/Category
Approach	Individual moves to within three body lengths of another	Proximity
In proximity	Individual is within three body lengths of another (recorded in seconds)	Proximity
Leave	Individual moves out of proximity (further than three body lengths away) of another	Proximity
Trunk towards	Extension of the trunk in the direction of another individual in proximity	Affiliative/associative
Trunk to mouth	Trunk makes contact with the mouth of another individual	Affiliative/associative
Trunk to gland	Trunk makes contact with the area between the eye and ear of another individual	Affiliative/associative
Trunk to eye	Trunk makes contact with the eye of another individual	Affiliative/associative
Trunk to trunk	The trunks of two individuals touch and/or intertwine	Affiliative/associative
Trunk to body	Trunk makes contact with any other area of the body not specified	Affiliative/associative
Head to head	Direct contact of two individuals' heads, resting together for 2 s or more	Affiliative/associative
Body contact	Nonaggressive body contact of any kind not specified	Affiliative/associative
Play fighting	Two or more individuals pushing one another non-aggressively	Affiliative/associative

Table 2. *Cont.*

Behaviour	Description	Function/Category
Back into	One individual walks backwards towards another and contact is made	Affiliative/associative
Follow	One individual leaves with another following within 5 s in the same direction	Affiliative/associative
Trunk to genitals	Trunk touches the area around the genitals/anus	Investigatory
Flehmen	Trunk touches the genital area, faeces, or urine of another, then touches individuals own mouth	Investigatory
Trunk slap	Aggressive swing of the trunk making contact with any area of the body on another individual	Dominance/aggression
Tusk stab/blow	Using the tusk to stab any area of another individual's body with force	Dominance/aggression
Pushing	Using the head, shoulders or side, or backside to nudge/push another, forcing them to take a minimum of two steps	Dominance/aggression
Displacement	One individual approaches another, with the focal individual leaving within 5 s	Submission
Low posturing	Ears are held out 90 degrees/perpendicular to the head with their head bowed towards another for more than 2 s	Submission
Turn around	One individual approaches another, with the other turning 90 degrees away within 5 s	Submission
Back towards	One individual walks backwards towards another when in proximity	Submission
Other	Any other social behaviour performed between twoindividuals not described	Other
Out of sight	Observed individual is out of sight/in house	Not visible

2.2.2. Individual Behaviour

The ethogram for individual behaviours (Table 3) was compiled from several different sources, as well as the authors' observations [23,25]. All included behaviours function for physiological maintenance and communication; those without these functions were classed as unusual behaviours, including stereotypy. All behaviours recorded were found to be non-normally distributed (Shapiro–Wilk, $p < 0.05$). Feeding was analysed separately from the other maintenance behaviours, as elephants spend a huge portion of their day feeding, and maintenance would, therefore, have a large skew. Drinking, elimination, and grooming behaviours were recorded as maintenance behaviours. Recipients or causes of some vocalisations cannot always be known; therefore, notes on the type, pitch, volume, and direction of the sound, as well as any possible cues, were recorded. Only human-audible vocalisations were recorded. The behaviours were grouped as follows: stereotypic, main-

tenance, sleep/rest, vocalisations, active temporal gland secretions, and other/unusual. These behaviours could not always be mutually exclusive as more than one could be performed simultaneously; for example, behaviour 13, temporal gland secretion, was nearly always recorded at the same time as a social interaction or during vocalisations or feeding. Therefore, in addition to in terms of expression within each minute (one or zero), stereotypic behaviour and sleep/rest were also recorded in time (seconds). All remaining behaviours were solely expressed as the average occurrence within each minute interval (one or zero) of behaviours within the observation periods. These data were analysed using the Mann–Whitney U test as the data were unpaired. Each group of behaviours was compared as one; for example, all those classed as 'maintenance' were analysed together. 'Feeding' was analysed separately to avoid a huge skew to 'maintenance' behaviours due to elephant ecology. Differences in observed temporal gland fluid secretion were analysed through a paired *t*-test. Stereotypic behaviour (seconds) was compared from *before transport* to *after transport* using a Mann–Whitney U test.

Table 3. Individual behaviours ethogram with a brief description of behaviours as well as their potential function for the individual.

