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Personality and behaviour of three captive African savannah elephants (*Loxodonta africana*)

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Abstract

This study explores the diversity in individual response for three captive African Savannah Elephants (*Loxodonta africana*) to variations in the daily number of zoo visitors. The nocturnal behaviour of the elephants was observed in two periods with a factor 5.1 difference in numbers of zoo visitors. Ten behavioural expressions for each elephant were compared for the two periods. Data was collected with surveillance cameras for ten hours (20:00 to 06:00) throughout six nights. Furthermore, the data was compared to a similar study on the same elephants performed two years earlier. Both studies revealed a significant difference in behaviour between low activity and high visitor activity periods for all three elephants in the behaviour 'Walk'. No overall significant difference was found in the other behavioural expressions. Clear difference in reaction norms was found between the matriarch and the two subordinates for the behaviours: 'Feed from ground', 'Inactive', 'Walk' and 'Other'. This study shows that elephants in captivity are influenced by an increase in the number of zoo visitors, and that the personality or social status of the elephant may provide them with different resilience to disturbance.

Keywords: Personality diversity; Reaction norms; Environmental conditions; Surveillance; Nocturnal behaviour.

الملخص

تستكشف هذه الدراسة التنوع في الاستجابة الفردية لثلاثة أفيال سافانا أفريقية أسيرة للتغيرات في العدد اليومي لزوار حديقة الحيوان. لوحظ السلوك الليلي للأفيال في فترتين مع اختلاف عامل 5.1 في عدد زوار حديقة الحيوان. تمت مقارنة عشرة تعبيرات سلوكية لكل فيل في الفترتين. تم جمع البيانات بكاميرات المراقبة لمدة عشر ساعات (20:00 حتى 06:00) على مدار ست ليالٍ ، وتمت مقارنة البيانات بدراسة مماثلة أجريت على نفس الأفيال قبل ذلك بعامين. كشفت كلتا الدراستين عن اختلاف كبير في السلوك بين فترات النشاط المنخفض والنشاط المرتفع للزائر لجميع الأفيال الثلاثة في "المشي" السلوكي. لم يتم العثور على اختلاف كبير بشكل عام في التعبيرات السلوكية الأخرى. تم العثور على اختلاف واضح في معايير رد الفعل بين الأم والمرؤوسين للسلوكيات: "تغذية من الأرض" ، "غير نشط" ، "المشي" و "أخرى". تظهر هذه الدراسة أن الأفيال في الأسر تتأثر بزيادة عدد زوار حديقة الحيوان ، وأن شخصية الفيل أو وضعه الاجتماعي قد يمنحهم مرونة مختلفة في مواجهة الاضطرابات.

الكلمات المفتاحية: تنوع الشخصية. قواعد رد الفعل الظروف البيئية؛ مراقبة؛ السلوك الليلي

Introduction

Personality of animals is characterized by an individual responding uniform to similar situations compared with other individuals (Alstrup et al. 2020). The individual personality consists of personality traits, when an individual responds in a similar way to different kinds of situations (Stamps 2007; Alstrup et al. 2020). African savannah elephants (*Loxodonta africana*) are living in complex societies (Yasui et al. 2012). They are expected to possess

exceptional capabilities within social proficiency and refined cognitive skills (Yasui et al. 2012), and they are able to express a wide range of differences in personalities and behavioural traits (Yasui et al. 2012). Examples of personality traits in elephants are attentiveness, sociability and aggressiveness (Seltmann et al. 2019). It has been established that individuals within the same species can express different behavioural reaction norms (Dingemanse et al. 2010; Briffa and Weiss 2010). Behavioural reaction norms can be seen as the set of behavioural phenotypes expressed by an individual in certain environments (Dingemanse et al. 2010). Behavioural reaction norms are here defined as an individual's average behaviour including how the behaviour might be different between two periods (Dingemanse et al. 2010). Furthermore, the relationship between an environmental condition and response value must be specified for the gradient (Dingemanse et al. 2010). This can result in diversity in an individual's personality. An example of environmental conditions in a zoo could be a change in number of visitors. The number of visitors can influence the environmental condition by causing loud and aversive noises or smells (Morgan and Tromborg 2007; Quadros et al. 2014). In captivity, societies and social relations between individuals are not formed in the same way that they would be in nature. In captivity the animals are limited to a certain area and do not have the opportunity to migrate. Furthermore, the composition of the group members is controlled by humans (Yasui et al. 2012). Visitors at most zoos can get relatively close to the enclosure, which may cause a stressful environment for the animals due to noise, smell or visual disturbance (Morgan and Tromborg 2007; Quadros et al. 2014; Greco et al. 2016).

Stressful environments and small enclosures can result in conflicts among the elephants and may lead to stereotypical behaviour varying according to their personality traits (Mason and Veasey 2010). Expression of stereotypical behaviour in elephants is associated with compromised welfare and can be used as an indicator of animal welfare in captivity. Stereotypic behaviour can be defined as a repeatable pattern in behaviour with no clear function or intention, for instance swaying or rocking (Rees 2009; Mason and Veasey 2010; Greco et al. 2016). Studies have shown that elephants in captivity display an increase in stereotypical behaviour when separated from social partners (Greco et al. 2016). It has also been found that stressors, such as, transfers, spatial restriction, food restriction, uncontrollable noise, and environmental exposure, e.g., artificial lightning and unpleasant temperatures contributes to stereotypical behaviour (Morgan and Tromborg 2007; Quadros et al. 2014; Greco et al. 2016). Managed activities during the day directed by the zookeepers may on the other hand have a positive effect on the elephants and reduce the risk of the elephants expressing stereotypical behaviour (Hosey 2008; Greco et al. 2016).

These activities include exercise sessions, training routines, feet- and skincare (Greco et al. 2016). Therefore, it is interesting to observe the nocturnal behaviour when the zookeepers are not present to conduct these activities. In addition, it has been shown that captive elephants are less active during night-time compared to daytime (Greco et al. 2016; Finch et al. 2021). Greco et al. (2016) also found that the elephants spent over 80% of their active time on feeding during the night. Wild elephants are generalist feeders, i.e., they feed on an abundance of numerous plants, but this will vary seasonally and regionally (Ullrey et al. 1997; Branco et al. 2019). Their diet consists of grasses, forbs, shrubs, sedges, and trees, but also bulbs, fruits, roots, and plant bases are occasionally eaten (Branco et al. 2019). The proportions of these foods depend greatly on their accessibility (Ullrey et al. 1997; Branco et al. 2019). Elephants utilize grazing and browsing to forage. Furthermore, if nourishment is not scarce, young plant parts are preferred (Ullrey et al. 1997).

In the present study the elephants had the opportunity to make use of the outdoor area throughout the night. During the previous study, Bertelsen et al. (2020) investigated the nocturnal behaviour of the same three elephants in the same enclosure, but without access to outdoor facilities. The previous study was conducted within the same area and time of the year. The opportunity to walk outside provided the elephants with a choice, and thereby a greater diversity of stimuli and resources. The availability to make choices has proven to reduce the time spent expressing stereotypical behaviour (Greco et al. 2016). It was hypothesized that: (1) visitor number have an impact on elephants' nocturnal behaviour; (2) there is a difference in the elephants' behaviour based on their different personalities; (3) behavioural reaction norms for the three elephants do not change over two years in terms of slopes and intercepts.

Methods and materials

Study design and animals

This study examined three adult (around 39 years) female African savannah elephants (’A’ "Tanja", ’B’ "Maj" and ’C’ "Bibi"). They were all born in the wild South Africa around 1982 and showcased to Aalborg Zoo in Denmark approximately three years later. Elephant ’A’ was considered the matriarch based on her behaviour. Elephant ’B’ was the second in the hierarchy, while elephant ’C’ was the most subordinate in the hierarchy. This ranking was based on own and zookeepers’ subjective opinions of the animal interactions and behaviour. The nocturnal behaviour in this study was compared with our previous study performed by Bertelsen et al. (2020). Bertelsen and co-workers revealed that the three elephants have different personalities due to their individual response. Thus, comparing the time spent on different behaviours with the study by Bertelsen et al. (2020) where a high visitor number (HA) and a low visitor number (LA) was investigated for three consecutive days for both periods. The number of daily visitors in Aalborg Zoo, varies throughout the year due to holidays and weekends.

