DER ZOOLOGISCHE GARTEN

THE ZOOLOGICAL GARDEN

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- news from zoological gardens
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Walking Less but Going Further – Male's Presence Reduces Walking Activity but Increases Space Use in a Group of Zoo-Kept Female African Elephants (*Loxodonta africana*)

Weniger gelaufen, aber weiter gekommen – die Anwesenheit eines Bullen reduziert die Laufaktivität, erhöht jedoch die Raumnutzung einer Kuhgruppe Afrikanischer Elefanten (*Loxodonta africana*) im Zoo

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Abstract

In their natural habitat, African elephants roam widely searching for water and food. To promote this behavior under zoo conditions, modern facilities are extending their elephant exhibits. The success of these investments can be determined by investigating the daily walking distances and the space coverage of the individual elephants. We did this in a group of 1.3 African elephants at Zoo Dresden. Attaching GPS trackers in an anklet to the elephants resulted in a total of 107 observation days under conditions with the dominant male present or absent for the night in the female group. With individual daily walking distances between 8.1 and 10.1 km, the locomotion activity was in the upper range reported for zoo elephants so far and in the median range of data from free-ranging elephants. On days with unlimited presence of the dominant male, all females showed reduced walking distances. Simultaneously they increased their coverage of the

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exhibit. We conclude that social factors impact walking activity in zoo-kept African elephants, and that a more balanced space use in this particular facility can be encouraged by making less-used enclosure parts more attractive with appropriate feeding and enrichment elements. Such evidence-based approaches will not only further improve zoo elephant husbandry, but continuously ensure elephant welfare in human care.

Keywords: GPS, locomotion, welfare, monitoring

Introduction

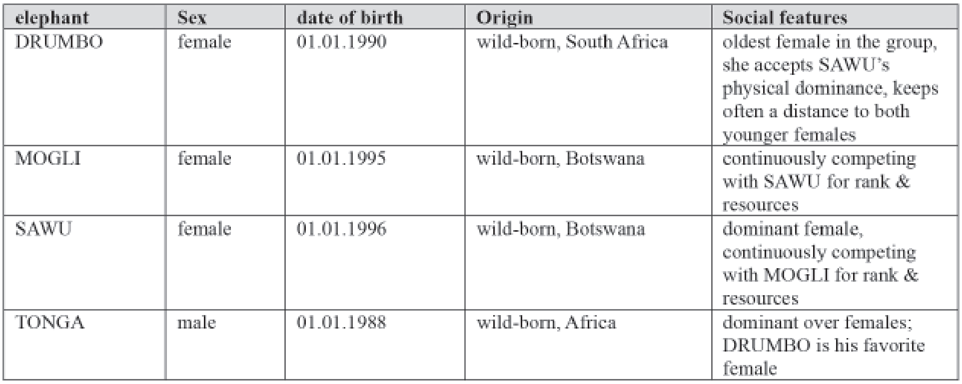
African elephants (*Loxodonta africana*) range across wide habitats in order to cover their dietary needs. Their home range heavily depends on the availability of water resources, plants to feed on and even mineral availability in their natural habitat (Weir, 1972; Douglas-Hamilton et al., 2005; Wall et al. 2006; Thomas et al., 2008; Wall et al., 2013; Sach et al., 2019; Sach et al., 2020). In addition, social aspects related to reproduction and the abundance of potential threats (e.g. predators or human-elephant conflict) impact the ranging pattern of the species (Douglas-Hamilton et al., 2005; Slotow et al., 2005; Ihwagi et al., 2024). In human care, elephants should ideally not be prone to any of these threats (Clauss & Schiffmann, 2022). At the same time, locomotion is crucial for their physical health, in particular regarding adequate foot wear, ideal body mass and body condition as well as their general musculoskeletal condition (Poole & Granli, 2008; Greco et al., 2016; Miller et al., 2016; Chusyd et al., 2021). In addition, only by a sufficient amount of daily walking activity it can be ensured that elephants in human care make use of their entire enclosure. Under zoo conditions, daily walking distances for African elephants have been reported in the range between 3.2 and 9.8 km (Reimers et al., 2001; Leighty et al., 2009; Rothwell et al., 2011; Miller et al., 2012; Rowell, 2014; Holdgate et al., 2016). In free-ranging African elephants average daily walking distances between 2.1 and 14.1 km have been observed (Guy, 1976; de Villiers & Kok, 1997; Slotow & van Dyk, 2004). Extreme distances up to nearly 30 km have been documented in free-ranging adult males (Rowell 2014).

This study pursued three distinct objectives: (I) The determination of the average daily walking distance of the elephants at Zoo Dresden as a parameter of physical activity and (II) a comparison of walking distances in the females in dependance of the presence of the adult male. According to the keepers’ impressions, it was hypothesized that the females express longer daily walking distances when they completely share the exhibit with the adult male, as compared to when the male is secluded overnight. As a third objective (III), we investigated the habitat use of the four elephants. And in doing so, we assessed whether the females show an altered habitat use during the male‘s presence.

Material and methods

This study covered a group of four (three females, one male) adult African elephants living at Zoo Dresden. At the time of the study, the females ranged between 28 and 33 years of age and were therefore in breeding age. The male was 35 years old and a proven breeder (Tab. 1). The elephant exhibit at Zoo Dresden consists of an outdoor yard measuring 3,000 m^2, outdoor paddocks of limited size for training and temporary separation and an indoor area of around 1,000 m^2 (Fig. 1). Both the indoor and outdoor areas have been extended during the past years (Brockmann, 2021). Across the entire exhibit, multiple feeding stations, natural substrates, a pool, mud wallows, sand piles, vertical tree trunks and additional enrichment items ensure a stimulating environment (Brockmann, 2021).

Tab. 1: Life history data and social features according to the keepers’ perception of the four African elephants living at Zoo Dresden.



elephant	Sex	date of birth	Origin	Social features
DRUMBO	female	01.01.1990	wild-born, South Africa	oldest female in the group, she accepts SAWU’s physical dominance, keeps often a distance to both younger females
MOGLI	female	01.01.1995	wild-born, Botswana	continuously competing with SAWU for rank & resources
SAWU	female	01.01.1996	wild-born, Botswana	dominant female, continuously competing with MOGLI for rank & resources
TONGA	male	01.01.1988	wild-born, Africa	dominant over females; DRUMBO is his favorite female

Data collection

Walking distances were recorded with GPS trackers designed for the use in companion animals with an online portal providing opportunities for data extraction (PAJ GPS Tracker, Allround Finder 2.0, PAJ GPS UG, Windeck-Hurst, Germany; https://v2.finder-portal.com/tabs/map). This approach has been proved functional in previous studies of zoo-kept African and Asian elephants (Miller et al., 2012; Holdgate et al., 2016; Linti, 2017). The trackers were incorporated in an anklet constructed of fire hoses and attached to the wrist at each elephant’s front limb after appropriate training (Fig. 2). The batteries of the GPS trackers required recharging every 3-4 days. Hence, the anklets needed to be taken off after three days of recording. Subsequently the batteries were charged for one day and afterwards attached with the anklets to the elephants again.

In order to assess the impact of the males’ presence on the daily walking distances, we applied an A-B-A-B study design. In doing so, we intended to measure the distances under baseline (male absent – condition A) and treatment (male present – condition B) conditions. According to the elephant husbandry program at Zoo Dresden, the dominant male is usually unrestrictedly sharing the habitat with the females. Due to management reasons the dominant male can be separated for the nighttime, which was common practice during the introduction phase after his arrival at Zoo Dresden (pers. comm. R. Moche). Therefore, all individuals are used to this kind of temporary separation. Given this situation, we defined condition A (male absent) as days when the male spent the daytime hours (7.00 am – 4.00 pm) with the female group but was separated in the indoor exhibit for the night (4.00 pm – 7.00 am). In contrast, the male remained under condition B outdoors with the females for 24 hours without access to the indoor yard. With these definitions, we ensured that the three females had the identical space (namely the entire outdoor yard, see Fig. 1) available independent of the condition.

The corresponding observation periods were defined with eight days of recording each. All periods were planned to be conducted in summer 2023, with the aim to reduce any potential impact of ambient temperature and daylight hours. Food provision across the enclosure was kept constant during the entire study, irrespective of the presence of the male or weather conditions. With this protocol, a potential habituation effect could be considered in the data analysis, and environmental conditions (e.g. ambient temperature) were supposed to be as constant as possible due to the summer season. No significant changes in the feeding enrichment, the substrates or the training routine were undertaken during the course of the study.

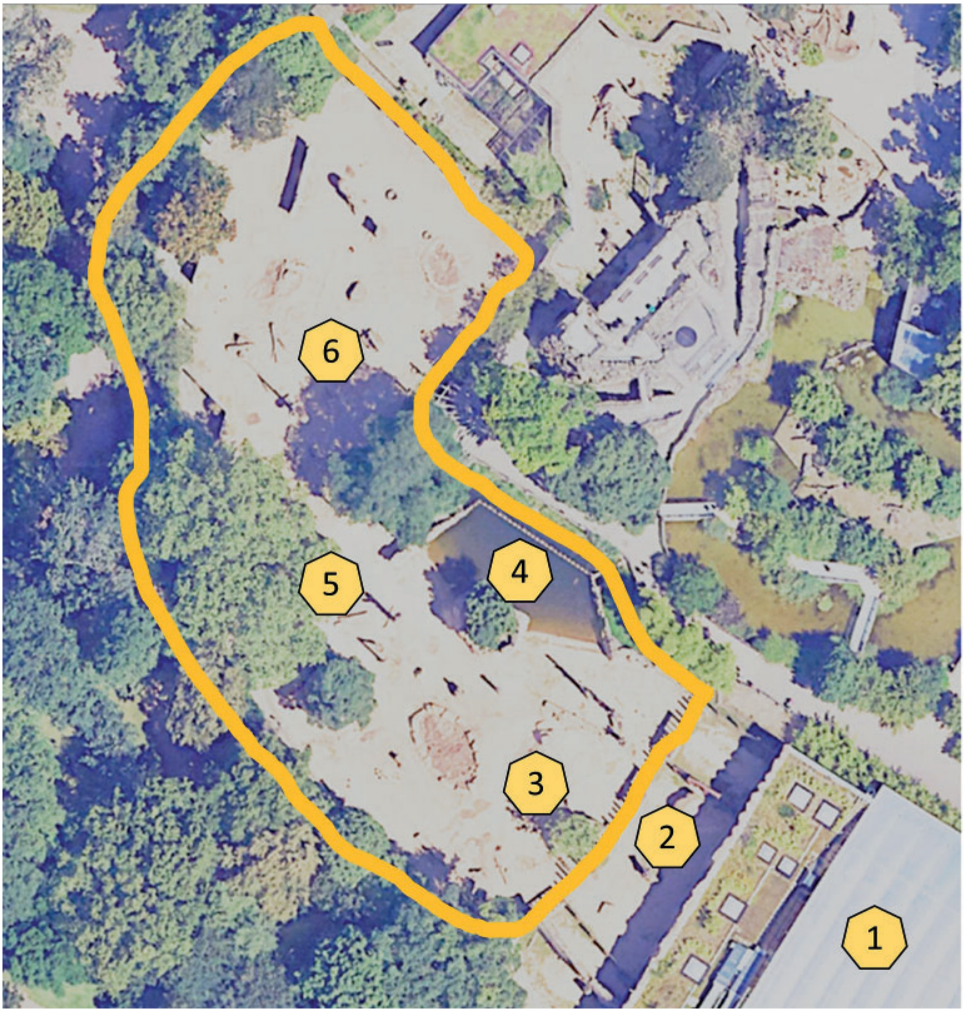


Fig. 1: Overview on the habitat with its major features. 1 – elephant house with indoor area, 2 – paddocks, 3 – mud wallow, sand pile and rubbing tree, 4 – pool, 5 – feeding station hay, 6 – top feeder. The orange line edges the entire outdoor yard available to the female group for 24 hours.

Statistical analysis

We assessed the distance travelled by the elephants during periods with or without presence of the dominant male using mixed-effects linear models, using R packages lmer and emmeans. The individual elephant was set as a random factor, the bull presence as a fixed factor, and the distance covered was the dependent variable; the normal distribution of the respective model residuals was confirmed with Shapiro-Wilk tests. This was performed for the whole 24-hour day as well as for those 15 hours only during which no keepers were present. The question

Fig. 2: The custom-made anklets made out of fire hoses and a physically protecting shed for the GPS tracker (a) and their position on the elephants wrist (b). Photos: Ronny Moche, Zoo Dresden)

whether there were significant differences in the distance walked between individual animals was assessed with a simple ANOVA and Tukey’s post hoc test for the entire observation period. The level of significance was set at $P < 0.05$.

Heat maps to determine habitat use

Based on the GPS data extracted from the commercial portal (https://v2.finder-portal.com/tabs/map), we were able to construct heat maps demonstrating the habitat use of the individual elephants. The heat maps were created using Excel®2016 (Microsoft®) on the basis of the GPS data with the wireframe contour diagram type. To do this, the data was first organized in a matrix, with the rows (latitude) and columns (longitude) representing the x and y values and the cells within the matrix containing the corresponding z values (sum of all data points in the respective quadrant). The elephant enclosure was selected as the background image. The wireframe model is a three-dimensional representation that visualizes the relationship between three variables. The wireframe consists of a grid of lines representing the height values (z-values). The wireframe model helps to identify positions in the enclosure that are frequently visited by the individuals and thus allows conclusions to be drawn about habitat use.

Results

We determined the walking distance of the four elephants for a total of 107 complete 24 hour cycles. The distribution of these cycles with respect to the study periods is given in Table 2. In addition, we separately considered the 15 hour time span from 4.00 pm to 7.00am. In this time the keepers were not on site at the elephant facilities. This approach resulted in 115 recordings over the four periods (Tab. 3). The variability in recording day numbers between the periods was caused by inappropriate weather conditions or due to management reasons. In DRUMBO, one recording is missing in period 1 due to a low battery status of the GPS tracker.

Tab. 2: Number of the 24h recordings with respect to the study periods. In period 1 and 3 the male was present, while he was absent in period 2 and 4.

Walking distance 24h	N period 1	N period 2	N period 3	N period 4	N total
DRUMBO	4	9	10	3	26
MOGLI	5	9	10	3	27
SAWU	5	9	10	3	27
TONGA	5	9	10	3	27
Total	19	36	40	12	107

Tab. 3: Number of the 15h recordings (4.00 pm – 7.00 am) with respect to the study periods. In period 1 and 3 the male was present, while he was absent in period 2 and 4.

Walking distance 15h	N period 1	N period 2	N period 3	N period 4	N total
DRUMBO	5	10	10	3	28
MOGLI	6	10	10	3	29
SAWU	6	10	10	3	29
TONGA	6	10	10	3	29
Total	23	40	40	12	115

There were significant differences between the individual elephants in the distance covered (24h: $P = 0.001$; 15h: $P = 0.009$). Significant differences between individuals based on Tukey's post hoc test are indicated in Table 4 and 5; in both the 24 h and the 15 h periods, MOGLI moved significantly less than DRUMBO and SAWU, whereas DRUMBO and SAWU did not differ significantly. Although the average distance covered per hour was numerically lower during the 15 h period that included the night, these differences were in the magnitude of 15-43 m /h.

Tab. 4: Mean daily walking distances of the four elephants over the entire study (24 h-periods).

Walking distance 15h	N period 1	N period 2	N period 3	N period 4	N total
DRUMBO	5	10	10	3	28
MOGLI	6	10	10	3	29
SAWU	6	10	10	3	29
TONGA	6	10	10	3	29
Total	23	40	40	12	115

Elephants that do not share a superscript (A, B, C) differ significantly (Tukey's post hoc test, $P < 0.05$).

Tab. 5: Mean walking distances during the daily absence of the elephant keepers over the entire study (15 h-periods).

Covered distance in 15h [km]	DRUMBO	MOGLI	SAWU	TONGA
Mean	5.68^{A}	4.67^{B}	5.71^{A}	5.16^{AB}
standard deviation	1.02	0.98	1.57	1.58
km/h	0.38	0.31	0.38	0.34

Elephants that do not share a superscript (A, B, C) differ significantly (Tukey's post hoc test, $P < 0.05$).

For both the 24-hour day and the 15-hour period, the presence of the dominant male had a significant effect on the distance covered ($P < 0.001$ and $P = 0.001$, respectively) (Figs 3 and

S1). This pattern was also evident during the daytime hours with keepers present (Fig. S2). With the dominant male unrestrictedly sharing the exhibit with the females, all elephants covered less distance, with the respective marginal means being 8.48 (95% confidence interval: 7.16-9.80) km and 9.82 (8.53-11.12) km with and without the male during 24 h, and 4.94 (4.21-5.67) km and 5.74 (5.02-6.46) km with and without the male during the 15-h period.