Behaviour	Description	Function/Category
Stereotypic	Individual stereotypy (rocking, bobbing, swaying, air blowing, pacing), time in seconds	Stereotypy
Drinking	Ingestion of water	Maintenance
Feeding	Ingestion of feed	Feeding
Elimination	Urination/defecation	Maintenance
Dusting	With mud, sand, etc.	Maintenance
Bathing	Splashing with water/swimming/mud wallowing	Maintenance
Ear flap	Using repetitive ear movements to cool	Maintenance
Sleep/rest	Standing/lying/leaning, time in seconds	Maintenance
Social vocalisation	Vocalisation directed at another elephant as a greeting or for an affiliative purpose	Communication
Trumpet	Taking note of potential cause (other elephant, environmental stimulus)	Communication
Purr/rumble	Taking note of potential cause (other elephant, environmental stimulus)	Communication
Other vocalisation	Any other audible vocalisation, taking note of potential cause	Communication
Draining	Visible drainage/squirting secretion from temporal gland	Communication
Unusual	Any behaviour not classed as stereotypical that is rarely seen, with given description/duration	
Other	Any other behaviour thought to be worth noting, with given description/duration	

2.3. Ethical Consideration

Permission was received from all relevant departments at Knowsley Safari prior to commencing the study. As the animal transport was already planned and the elephants were not interacted or interfered with at any stage for this research, their daily behaviours were not influenced by any data collection or observations.

3. Results

3.1. Social Behaviour

Regardless of two fewer possibilities for interactions, with the transport and, therefore, removal of two individuals (Juba and Ashanti), Tana's time spent in proximity to another elephant showed no change, spending on average 16.54 min with another individual per observation session before transport, compared with 15.82 min after transport. After transport, Nala also spent on average 15.82 min with another elephant, slightly less than the average 17.03 min before transport. However, Nala's play behaviours after transport showed a highly significant decrease (u = 171.1, $p < 0.001$, df = 22), with nearly all of the play fighting behaviours (behaviour 1, Table 2) initiated and received by Nala beforehand being towards or from Ashanti. Of the time spent in proximity to another elephant, 100% *after transport* was between Tana and Nala, compared to 66% of time in proximity to another elephant being between the pair before transport. It is also worth noting that 46% of time spent in proximity to another elephant was when all four individuals were all together and, therefore, not in pairs or three together.

Affiliative interactions between the pair increased after transport for Tana → Nala (u = 129, $p < 0.05$, df = 22), initiating tactile or directional affiliative behaviours, but there was no change for Nala → Tana (u = 168.4, $p > 0.05$, df = 22). Both Tana and Nala's investigatory and aggressive behaviours remained at low frequencies for each study period. However, the data for Nala → Tana submissive behaviours increased significantly (t = 51, $p < 0.05$, df = 22) after transport. No submissive behaviours from Tana → Nala were observed before transport or after transport.

3.2. Individual Behaviour

Most significant changes observed in Tana and Nala's behaviour were in their individual behaviours (Figures 2 and 3, respectively). Most maintenance behaviours (Table 3, 2–7) did not change in their expression/interval after transport. Figures 2 and 3 detail individual behaviours, not social behaviours (which could have been performed simultaneously). The apparent ratios of feeding to other individual behaviours decreased, but behaviour 8, sleep or standing rest, increased for both Tana and Nala (t = 72, $p < 0.001$, df = 22) following transport (Figures 4 and 5). Behaviours 9–12, various human-audible vocalisations, significantly increased in frequency after transport for Tana and Nala (t = 69, $p < 0.001$, df = 22; t = 69, $p < 0.001$, df = 22 respectively). Both elephants showed a significantly increased incidence of active temporal gland secretion after transport (t = 75, $p < 0.001$, df = 22).