Housing and care

The three elephants were group housed in daytime, while two of the elephants, ’A’ and ’C’, were daily separated from ’B’ in the night from approximately 15:30 to 7:30, due to observed aggression between ’A’ and ’B’. Therefore, ’A’ and ’C’ shared two adjoining stables whereas ’B’ had its own stable. All elephants were able to see each other and put their trunk in the adjoining stable through metal bars which divided the stables. Each of the three stables were approximately 40 m^2 (Appendix 1). During the study period, the weather and recent improvements made to the enclosure in the form of plastic screens covering the entrances allowed the elephants to walk outside at any time during the night. ’A’ and ’C’ shared 1232 m^2 of outdoor area, while ’B’ had 288 m^2 outdoor area alone (Appendix 1). The outdoor area consisted of sand, trees, stones, and a small pool. For their activity the zookeepers added hay nets, tree trunks, a suspended tree trunk and tubes into the ground containing food. The zookeepers met every day at 7:30 and left latest 17:00. In addition to outdoor areas, the elephants also had access to a small indoor hall which connected the stables with the outdoor area. The hall for ’A’ and ’C’ was approximately 36 m^2 whereas the hall for ’B’ was 16 m^2 (Appendix 1). It was not possible to track the elephants’ behaviour in the hall due to the camera angles. The stables were enriched with objects, each with different functions to provide and care for the elephants. The elephants were fed 8-10 times per day at different time points during the day. Three feedings took place indoors whereas the rest were outside. The elephants received different kinds of food and nutrition every day which were grass straw, hay, branches, and food pellets (Kasper Faunafood and Dodson Horrell). Three times a day they got carrots, parsnips, and apples together with food pellets. The grass straw was placed on the floor and hay was placed in hay nets in each stable. The purpose of the hay nets was to activate the elephants. Each stable was also provided with a water tank with *ad libitum* access. In terms of appearance, the stables had concrete floors, wooden panels, and metal wires which made it impossible for the elephants to intrude the visitor area.

Data collection

The three elephants were observed during six nights (October 4th to October 7th and October 21st to October 24th 2021) for ten hours each night (20:00 to 06:00) (daylight-saving time). The number of visitors was on average 5.1 times higher during the HA compared with the LA period. The cameras (ABUS, 25 FPS) used during this study were provided by the zoo in advance. The cameras have been installed permanently which therefore did not cause a new disturbance for the elephants. One camera was pointed towards each respective stable, making the total number of cameras three (Appendix 1). Only indoor behaviour was observed as there was not enough light at night in the outdoor enclosure record behaviour. During examination of the footage, the individual behaviours for each elephant were observed and divided into multiple categories (Table 1).

Table 1: Ethogram of observed behaviours. Modified from Bertelsen et al. (2020) and Linder et al. (2020).

Behaviour	Description
Feed from ground	This includes both searching and feeding from ground in their own or adjacent box. The food can be hay, pellets, branches etc.
Feed from hay net	This behaviour includes reaching for the hay with trunk, eating hay directly from the net or eating hay from ground if it definitely comes from the net.
Drink	When the elephants have their trunk in the water tank and the intake of water through the mouth.
Inactive	No movement when the elephants are standing. This consists of the elephant sleeping or just standing still for a period of time.
Walk	Movement to the outdoor enclosure and movement without other activities such as feeding.
Lie	Lying down on the ground resting or sleeping.
Sway	Movement from side-to-side multiple times.
Stereotypy	When one movement or behaviour is repeated multiple times for a period of time (more than three seconds) with no obvious purpose or goal, e.g., pacing, touching the metal wires or scraping the ground.
Aggression	Threatening and violent behaviour, such as running towards the bars on the adjacent box or tear each other's trunk.
Other	This behaviour consists of scratching body, throwing hay, sand dust and faeces and gathering hay. It also includes when the elephants are clear from the camera angle.

Time intervals for each behaviour performed were listed with a start and end time. This was used to calculate how much time each elephant would spend on a given behaviour. Access to the outdoor area resulted in some time, where the elephants were outside, which made it impossible to observe the elephants' behaviour during this period. The listed behaviour in this time span was noted as 'Other'

Data analysis

All data of the study were processed and analysed with non-parametric statistical methods, since the data were non-normally distributed (Zar 2010). Only if the behaviours were observed minimum five times for each individual, it was used for statistical analysis. In cases with fewer than five observations, data was excluded. Median, skewness, kurtosis, and interquartile range (IQR) for all behaviours were calculated (Zar 2010; Gerstman 2015). Medians were compared with Mann-Whitney U test (pairwise) or Kruskal Wallis test (> 2 medians) (Forthofer et al. 2007; Zar 2010; Gerstman 2015). Confidence interval (CI) was calculated by the bootstrapping method to decide whether calculated skewness and kurtosis of the non-normal distribution were significantly different (Hastie et al. 2009). The test uses a resampling method to ensure representative data (Gerstman 2015; Fieberg et al. 2020). P-values of < 0.05 was considered as significant (Forthofer et al. 2007; Hastie et al. 2009; Zar 2010).
Time budgets for nocturnal behaviour were created for LA and HA (Linder et al. 2020). This was done by dividing the amount of time spent on a given behaviour, e.g., feeding with the total amount of time the elephants were recorded over three nights (HA or LA). Thereby the three nights make up 100% and a previously performed behaviour make up a percentage of the three nights. Behaviours that constitute less than 5% are all put in the same

group, 'Other*'. To test if there was a significant difference between the elephants' performed behaviours, χ^2 tests were used to find p-values (Forthofer et al. 2007; Zar 2010). The performed statistical tests were considered significant if $p < 0.05$. A χ^2 two sample test was used to test for differences in proportion of time spent on a given behaviour (Zar 2010). Identical tests were used in Bertelsen et al. (2020

Results

Comparison between the three elephants within respectively HA and LA

For the behaviours in LA there was a significant difference in the median time spent feeding from ground between the matriarch 'A' *versus* 'B' ($p < 0.01$) and 'A' *versus* 'C' ($p < 0.001$) where 'A' was significantly lower than the two others (Table 2). Test for skewness and kurtosis showed a significant difference in the behaviour 'Walk' between 'A' *versus* 'B' ($p < 0.05$) and 'A' *versus* 'C' ($p < 0.05$), where 'A' was significantly lower. All three were highly positively skewed for 'Walk', which indicates many short observed periods for these behaviours and a unpredictable pattern. For kurtosis, 'B' and 'C' were mesokurtic, whereas 'A' was leptokurtic and therefore a more fluctuating behavioural pattern (Table 2).

For the behaviours in HA there was found a significantly higher value for 'C' in the median time spent on the behaviours 'Feed from ground' ($p < 0.01$) and 'Inactive' ($p < 0.05$) than 'A' (Table 2). The test also showed a significant higher value for 'C' *versus* 'A' ($p < 0.01$) and 'C' *versus* 'B' ($p < 0.05$) for the behaviour 'Other'. The test for skewness showed a significant lower value for 'B' in the behaviours 'Feed from ground' and 'Other' between 'B' *versus* 'A' ($p < 0.05$) and 'B' *versus* 'C' ($p < 0.05$) during HA. In 'Feed from ground' all elephants were moderately to highly positively skewed. For the behaviour 'Other' all three elephants were highly positively skewed (Table 2). Positively skewed results indicate many short observed periods and a unpredictable pattern for these behaviours.

The results for kurtosis showed a significant difference between 'B' *versus* 'C' in the behaviours 'Feed from ground' and 'Other' where 'B' was significantly lower for 'Feed from ground' ($p < 0.05$) and higher for 'Other' ($p < 0.05$). Both 'B' and 'C' were platykurtic for 'Feed from ground', which indicates a homogeneous behavioural pattern. For the behaviour 'Other', Elephant 'B' was leptokurtic and 'C' was platykurtic. In addition, 'B' was also significantly higher than 'A' in the behaviour 'Other' ($p < 0.05$) where both 'A' and 'B' were leptokurtic and therefore showed a fluctuating behavioural pattern (Table 2).

The table is divided in high activity (HA) and low activity (LA). 'No. of tests' shows how many tests are possible to make for each row. 'ns' indicates that there is no significant difference between the two tested groups. '-' indicates that it is not possible to make any statistic tests with this data due to too few observations. When percentage is stated, it indicates how many of the tests are significant. The angle brackets indicate which elephant has the highest value of the two tested. Different significant levels are indicated with asterisk, '***' when $p<0.001$, '**' when $p<0.01$ and '*' when $p<0.05$.

Comparison between HA and LA within each individual elephant

Skewness ($p < 0.05$) and kurtosis ($p < 0.05$) for the behaviour 'Walk', 'A' was significantly higher during LA than during HA. The behaviour 'Walk' was highly positively skewed in both HA and LA, however the behaviour was more skewed in LA, which implies short time intervals and unpredictable pattern for this behaviour. For kurtosis, 'Walk' was leptokurtic in LA, which indicates a fluctuating behavioural pattern. However, the behaviour was platykurtic in HA, which indicates a fluctuating behavioural pattern. For elephant 'B' the median time spent on 'Walk' ($p < 0.05$) was significantly higher during LA than during HA. The behaviour 'Other' performed by 'B' was significantly lower in LA than HA for both skewness ($p < 0.05$) and kurtosis ($p < 0.05$). The results of skewness, 'Other' was moderately positively skewed in LA, whereas the behaviour was highly positively skewed in HA. This result indicates that the behaviour had short time intervals and a unpredictable pattern in both HA and LA. 'Other' was platykurtic in both HA and LA, which indicates a fluctuating behavioural pattern. For 'C' the

median time spent on the behaviour 'Walk' ($p < 0.05$) was significantly higher during LA than during HA (Table 3).