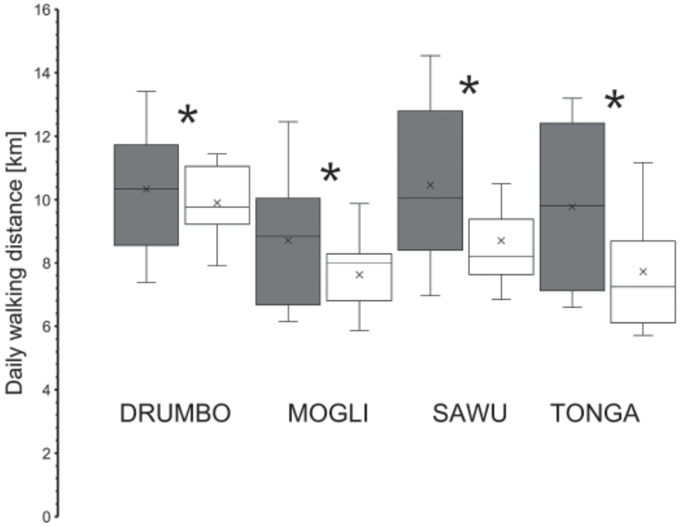


Fig. 3: Box plots demonstrating the walking distance for the four elephants over 24 hours with the male absent (grey bars) and present (white bars). All individuals (including the male) showed a decreased daily walking distance when the male was present in the group. The difference was significant (*) for every individual. Boxes extend from the first to third quartiles, with median indicated by a black line and mean by an "x". The fences extend to 1.5 times the interquartile range.

When investigating the daily walking distances over the course of the study, an increase between recording days 5 and 10 (21.07.2023-01.08.2023) with a distinct and stable decrease after day 10 is evident in all individuals (Fig. 4). This drop in daily walking distances was also evident when considering separately the time spans without (4.00 pm – 7.00 am) and with (7.00 am – 4.00 pm) keeper presence. In the oldest female DRUMBO the drop in daily walking distance was only slight, nonetheless her peak daily distances occurred between day 5 and 10 (Figs S3 and S4).

As a third objective, we investigated the habitat use of the four elephants. And in doing so, also visualized whether the females do show an altered habitat use pattern during the male`s presence. We made use of heat maps to demonstrate the habitat use in a descriptive fashion (Figs 5 and 6) and put this into relation to features of the various exhibit areas. Considering all individuals over all conditions, this qualitative approach revealed one major area of preference and one further area covered frequently (Fig. 5).

Comparing the habitat use of the individual female elephants, we found a consistent pattern in both conditions (Fig. 5). While all females shared their favorite spot adjacent to the paddocks, they seem to differ in the size of this area. The most dominant female SAWU covers a smaller area (Fig. 6c) than both sub-ordinate females do (Figs 6a, b). DRUMBO in her position as an outcast, covers the largest area of all of them (Fig. 6a). The most frequented areas of the

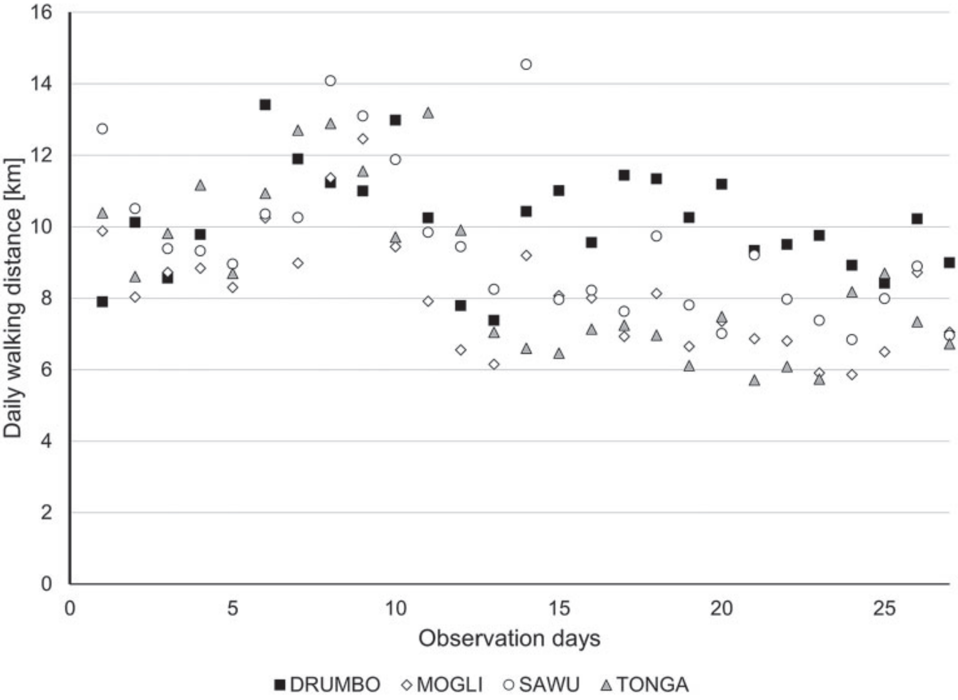


Fig. 4: Individual daily walking distances over the course of the study. Note the distinct decrease in all elephants at around day 10.

females seem to shrink in the absence of the male, an effect which seems to be most strongly pronounced in the two sub-ordinate females (Figs 6a, b). In addition, all females expressed an increased space use when the male was present (Fig. 6).

Discussion

The method applied here to determine daily walking distances has been shown to work in zoo elephants (Miller et al., 2012; Holdgate et al., 2016; Linti, 2017). The present study covers full 24 h-cycles, which has only been done by very few reports (Rowell, 2014), presumably due to the required work load for the elephant care staff and the reliable compliance of the individual elephants. Far more common, the daily walking rates have been extrapolated from measurements over several hours or a keeper working day (Rowell, 2014). We based our analysis exclusively on recordings of entire 24h cycles and hope this will ensure reliable results. With individual mean daily walking distances ranging from 8.10 to 10.10 km, the elephants at Dresden Zoo express walking activities in the upper level of what has been reported for zoo-kept African elephants so far (Leighty et al., 2009; Miller et al., 2012). Taking the average daily distances covered by zoo elephants in North America as comparison, the elephants at Zoo Dresden showed distinctly longer daily walking distances (Holdgate et al., 2016). Compared to data from free-ranging populations (2.10 – 14.10 kilometers/day), these values are in the mediate to upper range (Guy, 1976; de Villiers & Kok, 1997; Slotow & van Dyk, 2004; Rowell, 2014). It must be

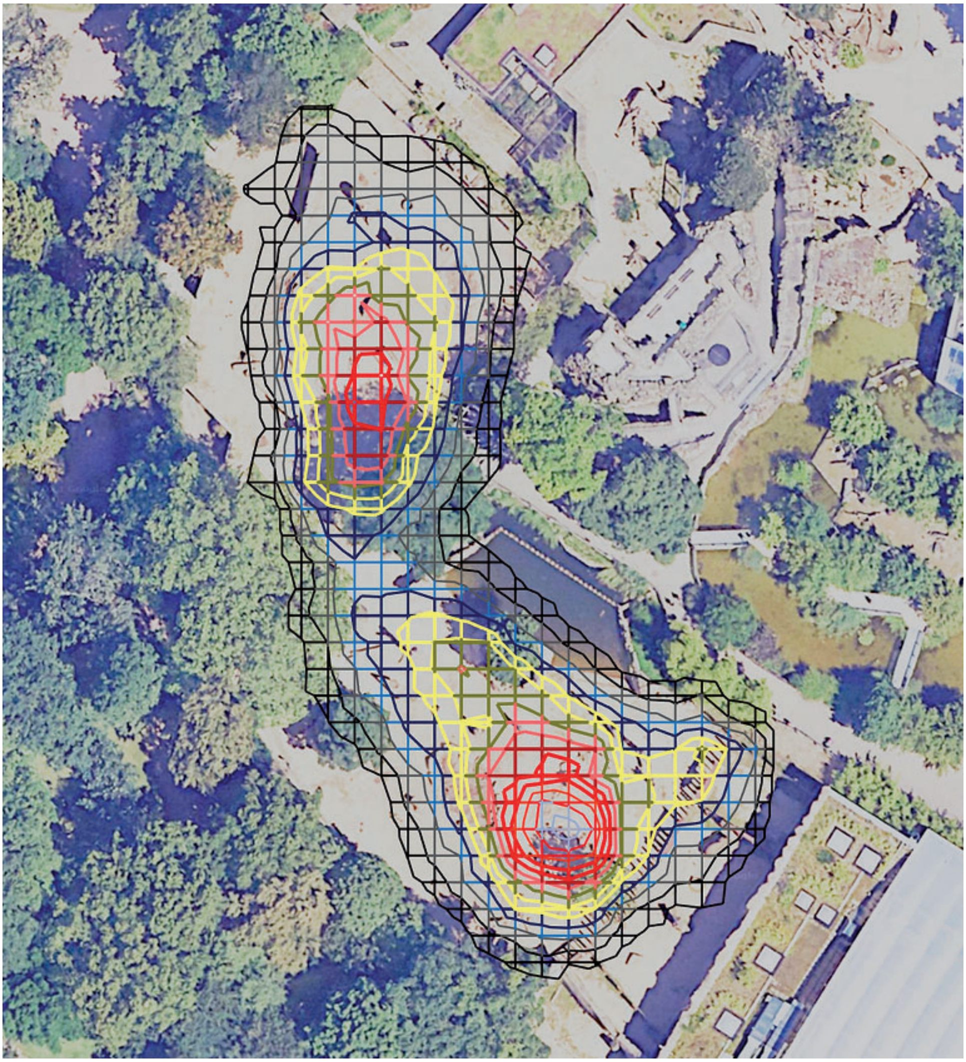


Fig. 5: Heat map for all individuals under all conditions. The more intense colors indicate a higher frequency for these locations.

emphasized that the walking distances of free-ranging elephants seem to vary enormously, leading to a huge range in the data reported so far. Considering the natural needs such as water, food and social partners as motivators for movement in free-ranging elephants (Thomas et al., 2008; Sach et al., 2019; Sach et al., 2020) as well as human impact on the available habitat (Wall et al., 2021), it only makes sense that the motivation to walk is far less variable under zoo conditions, where all these resources are constantly provided in a safe environment.

The female DRUMBO covered the largest daily distance, while MOGLI walked the least distance. By comparing their constitution and body condition, differences are obvious with DRUMBO being in the ideal range of body condition (BCS 5/9) and MOGLI significantly over-conditioned (BCS 7/9) (Fig. 7). Of course, this report can only provide limited evidence

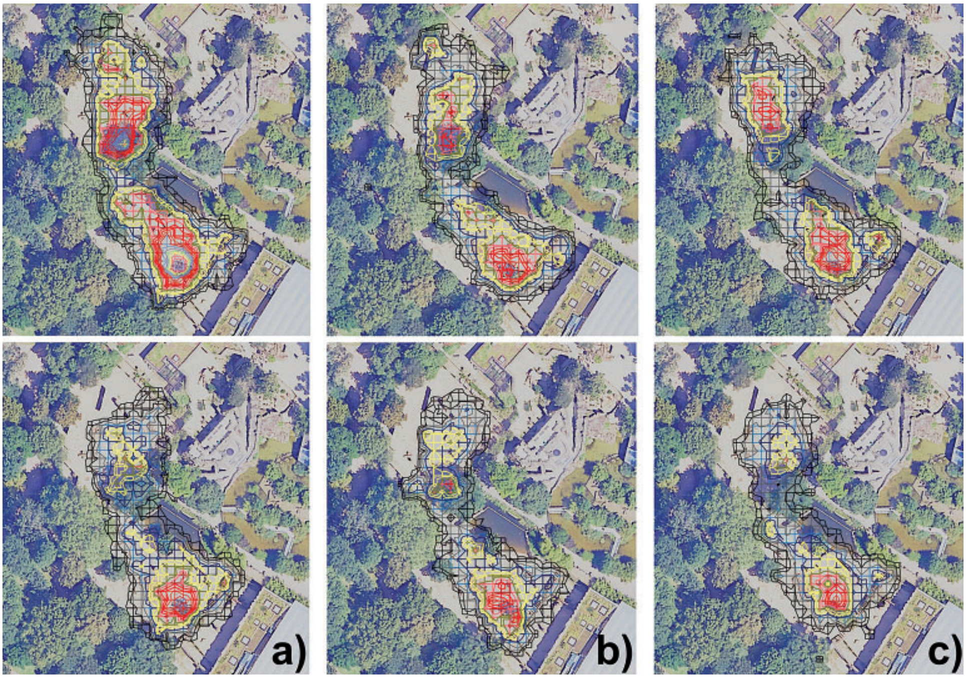


Fig. 6: Heat maps for the three females (columns a-c) when the male was present (upper row) in contrast to when he was absent (lower row). Note the reduced coverage of the exhibit in the lower row (male absent) in comparison to the coverage in the upper row (male present). a) female DRUMBO, b) female MOGLI, c) female SAWU.

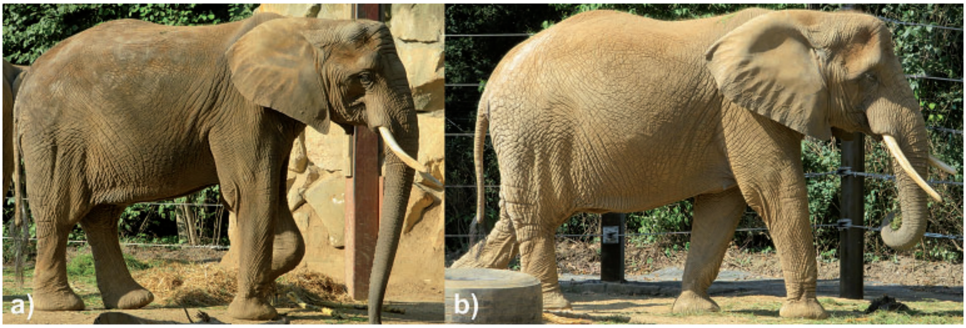


Fig. 7: The females DRUMBO (a) and MOGLI (b) in lateral profile. Note the difference in their body condition with DRUMBO in the ideal range (5/9) and MOGLI being overweight (7/9) according to Schiffmann et al. (2018). Mel dl p7Ol kkv J l ` eb) Wl l Adbpabk+

for a causative correlation between daily walking distance and physical condition. A previous report determined only a staff-directed walking exercise of at least 14 hours per week to reduce a zoo elephants risk for being over-conditioned (Morfeld et al., 2016). Whether this association can be transferred to voluntary walking activity would need to be further investigated.

The evaluation of the daily walking distances during the observation period shows higher daily walking distances covered in the first 10 observation days and then a general decrease after the

10th observation day (Fig. 4). At the same time the individuals walking the largest daily distance varied significantly before day 10. On the subsequent observation days, the female DRUMBO consistently walked the largest daily distances with only a few exceptions (Fig. 4). Based on the pattern observed in the admittedly limited time span of our recordings, we consider the walking distances after day 10 as baseline locomotion activity (Fig. 4). We can only speculate on the reasons for the distinct increase in walking activity between observation day 1 and 10. One explanation may be the females´ estrous cycles. The latter might not only increase the walking activity of the females as known for cattle (Kiddy 1977), but also increase the motivation of the male for being close to the receptive female. Assuming that the females at Zoo Dresden may at least temporarily show avoidance behavior towards the male, a chasing behavior of the male (although focused on only one female) may lead to an increased locomotion of the entire group. At Zoo Dresden, the three females are constantly monitored for their reproductive cycle by weekly urine analysis. Based on these data, we know that SAWU and MOGLI were in estrous between 8th of July and 2nd of August (corresponding with observation days 1-11), supporting this hypothesis. Given that the maximum daily walking distances by the male TONGA also occurred exactly in this time period (Fig. 4), this assumption appears plausible. We are not aware of any report already observing such a correlation between walking activity and reproductive cycle in female African elephants. Further research with data recording over several reproductive cycles would be required to elucidate this pattern. Such investigations might also reveal the potential of daily walking activity surveillance in reproductive cycle monitoring of zoo elephants, given that a less invasive recording method can be established (Brady et al., 2021).

In clear contrast to the assumption of the keepers, all individuals showed a significantly increased walking activity on days when the adult male was separated for the night (Fig. 3). Several aspects may explain this finding. The adult male is considered a dominant character, sometimes showing rather rough behavior towards the females (R. Moche, pers. obs.). This might have led to a restricted moving pattern of the females as an avoidance behavior. This is in line with the more extended habitat use we found in the heat maps on days with the male present for 24 hours (Fig. 6). Although not observed by the elephant keepers, one might think of a stereotypical pacing behavior in the male during the separation from the females, which might increase his walking distance. If this assumption was valid, we would expect an even more pronounced difference in the walking rates of the two conditions during the night. Checking for this in the 15-hour dataset, we found a less pronounced increase in the male (and also the females) during the nights separated compared to the complete 24h cycles (Fig. S1). Therefore, we consider this hypothesis invalid. In addition to the more extended habitat use under the male's presence, the heat maps demonstrate a strong preference for one particular area of the habitat (Figs 5 and 6). Independent of the social constellation, all elephants seem to spend most of their time in a relatively small area close to the paddocks connecting the outdoor yard with the indoor area (Figs 1 and 5). Remarkably, no feeding station is located in this area. With a rubbing tree and a sand pile, this area provides opportunities for comfort behaviors of the elephants including an appropriate place to have recumbent rest at night. At the same time, the elephants will spend time in this area while waiting for access to the indoor area. Given that the indoor area means a shelter with food and positive experiences such as routine medical trainings, waiting for access may present an anticipatory behavior for the entire elephant group. If this should be the case, one should consider ways of providing free access to the indoor and outdoor area as often as possible. Ideally, this would lead to a more balanced habitat use and reduced anticipatory behavior as shown in previous research (Lucas & Stanyon, 2016; Schiffmann et al., 2019; Glaeser et al., 2021). A more balanced habitat use might be further encouraged by the installation of attractive experiences in the far end of the outdoor yard, such as an outdoor training wall or additional puzzle feeders. Furthermore, the heat maps for the three females reveal an inter-individual difference in their habitat use. While the oldest female with her role as an outcast (column a in Fig. 6) seems to be more flexible in her preferred area, both younger females showed a narrower area of preference. Under the assumption that this may be due to social tensions in this group of unrelated females, the mentioned options to encourage a more balanced exhibit use may become even more beneficial.