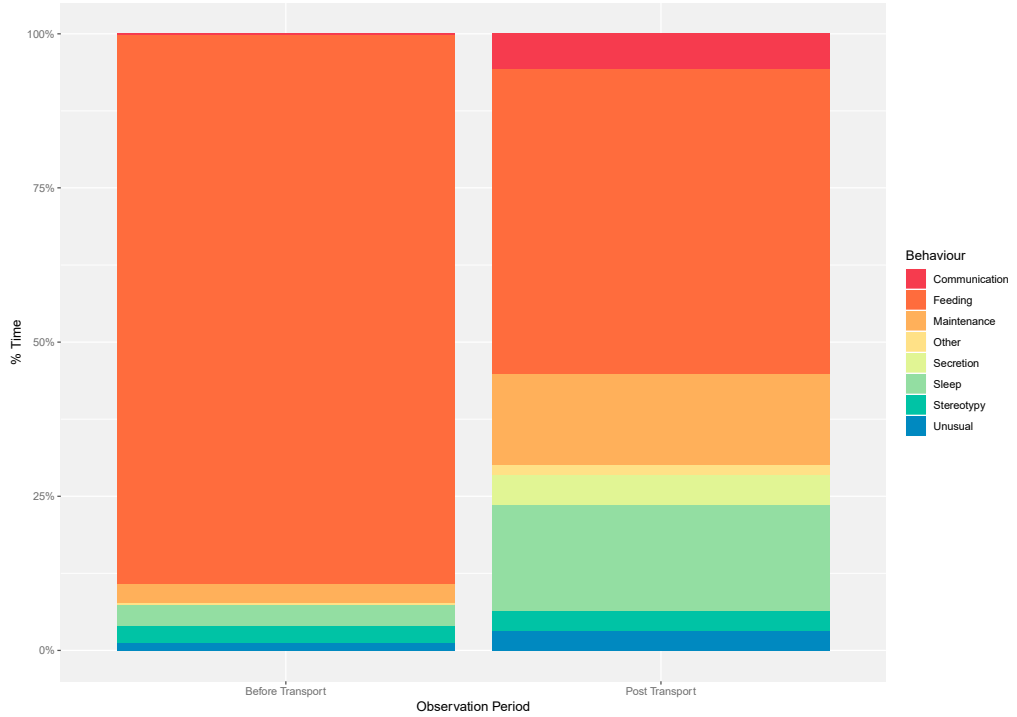

Figure 2. Average percentage of the total number of intervals (minutes) during observation sessions in which individual behaviours were expressed at least once (Hansen's frequency, found through one-zero sampling) by Tana before and after transport. These were calculated as a percentage of total time spent on individual behaviours for each observation period; behaviours were not mutually exclusive and do not reflect time (seconds).

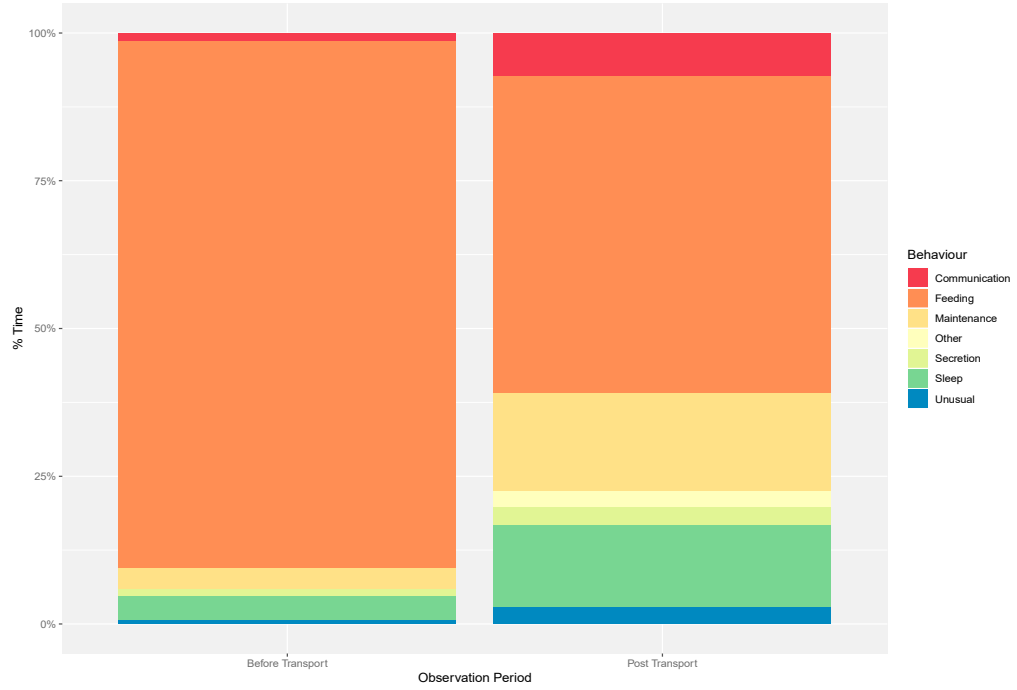

Figure 3. Average percentage of the total number of intervals (minutes) during observation sessions in which individual behaviours were expressed at least once (Hansen's frequency, found through one-zero sampling) by Nala before and after transport. These were calculated as a percentage of total time spent on individual behaviours for each observation period; behaviours were not mutually exclusive and do not reflect time (seconds).