Table 2: Results from Mann-Whitney U test for medians, Kruskal Wallis for medians, skewness (95% CI) and kurtosis (95% CI) between the three elephants.

	Behaviour	No. of tests	Mann-Whitney	Kruskal Wallis	Skewness	Kurtosis
LA	Feed from ground	3	(A<B)** 33% (A<C)*** 33% (B-C) ns	ns	ns	ns
	Feed from hay net	3	ns	ns	ns	ns
	Drink	1	(A) – (B-C) ns	(A) – (B-C) ns	(A) – (B-C) ns	(A) – (B-C) ns
	Inactive	3	ns	ns	ns	ns
	Walk	3	ns	ns	(A<B)* 33% (A<C)* 33% (B-C) ns	(A<B)* 33% (A<C)* 33% (B-C) ns
	Lie	3	ns	ns	ns	ns
	Sway	1	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –
	Stereotypy	1	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –
	Aggression	0	–	–	–	–
	Other	3	ns	ns	ns	ns
HA	Feed from ground	3	(A-B) ns (A<C)** 33% (B-C) ns	ns	(A>B)* 33% (A-C) ns (B<C)* 33%	(A-B) ns (A-C) ns (B<C)* 33%
	Feed from hay net	3	ns	ns	ns	ns
	Drink	3	ns	ns	ns	ns
	Inactive	3	(A-B) ns (A<C)* 33% (B-C) ns	ns	ns	ns
	Walk	3	ns	ns	ns	ns
	Lie	3	ns	ns	ns	ns
	Sway	1	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –
	Stereotypy	1	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –	(A-B) ns (C) –
	Aggression	0	–	–	–	–
	Other	3	(A-B) ns (A<C)** 33% (B<C)* 33%	(A-C) ns	(A<B)* 33% (A-C) ns (B>C)* 33%	(A<B)* 33% (A-C) ns (B>C)* 33%

The table 3 is divided in 'A', 'B' and 'C'. 'No. of tests' showed how many tests are possible to calculate for each row. The table is divided in high activity (HA) and low activity (LA). 'No. of tests' shows how many tests are possible to make for each row. 'ns' indicates that there is no significant difference between the two tested groups. '-' indicates that it is not possible to make any statistic tests with this data due to too few observations. When percentage is stated, it indicates how many of the tests are significant. The angle brackets indicate which elephant has the highest value of the two tested. Different significant levels are indicated with asterisk, '***' when $p<0.001$, '**' when $p<0.01$ and '*' when $p<0.05$.

Table 3: Results from Mann-Whitney U test for medians, Kruskal Wallis for medians, skewness (95% CI) and kurtosis (95% CI) between high activity (HA) and low activity (LA) within each individual elephant.

	Behaviour	No. of tests	Mann-Whitney	Kruskal Wallis	Skewness	Kurtosis
A	Feed from ground	1	ns	ns	ns	ns
	Feed from hay net	1	ns	ns	ns	ns
	Drink	0	–	–	–	–
	Inactive	1	ns	ns	ns	ns
	Walk	1	ns	ns	(LA>HA) 100%	(LA>HA) 100%
	Lie	1	ns	ns	ns	ns
	Sway	1	ns	ns	ns	ns
	Stereotypy	1	ns	ns	ns	ns
	Aggression	0	–	–	–	–
	Other	1	ns	ns	ns	ns
B	Feed from ground	1	(LA>HA) 100%	ns	ns	ns
	Feed from hay net	1	ns	ns	ns	ns
	Drink	1	ns	ns	ns	ns
	Inactive	1	ns	ns	ns	ns
	Walk	1	(LA>HA) 100%	ns	ns	ns
	Lie	1	ns	ns	ns	ns
	Sway	1	ns	ns	ns	ns
	Stereotypy	1	ns	ns	ns	ns
	Aggression	0	–	–	–	–
	Other	1	ns	ns	(LA<HA) 100%	(LA<HA) 100%
C	Feed from ground	1	ns	ns	ns	ns
	Feed from hay net	1	ns	ns	ns	ns
	Drink	1	ns	ns	ns	ns
	Inactive	1	ns	ns	ns	ns
	Walk	1	(LA>HA) 100%	ns	ns	ns
	Lie	1	ns	ns	ns	ns
	Sway	0	–	–	–	–
	Stereotypy	0	–	–	–	–
	Aggression	0	–	–	–	–
	Other	1	ns	ns	ns	ns

Reaction norms between individuals and behaviours

Median, IQR, skewness and kurtosis for all behaviours were compared between all three individuals for LA and HA periods (Figure 1-4). Lines without any slope or regression indicated not enough observed behaviour data. Generally, medians for all three elephants showed similar reaction norms for 'Feed from ground', 'Inactive', 'Walk' and 'Stereotypy' (Figure 1). Even though 'A' and 'B' were significantly different in most behaviours, they displayed a similar reaction norm. The results from χ^2-tests showed that slopes for 'Feed from ground' ($p < 0.001$), 'Feed from hay net' ($p < 0.001$) and 'Other' ($p < 0.001$) were significantly higher for 'A' than for 'B'. *Vice versa*, the slopes for the behaviours 'Inactive' ($p < 0.001$), 'Lie' ($p < 0.001$), 'Sway' ($p < 0.001$) and 'Stereotypy' ($p < 0.01$) were significantly higher for 'B' than the slopes for 'A'. The results showed slopes the behaviours 'Feed from ground' ($p < 0.001$), 'Lie' ($p < 0.001$) and 'Other' ($p < 0.001$) were significantly higher for 'A' than the

slopes for 'C'. Results also showed, the slopes for the behaviours 'Feed from hay net' ($p < 0.001$) and 'Inactive' ($p < 0.001$) were significantly higher for 'C' than the slopes for 'A'. Furthermore, slopes for the behaviours 'Feed from ground' ($p < 0.05$), 'Drink' ($p < 0.01$), 'Lie' ($p < 0.001$) and 'Other' ($p < 0.001$) were significantly higher for 'B' than the slopes for 'C'. Moreover, the slopes for the behaviours 'Feed from hay net' ($p < 0.001$) and 'Inactive' ($p < 0.001$) were significantly higher for 'C' than the slopes for 'B' (Figure 1).

The tendency for IQR displayed that 'A' and 'B' showed similar reaction norms in the behaviours 'Feed from ground', 'Feed from hay net', 'Inactive', 'Walk', 'Stereotypy' and 'Other'. Despite this, the χ^2-tests showed significant difference between most of the behaviours (Figure 2). The χ^2-tests showed the slopes for the behaviours 'Feed from ground' ($p < 0.001$), 'Feed from hay net' ($p < 0.001$), 'Inactive' ($p < 0.001$), 'Walk' ($p < 0.001$), 'Lie' ($p < 0.001$), 'Stereotypy' ($p < 0.01$) and 'Other' ($p < 0.01$) were significantly higher for 'A' than the slopes for 'B'. In contrast, the slope for 'Sway' ($p < 0.001$) performed by 'B' was significantly higher than 'A'. The significant difference between 'A' and 'C' showed the slopes for the behaviours 'Feed from ground' ($p < 0.001$) and 'Lie' ($p < 0.001$) were higher for 'A' than the slopes for 'C'. *Vice versa*, the slopes for 'Feed from hay net' ($p < 0.001$) and 'Inactive' ($p < 0.001$) were significantly higher for 'C' than the slopes for 'A'. Finally, slopes for the behaviours 'Feed from ground' ($p < 0.001$) and 'Drink' ($p < 0.001$) were significantly higher for 'B' than the slopes for 'C'. Significantly higher slopes for 'Feed from hay net' ($p < 0.001$), 'Inactive' ($p < 0.001$), 'Walk' ($p < 0.01$), 'Lie' ($p < 0.001$) and 'Other' ($p < 0.001$) were found for 'C' than for 'B' (Figure 2).

Skewness for the behaviour 'Walk' ($p < 0.05$) was significantly different between the slopes for 'A' and 'C', where 'Walk' for 'C' had a higher slope. Generally, the behaviours displayed different gradients and therefore no clear tendencies (Figure 3). The results from comparing slopes for kurtosis showed significantly higher slopes in the behaviours 'Walk' ($p < 0.001$), 'Stereotypy ($p < 0.01$) and 'Other' ($p < 0.001$) for 'B' than for 'A'. For kurtosis, there was a significantly higher slope for the behaviour 'Feed from ground' ($p < 0.01$) for 'C' compared to 'A'. *Vice versa*, the slope for the behaviour 'Inactive' ($p < 0.01$) for kurtosis was significantly higher for 'A' than 'C'. Finally, slopes for the behaviours 'Feed from ground' ($p < 0.01$) and 'Drink' ($p < 0.05$) were significantly higher for 'C' than for 'B'. Whereas slopes for the behaviours 'Other' ($p < 0.01$) and 'Lie' ($p < 0.05$) were significantly higher for 'B' than for 'C' (Figure 4).