As usual in zoo research with a multitude of uncontrollable variables, this study contains several limitations. Going for a balanced A-B-A-B study design, we targeted a number of eight complete 24h recordings for each period. Due to inappropriate weather conditions not allowing the use of exhibit areas according to the study plan or management reasons, the recorded data were not as balanced as intended. Nevertheless, in total a nearly equivalent number of recordings for both conditions were reached (Tabs 2 and 3). Another limitation was the accuracy of GPS data. Although the measuring of walking distances by GPS has been reported as a practical approach in zoo elephants (Miller et al., 2012; Holdgate et al., 2016; Linti, 2017), we assume that the accuracy will have limitations. The latter might bias the absolute distances covered, but not the comparison between individuals. Due to the method of calculating walking distance from GPS coordinates, we do not assume stereotypical swaying to have an impact on the recordings. But we observed a shorter charging interval for the tracker in one female known to express significant swaying behavior. This aspect should be considered when conducting similar research.

In conclusion, we were able to determine the absolute daily walking distance in the African elephant group at Zoo Dresden. Ranging from 8.1 to 10.1 km, these distances are in the upper level compared to previous research in zoos and in the intermediate range of data reported for free-ranging individuals. Although activity levels do vary significantly between individuals, our current findings provide further support that also in exhibits of limited size, adequate walking activity can be reached in zoo elephants. The presence of a dominant male had a demonstrable impact on the space use and the walking activity in the females. Maximum space use has several beneficial aspects and should be encouraged in zoo housed elephants. To do so, a monitoring of the exhibit use before and after introduced changes is recommended.

Acknowledgements

Our special thanks go to the entire elephant team at Zoo Dresden. Without their dedication and perseverance, it would never have been possible to gather a such complete set of data over an extended period.

Zusammenfassung

In seinem natürlichen Habitat legt der Afrikanische Elefant täglich erhebliche Strecken zurück, um Zugang zu ausreichend Futter und Wasser zu haben. Um diese natürliche Laufaktivität auch bei der Haltung in Menschenhand zu ermöglichen, bemühen sich zahlreiche moderne Haltungsstätten um die Erweiterung ihrer Elefantenanlagen. Eine entsprechende bauliche Optimierung wurde im Zoo Dresden für die dort lebenden 1,3 Afrikanischen Elefanten realisiert. Zur Untersuchung der tatsächlichen Anlagennutzung durch die Elefanten bietet sich die Messung der täglichen Laufdistanzen an. Solche Messungen konnten wir durch Anbringen eines GPS-Trackers am Carpalgelenk der Elefanten erreichen, womit wir für insgesamt 107 Tage Daten aufzeichnen konnten. Dies geschah unter zwei verschiedenen Bedingungen. Nämlich mit

dem adulten Bullen in der Kuhgruppe während 24 Stunden, oder bei dessen Separierung für die Nacht. Die von uns gemessenen täglichen Laufdistanzen zwischen 8,1 und 10,1 km befinden sich im oberen Bereich der bisher für Zooelefanten ermittelten Daten. Im Vergleich zu Daten aus dem Freiland bewegen sich die Werte im mittleren Bereich. Bei ganztägiger Anwesenheit des Bullen wiesen alle Elefantenkühe geringere Laufstrecken auf, nutzten jedoch größere Bereiche der Anlage. Wir schließen daraus, dass die soziale Konstellation einen bedeutsamen Einfluss auf die Laufaktivität Afrikanischer Elefanten im Zoo haben kann. Durch Aufwertung wenig attraktiver Bereiche des Geheges zum Beispiel mittels weiterer Futterstellen und Beschäftigungsmöglichkeiten könnte vermutlich eine ausgeglichenere Nutzung der gesamten Anlage gefördert werden. Untersuchungen zum Verhalten der Elefanten in menschlicher Obhut und dem Einfluss moderner Managementstrategien, sind maßgeblich für die Weiterentwicklung der Elefantenhaltung und sichern das Wohlbefinden dieser Tierriesen in zoologischen Einrichtungen.

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The First Behavioural Survey of ex-situ Bengal Floricans (*Houbaropsis bengalensis blandini*)

Die erste Verhaltensbeobachtung bei ex-situ gehaltenen Bengaltrappen (*Houbaropsis bengalensis blandini*)

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Abstract

The Bengal florican (*Houbaropsis bengalensis*) is the rarest member of the bustard order Otidiformes and is classified as Critically Endangered by the IUCN. The Southeast Asian subspecies, *Houbaropsis bengalensis blandini*, only occurs in Cambodia, where it inhabits seasonally inundated floodplains of the Northern Tonle Sap protected landscape during the breeding season, and migrates to transitional woodlands outside the breeding season. The species has a declining population due to habitat destruction. Serving as both a flagship and umbrella species, understanding Bengal florican behaviour is crucial for the development of biodiversity conservation strategies for the species in both captivity and in the wild. The study was carried out over ten days during the non-breeding season at the ex-situ facility, the Angkor Centre for Conservation and Biodiversity, in Cambodia. The three focal birds included two habituated males, one adult and one juvenile, and one unhabituated adult female. The variables recorded were bird activity, time of day, presence of disturbances, presence of other animal vocalizations, location of bird in its enclosure, the distance of bird to a conspecific, the distance of bird to the researcher, and if the bird gaze was directed at the researcher. The majority of behaviours performed by all focal individuals was sitting (23.3%), standing (41.1%), or walking (23.9%). More rare behaviours included preening (3.7%), foraging (0.8%), crouching (0.4%), stretching (0.5%), or

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trotting (0.4%). A linear regression found correlations between Bengal florican behaviour and time, behaviour and humidity, and behaviour and external disturbances.

Keywords: Bengal florican, Cambodia, ex-situ, activity budget, behavioural survey, ethogram

Introduction

The Bengal florican (*Houbaropsis bengalensis*) (Figs 1a, b) is the only bustard taxon in Southeast Asia (Packman, 2011) and is the rarest member of the bustard order, Otidiformes. The total global population for this species is tentatively placed at fewer than 1000 mature individuals (Baral et al., 2020). The species is classified by the IUCN as Critically Endangered and listed as Appendix 1 in CITES (BirdLife International, 2018). It is unknown how many individuals of *H. bengalensis bengalensis* remain in India but less than 100 remain in Nepal (Baral et al., 2020). All Bengal floricans are mainly confined to established protected areas, including the sub-species found in Cambodia (*Houbaropsis bengalensis blandini*) of which there is an estimate of 432 (Packman et al., 2014), although the numbers are believed to have increased slightly since the 2014 study due to conservation efforts and/or improved techniques of assessment.

Fig. 1a: Young male. Photo: ACCB/Maria Blümm

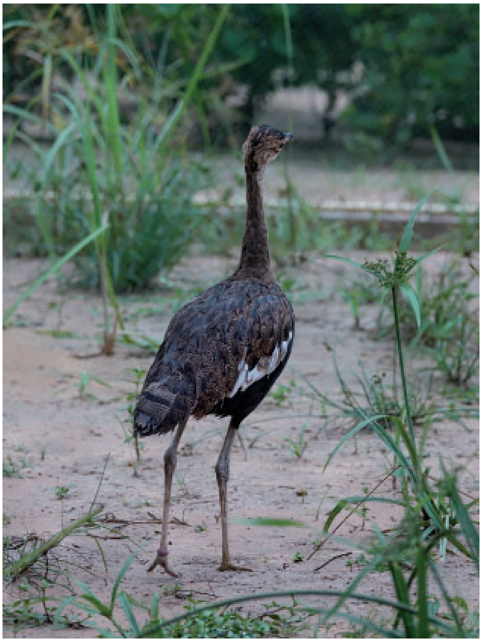

Fig. 1b: Adult male. Photo: ACCB/Pau Puigcerver

Occupying habitat at or near floodplains of the Northern Tonle Sap Protected Area (NTSPA) and restricted to habitats of low-land and seasonally inundated grasslands during their breeding season (Gray et al., 2009a), *H. bengalensis blandini* require large expanses of land to carry out lek-breeding behaviour and exaggerated displays of movement (Gray et al., 2009b). They are known to seek alternative sites if grassland decreases in size to less than

25 km^2 (Mahood, 2019a). During monsoonal rain periods, they often migrate to open deciduous dipterocarp forests beyond the floodplains and return to grasslands when the area is less flooded for their breeding season (Packman et al., 2013).

The improper management of the grassland on the Tonle Sap Lake through slash-and-burn fires and unsustainable grassland modification for rice cultivation has caused a rapid decline of their habitat, resulting in the near extinction of this species (Mahood, 2019a). This contradicts earlier findings by Jha et al. (2018) who claimed that effects of human disturbance are weak and that annual burning before march is important in maintaining suitable habitat for the species. The increase in human development, such as the construction of hydroelectric dams, irrigation systems, and the allocation of concessions, has also caused a decrease in this population (Packman et al., 2013). In other countries where the species occurs, domesticated and feral dogs, and poachers are also high on the list of threats (Baral et al., 2020). This is likely due to female nesting habits within the grassland increasing their vulnerability to habitat changes and predators (Chakdar et al., 2021), although it is unknown if these are a threat to the subspecies in Cambodia. Other threats include poachers that use snare traps to capture females that are guarding their nests in order to collect their eggs, resulting in lower populations of females and juveniles in the wild. Males are also hunted to sell or for bushmeat (Gray et al., 2009a), and eggs may be accidentally trampled by other animals (Gadhvi, 2003). It is estimated that population numbers have dramatically dropped from 461 individuals between 2005 and 2007 to 143 individuals in 2018 (Gray et al., 2009; Mahood et al., 2019a). Packman et al. (2013) highlighted the urgency of the situation, alerting that if this rate continued the species would be extinct by 2023. Thankfully, with in-situ conservation strategies in place, the overall population estimation across the NTSPA reached 551 individuals in 2021, with the Baray Bengal Florican Conservation Area (BFCA) and its wider area supporting the largest population (WCS, unpublished data, 2022). Numbers are stable at both the Stoung-Chikreng and Baray BFCAs, suggesting that the conservation activities conducted are stabilizing florican numbers at those sites.

Conservation of the Bengal florican should be a priority due to its role as a flagship for grassland habitats (Baral et al., 2020). They provide a vital example of the impacts of human disturbances on wildlife. Their Critically Endangered classification and EDGE score of 5.80 can serve as a marketing technique to inspire locals and authorities to prioritize this species (Mahood et al., 2019b). Through direct conservation efforts and funding for the Bengal florican habitat, other endemic bird species will benefit (Baral et al., 2020), such as the sarus crane (*Grus antigone*) (Ibbett et al., 2019). Man-made replication of their habitat is difficult because Bengal floricans require a specific niche to survive; therefore, emphasis on the conservation of what remains of the natural grasslands is crucial (Sinhas et al., 2012). Bengal floricans feed on various insects and plants, including grasshoppers, beetles, centipedes, worms, leaves, and berries (Bhardwaj et al., 2011), and their extinction may impact the various trophic interactions of these organisms.

Since the early 2000s, the Tonle Sap floodplain grasslands have gained interest from international and regional conservation organizations, such as the Wildlife Conservation Society (WCS), the World Wildlife Fund (WWF), and Fauna & Flora. Partnerships with organizations, authorities and locals have developed monitoring and conservation programs to protect the local biodiversity of the area (Arias et al., 2013). The Ministry of Environment (MoE) and WCS are currently employing rangers as a means of avian conservation enforcement, where local people are hired to patrol the floodplains on Tonle Sap Lake to limit illegal activity. They also conduct population and nest counts of several other bird species to foster research and conservation efforts (Moreto et al., 2019). In 2008 and 2009, training and education programs took place in 71 villages to increase awareness about the importance of preserving biodiversity. In 2023 eight community awareness-raising activities focusing on Bengal florican conservation, eco-tourism, and climate change and global warming were conducted at five primary schools around Stoung Bengal Florican Conservation Area, reaching 1320 students (WCS, unpublished, 2023). Villagers continue to receive training and financial rewards for reporting nests to support patrolling and effective guarding of viable nests. By taking the initiative, personal motivation for protecting local bird populations increased, which decreased poaching incidences (BirdLife International, 2018).

Furthermore, in 2008, MoE, WCS, BirdLife International and local governments created Bengal Florican Conservation Areas (BFCAs) that designated 173 km^2 of breeding habitats and 138 km^2 of non-breeding habitat. A ministerial Sub-Decree to protect the Bakan grassland, south of the Tonle Sap, was implemented in 2023. These protected areas, along with regular patrols, satellite monitoring (BirdLife International, 2018), and regulations forbidding bird hunting and developments, aim to decrease human and habitat disturbance conflicts that threaten Bengal floricans (Ibbett et al., 2019).

However, the increase in regulations, enforcement, and protected areas restricts land use for people to have farms, mainly dry-season rice cultivation. This negatively impacts their livelihoods and potential to earn an income, which hinders conservation efforts (Ibbett et al., 2019). There is also significant hunting for various bird species on the Tonle Sap for bush meat, and it is predicted that hunting of Bengal floricans is mainly opportunistic and serves as a dietary component for locals. However, mitigation of hunting is made difficult when communities rely on the local birds for food or to sell (Ibbett et al., 2019).

Ex-situ conservation programs are essential for populations declining at fast rates and facing extinction. They protect vulnerable species from predators and human conflicts, allowing for more effective habitat conservation efforts, such as legislation and enforcement, to rebuild their habitat. Programs can provide various management and procedural strategies, along with close-range research of behavioural activities and habitat preferences that can be used for in-situ conservation (Rose, 2021). Activity budgets are used as a reference to understand the behaviours of species that increase their capacity to survive in changing environments. Influences on bird activity include food availability, temperature, and reproduction (Koladiya et al., 2012). The patterns recorded can give insight into sex-specific behaviours, the effect of disturbances, and correlations between activities (Ross & Deeming, 1998).

Early in 2019, Angkor Centre for Conservation and Biodiversity (ACCB), (WCS), and relevant government stakeholders conducted an ex-situ feasibility assessment for Bengal floricans, following the IUCN Species Survival Commission guidelines on the use of ex-situ management for species conservation (IUCN/SSC, 2014). The assessments, supported by long-term in-situ monitoring data, computer models, and personal experiences, concluded that an ex-situ conservation breeding program has a high chance of success to contribute towards the survival of the Southeast Asian subspecies of Bengal florican (Mahood et al., 2019a, b, 2021). This conservation breeding program was established in 2019 and and by February 2024 the global insurance population consists of thirteen individuals, all housed at ACCB. Of this, nine individuals have been successfully incubated and reared at ACCB after the eggs were obtained from the wild between 2019 and 2023.

Understanding Bengal florican behaviour will contribute to developing a successful species-specific reintroduction program once the ex-situ insurance population is viable and threats to their habitat are reduced. Although the study was focused on Bengal floricans under human care, it will create consistent and specific data that will produce a control survey of non-breeding behaviours that can be referred to by future researchers. Also, by understanding their behavioural patterns conservationists can work with locals to mitigate livelihood and conservation issues. These behaviours can also indicate welfare in captivity and be used to create an ethical foundation for other ex-situ programs of Bengal floricans.

Methods

This study took place at the Angkor Centre for Conservation and Biodiversity (ACCB), established in 2003 at the edge of Kbal Spean in the Phnom Kulen National Park (13.6783° N, 104.0259° E). It is a conservation center of the Allwetterzoo Münster in Germany developed to provide in-situ and ex-situ conservation support for Endangered and Critically Endangered turtle and bird species native to Cambodia.

Two male Bengal floricans (6 months old and ~ 3 years old) and one female (~ 3 years old) were selected as the focal species for the study based on advice from the ACCB team. Both males were habituated to humans and the female was not. These birds were selected to provide representative information on male and female behavioural characteristics, differences between adult and juvenile as well as habituated and unhabituated individuals.

All birds were housed in a breeding facility covering nearly 1,700 m^2 which included twenty-two interconnected individual aviaries and an enclosed building serving as an animal food preparation area and 'nursery' for egg incubation and chick rearing. A service path surrounding all enclosures allowed keeper and researcher access. The entire facility was enclosed, offering protection from the elements and predators. The focal species were housed in enclosures measuring 12x6 m and 3.5 m in height with a covered area to protect from the elements (Appendix I). Enclosures were visually divided into an overlaid grid to record position of the bird at each interval. If the focal bird entered the nursery it was recorded as out of sight. Only the habituated juvenile had access to this area. Natural vegetation native to floodplain grasslands was planted in the enclosures. The habituated adult male shared two different interconnected aviaries, next to the juvenile, accompanied by a non-focal unhabituated female. Breeding season for Bengal floricans begins in May (Packman et al., 2014), so no breeding behaviours were noted or analysed in this study, which took place in November. The focal unhabituated adult female was housed alone with other Bengal Floricans on two sides of her enclosure.