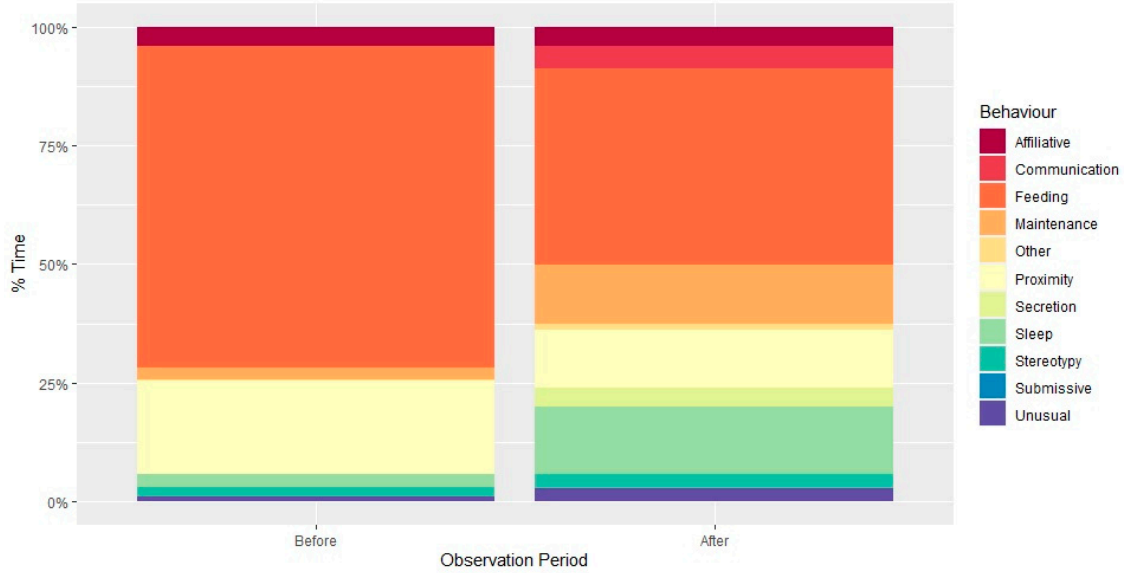

Figure 4. Average percentage of the total number of intervals (minutes) during observation sessions in which both individual and social behaviours were expressed at least once (Hansen's frequency, found through one-zero sampling) by Tana before and after transport. These were calculated as a percentage of total time spent on both individual and social behaviours for each observation period; behaviours were not mutually exclusive and do not reflect time (seconds).

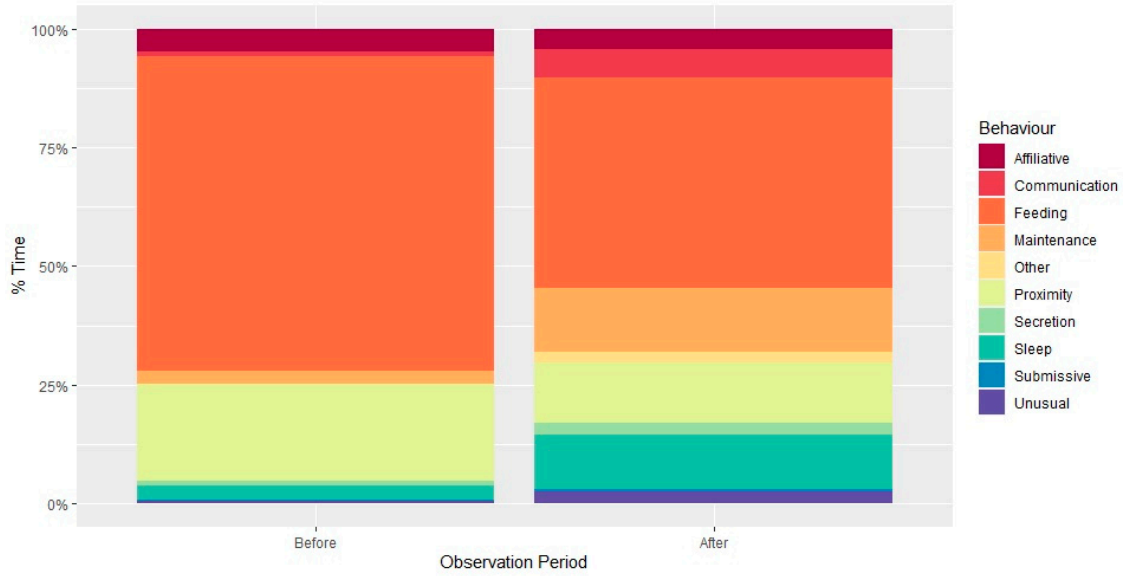

Figure 5. Average percentage of the total number of intervals (minutes) during observation sessions in which both individual and social behaviours were expressed at least once (Hansen's frequency, found through one-zero sampling) by Nala before and after transport. These were calculated as a percentage of total time spent on both individual and social behaviours for each observation period; behaviours were not mutually exclusive and do not reflect time (seconds).

Other/unusual behaviours increased significantly in both elephants ($t = 62$, $p < 0.01$, $df = 22$). For Nala, these behaviours were nearly always her holding her ears out to a 90-degree angle with one front foot poised on one toe for several seconds. Tana's unusual or other behaviours were nearly always using her trunk to lightly pull on her own nipples. Throughout both study periods, Nala showed no signs of having developed a stereotypic behaviour. Tana exhibited a stereotypic behaviour historically and in both study periods, in which she would hold her trunk in her mouth and blow across her tusk at the sulcus. After transport, Tana increased the incidence at which she performed her stereotypy when compared with before transport ($t = 171$, $p < 0.05$, $df = 22$).

4. Discussion

Although there is a now a focus on aiming to have multigenerational, highly related groups of elephants within captivity, in reality, the genetics of individuals within the available captive population available makes this unfeasible for many collections. However, despite most collections not currently reaching this aim, many of the same behaviours one would expect from a highly related herd are exhibited within captivity. The present study suggests that separating a group of elephants who have been housed together for decades had profound effects on the behaviours they exhibit.