Comparison between data from 2019 and 2021

Nine behaviours were compared with the study from 2019. The behaviour 'Aggression' was excluded since the behaviour was not investigated in 2019 and not enough data was collected in 2021. The results of χ^2-test for 'A' showed that median and IQR were significantly higher for all the tested behaviours in 2021 than in 2019 (Table 4). The behaviours 'Feed from ground', 'Feed from hay net', 'Inactive', 'Lie', 'Sway' and 'Other' for 'A' all had one common significance level ($p < 0.001$) in test for median and IQR between 2019 and 2021 (Table 4). Whereas 'Stereotypy' had a different significance level ($p < 0.01$) in test for median and 'Walk' had a different significance level ($p < 0.01$) in test for IQR between 2019 and 2021 (Table 4). Meanwhile, skewness and kurtosis showed variation in behaviours that were significant in proportion to which year had the higher value (Table 4). The results from skewness for 'A' showed significant difference between 2019 and 2021 in the behaviour 'Walk' ($p < 0.05$). The distribution for 'Walk' was highly positively skewed in 2021 and moderately positively skewed in 2019, which implies short time intervals and unpredictable pattern in both 2019 and 2021. Results from kurtosis for individual 'A' showed significant difference in the behaviours 'Feed from ground' ($p < 0.05$), 'Walk' ($p < 0.001$), 'Stereotypy' ($p < 0.05$) and 'Other' ($p < 0.05$). The distribution for the behaviour 'Feed from ground' was leptokurtic in 2019 and platykurtic in 2021, which means that there was a more fluctuating behavioural pattern for the behaviour in 2019 and more homogeneous behavioural pattern in 2021. Whereas 'Walk' and 'Stereotypy' were platykurtic in 2019 and leptokurtic in 2021. Finally, 'Other' had a leptokurtic distribution in 2019 and 2021, which indicates fluctuating behavioural pattern for both time periods.

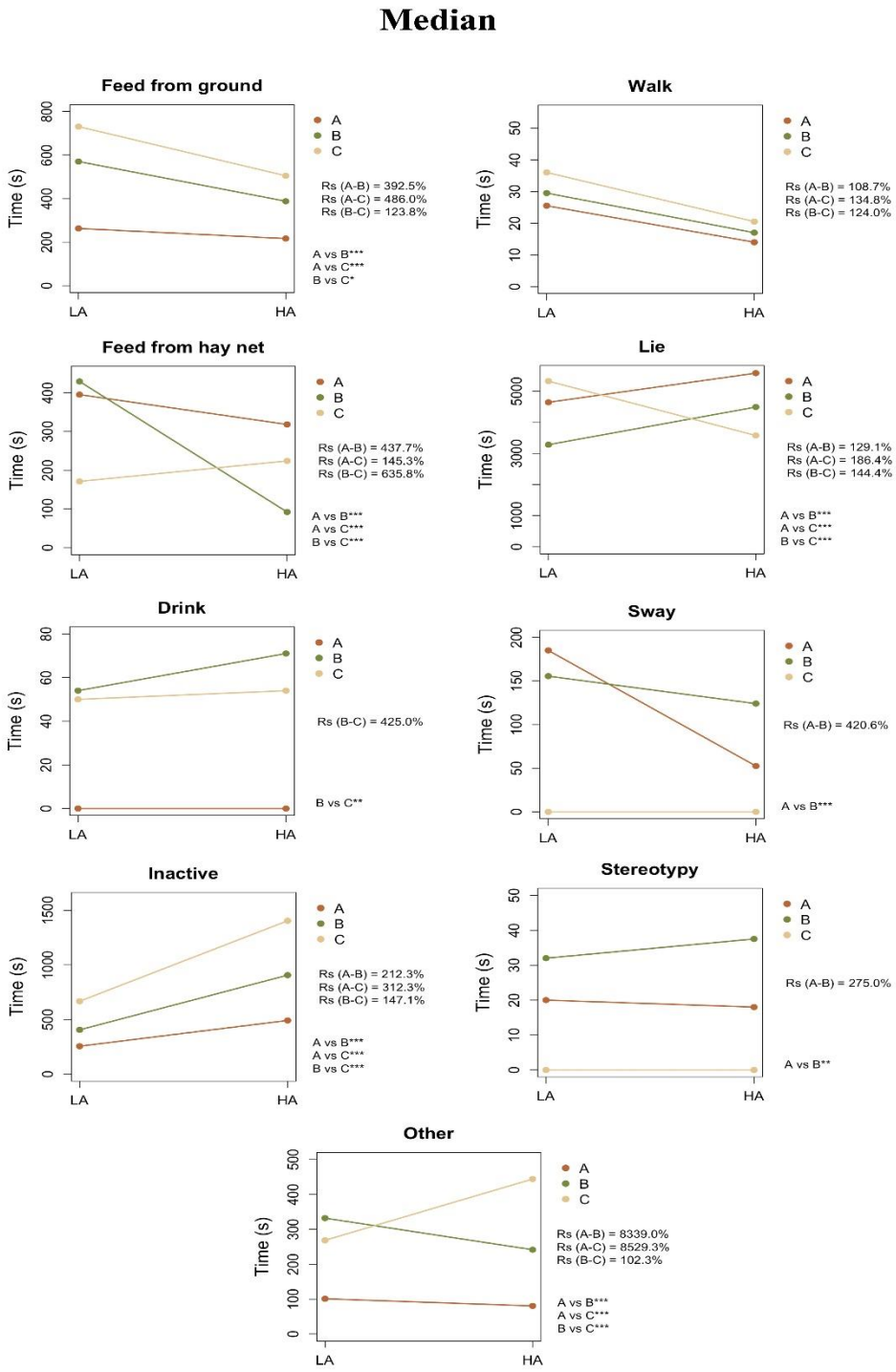

Figure 1: Comparison of medians for high activity (HA) and low activity (LA) including comparison between the three elephants. Red slope indicates elephant A, green slope indicates elephant B and yellow slope indicates elephant C. Significant differences are indicated with asterisk, '***' when $p < 0.001$, '**' when $p < 0.01$ and '*' when $p < 0.05$. 'Rs' indicates the relation between two slopes in percent

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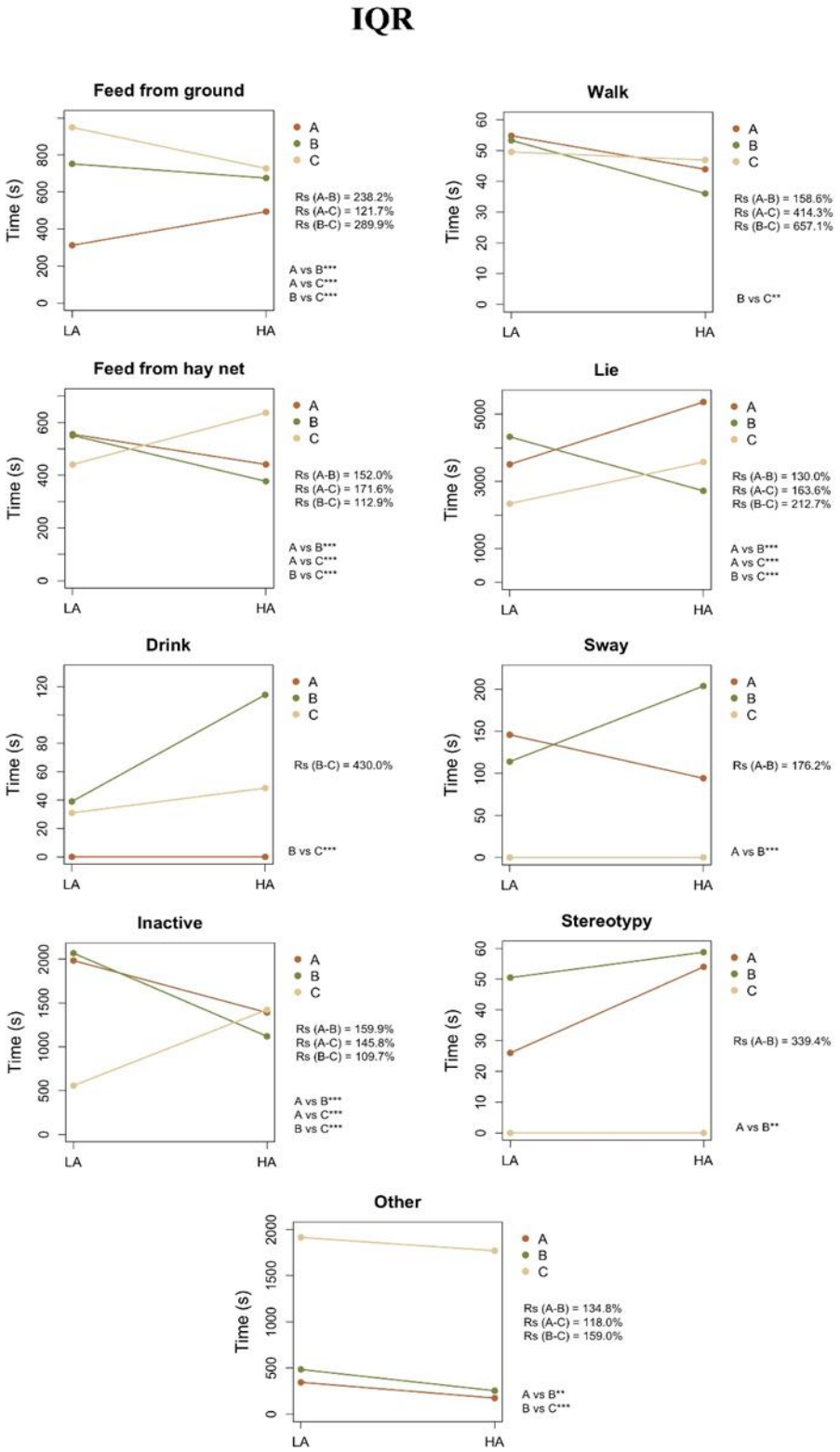