To date there is no literature on the general activity budget for Bengal floricans, in the wild or in captivity. Therefore, the activity budget of houbara bustard, a species similar to the Bengal florican, was used to create an ethogram for this study (Launay & Paillat, 1990). State and Event behaviours were recorded at two-minute intervals (Altmann, 1974) for 110 minutes twice a day. Data was collected for ten days (14/11-20/11 and 22/11-25/11). Our study took place in November 2022, the beginning of the dry season. During week one, data was collected in the morning between 8:00 am – 12:00 pm. During week two data was collected during the afternoon between 1:00 pm – 05:00 pm. The birds were given ten minutes to adjust to the presence of the researchers before data collection commenced. Researchers were dressed in neutral colours (green, grey, brown) to blend with their surroundings. Behaviour was recorded by direct observation for the habituated adult and juvenile males. For the unhabituated female, a Sony handycam (model no. DCR-SR45E) was set up on a tripod and behaviour was recorded during playback.

A behavioural study conducted on adult houbara bustards provided illustrations of the resting, comfort, locomotion, feeding, social, and miscellaneous behaviour events we coded into our data sheet (Launay & Paillat, 1990). Being from the same family of bustards, it can be assumed that the behaviours may be similar. Observations of the following contextual variables were recorded every 30 minutes: temperature, humidity, and cloud cover. Observations of the following independent variables were recorded at two-minute intervals: time, presence of disturbances (e.g. keeper presence, loud car noises), presence of other species' vocalizations, zone in the enclosure, distance to conspecifics, distance to the observer, direction of the gaze of the bird (Appendix II). The activity, or behaviour, was the dependent variable.

A two-sample t-test was performed to determine if there was a significant difference in behaviour between the adult and juvenile males. SPSS software (version 26) was used to conduct correlation analyses between independent variables, and a linear regression analysis determined which independent variables were significantly correlated to behaviour. A time activity budget was then created to compare time spent performing the different behaviours, including resting, comfort, locomotion, foraging, social interaction, and miscellaneous behaviour patterns (Launay & Paillat, 1990). These were coded as follows: standing (ST), walking (WLK), sitting (SIT), crouching (CR), trotting (TR), pecking (PCK), foraging (FRG), preening (PRN), stretching (STR), and out of sight (OS).

Results

Adult and Juvenile Males

A two-sample t-test assuming equal variances found no significant difference in the activity budget for the juvenile (M=1.76, SD=0.92) and the adult (M=1.82, SD=0.88); (t(1698) = -1.259, p = 0.208). Therefore, their behaviours were collated for further analysis. The adult and juvenile spent approximately 41% of their time standing, 24% walking, and 23% sitting. The "other" category represents 3% of the time pecking, 1% of the time foraging, and 1% of the time stretching, with a <1% of the time crouching (n=7) or trotting (n=7) (Fig. 2).

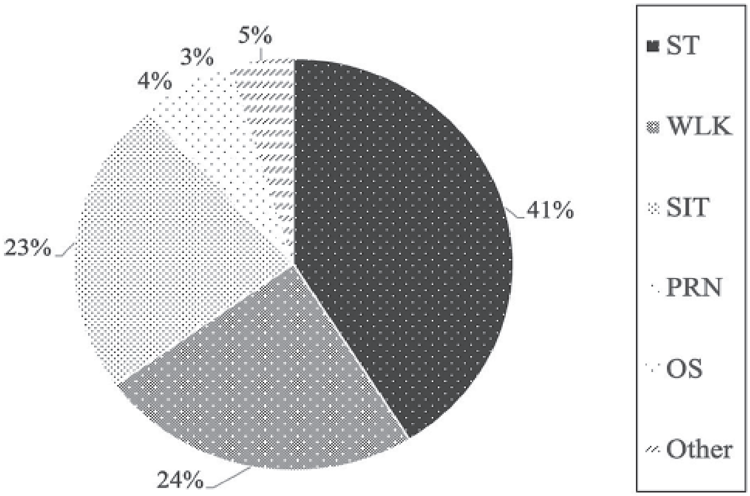

Fig. 2: Percentages of time of specific behaviours of male adult and juvenile Bengal floricans at ACCB, Nov 2022.

A Pearson correlation assessed the relationship between independent variables (time, temperature, humidity, presence of disturbances, presence of vocalizations of other species, proximity to conspecifics, and proximity to observer). Time was significantly correlated with temperature and humidity, as well as the presence of disturbances, proximity to conspecifics, and proximity to observers. The linear regression determined that time of day was significantly correlated with behaviour (F(7, 1742)=19.181, p=.000) (Fig. 3).

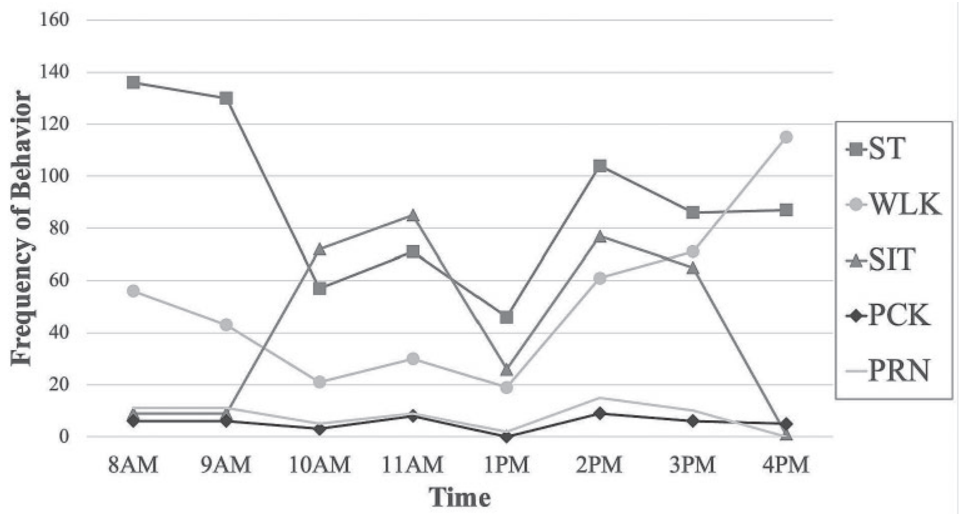

Fig. 3: The effect of time on the frequency of a behaviour of male adult and juvenile Bengal floricans at ACCB, Nov 2022. Standing (ST), walking (WLK), sitting (SIT), pecking (PCK), and preening (PRN) are shown.

Humidity levels were also significantly correlated with behaviour (F(7, 1742)=19.181, p=.033) (Fig. 4).

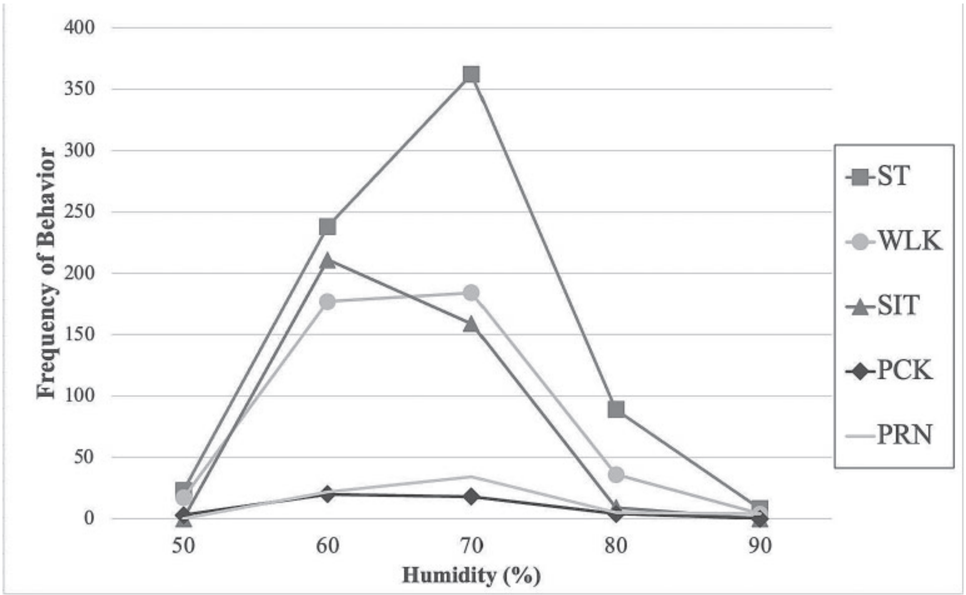

Fig. 4: The effect of humidity on occurrence of behaviour from adult and juvenile male Bengal floricans at ACCB, Nov 2022. Standing (ST), walking (WLK), sitting (SIT), pecking (PCK), and preening (PRN) illustrate the significant correlation between humidity and these behaviours.

The presence of external disturbances had a significant correlation with behaviour (F(7, 1742)=19.181, p=.000) (Fig. 5).

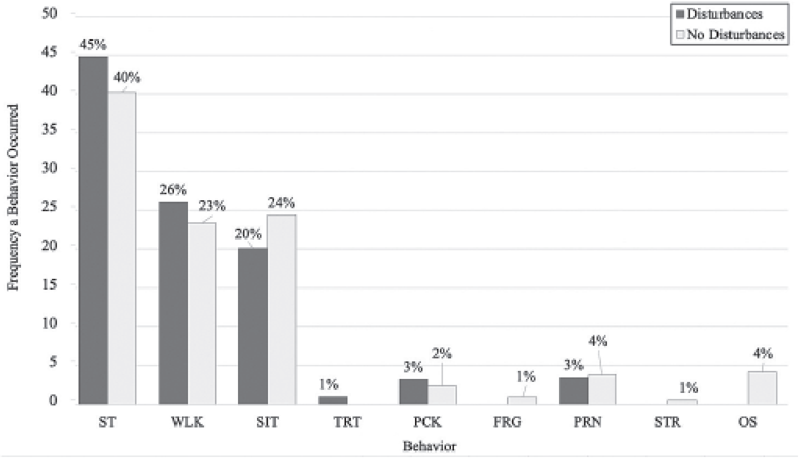

Fig. 5: The correlation of external disturbances and behaviour on male adult and juvenile Bengal floricans at ACCB, Nov 2022. Standing (ST), walking (WLK), sitting (SIT), trotting (TRT), pecking (PCK), foraging (FRG), preening (PRN), stretching (STR), and out of sight (OS). Percentages of behaviour observed with no disturbances compared to when a disturbance was recorded.

The presence of vocalizations of other species' also had a significant correlation to behaviour (F(7, 1742)=19.181, p=.000) (Fig. 6).

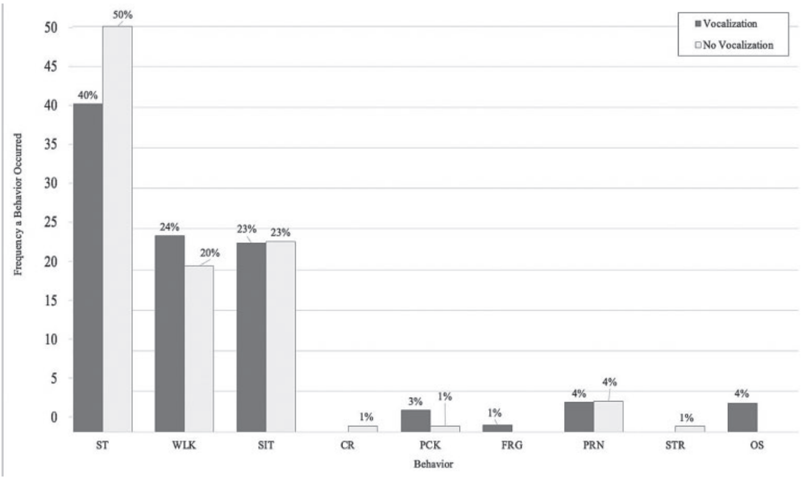

Fig. 6: The effect of vocalizations (of other species) on behaviour of male adult and juvenile Bengal floricans at ACCB, Nov 2022. Standing (ST), walking (WLK), sitting (SIT), trotting (TRT), pecking (PCK), foraging (FRG), preening (PRN), stretching (STR), and out of sight (OS). Percentages of time exhibiting behaviour when no external vocalizations are present compared to when an external vocalization was noted.

Unhabituated Female

Due to being unable to quantify independent variables (Appendix II) from replay of the video recordings, the unhabituated female activity budget was analysed separately from the male birds. Percentages of occurrence of behaviours observed were recorded. The female bird was out of sight for 47% of the data collection period. She spent 22% of the observable time walking, 20% of the observable time standing, and 11% of the observable time sitting. 0% of the time, the female was observed crouching or trotting (Fig. 7).

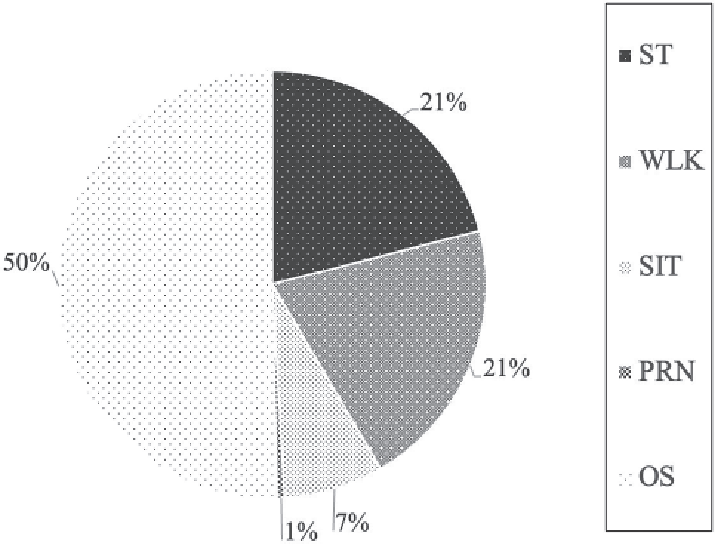

Fig. 7: Percentages of time displaying certain behaviours of unhabituated female Bengal florican at ACCB, Nov 2022. Standing (ST), walking (WLK), sitting (SIT), preening (PRN), and out of sight (OS) are shown.

Discussion

As there are no general behavioural studies of Bengal floricans, analyses of various avian species were used to interpret the behaviours exhibited during our observations; these included the kori bustard (*Ardeotis kori*) (Lichtenberg & Hallager, 2007), the great bustard (*Otis tarda*) (Martínez, 1999), the bridled white-eye (*Zosterops conspicillatus*) (Smith & Wassmer, 2016), the orange-chinned parakeets (*Brotogeris jugularis*) (Power, 1966), the houbara bustard (*Chlamydotis undulata macqueenii*) (Warren, 1996), the ground hornbill (*Bucorvus leadbeateri*) (Cooper & Jordan, 2013), and the northern bobwhite (*Colinus virginianus*) (Nuemann et al., 2022). Previous studies on various bird species interpreted that these behaviours were affected by factors including sex, age, and season (Martínez, 1999), along with variables associated with captivity, such as disturbances, enclosure size, and distance to other individuals. The main behaviours observed with the habituated adult male, habituated juvenile, and unhabituated female were standing (ST), sitting (SIT), walking (WLK), crouching (CR), preening (PRN), stretching (STR), foraging (FRG), and pecking (PCK). Also, behaviours that were not included in the statistical analysis due to a small sample size, but should be noted, were ruffling (RUF), flapping (FLP), trotting (TRT), jumping (JMP), and head-tilting (HD-TLT).

In a study of the kori bustard, it was found that standing, sitting, and crouching can be classified as comfort or resting behaviours. These behaviours are performed when the bird feels safe from predators and can rest (Lichtenberg & Hallager, 2007). Stretching, preening, foraging, and pecking occur in tandem with comfort behaviours, and all were noted in other bustard species as well as the Bengal floricans in this study. Stretching is often done after a long period of immobility (Ibid), and preening has been seen to be more common in males than females in a species similar to the Bengal florican, the great bustard (Martinez, 1999).

The bridled white-eye forages ants from the ground and plants within their enclosure because they are opportunistic foragers. They have been noted to peck repeatedly to eat or as a form of stereotypy in a captive environment (Smith & Wassmer, 2016). The Bengal floricans in our study exhibited foraging and pecking behaviour as well, but we cannot determine the target of their pecking. However, they have been observed by their keepers to peck at small stones, to aid in digestion, as well as invertebrates other than ants, such as worms, spiders and grasshoppers. Further studies are required to determine if the repeated pecking is a consequence of being in captivity and related to the onset of stereotypies or if this is a natural behaviour. The study of the captive ground hornbill showed that compared to wild ground hornbills, foraging was seen less often in captive individuals because they are given food rather than need to search for it (Cooper & Jordan, 2013). During our study period, feeding times were the same each day and the majority pecking recorded was when they were eating from the designated food provided.

A study involving orange-chinned parakeets described the idea of rigid and watchful immobility where an individual would remain still, either standing or sitting, along with alert eyesight or vocalizations, as a response to fear. The researchers suspected that their presence had a significant impact on the amount of immobility that the birds exhibited (Power, 1966). This corresponds to the 35.4% of time spent in a stationary position with an alert response of both the adult and juvenile.