4.1. Social Behaviour

Nala exhibited significant changes in the social behaviours investigated, with an increase in the occurrence of behaving submissively towards her mother, Tana. Before the transport of Juba and Ashanti, Tana was known to be submissive only to Juba, the herd's matriarch. With the most dominant elephant removed from the social hierarchy, Tana became the most dominant. To the authors' knowledge of the elephants' history (verbal communication and zoo records), this was the first time Tana had been the most dominant individual in any collection or herd she had been held in. When changes in social structure or herd dynamics occur, the hierarchy has to change accordingly. In situ, poaching for the ivory trade often removes older and often larger individuals, who would presumably hold high rank in their herd's hierarchy. It has been reported that hierarchal structures remain stable with the next availably dominant individual 'filling the gap' left by the removed individual [26]. Recorded results correlate with anecdotal observations made by the author of feed dominance at hay nets and when keepers were interacting with Tana and Nala after transport. Although always submissive to her mother, Nala's increased submission to Tana is explained through her recognising Tana's newly found standing in social structure. Without Juba in the same enclosure keeping a balance as 'matriarch', Tana was able to dominate food sources, as well as certain areas. In response to Tana's newfound dominance, Nala would protect herself by not challenging this behaviour, thus behaving submissively.

Although Tana (mother) initiated significantly more affiliative interactions with Nala (daughter), Nala's interactions with her mother did not change. Tana's increase could be simply explained through a reduction in social options; however, as Nala did not initiate more affiliative interactions, Tana's increase could also be explained through seeking tactile 'comfort'. However, overall, Nala initiated and received significantly fewer play behaviours after the departure of Ashanti, her half-sister. As the youngest elephants in the herd, Nala and Ashanti spent a lot of time with one another (averaging 16.7 min with each other before transport per observation session) and engaged in play behaviours during 86% of observations. Female African elephants in situ use play 'as one of many mechanisms to sustain their social, protective, and leadership roles within families' [6]. Play behaviours being such a large part of Nala and Ashanti's day shows the strength of their relationship. However, after transport, play was not observed, a negative for Nala when considering the array of functions attributed to play behaviours. Play behaviours have been described as extremely important for social learning and skill development [6] and, in captivity, an indicator of positive welfare, not just in elephants but across all taxa [27,28]. Ahead of 'suffering' being observed, welfare indicators need to be evaluated and improved [27]. In this case, valid reasons supported the two transports being separated by a 2-month interim period (environmental and individual responses to PC training). However, social behaviour results suggest the overall social and psychological consequences of the separation were potentially underestimated.

4.2. Individual Behaviour

Most of the differences observed in Tana and Nala were individual behaviours, with several maintenance behaviours for both changing significantly. Elephants are known to eat for up to 18 h throughout the day as they need to ingest huge quantities of plant

matter to gain enough nutrition from their relatively inefficient digestive systems [29]. It would, therefore, be expected that much of the time during observations would be taken up by physiological requirements. Before transport, all four of the elephants spent around 55% of the total time observed feeding, with the remaining time spent interacting with each other or their environment. After transport, 'feeding' reduced overall. Both Tana and Nala significantly increased their time spent resting/sleeping during the observation periods after transport compared with before. Before transport, sleep was not observed during observations, but standing rest was occasionally observed. After transport, Tana and Nala spent a large amount of time in standing rest during the day, especially when observed between 2:00 and 3:00 p.m. The decrease in feeding may be attributed to the increase in sleep/rest, which can in turn possibly be attributed to the lack of stimuli and social interactions the elephants had after transport.

Elephants communicate in multiple ways, chemically, vocally, tactile, and others, with communication being a vital aspect of their highly evolved social structure [24,30]. Both Tana and Nala significantly increased the occurrences of producing human-audible vocalisations. The vocalisations that were recorded were mostly quiet, low-pitch 'rumbles' with no obvious stimulant. Elephants have been observed to perform these types of rumbles 'in order to reduce the distance' between themselves and other individuals [31]. As Tana and Nala went from living in a herd of four to two, these vocalisations could have been a vocal reassurance that the other was still in proximity. There were also instances of more frequent loud greeting vocalisations performed by Nala towards Tana when they met in the paddock, even if they had been apart just a few minutes. It has been noted that elephants have intense greetings regardless of the separation time [32]. The increase in incidence of these greetings could also be interpreted as a possible reassurance to one another.