Figure 2: Comparison of IQR for high activity (HA) and low activity (LA) including comparison between the three elephants. Red slope indicates elephant A, green slope indicates elephant B and yellow slope indicates elephant C. Significant differences are indicated with asterisk, '***' when $p < 0.001$, '**' when $p < 0.01$ and '*' when $p < 0.05$. 'Rs' indicates the relation between two slopes in percent.

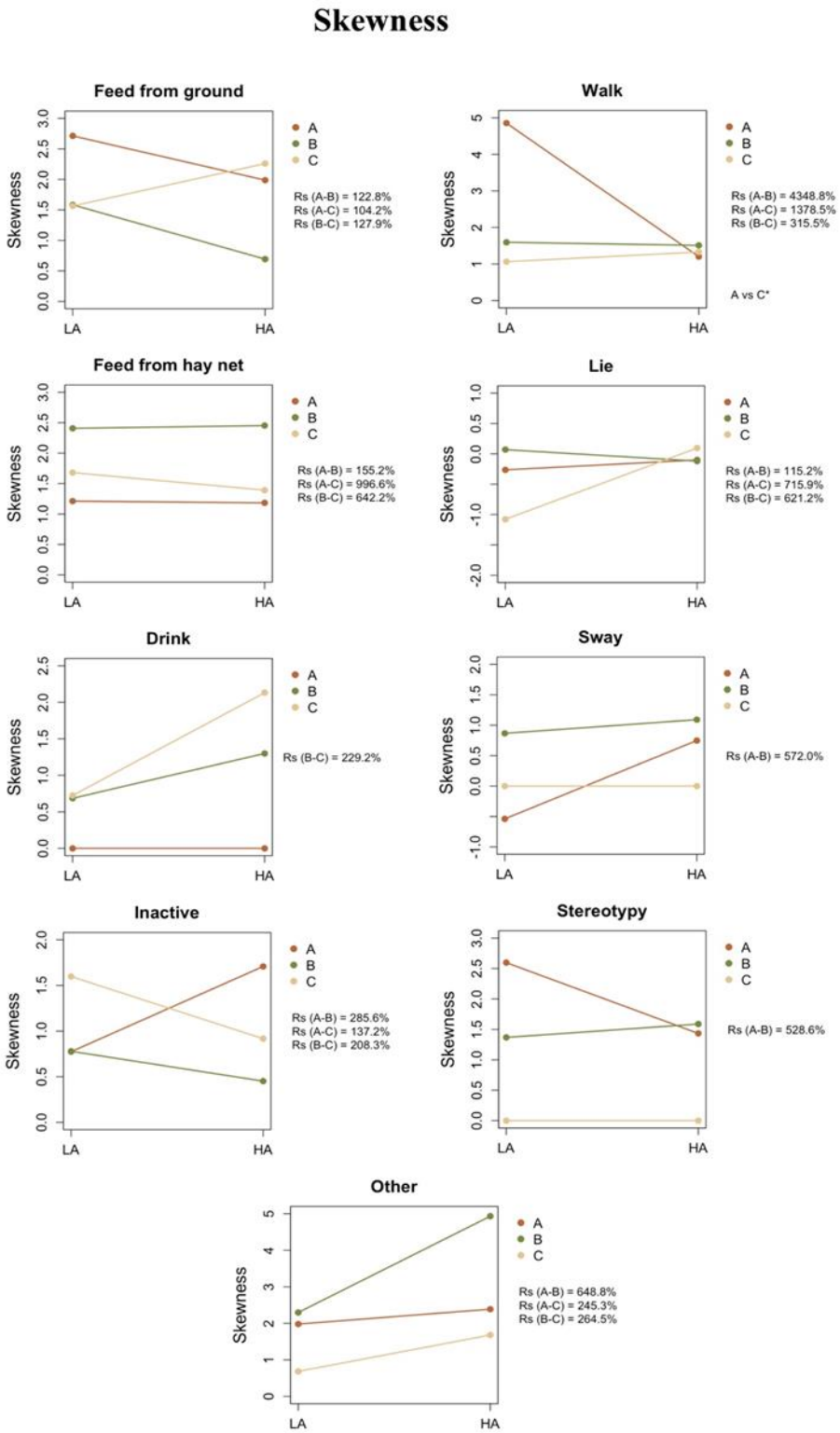

Figure 3: Comparison of skewness for high activity (HA) and low activity (LA) including comparison between the three elephants. Red slope indicates elephant A, green slope indicates elephant B and yellow slope indicates elephant C. Different significant levels are indicated with asterisk, '***' when p< 0.001, '**' when p< 0.01 and '*' when p< 0.05. 'Rs' indicates the relation between two slopes in percent.

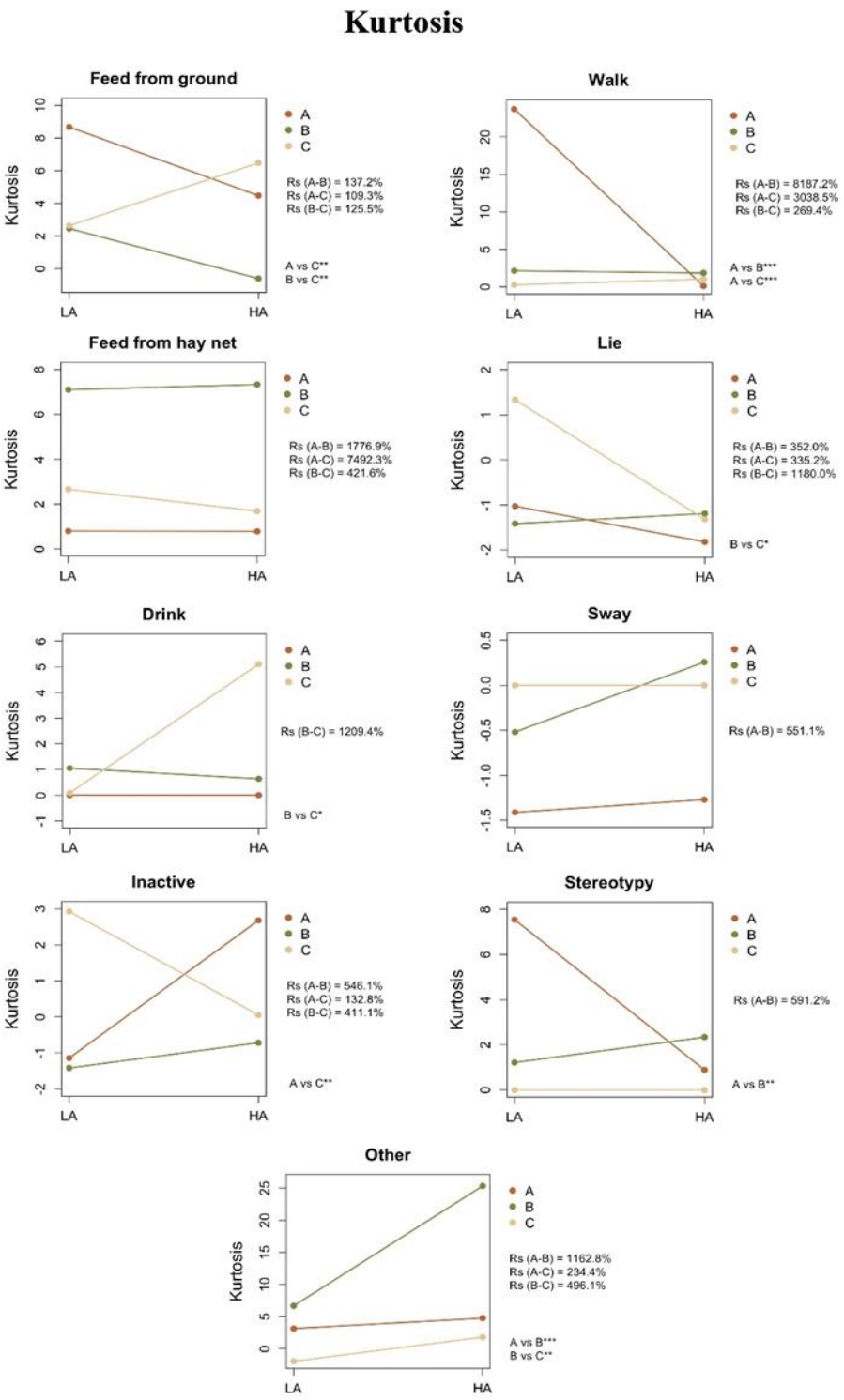

Figure 4: Comparison of kurtosis for high activity (HA) and low activity (LA) including comparison between the three elephants. Red slope indicates elephant A, green slope indicates elephant B and yellow slope indicates elephant C. Significant differences are indicated with asterisk, '***' when $p < 0.001$, '**' when $p < 0.01$ and '*' when $p < 0.05$. 'Rs' indicates the relation between two slopes in percent.