It was also noted during observations of the unhabituated female that she was out of sight (OS) from the researchers 45% of the time. It needs to be explored whether this was hiding behaviour as a response to fear or due to visibility issues from vegetation within the enclosure. The study of the houbara bustard described the common pattern of both female and male birds staying in the rear of their enclosures. The males tended to use more space, whereas the females typically hid in the back. This could be due to their need to feel secure and put distance between themselves and the observer or other threats (Warren, 1996). Although the statistical analysis proved that there was no correlation between behaviours and the distance to the observer, the individuals remained in the back portion of their enclosures, more than five meters away from the researchers. The female specifically would sit in the same bush in the back right of her enclosure for long periods. The habituated juvenile was raised as a chick in the nursery of his enclosure and likely feels secure there, which may explain why he spent 50.4% out of sight of his time in that section.

The Bengal floricans also spent a good portion of the time walking. The juvenile and adult males spent 25% of their total time walking and the female spent 22% of her time walking. These actions are typically used to move from one area to the next or to escape a predator (Power, 1966). The influences on crouching behaviour for the Bengal florican remain unknown. However, it is likely this is related to anti-predatory behaviour as seen in other ground dwelling birds such as pheasants (Rütting et al., 2007) and waterfowls (Atkins et al., 2019).

Behaviours that were observed but not included in the statistical analysis due to limited observations, or did not occur at the two-minute interval, were: ruffling, flapping, trotting, jumping, pacing, and tilted head position. Seen with the kori bustard, ruffling is done after preening (Lichtenberg & Hallager, 2007) and may be displayed during hot weather as a form of decreasing body temperature, sunbathing, to dry off after rain, or as a possible social behaviour (Launay & Paillat, 1990). Ruffling was observed only 0.2% of the time.

The kori bustard has been reported to trot, or run, as a means to get to another area faster than walking. They may also trot to escape predators (Lichtenberg & Hallager, 2007). Out of the five times trotting was observed with the Bengal floricans, all were by the habituated juvenile. Three out of the five had disturbances that occurred at the same time, possibly indicating that fear was the rationale behind trotting. Flapping both wings multiple times while standing, or in conjunction with jumping, may also be a response to predation or a surrounding fear (Dutra et al., 2016) but this display was not observed in this study.

Jumping was recorded by the habituated juvenile twice and the adult male once. Each jump was also in conjunction with flapping wings. There was no obvious connection to disturbances except for once when the habituated juvenile jumped because the keeper made a noise. Jumping has been seen as a way to catch flying insects in the wild (Power, 1966).

Pacing has also been prevalent in various captive bird species. The houbara bustard study indicates that pacing is a common form of a stereotypy (Warren, 1996) that results in walking repetitively along a route. Stereotypies, like pacing, occur when there is too little or too much stimulation, the restraints of natural behaviours, or feelings of fear (Smith & Wassmer, 2016). All three Bengal florican individuals were recorded to pace, typically along the fence line with an alert head position, at most for up to an hour without stopping. Repetitive actions may also be a sign of anticipatory behaviour. For example, in captivity animals are often fed at the same time each day; this behaviour may also be a result of anticipation to see the keeper or to be fed (Watters, 2014). Because this repetitive behaviour was recorded a significant amount of times during the study, more research is suggested to fully understand the reasoning behind it.

The alert behaviour was seen by the observers 41.1% of the time, indicating a possibility that this is either their natural rest posture or they have heightened alertness for a large portion of their activity budget. If the latter, this may have implications for long-term health and welfare. The alert posture in correspondence to a head tilt may give insight that they become more aware of their surroundings and possible predators by increasing their field of view. This posture was referenced as “skyward looking” in Lichtenberg & Hallager (2007) in their study on the kori bustard. It may also be a sign of the individual preparing to fly or flee, or in combination with a vocalization may be an attempt to communicate with others (Power, 1966). Further studies researching their visual and auditory abilities could be used to determine if a head tilt or skyward looking allows for better sight and hearing.

Although there was a correlation between temperature and humidity, temperature was not found to have a significant impact on behaviour, whereas humidity did. Possible reasons for this could be that the temperature only fluctuated a few degrees each day, whereas humidity was seen to have hourly changes. Most active behaviours occurred in the morning and late afternoon, and a lull of activity occurred around midday (Fig. 5). It was also found that between 31-32 °C and humidity higher than 70% there was a sharp decrease in activities. Despite this study lacking a clear understanding of why there were less frequent active behaviours that occurred around midday not driven by temperature but rather humidity, some assumptions can be made based on findings in other studies. The great bustard study observed that midday movements were less frequent due to the amount of sunlight and heat (Martínez, 1990). The northern bobwhite study also concluded that when the temperature rose, the bird became more sedentary

(Nuemann et al., 2022). Although there is no published literature on the impacts of humidity on avian behaviour, this study indicated that during the hottest and most humid climates the individuals remained standing or sitting, a total of 64.4% of the time, typically under bushes or in the shade. The Bengal floricans may use similar techniques as the northern bobwhite by finding refuge within their habitat to escape the heat (Nuemann et al., 2022). Exploring influence of humidity on florican behaviour is recommended.

In the ex-situ facility, other species were housed near the Bengal florican enclosure. It is typical for captive birds, especially highly sensitive individuals, to react severely to predators (Dutra et al., 2016). This study found a correlation between behaviour and the vocalizations of other species. Species that made vocalizations included birds of prey, pileated gibbons (*Hylobates pileatus)*, and smooth-coated otters (*Lutrogale perspicillata*). In the wild, birds are exposed to a variety of sounds that are natural to them. However, when these communications are replaced by vocalizations of foreign animals, it may create stress and lead to stereotypic behaviour (Williams et al., 2017). A study of saffron finches (*Sicalis flaveola*) noted that individuals had difficulty recognizing threats due to multiple generations living within captivity (Dutra et al., 2016). It is therefore a hopeful sign that the Bengal floricans in our study altered their behaviour when presented with vocalizations by potential threats.

The disturbances recorded during the study were categorized as any loud noise that was unnatural and not a vocalization by other species. It included traffic noise, keepers inside the enclosure talking or whistling, or other loud noises that occurred at the two-minute interval. Previous studies found that, depending on the severity of the disturbance, the individual's response will be limited. A study of various bird species determined that interference of noise, especially traffic, will limit the effectiveness of bird vocalizations and induce stress behaviours (Dooling & Popper, 2016). Research was also conducted on hornbills within a zoo that determined there was a significant change of behaviour when keepers or visitors were present. The birds typically became more alert and interested when humans were nearby. It highlighted that the response to the keeper was less than to visitors due to likely habituation (Rose et al., 2020). In the Bengal florican study, there were instances of behavioural changes around keepers and a possible correlation to disturbances made by the researchers.

Recommendations for Future Research

Conducting and analysing the first ethogram on Bengal floricans allows for more complex activity budgets to be created in the future, improving comprehension of their behaviour. It has also enabled a comparison of wild populations to determine how the species interact with their surroundings, if threats are present, and if management solutions are effective (Smith and Wassmer, 2016). Analysing behaviours also gives insight into welfare within captivity and provides a rationale for expanding enrichment (Padget, 2010).

Further research on this topic could include the creation of an ethogram in wild non-breeding Bengal floricans. It would be interesting to compare the behaviours of individuals that are not confined to an enclosure or face disturbances of traffic and researchers. Similar methods could also be used to create an ethogram of Bengal floricans during the breeding season, both in the wild and in captivity, to witness their lekking and social behaviour. An ethogram observing Bengal floricans over multiple seasons would allow for temporal variations to be recorded. This would clarify the confusing data on the impacts of humidity and analyse why temperature was found to have no correlation to behaviour.

There was also a behaviour observed that was not referred to in the publication from which we obtained the ethogram – the Skyward-Tilt. A future area of study could look further into this posture and determine what influences its occurrence. We also suggest future studies look into the visual or audible abilities of the Bengal florican which may aid us in understanding specific behaviours and postures.

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Zusammenfassung

Die Bengaltrappe (*Houbaropsis bengalensis*) ist das seltenste Mitglied der Ordnung Trappen (Otidiformes) und wird von der IUCN als vom Aussterben bedroht eingestuft. Die südostasiatische Unterart *Houbaropsis bengalensis blandini* kommt nur in Kambodscha vor, wo sie während der Brutzeit saisonal überschwemmte Auen der nördlichen Tonle-Sap-Schutzlandschaft bewohnt und außerhalb der Brutzeit in Übergangswälder abwandert. Aufgrund der Zerstörung des Lebensraums ist die Population der Art zurückgegangen. Da es sich sowohl um eine Flaggschiff- als auch um eine Schirmart handelt, ist das Verständnis des Verhaltens der Bengaltrappe von entscheidender Bedeutung für die Entwicklung von Strategien zum Schutz der Artenvielfalt sowohl in menschlicher Obhut als auch in der Wildbahn. Die Studie wurde über einen Zeitraum von zehn Tagen während der Nichtbrutzeit in der Ex-situ-Einrichtung, dem Angkor Center for Conservation and Biodiversity (ACCB) in Kambodscha, durchgeführt. Zu den drei Schwerpunktvögeln gehörten zwei habituierte Männchen, ein erwachsener und ein jugendlicher Vogel sowie ein nichthabituiertes erwachsenes Weibchen. Die aufgezeichneten Variablen waren Vogelaktivität, Tageszeit, Vorhandensein von Störungen, Vorhandensein anderer Tierlaute, Standort des Vogels in seinem Gehege, Abstand des Vogels zu einem Artgenossen, Abstand des Vogels zum Forscher und ob der Blick des Vogels auf den Forscher gerichtet war. Die meisten Verhaltensweisen aller Schwerpunktvögel waren Sitzen (23,3 %), Stehen (41,1 %) oder Gehen (23,9 %). Zu den selteneren Verhaltensweisen zählten Putzen (3,7 %), Nahrungssuche (0,8 %), Hocken (0,4 %), Strecken (0,5 %) oder Traben (0,4 %). Eine lineare Regression ergab Korrelationen zwischen dem Verhalten der Bengaltrappe und der Zeit, dem Verhalten und der Luftfeuchtigkeit sowie dem Verhalten und äußeren Störungen.

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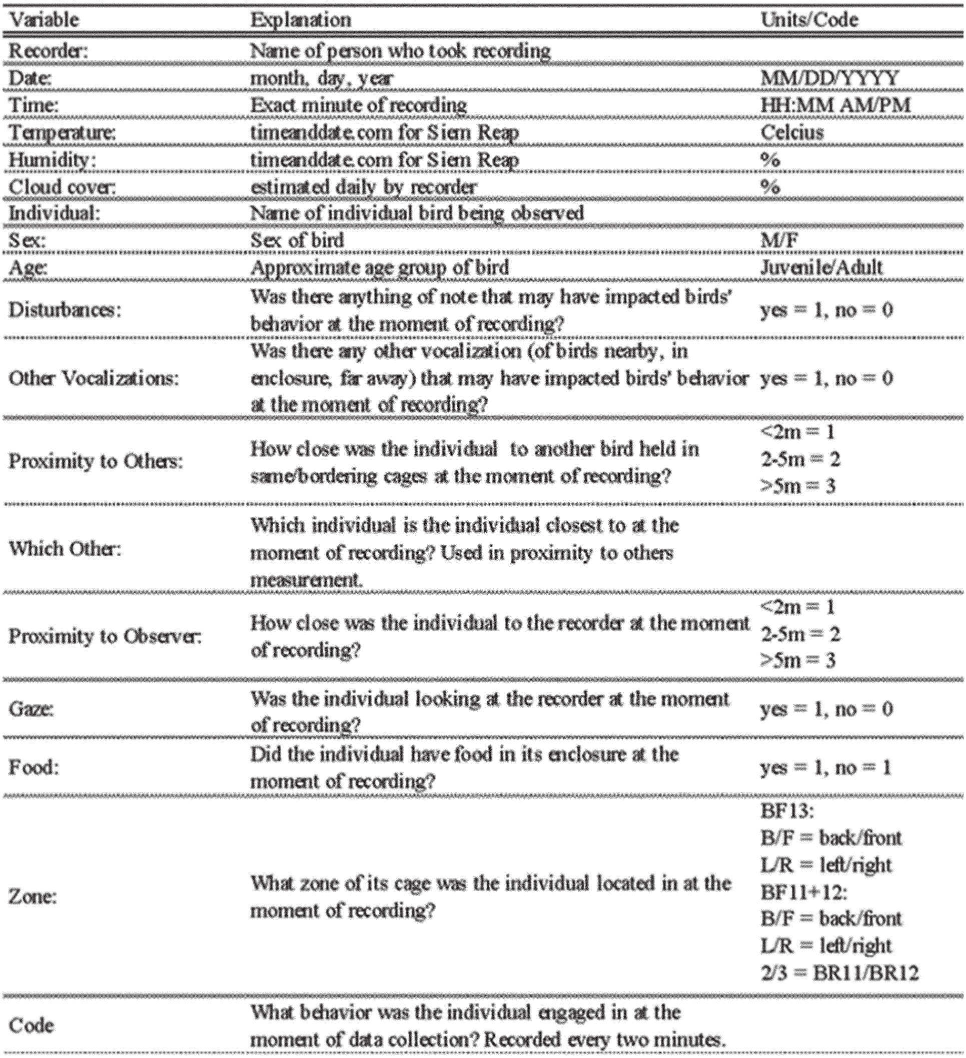
Appendix I

Appendix Ia: Layout of the Bengal florican enclosure at ACCB (ACCB, 2021).

Appendix Ib: Shelter within enclosures showing green tarps, or artificial hides (ACCB, 2022).

Appendix II.

Tab: 1: Description of independent variables measured.



Variable	Explanation	Units/Code
Recorder:	Name of person who took recording	
Date:	month, day, year	MM/DD/YYYY
Time:	Exact minute of recording	HH:MM AM/PM
Temperature:	timeanddate.com for Siem Reap	Celcius
Humidity:	timeanddate.com for Siem Reap	%
Cloud cover:	estimated daily by recorder	%
Individual:	Name of individual bird being observed	
Sex:	Sex of bird	M/F
Age:	Approximate age group of bird	Juvenile/Adult
Disturbances:	Was there anything of note that may have impacted birds' behavior at the moment of recording?	yes = 1, no = 0
Other Vocalizations:	Was there any other vocalization (of birds nearby, in enclosure, far away) that may have impacted birds' behavior at the moment of recording?	yes = 1, no = 0
Proximity to Others:	How close was the individual to another bird held in same/bordering cages at the moment of recording?	<2m = 1 2-5m = 2 >5m = 3
Which Other:	Which individual is the individual closest to at the moment of recording? Used in proximity to others measurement.	
Proximity to Observer:	How close was the individual to the recorder at the moment of recording?	<2m = 1 2-5m = 2 >5m = 3
Gaze:	Was the individual looking at the recorder at the moment of recording?	yes = 1, no = 0
Food:	Did the individual have food in its enclosure at the moment of recording?	yes = 1, no = 1
Zone:	What zone of its cage was the individual located in at the moment of recording?	BF13: B/F = back/front L/R = left/right BF11+12: B/F = back/front L/R = left/right 2/3 = BR11/BR12
Code	What behavior was the individual engaged in at the moment of data collection? Recorded every two minutes.	

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Taxonomy Goes Zoos: the Inevitable Relevance of Species Delimitation and Conservation Unit Recognition for Adequate *ex situ* Conservation Measures

Taxonomy goes Zoos: die unvermeidliche Bedeutung von Artabgrenzungen und der Anerkennung von Schutzeinheiten für angemessene *Ex-situ*-Erhaltungsmaßnahmen

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Abstract

The One Plan Approach to Conservation by the IUCN Conservation Planning Specialist Group (CPSG) proposes to combine in situ and *ex situ* conservation actions. However, the value of *ex situ* conservation programs run by respective zoos relies on sound scientific evidence of selected conservation units. Only when species and their geographic ranges are adequately defined, they can be properly protected. Accurate taxonomic information, based in particular on integrative analyses that combine several lines of evidence with the molecular assessments being among the most insightful, is not only important for proper identification of species or conservation units in zoo holdings but also for exclusion of hybrids from breeding programs. Molecular analyses, including phyloforensic research, are crucial for conservation units' delimitation and appropriate animal pairing and to prepare suitable restocking measures, to avoid artificial hybridization in conservation breeding facilities, releases in unsuitable regions, and genetic pollution. In this review, some topical vertebrate examples are provided to highlight the significance of sound taxonomy for subsequent conservation measures, including molecular diagnoses of independently evolving lineages for adequate One Plan Approach conservation practice.