Tactile communication sees elephants using their trunk to investigate the genitals and anus of other individuals, potentially to determine reproductive state through hormones and pheromones [22]. Chemical communication is often through the secretions of temporin from temporal glands [33,34]. Both Tana and Nala exhibited a marked increase in active temporal gland secretion after transport. Through extensive studies on African elephants, several potential functions for this secretion have been proposed, including chemical communication, a stress response (negative or positive), and aiding familiarity information when greeting another individual or herd [34]. Although historically thought to be related to stress and/or excitement, more recent work discusses the importance of combining behavioural and physical data to confirm, and the findings concluded that captive African elephants (*Loxodonta africana*) are more susceptible to social stressors than captive Asian elephants (*Elephas maximus*) [33]. The observed increase in secretions could be related to stress, potentially as a result of Tana and Nala being 'confused' by Juba and Ashanti no longer being in the same enclosure that the four had shared for the majority or all of their lives. The increase observed in Tana and Nala is also supported by work that found that temporal gland secretions increase when the number of individuals in the herd decrease [34]. As the two remaining elephants did not see the transport, it is unknown how much they understood about the departure, as infrasonic and chemical communication were not investigated. Elephants secrete more when separated from others for any period of time, long or short, before secreting again when reunited [35].

Several behaviours described under other/unusual were not observed in the focal herd before transport. The other/unusual behaviours that were observed most frequently after transport were Tana pulling lightly on her nipples and both Tana and Nala holding their ears out to a 90-degree angle, usually accompanied by lifting one of their front feet onto their toes for a second. This particular ear posturing is a known part of elephant behaviour. Depending on the context, several potential functions, such as listening, a submissive gesture, an aggressive gesture, and an unsure response to a new sensory stimulus or a change in surroundings, have been described [36–38]. Numerous studies discussed that elephants use structures in their feet to analyse infrasonic vibrations made

by other elephants through the ground, often across large distances, expressing presence, distance, and information sharing [39,40]. In this study, outright ear posturing was usually observed in response to a low rumble by the other elephant. However, there were several instances in which both Tana and Nala would stop what they were doing at the same time, to stand with ears outright with a front foot lifted. Without further research, the stimulus behind this is unknown.

Stereotypic behaviours in captive animals are well documented in many species and develop independently in different collections and different captive conditions. In elephants, stereotypies are recorded more frequently in wild-caught elephants [41]. These behaviours have several potential functions including but not limited to boredom, anticipation of feed or an activity at a particular time of day, a stress response, and a coping mechanism [42]. Due to the complexity of the neural pathways involved in the development of stereotypic behaviours and their triggers, no one explanation can be given. Tana's known stereotypy of blowing air from her trunk onto her tusk sulcus was exhibited in both observation periods but increased after transport. Tana's increase in stereotypy frequency can be attributed to an increase in stress due to the changes in herd structure and, therefore, hierarchy, as well as the uncertainty of Juba and Ashanti's departure. As Tana's rate of active temporal gland secretion also increased, the two combined strengthen the argument that the elephants were in a stress state. To accurately describe these changes in terms of physical stress, future research should utilise faecal glucocorticoid metabolites around the time of transport.

4.3. Limitations

The size of the focal group was a significant limitation of the present study, most notably on the power of statistical analysis. Furthermore, it was necessary for the study design to be compatible with a busy keeping routine. This, therefore, limited the data collection methods available. Whilst prolonged focal sampling would have been superior to one-zero sampling in providing the most robust data, the methodology described above was the only methodology that was reasonably practicable when taking into account the logistical challenges. One-zero sampling can underrepresent behaviour; therefore, the study is presented with the acknowledgement that the conclusions drawn are limited by design [43].

Nevertheless, the importance of keeper-generated research and their contributions to the literature cannot be overlooked [44]. Facilitating a keeper to propose and produce research that is feasible within their working day resulted in this case study. The findings are useful for both old and new collections to understand the individual elephants and their social dynamic. This knowledge could inform future decision making and impact individual elephant welfare. Furthermore, it could help provide guidance for other collections planning transport to relocate their elephants.

5. Conclusions

1. Even when housed in a nontypical grouping, captive African elephants exhibit similar responses to separation and uncertainty to wild elephants. Although there is correctly a focus on high relatability in captive elephant herds, not all institutions have this, and the same allowances for herds with low or no relatability need to be made when collection planning.
2. Reduced social capacity and play opportunities, combined with increases in stereotypy and temporal gland secretion, all indicate reduced welfare.
3. Temporary separation in this case was necessary due to logistics and safety; however, when arranging transports for any animal, the psychological repercussions of separations, be they temporary or permanent, must be taken into account, and alternative methods should be explored for all social species.
4. In the future, when transports or major events changing social structure or individual behavioural opportunities occur, where possible, there should also be a focus on

behavioural and physical data collection prior to, during, and after. The subsequent analysis, publication, and incorporation into actual procedure and protocol are vital to continue improving captive welfare.

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Informed Consent Statement: Not applicable.

Data Availability Statement: Raw data are available from the corresponding author upon reasonable request.