All tested behaviours for median were significant different between 2019 and 2021 for 'B', except 'Sway' (Table 4). The data from 2021 had higher median for six out of eight behaviours for 'B', and a higher IQR in six out of eight behaviours for 'B'. All behaviours in median had a significance level at $p < 0.001$. Results from IQR showed the same significance level for all behaviours that were significant ($p < 0.001$) (Table 4). There was one significant difference in kurtosis for the behaviour 'Lie', where the behaviour was significantly higher in 2019 than in 2021. Results for kurtosis also displayed that 'Lie' was platykurtic in 2019 and leptokurtic in 2021. This indicates a fluctuating behavioural pattern in 2021 and a homogeneous behavioural pattern in 2019.

For 'C' the behaviours 'Sway' and 'Stereotypy' were not tested. In the data from 2021, 'C' had higher median in five out of seven behaviours and a higher IQR for all behaviours than in the data from 2019 (Table 4). Median results showed the same significance level ($p < 0.001$) for the behaviours 'Feed from ground', 'Feed from hay net', 'Inactive', 'Walk', 'Lie' and 'Other'. The significance level found for the behaviour 'Drink' was $p < 0.05$. Furthermore, the results from IQR displayed the same significance level ($p < 0.001$) for all the behaviours that were significant between the two studies (Table 4). Kurtosis results showed a leptokurtic distribution for 'Feed from ground' in 2019 and 2021, therefore a fluctuating behavioural pattern for both time periods. A platykurtic distribution for 'Drink' and 'Lie' was seen in 2019 and 2021, which indicates a homogeneous behavioural pattern for the elephants. The behaviours 'Feed from hay net' and 'Other' had a leptokurtic distribution, and therefore a fluctuating behavioural pattern, in 2019 and platykurtic distribution and therefor a homogeneous behavioural pattern in 2021 (Table 4).

'No. of tests' shows how many tests are possible to make for each row. 'ns' indicates that there is no significant difference between the two tested groups. '-' indicates that it is not possible to make any statistic tests with this data due to too few observations. When percentage is stated, it indicates how many of the tests are significant. The angle brackets indicate which elephant has the highest value of the two tested. Different significant levels are indicated with asterisk, '***' when $p< 0.001$, '**' when $p< 0.01$ and '*' when $p< 0.05$.

Time budgets

During both HA and LA, 'C' ate more from ground than the two other elephants (Figure 5-6). Moreover, 'A' ate significantly less from ground than 'B' ($p < 0.05$) and 'C' ($p < 0.01$) during LA (Figure 6). 'A' was significantly more inactive than 'C' ($p < 0.05$) during HA and LA and significantly more inactive than 'B' ($p < 0.01$) during HA (Figure 5-6). The behaviours 'Feed from hay net', 'Lie' and 'Other*' did not show any significant difference between the three elephants neither during HA nor LA. The most observed nocturnal behaviour was 'Lie' during LA and HA. The average of the three individuals for this behaviour was approximately 30 ± 8%. However, if the behaviours 'Feed from ground' and 'Feed from hay net' is combined, then feeding would be the most observed behaviour with an average of approximately 35 ± 12% (Figure 5-6).

Table 4: Median, IQR, skewness and kurtosis for data between 2019 and 2021.

	Behaviour	No. of tests	Median	IQR	Skewness	Kurtosis
A	Feed from ground	1	(2019<2021)***	(2019<2021)***	ns	(2019<2021)*
	Feed from hay net	1	(2019<2021)***	(2019<2021)***	ns	ns
	Drink	1	–	–	–	–
	Inactive	1	(2019<2021)***	(2019<2021)***	ns	ns
	Walk	1	(2019<2021)***	(2019<2021)**	(2019<2021)*	(2019<2021)***
	Lie	1	(2019<2021)***	(2019<2021)***	ns	ns
	Sway	1	(2019<2021)***	(2019<2021)***	ns	ns
	Stereotypy	1	(2019<2021)*	(2019<2021)***	ns	(2019<2021)*
	Other	1	(2019<2021)***	(2019<2021)***	ns	(2019>2021)*
B	Feed from ground	1	(2019<2021)***	(2019<2021)***	ns	ns
	Feed from hay net	1	(2019<2021)***	ns	ns	ns
	Drink	1	(2019<2021)***	(2019>2021)***	ns	ns
	Inactive	1	(2019<2021)***	(2019<2021)***	ns	ns
	Walk	1	(2019<2021)***	(2019<2021)***	ns	ns
	Lie	1	(2019>2021)***	(2019<2021)***	ns	(2019>2021)*
	Sway	1	ns	(2019>2021)***	ns	ns
	Stereotypy	1	(2019>2021)***	(2019<2021)***	ns	ns
	Other	1	(2019<2021)***	(2019<2021)***	ns	ns
C	Feed from ground	1	(2019<2021)***	(2019<2021)***	ns	(2019>2021)*
	Feed from hay net	1	(2019>2021)***	(2019<2021)***	ns	(2019>2021)**
	Drink	1	(2019<2021)*	(2019<2021)***	ns	(2019<2021)***
	Inactive	1	(2019<2021)***	(2019<2021)***	ns	ns
	Walk	1	(2019<2021)***	ns	ns	ns
	Lie	1	(2019>2021)***	(2019<2021)***	ns	(2019>2021)*
	Sway	1	–	–	–	–
	Stereotypy	1	–	–	–	–
	Other	1	(2019<2021)***	(2019<2021)***	ns	(2019>2021)*

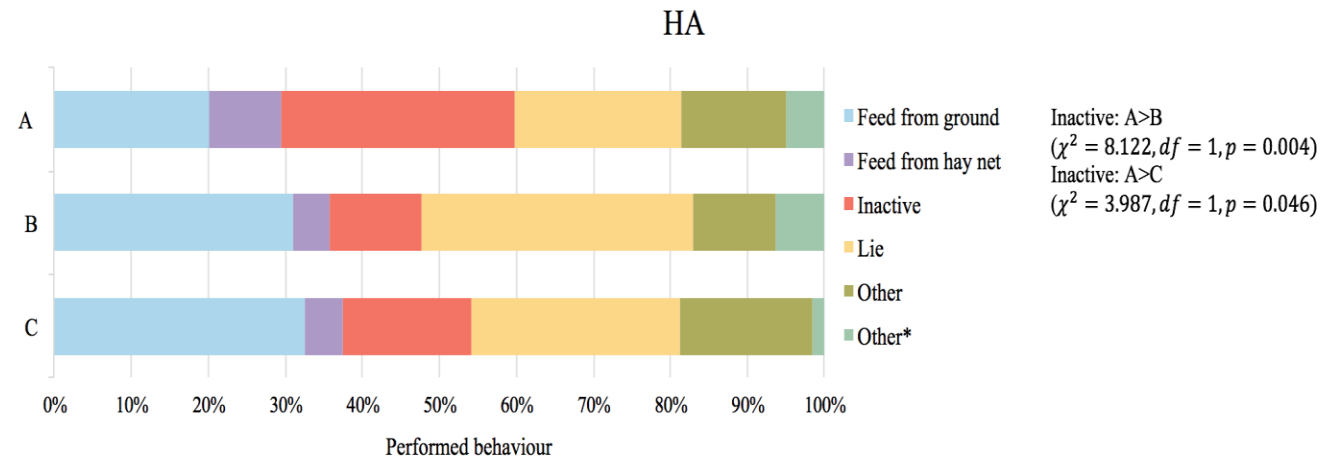

Figure 5: Time budget comparing the proportion of time each elephant did a specific behaviour during high activity (HA) period. Each bar represents one elephant. The proportions of behaviours that are significantly different ($p < 0.05$) are showed to the right on the figure. 'Other∗' indicates all behaviours which proportion is < 5%.