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There is an underground conflict within the discipline of conservation biology between those interested to prevent populations from becoming too small to retain genetic diversity by adopting a more inclusive Evolutionary Significant Unit (ESU) definition and those that continue to highlight the need for an objective and evolutionary approach to ESU‘s delimitation even if this means having a greater number of conservation units with inevitably smaller ranges and a lower number of individuals (Zachos et al., 2013; Senn et al., 2014; Gippoliti et al., 2018; Gippoliti & Groves, 2020) and thus more prone to extinction. This is an ill-conceived scientific dilemma, as the study of biodiversity and delimitation of species are complex autonomous scientific issues that should be left unaffected from extra-scientific practical management problems (Dubois, 2003). At present there is also an extensive scientific debate around the species‘ concept which shall be applied, of which some conservationists and biologists seem unaware (cf. Zachos, 2016). The aforementioned visions collide when a distinct ESU established by a population geneticist is considered a distinct species by a taxonomist following an evolutionary species concept (Goldstein et al., 2000), the latter move being perceived as ‚anarchic‘ by some biologists (Garnett & Christidis, 2017). Therefore, conservation biologists and zoo managers should be prepared to coexist with taxonomic conflicts and scientific debates. Yet this seems not always the case at present.

This conflict may appear far and mostly ‚academic‘ in several fields of conservation biology, and specifically for in situ conservation as the apparent value of a protected area may not be changed if it protects a population labelled as *Ursus arctos* Linnaeus, 1758, *Ursus arctos isabellinus* Horsfield, 1826 or *Ursus isabellinus*, (but see Hazevoet, 1996; Gippoliti & Amori, 2012). However, the same certainly cannot be said when we are dealing with *ex situ* conservation in zoos and other dedicated facilities (van Bemmel, 1971; Dathe, 1978; Ziegler et al., 2015; Gippoliti, 2019). The following case examples reinforce that exchange and networking with taxonomists positively pave the way for improved One Plan Approach conservation.

A classical recent example originated from the IUCN/SSC Felid Specialist Group attempt to develop a consistent felid taxonomy as a basis for conservation efforts. The results presented by Kitchener et al. (2017) led to a severe contraction of the recognised tiger *Panthera tigris* (Linnaeus, 1758) subspecies. If this taxonomic contraction had been immediately accepted by the zoo community, it would have led to the dismissal of several coordinated *ex situ* breeding programs for tiger subspecies (Luo et al., 2010) if a subsequent study had not contradicted these results (Liu et al., 2018), confirming the validity (‚reality‘) of the classically accepted tiger subspecies. The same problem arises with the lumping of North China and Amur subspecies of leopards, *Panthera pardus japonensis* (Gray, 1862) and *P. pardus orientalis* (Schlegel, 1857) respectively, that could result in terminating the *ex situ* breeding program for the most threatened leopard taxon on Earth, the Amur leopard (Uphyrkina & O’Brien, 2003).

These extreme episodes demonstrate the critical importance of taxonomy, even because one of these subspecies, the Chinese tiger *Panthera tigris amoyensis* (Hilzhemier, 1905), exists only as an *ex situ* population. Although a single paper is often sufficient to terminate the validity of a taxon and thus deleting it from the conservation agenda, this needs extreme caution because synonymizations have frequently been subsequently reversed, for example when new datasets with new evidence were available. An example is the Northwestern African crocodile *Crocodylus suchus* E. Geoffroy, 1807, for long time hidden under the Nile crocodile *C. niloticus* (Laurenti, 1768), also in zoo collection holdings (Ziegler et al., 2015). Best studied species, such as tiger, may also be separated in a number of units for conservation (Hoelzel, 2023) but this extra-taxonomic option is precluded to most organisms at present.

Fig. 1: Amur leopard (*Panthera pardus orientalis*). Photo: S. Gippoliti

Fig. 2: Mhorr gazelle (*Nanger mhorr*). Photo: S. Gippoliti

Fig. 3: West African crocodile (*Crocodylus suchus*). Photo: A. Rauhaus

The simple fact that the number of currently recognised mammal species has grown to 6,495 compared to the 5,416 in 2005 – an increase of 1,079 species in about 13 years (Burgin et al., 2018); and in September 2024 the number raised at 6,753 (mammaldiversity.org) shows that increasing species number is a reality even for the most well-known taxonomic groups.

In general, careful consideration is recommended in the treatment of populations from different geographic lineages under *ex situ* conditions, in particular if different conservation breeding units or even taxa could be involved. Molecular analyses are thus crucial for separating different conservation units, carrying out proper population planning, and preparing suitable restocking measures to strengthen natural populations (Pohlová et al., 2014; Norman et al., 2018). A prominent example from herpetology is the Chinese softshell turtle *Pelodiscus sinensis* (Wiegmann, 1835) complex, a species listed as Vulnerable by the IUCN Red List and previously believed to be widespread, but now consisting of six species with smaller ranges and thus also being more threatened (Gong et al., 2021). Recently, a first conservation breeding program has been established for the taxonomically distinct conservation unit from northern Vietnam (Ziegler et al., 2020a). The black knobby newt *Tylototriton asperrimus* Unterstein, 1930 was also believed to be widespread and kept by both hobbyists and zoos, but now consists of a continuously growing number of micro-endemic species, that have to be dealt with independently (Bernardes et al., 2013).

This is in particular important taking the IUCN CPSG's One Plan Approach to Conservation into account, which combines *in situ* and *ex situ* conservation measures (Byers et al., 2013). In the Four-eyed turtle *Sacalia quadriocellata* (Siebenrock, 1903) several conservation units were identified recently applying a molecular analysis in a phylogeographical context. This is crucial on the one hand for building up adequate conservation breeding groups as suitable assurance colonies for later restocking measures to stabilize diminished natural populations. On the other hand, this knowledge helps to avoid genetic pollution by releasing individuals from confiscations in unsuitable populations and locations. Release in unsuitable regions could also lead to animal losses, if for example individuals from southern populations are transferred into the much cooler north during the winter time (Le et al., 2020). Such phyloforensic research also

Fig. 4: Four-eyed turtle (*Sacalia quadriocellata*). Photo: T. Ziegler

Fig. 5: Vietnamese crocodile lizard (*Shinisaurus crocodilurus vietnamensis*). Photo: T. Ziegler

has recently been performed for the water monitor lizard *Varanus salvator* species complex (Welton et al., 2013) and the crocodile lizard *Shinisaurus crocodilurus* Ahl, 1930, which were revealed to consist respectively of several taxa and conservation units. Genetic screening of zoo stocks was crucial to allocate held individuals to respective lineages (Ngo et al., 2020). Molecular analyses helped to allocate individuals to populations and geographic lineages, to identify hybrids and care for proper species identification and zoogeographical allocation. A recent example from ichthyology is the Malagasy rainbowfish *Bedotia madagascariensis* Regan, 1903, which was previously misidentified in European zoo holdings as *B. geayi* Pellegrin, 1907 until molecular identification took place (Ziegler et al., 2020b).

The mixing of different lineages or subspecies, as in the case of *Nanger dama* (Pallas, 1766), the dama gazelle (Senn et al., 2014), with the subspecies *Nanger dama mhorr* (Bennett, 1833) having a very small number of founders, must be carefully considered. It only seems to be justified, when total extinction of a taxon has to be prevented. Scientific evidence about the original genetic population structure, its origin and adaptive significance is crucial here, but often lacking (Thakur et al., 2018; Schreiber et al., 2018; Schreiber, 2022). For comparison, it is interesting to note that despite a long history of scientific debate whether the red wolf *Canis rufus* Audubon et Bachman, 1851, viz. was a true species or rather hybrids between coyotes and wolves (National Academies of Sciences, Engineering, and Medicine, 2019), the US Fish and Wildlife Service continues to support *ex situ* efforts and new reintroduction has recently taken place (Hinton et al., 2013; Gese et al., 2015).

Maintaining viable *ex situ* populations is at present one of the most important goal of modern zoological gardens (Robovský et al., 2020). Although greater emphasis is directed toward genetic and demographic goals, the value of these *ex situ* programs relies on the soundness of selected conservation units. As the recent case of the Chinese giant salamanders (genus *Andrias* Tschudi, 1837) highlights, breeding and releasing individuals without the due care of the taxonomic reality may exacerbate problems rather than being a solution (Yan et al., 2018). Formerly believed monotypic with a unique species, *Andrias davidianus* (Blanchard, 1871), Chinese authorities supported breeding and reintroduction programs that de facto mixed the four species currently recognised based on molecular analyses (Turvey et al., 2019). The *Andrias* case demonstrates that the arguments for a due attention to solid taxonomic evaluation before performing *ex situ* conservation and translocations (Dubois, 2006; Gippoliti et al., 2021) were well-founded. Another similar example concerns the genus *Tupinambis* Daudin, 1802, for which taxonomic revisions revealed the presence of multiple species in this once monotypic genus. However, individuals held in zoos continued to be associated to only one species, *T. teguixin* (Linnaeus, 1758), which was described more than 260 years ago. Thus, it was not surprising that first molecular analyses revealed more than one tegu species being held among zoos (Ziegler et al., 2019a). It should be noted that zoo support to taxonomic-phylogenetic research should always be positive if, as in the case of the Ethiopian endemic primate *Theropithecus gelada* (Ruppell, 1835), it helps to identify distinct ESUs that should be the target of in situ conservation programs (Zinner et al., 2018).

These examples reinforce the idea that zoo stocks should be carefully checked regarding both taxonomic affiliation and purity of breeding, because only properly identified and pure-bred zoo stocks are of conservation value in the sense of IUCN's One Plan Approach to Conservation. For example, if crocodiles with farm origin should be included in conservation breeding and restocking projects, genetic testing of purity of breeding is crucial, as hybrids were reported, e.g. among held Siamese crocodiles *Crocodylus siamensis* (Schneider, 1801) and Philippine crocodiles *C. mindorensis* Schmidt, 1935 (Ziegler et al., 2015). The case of another charismatic zoo animal, the giraffe, is emblematic here, as holdings of animals of different provenances were encouraged by a general lack of credibility that surrounded taxonomy and the subspecies concept in biological circles (Geist, 2007; Vinarski 2015a; 2015b) during most of the twentieth

Fig. 6: Cryptic golden tegu (*Tupinambis cryptus*). Photo: T. Ziegler

Fig. 7: Philippine crocodile (*Crocodylus mindorensis*). Photo: T. Ziegler

century. Giraffes now are recognised as belonging to a still unstable number of species and subspecies (Groves & Grubb, 2011; Fennesy et al., 2016; Petzold et al., 2020) with obvious hybrid *ex situ* subpopulations without any conservation significance having to be excluded from zoo breeding programs.

While debates about the taxonomic status of hidden or overlooked populations among higher vertebrates have been relatively common in recent years (Gippoliti & Groves, 2018; Taylor et al., 2019), true discoveries happen still regularly and scientific descriptions are continuously released among lower vertebrates. An impressive example is the megadiverse gecko genus *Cyrtodactylus* Gray, 1827 from Southeast Asia, with far more than 300 nominal species and thus representing the most diverse genus of the Gekkonidae. The species number of bent-toed geckos reported from Laos and Vietnam has remarkably increased from five in 1997 to 71 species in 2021 (Ngo et al., 2022). Only when species and their ranges are defined, they can be properly protected, because we can only protect what we know.

This is not where research ends, it is rather beginning with the adequate taxonomy. Next, habitat requirements and ecological adaptations must be determined to better understand the species' niche occupancy but also for the proper set up of keeping conditions for the build-up of conservation breeding programs in zoos (Ziegler et al., 2019b). To reach an official or increased legal protection status (i.e. IUCN Red List, CITES, new protected areas) population and threat analyses must follow, as they were performed recently for crocodile and warty newts, for genera such as *Tylototriton* Anderson, 1871, and *Paramesotriton* Chang, 1935, the Psychedelic Rock Gecko *Cnemaspis psychedelica* Grismer, Ngo & Grismer, 2010, tiger geckos *Goniurosaurus* Barbour, 1908, and the Green Water Dragon *Physignathus cocincinus* (G. Cuvier, 1829) (Bernardes et al., 2020; Nguyen et al. 2018, Ngo et al. 2016; Ngo et al., 2019, Gewiss et al. 2020). Several higher taxa, such as amphibians, constitute a diverse yet still incompletely characterised clade of vertebrates, in which new species are still being discovered and described at a high rate (Vietes et al., 2009; Streicher et al., 2020). Regardless of whether divergent lineages should or should not be recognized and described as distinct species, even conspecific divergence is important in *ex situ* conservation programmes. Nominally conspecific yet divergent lineages represent allopatric populations that may have genetic variants that represent incompatibilities or local adaptations and perhaps cannot or should not be interbred in human hands (Crawford et al., 2013). This highlights the significance of sound taxonomy for subsequent research and adequate One Plan Approach conservation measures.

Fig. 8: Cryptic bent-toed gecko (*Cyrtodactylus cryptus*). Photo: T. Ziegler

Fig. 9: Vietnamese crocodile newt (*Tylototriton vietnamensis*). Photo: A. Rauhaus

For the impact on biodiversity conservation worldwide, an increased attention to taxonomy and a stronger collaboration with the taxonomic community may prove highly beneficializing to both *ex situ* and *in situ* conservation. In the end, continuing discoveries of Earth biodiversity may prove a further force to increase awareness of the need to maintain its ecological properties among new generations of humans.

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Investigating the Effect of Food Presentation on Black Lemur Behaviour

Untersuchung des Effekts der Futterpräsentation auf das Verhalten von Mohrenmakis

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Abstract

Diets for captive primates are frequently chopped into small pieces, despite the growing body of evidence that suggests the animals may not need small, chopped food items. In the wild, frugivorous primates would typically find larger fruit items that require manipulation to be eaten. Additionally, the chopping of food items is believed to reduce nutritional value, increase the risk of contamination, and may be costly in terms of keeper time. To determine whether the chopped feeding style has any benefits, research was conducted on a family group of four black lemurs (*Eulemur macaco)* housed at Sparsholt College's Animal Health and Welfare Research Centre. Food was provided in two different presentation styles: chopped into small or large particle sizes. The food items used were the same for both conditions. To investigate the effects of food presentation, one-zero focal sampling was used to monitor lemur behaviour, focusing particularly on aggressive, affiliative and food-based behaviours. Poisson regressions were used to investigate the impact of food type, and also time of day and individual lemur effects on behaviour. Overall, the large food style significantly reduced the frequency of aggressive behaviours such as biting, chasing, cuffing, stealing food and purring (but not screeching), whilst increasing allogrooming. Food-based behaviours such as foraging, moving with food and sitting up with food significantly increased when large foods were provided. Overall, lemurs were more likely to carry larger food items up to remote parts of their enclosure, thus reducing competition over food sources and reducing conflict. Provision of large food items such as fruits for captive pri-

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mates may therefore have value in terms of reduced conflict and improved group cohesion, along with more naturalistic feeding opportunities. Further study across a wide range of frugivorous, group-housed primates would therefore be valuable.

Keywords: chopped food, *Eulemur macaco*, food presentation, Lemuridae, animal welfare

Introduction

Modern zos and aquaria place animal welfare as one of their core principles, and in order to ensure that their animals are well cared for, management practices should be based on scientific evidence (Melfi, 2009). Zoos and aquaria are responsible for the management of thousands of animal species, with diverse biology, behaviour and management needs (Mason, 2010). Many of these species have not yet been formally studied, and so it is important that research on husbandry practices continues to be embedded into the work of zoos. One form of husbandry practice that benefits from research interest is zoo food presentation.

Should primate foods be chopped?

Food provided for captive animals is often chopped into small, bitesize pieces, even when the animals naturally tackle much larger items (Plowman et al., 2006). The practice of chopping food is surprisingly ubiquitous throughout captive environments, with chopped foods used in the diets of a myriad of domestic and zoo animals (Young, 1997; Griffin & Brereton, 2021). Diets containing chopped food may be especially common for primates, as many species are traditionally fed fruits or vegetables in captivity (Britt et al., 2015).

Despite its common use, chopping food results in several disadvantages, including loss of keeper time (Quintanilla et al., 2023), food nutrient deterioration (Hodges & Toivonen, 2008; Brereton et al., 2024) and risk of bacterial contamination of food. There is evidence that some animals actually prefer larger food items, and are willing to work for them (Rozek et al., 2010; Rozek & Millam, 2011). From an evidence-based perspective, it is therefore important that caregivers determine whether chopped food provides any benefits to the animals being fed (Melfi, 2009).

It is not clear from the literature why chopped food is frequently used in animal diets, though keepers sometimes justify food chopping as an attempt to reduce aggression in group-housed animals, reduce stealing, and encourage foraging (Plowman et al., 2006; Brereton, 2020; Waasdorp et al., 2021). However, literature on chopped food for primates does not demonstrate all these benefits. Contrary to these anecdotes, Barbary macaques (*Macaca sylvanus*) reduced aggressive interactions when fed whole foods (Sandri et al., 2017). For lion-tailed (*Macaca silenus*) and Sulawesi macaques (*Macaca nigra)*, dietary diversity and the amount of food eaten by submissive individuals increased (Smither et al., 1989; Plowman et al., 2006) wen whole food were provided. Theoretically, less prepared food requires more manipulation by animals. Consequently, they should have less time to engage in conflict with others. There is also a suggestion that animals are more likely to transport large food items to safer locations to eat, thus reducing conflict (Shora et al., 2018). To date, only one published study has demonstrated an increase in aggression association with whole foods (Mathy & Isbell, 2001). However, the study methodology involved throwing two food items in for a group of 70 macaques (*Macaca mulatta*): naturally, this may have increased competition. While macaques have been well studied, there remains scope to extend research on food presentation for a wider range of primate species. It is particularly important to engage in further research, because different primate species are likely to respond differently on account of their natural feeding ecology and social structure (Waasdorp et al., 2021). Prosimians, such as lemurs, represent an excellent opportunity to investigate food presentation impacts further (Britt, 1998), as they are largely frugivorous, social animals, and are frequently found in zoos globally.