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References

1. Moss, C.J.; Poole, J.H. Relationship and social structure in African Elephants. In *Primate Social Relationships: An Integrated Approach*; Hinde, R.A., Ed.; Blackwell Scientific: Oxford, UK, 1983; pp. 315–325.
2. Hoare, R. African elephants and humans in conflict: The outlook for co-existence. *Oryx* **2000**, *34*, 34–38. [CrossRef]
3. Cameron, E.; Ryan, S. Welfare at Multiple Scales: Importance of Zoo Elephant Population Welfare in a World of Declining Wild Populations. *PLoS ONE* **2016**, *11*, e0158701. [CrossRef]
4. Poulsen, J.R.; Koerner, S.E.; Moore, S.; Medjibe, V.P.; Blake, S.; Clark, C.J.; Akou, M.E.; Fay, M.; Meier, A.; Okouyi, J.; et al. Poaching empties critical Central African wilderness of forest elephants. *Curr. Biol.* **2017**, *27*, 134–135. [CrossRef] [PubMed]
5. Poole, J.; Payne, K.; Langbauer, W.R.; Moss, C. The social contexts of some very low frequency calls of African Elephants. *Behav. Ecol. Sociobiol.* **1988**, *22*, 385–392. [CrossRef]
6. Lee, P.; Moss, C. African Elephant Play, Competence and Social Complexity. *Anim. Behav. Cogn.* **2016**, *1*, 144–156. [CrossRef]
7. Moss, C.J.; Croze, H.; Lee, P.C. (Eds.) *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*; University of Chicago Press: Chicago, IL, USA, 2011.
8. Lucas, C.; Stanyon, B. Improving the welfare of African elephants *Loxodonta africana* in zoological institutions through enclosure design and husbandry management: An example from Blair Drummond Safari and Adventure Park. *Int. Zoo Yearb.* **2017**, *51*, 248–257. [CrossRef]
9. Harris, M.; Sherwin, C.; Harris, S. The Welfare, Housing and Husbandry of Elephants in UK Zoos. Report. Available online: http://randd.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=None&ProjectID=13192&FromSearch=Y&Publisher=1&SearchText=wc05007&SortString=ProjectCode&SortOrder=Asc&Paging=10 (accessed on 5 January 2019).
10. Stevenson, M.; Walter, O.; British & Irish Association of Zoos & Aquariums. *Management Guidelines for the Welfare of Zoo Animals: Elephants, Loxodonta africana and Elephas Maximus*; British & Irish Association of Zoos & Aquariums: London, UK, 2006.
11. Williams, E.; Chadwick, C.; Yon, L.; Asher, L. A review of current indicators of welfare in captive elephants (*Loxodonta africana* and *Elephas maximus*). *Anim. Welf.* **2018**, *27*, 235–249. [CrossRef]
12. Garstang, M. *Elephant Sense and Sensibility*; Academic Press: Cambridge, MA, USA, 2015.
13. Barkai, R. Elephants are people, people are elephants: Human–proboscideans similarities as a case for cross cultural animal humanization in recent and Paleolithic times. *Quat. Int.* **2016**, *406*, 239–245.
14. Elephant Welfare Group; British & Irish Association of Zoos & Aquariums Elephant Welfare Group. BIAZA Website 2016. Available online: https://biaza.org.uk/elephant-care-management (accessed on 5 January 2019).
15. Chadwick, C.; Williams, E.; Asher, L.; Yon, L. Incorporating stakeholder perspectives into the assessment and provision of captive elephant welfare. *Anim. Welf.* **2017**, *26*, 461–472. [CrossRef]
16. Whittaker, M.; Laule, G. Protected contact and elephant welfare. In *An Elephant in the Room: The Science and Well-Being of Elephants in Captivity*; Tufts Center for Animals and Public Policy: Medford, MA, USA, 2009.
17. Wilson, M.; Perdue, B.; Bloomsmith, M.; Maple, T. Rates of reinforcement and measures of compliance in free and protected contact elephant management systems. *Zoo Biol.* **2015**, *34*, 431–437. [CrossRef] [PubMed]