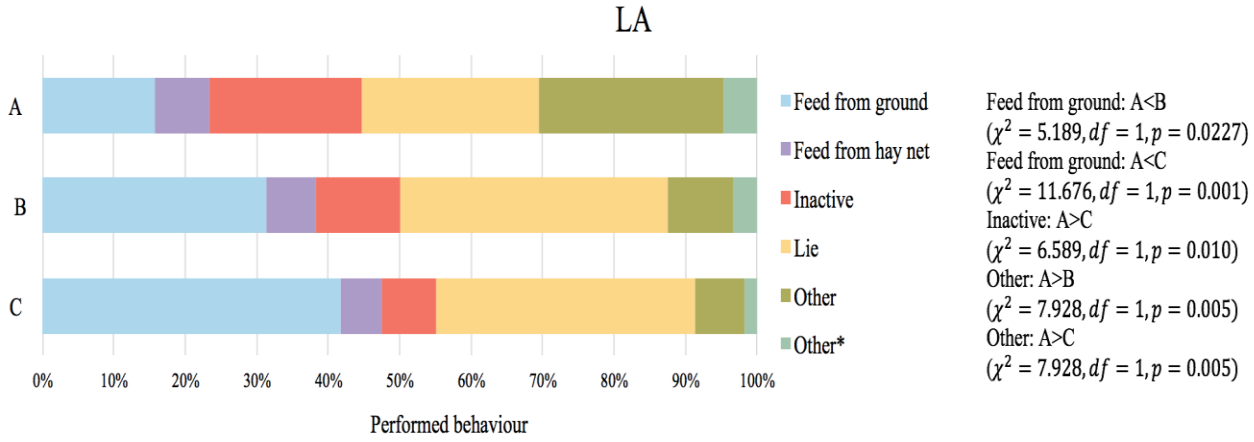

Figure 6: Time budget comparing the proportion of time each elephants did a specific behaviour during low activity (LA) period. Each bar represents one elephant. The proportions of behaviours that are significant different ($p < 0.05$) are showed to the right on the figure. 'Other∗' indicates all behaviours which proportion is < 5%.

Discussion

Comparison between the three elephants within respectively HA and LA

The behavioural differences observed between the elephants indicate that the hierarchy status may have an influence on behaviour since the matriarch 'A' differed from the two others in several performed behaviours. This is in agreement with Larrieu et al. (2017), who found that dominant individuals were susceptible to stress-like behaviour (Larrieu et al. 2017). However, on most occasions no significant difference was found between the elephants in this study.

Comparison between HA and LA for each individual elephant

Few significant results were found when comparing the three elephants during HA and LA periods. Lower time was spend walking during the night in HA compared to the LA, which may be explained by stressors, such as noise due to an increase in the number of visitors during the day (Table 3) (Morgan and Tromborg 2007; Quadros et al. 2014). A response to disturbing noise can be expressed in different ways, such as an increase or decrease in locomotive activity (Morgan and Tromborg 2007; Quadros et al. 2014). This could explain the observed decrease in locomotive activity for 'B' and 'C' during HA (Table 3). A similar response could be expected for the distribution of the intervals for the behaviour 'Lie', but due to the small sample size, the margin of error has increased (Zar 2010; Agresti and Franklin 2014; Boyle et al. 2015).

The behavioural differences observed for 'A' between HA and LA showed an alteration in the pattern of walking when data were compared which indicate that HA may disturb the elephant. Both HA and LA were positively skewed, and the majority of the values lie to the left. Therefore, the observed intervals for the behaviour were short. LA was more positively skewed than HA, which means the intervals were shorter during LA than during HA. This unpredictable pattern could be a response to different environmental conditions (Dingemanse et al. 2010; Greco et al. 2016). Distributions for 'A' showed a change in the pattern of walking between LA and HA which could be due to stressors during HA. Behavioural differences among elephants could be explained by individual personality traits, where some elephants exhibit increased investigatory behaviour and others become sceptical (Morgan and Tromborg 2007; Montiglio et al. 2012). This may be the reason for different results respectively for 'A', 'B' and 'C' in the different behaviours in LA and HA.

This study and the previous study by Bertelsen et al. (2020) showed opposite results for time spend walking between HA and LA, which indicates a change in behaviour and reaction norms for 'B' and 'C' over the time span of two years (Montiglio et al. 2012; Turcsán et al. 2020). All three elephants spent more time on walking in 2021 than in 2019, which may be due to the possibility to walk outside in 2021, which was not possible in 2019. It was not possible to observe their behaviour in the outside area, accordingly the results for walking might be misrepresenting, considering the possibility that the elephants are walking when being outside.

Reaction norms between individuals and behaviours

This study demonstrates the diversity of personality and how visitor number contribute to a variation in percentage distribution of the behaviours. High-significant differences in medians were found across several behaviours between the elephants (Figure 1). Furthermore, the IQR documented asymmetry in all tested behaviours between the three individuals. We therefore assume, that the three elephants show different personalities due to a difference in gradients for reaction norms. Moreover, the results from skewness and kurtosis showed that the distributions were different for many of the behaviours between the individuals, which support the statement about different personalities (Montiglio et al. 2012). The significant result in skewness between 'A' and 'C' for the behaviour 'Walk' implies two different and unpredictable patterns for both elephants. This can be a result of interactions between the two elephants which may cause them to change each other's walking pattern.

Comparing data from 2019 and 2021

Median and IQR's for most of the observed behaviours differs significantly between 2019 and 2021 in both median and IQR (Table 4). For the observed behavioural differences in median time for 'A' between 2019 and 2021, all behaviours had a higher median value in 2021. Therefore, the behaviour 'Stereotypy' and 'Sway' had a higher median value in 2021. This could be explained by dominant individuals are more prone to exhibit stress-related behaviour (Larrieu et al. 2017). The zookeepers always seek to challenge

the elephants' senses by presenting new ways of stimuli. Feeding stimuli included hiding small pieces of vegetables or fruits in different places, e.g., in tree trunks, or holes in the ground and walls (Carlstead, Paris, and Brown 2019). The time spent on feeding could therefore be higher in 2021, because the elephants may spend more time searching for food. Differences for the observed behaviours for 'B' suggest that the elephant may have had better stimuli in 2021 than in 2019 (Greco et al. 2016). Moreover, 'Lie' and 'Stereotypy' had a higher median value in 2019 for 'B' than in 2021. 'C' had a higher median time spent on lying down in 2019 than in 2021.

Boyle et al. (2015) found that older animals spend less time lying down than younger animals. Time spend lying down can be interpreted as a positive welfare indicator, as less time spend lying down is associated with poor social compatibility (Finch et al. 2021). The more time spend on 'Lie' in 2021 can be caused by lower stress level (Boyle et al. 2015). It is therefore reasonable to assume that the new initiatives, such as the possibility to walk outside, may have had a positive influence on 'B' (Greco et al. 2016).

IQR results stated the 50% of the middle values for the distribution from 2021 were spread out further than for the distribution in 2019. The fact that the elephants had a larger variability in time intervals for the observed behaviours in 2021 than in 2019 may be due to that they had more options in 2021 (Greco et al. 2016). In 2019 the elephants could not walk outside. These results demonstrates that the same three elephants responded differently to particular situations, which contradict the statement and hypothesis that elephants do not change their personality and reaction norms over time (Turcsán et al. 2020). Due to few significant differences for skewness and kurtosis between 2019 and 2021, there is no clear tendency regarding difference in distributions for the tested behaviours.

Time budgets

The most frequent behaviour observed was feeding, where the elephants spend 35 ± 12%. This is consistent with the previous study from Bertelsen et al. (2020), where the elephants spending 43 ± 6% of their time on feeding. The second most common behaviour in both studies were lying down which where equivalent to 28 ± 5% in 2019 and 30 ± 8% in 2021. Wild African elephants approximately eat about 1.0 − 1.5% of their body weight a day (Ullrey et al. 1997). Ullrey and co-workers (1997) also found that the daily intake of food was about 1.4 − 1.6% of their body weight for captive female African elephants. We found that the elephants ate 4.5 − 7.5% of their body weight per day, which appear to be considerably more. Therefore, the large amount of food received must be taken into account to interpret our results, as this may have encouraged the elephants to spend more time on eating than in other studies. When the data from HA periods are compared with the data from LA periods, a clear pattern in the individual's personality traits is evident, e.g., the behaviour 'Feed from ground' (Figure 5-6). A similar tendency for personality traits was found in the data from 2019 by Bertelsen et al. (2020). Furthermore, these results support the hypothesis that elephants are not changing behavioural reaction norms over time (2 years).

Limitations

The number of animals in the zoo are always very limited and therefore it was not possible to obtain the same statistical power compared to a laboratory setting. A small sample size increases the risk of type I error which will result in rejection of a true hypothesis. However, many significant results were found in this study and a substantial amount were relatively powerful. Elephant 'A' and 'B' were clearly aggressive in their behaviour, but due to small sample size the behaviour could not be investigated further statistically. Outliers were not removed due to the small sample size. If outliers were removed, this could have reduced the variability (Zar 2010; Gerstman 2015). Furthermore, a limited selection of behaviours was chosen in this study for the purpose of a direct comparison with the study performed by Bertelsen et al. (2020). Therefore, this did not allow a full representation of all the behaviours the elephants might convey. When comparing the results from 2021 with data from 2019 a possible explanation for variation in data

was found. It was possible to monitor the elephants constantly in 2019 since they had no access to the outside area and remained indoors at all times (Bertelsen et al. 2020).