The black lemur

The black lemur (*Eulemur macaco)* is a frugivorous, cathemeral primate endemic to Madagascar (Gosset & Roeder, 2001). As in all *Eulemur* species, *Eulemur macaco* diets contain high proportions of fruits, as wild diets can exceed 78% fruit (Birkinshaw, 2001). Occasional non-fruit food items include leaves and flowers (Simmen et al., 2007). Black lemurs have been observed feeding on over 70 different fruit species in the wild, and food selection varies between day and night (Andrews & Birkinshaw, 1998; Birkinshaw, 2001). The species naturally lives in small family groups with a hierarchical structure in which adult females tend to be dominant (Birkinshaw, 2001).

In captivity, black lemurs are often fed a range of fruit items, and aggression and food-based interactions have previously been noted (Gosset & Roeder, 2001). This species is categorized as Endangered by the International Union for Conservation of Nature (IUCN) (Andriantsimanarilafy et al., 2020), and zoological collections currently maintain a captive population of around 160 individuals in total (Species360, 2022). It is important, therefore, that management practices and feed presentation methods are developed for this species, so as to continue to improve welfare. The purpose of this study, therefore, was to determine whether larger food items would affect the behaviour of a group of zoo-housed black lemurs.

Materials and Methods

Study site and subjects

Following ethical approval, a behavioural study was commenced at the Animal Health & Welfare Research Centre at Sparsholt College, Hampshire. Observations took place throughout January and February 2022, and focused on a group of four black lemurs (Tab. 1). Lemurs were kept in a large enclosure containing an indoor and outdoor component. The outdoor enclosure consisted of a large, netted exhibit, containing tree ferns and posts for climbing. The indoor exhibit included a climbing frame, and sawdust was provided as the substrate.

Tab. 1: Information on black lemur individuals in study.

GAN	Name	Sex	Birth date	Birth location	Parents
27353930	Bee	Female	5 Apr 2008	Bioparc Fuengirola,	Unknown
26499789	Lemar	Male	27 Jun 2008	Prague Zoo, Prague	Unknown
NRP14-00760	Caitlin	Female	4 Apr 2014	Sparsholt College, UK	Bee and Lemar
NRP21-02167	Lokobe	Male	19 May 2021	Sparsholt College, UK	Bee and Lemar

Diet preparation

The lemurs were fed twice per day (09:00 and 14:00) as per the normal husbandry routine, but the diet always consisted of a range of fruits and vegetables, together with 140g of Mazuri™ leafeater pellet. For the study, diets were prepared in two formats: chopped small (chopped into 2cm^3 cubes) and large (entire fruit items where possible or chopped where food items were especially large). The leafeater pellets were similarly provided in two formats: small (25mm length x 15mm width, as sold by Mazuri™) and large (50mm length x 30mm width) (Fig. 1). The large pellets were prepared on site by grinding the original leafeater pellets into dust, adding water to the dust to form a paste, moulding the paste into the new pellet size required, and removing the excess water using a cryo-desiccator. This meant that the small and large pellets were near identical in terms of their nutrient value. The small pellets were always provided with the chopped food, and the large pellets with the large food. The food was provided on four platforms throughout the indoor enclosure, and additionally was scattered over the floor. The order in which food condition (small or large) was provided to the lemurs was randomised, but both food conditions were offered an equal number of times.

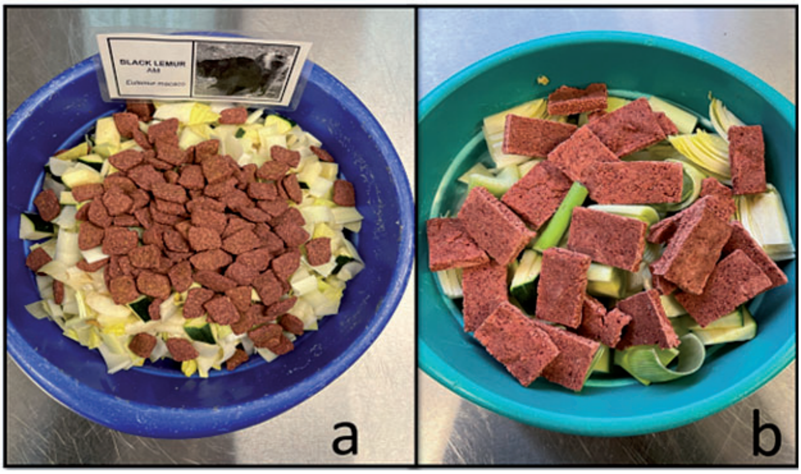

Fig. 1: Diet preparation for black lemurs. a) Small pieces with small pellets and b) large pieces with large pellets. Photo: R. Panayi

Data collection

Observations of both morning and afternoon feeds took place throughout the study period. Lemur observations were conducted using one-zero focal sampling (Altmann, 1974; Brereton et al., 2022) at one-minute intervals for all lemurs, for three-hour observation periods. Observations began directly after food was placed within the exhibits. An ethogram was developed to investigate the effect of food presentation aggressive, affiliative, and food-based behaviours (Tab. 2).

Data analysis

Data were collected into a Microsoft™ Excel 2016 spreadsheet, and data analysis was undertaken using Minitab, version 23. Behavioural data were analysed using a series of Poisson

Tab. 2: Ethogram for black lemurs observed in study.

Behaviour category	Behaviour	Description
Affiliative	Allogroom	Lemur uses grooming claw or tooth comb to clean another individual.
	Huddle	Lemur is touching another animal, usually accompanied by grabbing the other animal with limbs and wrapping tail around the other animal.
	Play	One animal grabs another animal and engages in non-aggressive wrestling.
Aggressive	Bite	Lemur attacks another individual using their teeth in an aggressive manner.
	Chase	Lemur moves at a fast pace after another animal.
	Cuff	Lemur hits another individual using their hand in an aggressive manner.
	Purr	Lemur emits a vibrating sound from the throat.
	Screech	Lemur emits a short, high pitch noise.
	Steal food	Lemur grabs a food item from another individual’s hands.
Food-based	Drink	Lemur leans head down to water bowl and flicks tongue into water to ingest water.
	Forage	Lemur searches for and ingests food in the enclosure either by actively moving through the enclosure or by visually searching for food items.
	Move with food	Lemur holds a food item in its hands or feet and locomotes around enclosure.
	Sit up with food	Lemur uses one of its hands or feet to pick up and hold a food item after, while or followed by sitting up.
General	Climb	The animal moves about on a vertical structure, including platforms, ropes and mesh.
	Groom	Lemur uses the grooming claw or tooth comb to clean itself.
	Inactive	Lemur is sitting, resting or sleeping.
	Jump	Lemur leaps from one climbing structure to ground or another climbing structure.
	Locomotion	Lemur walks or runs around enclosure.
	Scent mark	The animal uses glands to mark surfaces
	Sunning	Lemur moves into the sunlight, torso vertical, forelimbs extended and allows solar rays to warm the body.

regressions. For the regressions, the selected behaviour (frequency per hour) was inputted as the response, and the food type (small or large), individual lemur and time (morning versus afternoon) were inputted as predictors. The alpha value was set to 0.05.

Results

A graph was generated to show the impact of food condition on the rate of general behaviour per lemur per hour (Figs 2, 3). To show more detail on affiliative, aggressive and food-based behaviours, further figures were generated to show the specific behaviours identified (Figs 4, 5, 6). Poisson regressions were run for all behaviours (Tab. 3): while all models were significant, food type was a significant predictor of 14 behaviours, with climbing, inactive, allogroom, forage, move with food and sit up with food occurring significantly more often for the large food condition, and jump, , bite, chase, drink, cuff, purr, screech and steal food occurring significantly less often.

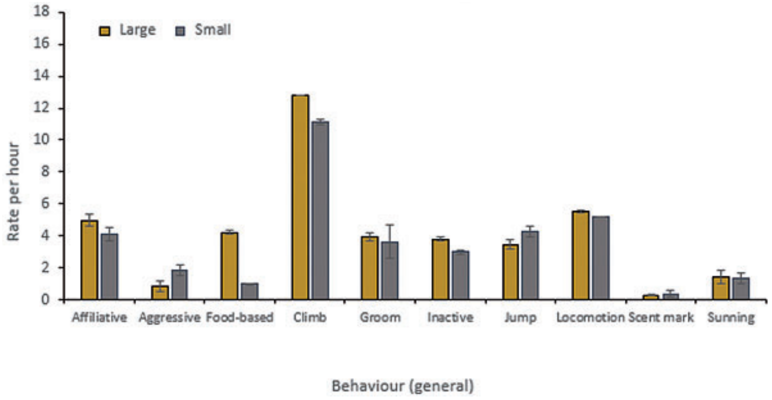

Fig. 2: Behaviour rate per hour, broken down by food type (+/- standard error). All affiliative, aggressive and food-based behaviours have been pooled for the purpose of this figure. Further detail on these behaviour types can be seen in the figures below. Large and small indicate the food types provided.

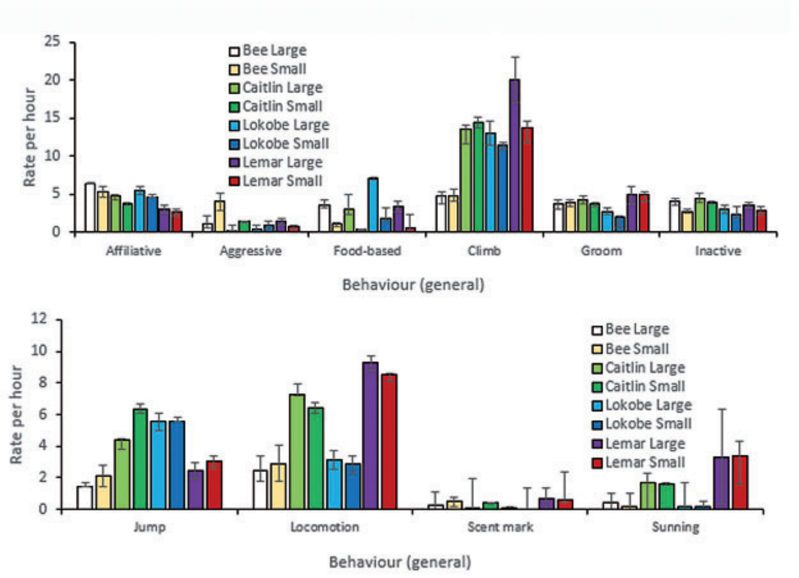

Fig. 3: Behaviour rate per hour, broken down by lemur and food type (+/- standard error). All affiliative, aggressive and food-based behaviours have been pooled for the purpose of this figure. Further detail on these behaviour types can be seen in the figures below. Large and small indicate the food types provided.

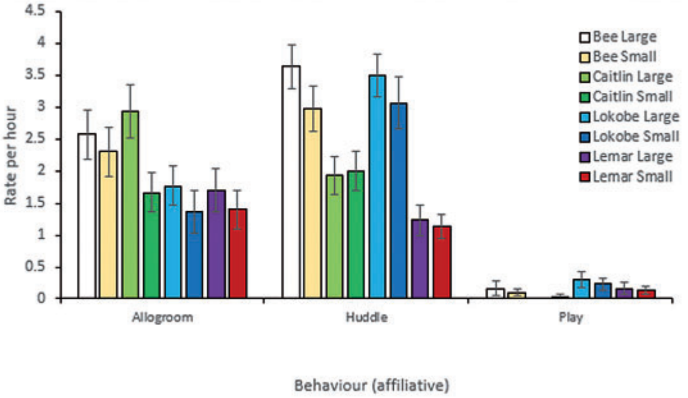

Fig. 4: Affiliative behaviour rate per hour, broken down by lemur and food type (+/- standard error).

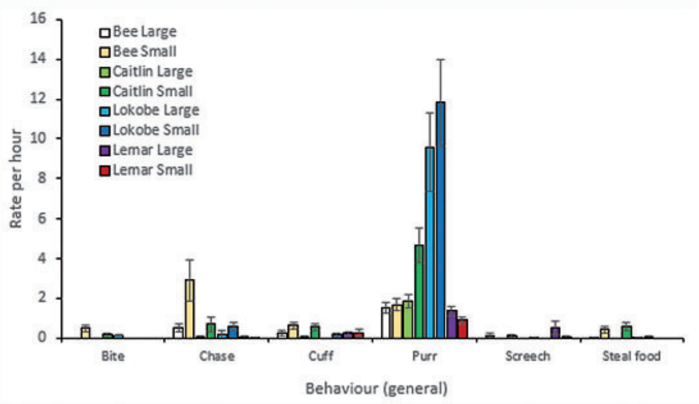

Fig. 5: Aggressive behaviour rate per hour, broken down by lemur and food type (+/- standard error).

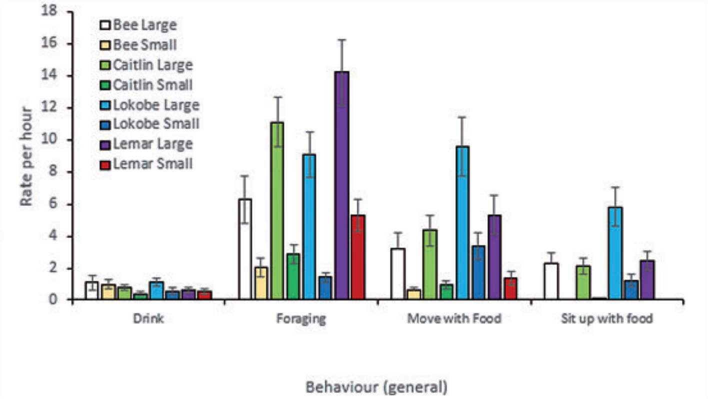

Fig. 6: Food-based behaviour rate per hour, broken down by lemur and food type (+/- standard error). * denotes a significant value.

Tab. 3: Output of Poisson regressions for lemur behaviour.

Behaviour	R^2	Predictor	DF	SE Predictor	X^2	P
Climb	20.56%	Model	5	0.065	432.92	<0.001 *
		Food type	1	0.037	14.88	<0.001 *
		Lemur	3	0.068	359.69	<0.001 *
		Time of day	1	0.038	58.35	<0.001 *
Groom	6.78%	Model	5	0.080	52.31	<0.001 *
		Food type	1	0.067	1.68	0.195
		Lemur	3	0.082	50.62	<0.001 *
		Time of day	1	0.065	0.01	0.921
Inactive	7.51%	Model	5	0.084	30.06	<0.001 *
		Food type	1	0.071	11.52	0.001 *
		Lemur	3	0.093	18.44	<0.001 *
		Time of day	1	0.070	0.10	0.752
Jump	19.82%	Model	5	0.108	166.94	<0.001 *
		Food type	1	0.066	10.09	0.001 *
		Lemur	3	0.112	155.94	<0.001 *
		Time of day	1	0.065	0.91	0.341
Locomotion	29.69%	Model	5	0.091	387.11	<0.001 *
		Food type	1	0.056	1.37	0.242
		Lemur	3	0.093	279.07	<0.001 *
		Time of day	1	0.059	106.67	<0.001 *
Scent mark	12.62%	Model	5	0.280	29.37	<0.001 *
		Food type	1	0.231	2.17	0.140
		Lemur	3	0.344	25.00	<0.001 *
		Time of day	1	0.231	2.17	0.140
Sunning	43.45%	Model	5	0.242	182.39	<0.001 *
		Food type	1	0.110	0.15	0.700
		Lemur	3	0.250	182.20	<0.001 *
		Time of day	1	0.110	0.03	0.869
Allogroom	5.57%	Model	5	0.101	32.98	<0.001 *
		Food type	1	0.093	9.47	0.002 *
		Lemur	3	0.119	19.96	<0.001 *
		Time of day	1	0.093	3.56	0.059
Huddle	21.30%	Model	5	0.089	83.26	<0.001 *
		Food type	1	0.084	1.98	0.160
		Lemur	3	0.116	75.14	<0.001 *
		Time of day	1	0.083	6.14	0.013*

Tab. 3: Continued.

Behaviour	R^2	Predictor	DF	SE Predictor	X^2	P
Play	19.58%	Model	5	0.565	22.80	<0.001 *
		Food type	1	0.345	0.47	0.494
		Lemur	3	1.060	9.15	0.027 *
		Time of day	1	0.484	13.18	<0.001 *
Bite	26.87%	Model	5	0.693	23.37	<0.001 *
		Food type	1	0.619	9.39	0.002 *
		Lemur	3	0.516	9.17	0.027 *
		Time of day	1	0.475	4.81	0.028 *
Chase	30.45%	Model	5	0.229	162.27	<0.001 *
		Food type	1	0.215	54.29	<0.001 *
		Lemur	3	0.231	98.26	<0.001 *
		Time of day	1	0.167	9.72	0.002 *
Cuff	22.83%	Model	5	0.16	48.94	<0.001 *
		Food type	1	0.392	15.11	<0.001 *
		Lemur	3	0.288	12.24	0.007 *
		Time of day	1	0.302	21.59	<0.001 *
Purr	33.44%	Model	5	0.111	718.99	<0.001 *
		Food type	1	0.064	20.33	<0.001 *
		Lemur	3	0.125	641.69	<0.001 *
		Time of day	1	0.065	56.98	<0.001 *
Screech	22.02%	Model	5	0.529	29.75	<0.001 *
		Food type	1	0.737	10.98	0.001 *
		Lemur	3	0.764	17.78	<0.001 *
		Time of day	1	0.408	0.99	0.321
Steal food	36.50%	Model	5	0.745	29.07	<0.001 *
		Food type	1	0.728	14.82	<0.001 *
		Lemur	3	0.356	8.26	0.041 *
		Time of day	1	0.374	6.00	0.014 *
Drink	7.54%	Model	5	0.150	34.84	<0.001 *
		Food type	1	0.150	6.54	0.011 *
		Lemur	3	0.209	11.31	0.010 *
		Time of day	1	0.155	16.98	<0.001 *
Forage	36.59%	Model	5	0.073	691.11	<0.001 *
		Food type	1	0.061	421.79	<0.001 *
		Lemur	3	0.080	157.11	<0.001 *
		Time of day	1	0.053	112.20	<0.001 *

Tab. 3: Continued.