18. Csuti, B. Elephants in captivity. In *Biology, Medicine, and Surgery of Elephants*, 1st ed.; Fowler, M., Mikota, S., Eds.; John Wiley & Sons: Hoboken, NJ, USA, 2006; pp. 15–22.
19. Stoinski, T.; Daniel, E.; Maple, T. A preliminary study of the behavioral effects of feeding enrichment on African elephants. *Zoo Biol. Publ. Affil. Am. Zoo Aquar. Assoc.* **2000**, *19*, 485–493. [CrossRef]
20. Laws, N.; Ganswindt, A.; Ganswindt, A.; Heistermann, M.; Harris, S.; Sherwin, C. A Case Study: Fecal Corticosteroid and Behavior as Indicators of Welfare During Relocation of an Asian Elephant. *J. Appl. Anim. Welf. Sci.* **2007**, *10*, 349–358. [CrossRef]
21. Bateson, M.; Martin, P. *Measuring Behavior: An Introductory Guide*, 4th ed.; Cambridge University Press: Cambridge, UK, 2021; pp. 105–106.
22. Bagley, K.; Goodwin, T.; Rasmussen, L.; Schulte, B. Male African elephants, *Loxodonta africana*, can distinguish oestrous status via urinary signals. *Anim. Behav.* **2006**, *71*, 439–1445. [CrossRef]
23. Gruber, T.; Friend, T.; Gardner, J.; Packard, J.; Beaver, B.; Bushong, D. Variation in stereotypic behavior related to restraint in circus elephants. *Zoo Biol.* **2000**, *19*, 209–221. [CrossRef]
24. Langbauer, W. Elephant communication. *Zoo Biol.* **2000**, *19*, 425–445. [CrossRef]
25. Olson, D. (Ed.) Ethogram of elephant behaviors. In *Elephant Husbandry Resource Guide*; Allen Press: Lawrence, KS, USA, 2004; pp. 103–121.
26. Goldenberg, S.; Douglas-Hamilton, I.; Wittemyer, G. Vertical transmission of social roles drives resilience to poaching in elephant networks. *Curr. Biol.* **2016**, *26*, 75–79. [CrossRef] [PubMed]
27. Veasey, J. Concepts in the care and welfare of captive elephants. *Int. Zoo Yearb.* **2006**, *40*, 63–79. [CrossRef]
28. Held, S.; Špinka, M. Animal play and animal welfare. *Anim. Behav.* **2011**, *81*, 891–899. [CrossRef]
29. Buss, I. Some observations of food habits and behaviour of African Elephants. *J. Wildl. Manag.* **1961**, *25*, 131–148. [CrossRef]
30. Vicino, G.; Marcacci, E. Intensity of play behavior as a potential measure of welfare: A novel method for quantifying the integrated intensity of behavior in African elephants. *Zoo Biol.* **2015**, *34*, 492–496. [CrossRef]
31. Leighty, K.A.; Soltis, J.; Wesolek, C.M.; Savage, A. Rumble vocalizations mediate interpartner distance in African elephants, *Loxodonta africana*. *Anim. Behav.* **2008**, *76*, 1601–1608. [CrossRef]
32. Poole, J. Elephant Trunk Calls. *Swara* **1988**, *6*, 29–31.
33. Brown, J.L.; Carlstead, K.; Bray, J.D.; Dickey, D.; Farin, C.; Ange-van Heugten, K. Individual and environmental risk factors associated with fecal glucocorticoid metabolite concentrations in zoo-housed Asian and African elephants. *PLoS ONE* **2019**, *14*, e0217326. [CrossRef] [PubMed]
34. Kioko, J.; Taylor, K.; Milne, H.; Hayes, K.; Kiffner, C. Temporal gland secretion in African elephants (*Loxodonta africana*). *Mamm. Biol.* **2017**, *82*, 34–40. [CrossRef]
35. Poole, J.; Granli, P. Mind and movement: Meeting the interests of elephants. In *An Elephant in the Room: The Science and Well Being of Elephants in Captivity*; Forthman, D.L., Kane, F.L., Hancocks, D., Waldau, P.F., Eds.; Center for Animals and Public Policy, Cummings School of Veterinary Medicine, Tufts University: Medford, MA, USA, 2009.
36. O'Connell-Rodwell, C. Keeping an "ear" to the ground: Seismic communication in elephants. *Physiology* **2007**, *22*, 287–294. [CrossRef]
37. Buss, I.; Estes, J. The functional significance of movements and positions of the pinnae of the African elephant, *Loxodonta africana*. *J. Mammal.* **1971**, *52*, 21–27. [CrossRef]
38. Langbauer, W.R.; Payne, K.B.; Charif, R.A.; Rapaport, L.; Osborn, F. African elephants respond to distant playbacks of low frequency conspecific calls. *J. Exp. Biol.* **1991**, *157*, 35–46. [CrossRef]
39. McComb, K. Studying vocal communication in elephants. In *Studying Elephants*; African Wildlife Foundation: Nairobi, Kenya, 1996; pp. 112–119.
40. McComb, K.; Reby, D.; Baker, L.; Moss, C.; Sayialel, S. Long-distance communication of acoustic cues to social identity in African elephants. *Anim. Behav.* **2003**, *65*, 317–329. [CrossRef]
41. Mason, G.J.; Latham, N. Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Anim. Welf.* **2004**, *13*, 57–69.
42. Greco, B.; Meehan, C.; Hogan, J.; Leighty, K.; Mellen, J.; Mason, G.; Mench, J. The days and nights of zoo elephants: Using epidemiology to better understand stereotypic behavior of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. *PLoS ONE* **2016**, *11*, e0144276.
43. Powell, D.; Baskir, E. A matter of time: Comparing observation methods. In *Exploring Animal Behavior in Laboratory and Field*; Academic Press: Cambridge, MA, USA, 2021; pp. 49–61.
44. Margulis, S.; Westhus, E. Evaluation of different observational sampling regimes for use in zoological parks. *Appl. Anim. Behav. Sci.* **2008**, *110*, 363–376. [CrossRef]