Conclusion

The results revealed a significant difference between the behaviours during low activity and high activity for all three elephants. However, there were not enough evidence to suggest that number of visitors had an influence on the elephants' reaction norms. Clear differences in reaction norms of various behaviours were found between the three elephants indicating personality diversity. Although, time budgets did not reveal any change in personality for the individuals over the two years, the tests for comparison forms evidence for some personality change between 2019 and 2021.

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Conflicts of Interest

The authors declare no conflicts of interest.

References

Agresti A, Franklin C. 2014. *Statistics: The Art and Science of Learning from Data*. Pearson Education Limited, *Volume:* 3.

Alstrup AKO, Jensen TH, Pagh S. 2020. Personlighed hos dyr [in Danish]. *Dyrlægen* 5, 18- 23.

Bertelsen SS. et al. 2020. Nocturnal behaviour of three zoo elephants *(Loxodonta Africana)*. *Genetics and Biodiversity Journal.* Special issue 93-113.

Boyle A. et al. 2015. Assessment of flooring renovations on African elephant (*Loxodonta africana*) behavior and glucocorticoid response. *PLOS ONE* 11, 10. doi: 10.1371/ jour nal.pone.0141009.

Branco PS. et al. 2019. Determinants of elephant foraging behaviour in a coupled human-natural system: Is brown the new green? *Animal Ecology* 88, 5, 780–792. doi: https://doi.org/10.1111/1365-2656.12971.

Briffa M, Weiss A. 2010. Animal personality. *Current Biology* 20, 21, R912–R914. doi: 10.1016/j.cub.2010.09.019

Carlstead K, Paris A, Brown JL. 2019. Good keeper-elephant relationships in North American zoos are mutually beneficial to welfare. Applied Animal Behaviour Science 211, 103–111. Doi: https://doi.org/10.1016/j.applanim.2018.11.003.

Dingemanse NJ et al. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology & Evolution. 2010, 25, 81–89. doi: 10.1016/j.tree.2009.07.013.

Fieberg JR, Vitense K, Johnson DH. 2020. Resampling-based methods for biologists. PeerJ 8, e9089. doi: 10.7717/peerj.9089.

Finch K et al. 2021. Insights into activity of zoo housed Asian elephants (*Elephas maximus*) during periods of limited staff and visitor presence, a Focus on resting behaviour. *Zoological and Botanical Gardens* 2, 101–114. doi: https://doi.org/10.3390/jzbg2010008.

Forthofer RN, Lee ES, Hernandez M. 2007. *Biostatistics*. 30 Corporate Drive, Suite 400, Burlington, MA 01803, USA: Academic Press.

Gerstman BB 2015. *Basic biostatistics*. 5 Wall Street, Burlington, MA 01803, USA: Jones and Bartlett Learning.

Greco BJ et al. 2016. The days and nights of zoo elephants: Using epidemiology to better understand stereotypic behavior of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maxi mus*) in North American zoos. PLoS One 2016, 14; *ProQuest* 11. doi: 10.1371/journal.pone.0144276.

Hastie T, Tibshirani R, Friedman J. 2009. *The elements of statistical learning*. Stanford University, Stanford, CA 94305, USA: Springer.

Hosey G. 2008. A preliminary model of human–animal relationships in the zoo. Applied Animal Science 109, *2-4*, 105–127. doi: https://doi.org/10.1016/j.applanim.2007.04.013.

Larrieu T et al. 2017. Hierarchical status predicts behavioral vulnerability and nucleus accumbens metabolic profile following chronic social defeat stress. Current Biology *14*, 27, 2202–2210. doi: https://doi.org/10.1016/j.cub.2017.06.027.

Linder AC et al. 2020. Using behavioral instability to investigate behavioral reaction norms in captive animals: Theoretical implications and future ferspectives. *Symmetry* 12, 603. doi: https://doi.org/10.3390/sym12040603.

Mason J, Veasey JS. 2010. What do population-level welfare indices suggest about the well-being of zoo elephants. *Zoo Biology* 2010, 29, 256–273. doi: DOI10.1002/zoo.20303.

Montiglio P-O et al. 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. Animal Behaviour 84, *4*, 1071–1079. doi: 10.1016/j.anbehav.2012.08.010.

Morgan KN, Trombor CT. 2007. Sources of stress in captivity individual plasticity. *Applied Animal Behaviour Science 3–4,* 102, 262–302. doi: 10.1016/j.applanim.2006.05.032.

Quadros S et al. 2014. Zoo visitor effect on mammal behaviour: Does noise matter? *Applied Animal Behaviour Science* 156, 78–84. doi: 10.1016/j.applanim.2014.04.002.

Rees PA. 2009. Activity budgets and the relationship between feeding and stereotypic behaviors in Asian elephants (*Elephas maximus*) in a Zoo. *Zoo Biology* 28, 79–97 doi: https://doi.org/10.1002/zoo.20200.

Seltmann MW et al. 2019. Males have more aggressive and less sociable personalities than females in semi-captive Asian elephants. *Scientific Reports 9 1*. doi: DOI:10.1038/s41598-019-39915-7.

Stamps JA. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters* 10.5, 355–363. doi: https://doi.org/10.1111/j.1461-0248.2007.01034.x.

Turcsán B et al. 2020. Individual and group level personality change across the lifespan in dogs. *Scientific Reports* 10, 16276. doi: https://doi.org/10.1038/s41598-020-74310-7.

Ullrey DE, Crissey SD, Hintz HF. 1997. Elephants: Nutrition and Dietary Husbandry: Nutrition Advisory Group Handbook. Fact Sheet 004, Page 20.

Yasui S et al. 2012. Personality assessment and its association with genetic factors in captive Asian and African elephants. *Zoobiology* 2013, 32 (1), 70-78. doi: https: //doi.org/10.1002/zoo.21045.

Zar JH. 2010. *Biostatistical Analysis*. Upper Saddle River, New Jersey 07458: Pearson Education International.

Appendix 1

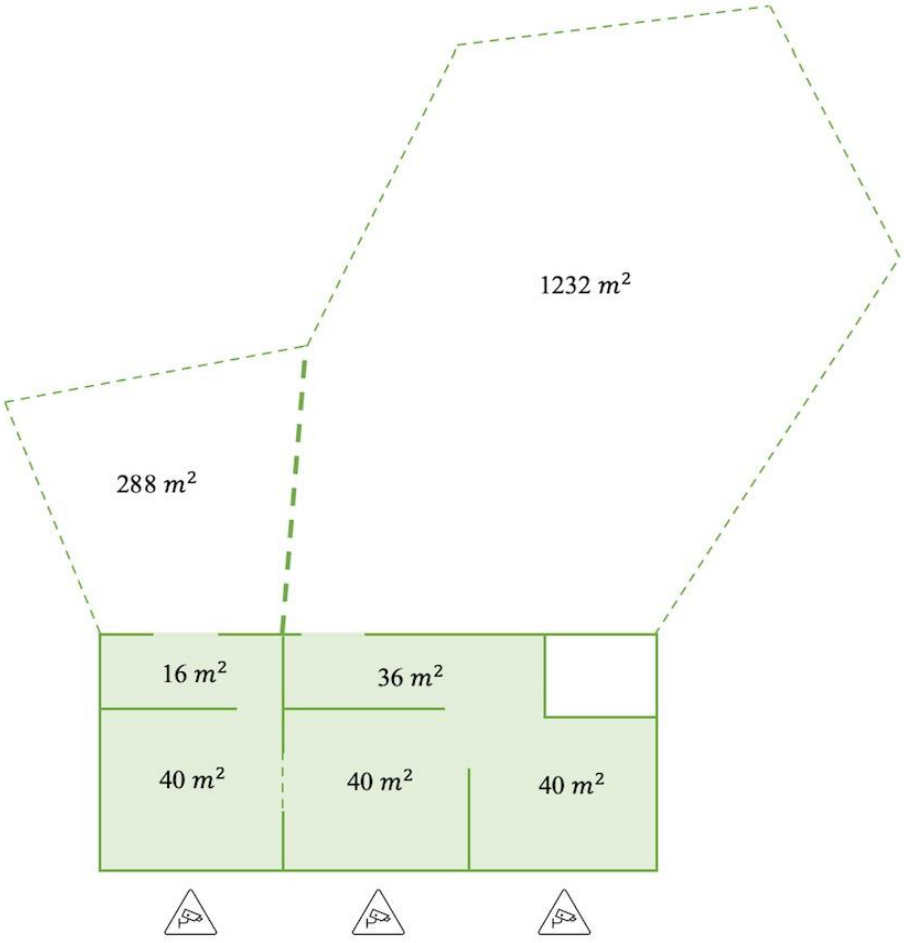

Figure 7: Floor plan of elephant enclosure in Aalborg Zoo. Modified from Bertelsen et al