Behaviour	R^2	Predictor	DF	SE Predictor	X^2	P
Move with food	26.68%	Model	5	0.103	438.53	<0.001 *
		Food type	1	0.082	238.27	<0.001 *
		Lemur	3	0.122	185.59	<0.001 *
		Time of day	1	0.069	14.68	<0.001 *
Sit up with food	38.40%	Model	5	0.134	327.01	<0.001 *
		Food type	1	0.170	184.55	<0.001 *
		Lemur	3	0.172	130.60	<0.001 *
		Time of day	1	0.138	11.86	0.001 *

Discussion

Overall, food type (small or large) was a significant predictor of 14 key lemur behaviours. Briefly, the large food type was a significant predictor of increased allogrooming behaviour, reduced aggressive interactions (except screeching), and increased foraging and moving and sitting up with food. Individual lemur was a significant predictor for all behaviours and helped to explain much of the variance in behavioural expression. This suggests that there are considerable differences in behaviour between individual lemurs, likely as a result of sex, age and role in family (Andrews & Birkinshaw, 1988).

When provided with large food, lemurs significantly increased the frequency of foraging, sitting up with food and moving with food, whereas drinking behaviour decreased. Large food items may take more time to eat, and therefore movement away from feeding areas is incentivised. For the small food type, it would not be time-effective to transport each food item any distance before feeding, as this would necessitate many trips. Similar trends have been observed in other species in terms of food transport. For rats (*Rattus norvegicus*), larger food particle size is a significant predictor of increased carrying behaviour, and also hoarding behaviour (Whishaw & Tomie, 1989; Whishaw & Dringenberg, 1991; Davison et al., 2024). A similar preference for, and movement of larger food items has been observed in coatis (*Nasua nasua)* (Shora et al., 2018), binturong (*Arctictis binturong)* (Vine et al., 2024) and agouti (*Dasyprocta leporina*) (Dookie et al., 2018). These similar findings in terms of carrying of large food items across multiple mammalian Classes (i.e. Rodentia, Carnivora and Primates) suggests that this behavioural tendency transcends taxonomic grouping. From a social cohesion standpoint, this carrying of food may be beneficial, as it reduces competition over a single food source (e.g. scattered small food particles) that could be dominated by a single, aggressive individual. Instead, animals may quickly grab one item and then proceed to eat in relative safety, for example on an elevated platform.

Large food items may have other benefits in terms of natural behaviour. These larger items required lemurs to use both hands for grasping and manipulating food, thus encouraging them to adjust their posture accordingly and use their dentition for shearing and chewing. This alteration to position and movement of lemurs may have benefits in terms of natural behaviour, particularly as wild lemur foods also require significant manipulation (Mertl-Millhollen et al., 2003; Bennett et al., 2016). According to Birkinshaw (2001), the majority of black lemur fruits were over 1cm in length, and many species had a thick skin or shell requiring removal. Lemurs also tended to feed high within the trees (2-15m up by day and over 15m by night) (Andrews & Birkinshaw, 1998). The incentivisation of movement with food and manipulation may enhance activity levels and overall fitness and behavioural flexibility in lemurs.

In terms of aggression, the large food type was a significant predictor for reduced biting, chasing, cuffing, purring and stealing, whereas screeching appeared more often when large foods were provided. The reduced incidence of aggressive behaviours contrasts with the findings of Waasdorp et al. (2021) and Mathy & Isbell (2001), who demonstrated increased aggression with larger food items. The reduction in aggression may have been associated with movement of animals. Lemurs were significantly more likely to carry larger food items (rather than small items) to a new location in order to eat. This meant that individuals were in remote, less accessible positions when feeding, which may therefore have reduced conflict over food resources. Similar findings have been demonstrated for the ring-tailed coati when housed in small social groups. This may have also reduced the incidence of stealing behaviour, as lemurs tended to be in less accessible locations for feeding, rather than clustered on shared platforms. Aggression has been a management problem for the black lemur, as adult females may engage in food-based aggression, particularly directed toward males (Simmen et al., 2003, 2007). Anecdotally, the keepers had noted that the adult female lemur, Bee, at the collection often engaged in aggressive behaviours toward the adult male, Lemar. The reduction in aggression, particularly from the adult female, is therefore a promising sign.

Of all aggressive behaviours, only screeching was increased during the large food observations. Screech behaviour was relatively rare during all observations, but this behaviour occurred significantly more frequently when large food was provided. Of all lemurs, the adult male Lemar engaged in this behaviour most often. It is not clear why this behaviour occurred more often during large food observations.

For affiliative interactions, allogrooming was significantly influenced by food type. Overall, allogrooming behaviour appeared more frequently during the large food condition. Again, the underlying reason why this behaviour occurred more frequently is difficult to unpick, though the behaviour may be associated with better group cohesion (Jaeggi & van Schaik, 2011). Individuals were engaging in less conflict, and therefore may have spent less time avoiding one another following bouts of aggression at feeding. Huddling and play behaviour, however, were not influenced by food type, but rather by time of day and individual.

It should be noted that inactivity levels did rise when large foods were provided. For captive lemurs who often spend long periods of time inactive, this can be a concern, particularly where diets are more calorific than those experienced by wild individuals (Hansell et al., 2017). Changes in inactivity were relatively slight but should be monitored overall.

Future directions

This is a small-scale study, and due to species-availability, the study was carried out on a single family group of lemurs. As such, the study resembles a case report, rather than a full cohort study. While the Poisson regressions controlled for, and quantified, the amount of behavioural variation that occurred between individuals, replication across a wider range of black lemur groups would be beneficial. It must also be noted that the number of tests run in this study is considerable, and this increases the risk of a type 1 (false positive) error. Care should therefore be taken when interpreting the behavioural differences that were observed in this study.

Several interesting trends have been identified in this study that appear to transcend species differences, such as the tendency to transport larger food items, and the resulting reduction in aggression. The aggression reduction appears to result from distance between individuals and lack of competition over a single, immobile resource (finely chopped food items in a bowl or on a platform). As a result, future studies could be trialled for other group-housed primates where aggression may become a challenge. Examples could include squirrel monkeys (*Saimiri sciureus)* or mandrills (*Mandrillus sphinx*).

Research could also include investigations of food intake, ideally comparing between individuals. In some species, such as lemurs and macaques, food-based aggression can result in concerns that not all individuals are receiving equal portions of food (Plowman et al., 2006; Junge et al., 2009). Investigations of food intake and the types of food eaten would add value for future researchers and keepers. Similarly, quantification of concerns that keepers may have over food presentation changes, or anecdotal evidence of suitability, would have merit in terms of informing current feeding strategies (Hammerton et al., 2019).

Conclusion

From an animal welfare perspective, the provision of large food items seems to have improved black lemur behaviour by reducing group conflict, improving allogrooming and naturalised the range of food-based behaviours shown. Lemurs engaged more frequently in carrying behaviour, thus avoiding conflict by eating in remote parts of their enclosure. The reduction in conflict was particularly noticeable from the adult female lemur, who regularly engaged in chasing, particularly towards the adult male. Given that there are concerns regarding male-directed aggression by females in captive lemurs, this feeding style appears to be a positive strategy for reducing conflict frequency. It also may reduce the requirement by zoos to separate troop members during feeding times. While a relatively small-scale study, similar research could be trialled across a range of frugivorous, group-housed primates with a view to determining welfare impacts.

Statements

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Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Zusammenfassung

Das Futter für in Gefangenschaft lebende Primaten wird häufig in kleine Stücke geschnitten, obwohl obwohl es immer mehr Belege dafür gibt, dass die Tiere keine zerkleinerte Nahrung benötigen. In freier Wildbahn finden frugivore Primaten normalerweise größere Früchte, die zum Verzehr manipuliert werden müssen. Außerdem wird angenommen, dass das Zerkleinern von Nahrungsmitteln den Nährwert verringert, das Verunreinigungsrisiko erhöht und es kann einen hohen Zeitaufwand für die Tierpfleger mit sich bringen. Um festzustellen, ob die zerkleinerte Fütterung irgendwelche Vorteile hat, wurde eine Studie an einer Familiengruppe von vier Mohrenmakis (*Eulemur macaco*) durchgeführt, die im Sparsholt Colleges Animal Health and Welfare Research Centre untergebracht ist. Das Futter wurde in zwei verschiedenen Darreichungsformen angeboten: in kleiner oder großer Partikelgröße. Die verwendeten Futtermittel waren für beide Bedingungen gleich. Um die Auswirkungen der Futterpräsentation zu untersuchen, wurden Eins-Null-Stichproben verwendet, um das Verhalten der Lemuren zu beobachten, wobei der Schwerpunkt auf aggressiven, affiliativen und futterbezogenen Verhaltensweisen. Poisson-Regressionen wurden verwendet, um den Einfluss der Futterart, der Tageszeit und der individuellen Lemuren auf das Verhalten zu untersuchen. Insgesamt verringerte der große Futtertyp deutlich die Häufigkeit von aggressiven Verhaltensweisen wie Beißen, Jagen, Kuscheln, Stehlen von Futter und Schnurren (aber nicht Kreischen), während das Fremdputzen zunahm. Futterbezogene Verhaltensweisen wie Futtersuche, Bewegung mit Futter und Aufsitzen mit dem Futter nahmen signifikant zu, wenn großes Futter angeboten wurde. Insgesamt war es wahrscheinlicher, dass die Lemuren größere Futterstücke in entlegene Teile ihres Geheges trugen, wodurch der Wettbewerb um die Futterquellen und Konflikte reduziert wurde. Die Bereitstellung von großen Nahrungsmitteln wie Früchten für in Gefangenschaft Primaten in Gefangenschaft kann daher zu weniger Konflikten und einem besseren Gruppenzusammenhalt führen, zusammen mit natürlicheren Fütterungsmöglichkeiten. Weitere Studien über eine breite Palette von frugivoren, in Gruppen gehaltenen Primaten wäre daher wertvoll.

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Enclosure use of a group of yellow-breasted capuchins (*Sapajus xanthosternos*) at Allwetterzoo Münster

Gehegenutzung einer Gruppe von Gelbbrustkapuzinern (*Sapajus xanthosternos*) im Allwetterzoo Münster

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Abstract

Exploring enclosure use is an approach that has recently gained popularity and has already been applied to a variety of animal species, including various primates. Investigating enclosure utilization of animals in human care can help assessing the quality of husbandry conditions and provide information about animal welfare. By examining reasons for preference of certain enclosure areas, zoo professionals can identify potentials for husbandry improvement. In this study, we examined the outdoor enclosure use by a group of 27 yellow-breasted capuchin monkeys (*Sapajus xanthosternos* Wied, 1826) at Allwetterzoo Münster, Germany. Apart from the indoor enclosure and two outdoor cages, the group had access to a large outdoor enclosure. We used instantaneous scan sampling and focal animal sampling to record the intensity of use of and the behaviors performed in this outdoor enclosure.

We found that the monkeys did not use the space randomly, but preferred locations that were suitable for certain behaviors. They performed a limited range of behaviors in the outdoor enclosure and exhibited a pronounced daily routine. The capuchins preferred to stay in the

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structurally rich central areas of the enclosure and visited the structurally poor peripheral areas only to forage.

The animals utilized the enclosure complex, comprising indoor enclosures, two outdoor cages, and the main outdoor enclosure, as distinct functional zones, each supporting different behaviors or proportions of behaviors and being frequented to varying degrees. Social rank influenced the use of the outdoor enclosure, with low-ranking individuals spending more time outside and displaying different behavior patterns compared to high-ranking individuals. These findings suggest that the outdoor enclosure can serve as a retreat for low-ranking animals and that the exhibit does not offer equal habitat quality to all group members. Some animals may select locations based on factors beyond behavioral intentions or personal preferences, but instead for social reasons. Overall, the naturalistic design of the outdoor enclosure provides the animals with opportunities to display natural behaviors and seems to play a crucial role in alleviating social tensions by giving opportunities for choice and action, which is likely to have a positive impact on the welfare of all, but especially the lower-ranking animals.

Keywords: enclosure use, capuchin monkey, *Sapajus*, behavioral biology, husbandry

Introduction

Understanding the factors influencing space use of zoo animals is essential for effective enclosure design and to maximize animal welfare in the available space (Ross et al., 2011; Maple & Perdue, 2013; Hunter et al., 2014). Although the amount of space available to animals is an important factor, especially in terms of minimum requirements to promote good health and welfare, the functionality of the space is equally or even more significant. Even large enclosures may hold limited value for animals if they cannot utilize the available space effectively (Paulk et al., 1977; Kerl & Rothe, 1996; Schapiro et al., 1997; Jensvold et al., 2001). Enclosure designs appropriate for the species should facilitate and encourage natural behaviors (Meier, 2009; EAZA, 2021). Conversely, inadequate physical and social features of the housing environment can cause discomfort and stress leading to welfare issues (Barnes et al., 2002; Bashaw et al., 2007; Maple & Perdue, 2013). The environment created for a species plays an important role in the range and diversity of activities and behavioral budgets of captive animals (Reinhardt et al., 1996; Schapiro et al., 1997; Seidensticker & Forthman, 1998; Jensvold et al., 2001; Ross et al. 2011; Clark et al., 2012; Rose & Roffe, 2013). Consequently, the characteristics of the space provided for animals in zoological gardens determine their ability to exhibit species-typical behaviors and influence factors that contribute to an individual animal's social situation as well as the ability of zookeepers to manage the group in a way that promotes individual welfare (Jennings et al., 2009; EAZA, 2021).

To ensure that a specific enclosure design fulfills its purpose and has the intended effects on optimal husbandry, it is crucial to determine whether and how animals use the resources provided to them (Ross et al., 2009; Tan et al., 2013). An enclosure that is designed to closely resemble the look of a species' natural habitat will fail to serve its purpose if the occupants are unable to exhibit species-specific behaviors or if the animals actively avoid much of the available space (Hediger, 1964; Blount & Taylor, 2000). For primates, assessments of enclosure use have primarily focused on great apes (Hedeen, 1983; Traylor-Holzer & Fritz, 1985; Bloomsmith et al., 1991; Perkins, 1992; Bettinger et al., 1994; Jensvold et al., 2001; Stoinski et al., 2001; Ross et al., 2006/2009/2011; Bonnie et al., 2016), but lion-tailed macaques (*Macaca silenus* Linnaeus, 1758), for example, also have been subjects of enclosure use studies under zoo conditions (Hornshaw, 1975; Mallapur et al., 2005).

In a group of female chimpanzees (*Pan troglodytes* Blumenbach, 1775), every individual had a preferred site where it spent the majority of its time (Bettinger et al., 1994). In lion-tailed macaques, it has been found that animals housed in sparse enclosures utilized the edge areas at a higher rate than individuals in more complex enclosures (Mallapur et al., 2005). Similar results are available for great apes: In an older, low-structure, low-natural design enclosure, both gorillas (*Gorilla gorilla* Savage, 1847) and chimpanzees preferred residing at grid or net barriers and in corners while avoiding open spaces that were not adjacent to a physical structure (Ross et al., 2009). In a new and naturally designed exhibit, preferred positions in the enclosure area changed for both species (Ross et al., 2009). From this, it could be inferred for the target-oriented design of animal enclosures that size alone misses its purpose if the enclosure area does not encourage the animal to use it through structure-rich design (Ross et al., 2009). Neither chimpanzees nor gorillas were observed to avoid the areas of their enclosure closest to zoo visitors as the number of visitors increased, which is taken to indicate that well-designed zoo enclosures can prevent the negative effects zoo visitors potentially have (Bonnie et al., 2016).

In this study, we examined how a group of yellow-breasted capuchin monkeys (*Sapajus xanthosternos* Wied, 1826, hereafter abbreviated as YBC) utilized a large and structurally complex outdoor enclosure at Allwetterzoo Münster (Germany). Particularly, we asked (1.) how intensive this enclosure was used in comparison to the other elements of the housing complex (indoor and outdoor cages) and (2.) whether there were differences between morning and afternoon indicating some kind of daily routine, as well as (3.) how enclosure use varied within the different areas of the outdoor enclosure. Here we examined whether different zones of the outdoor enclosure were used uniformly in relation to the size (area) of the zones. Based on the results of similar studies with other species, including primates, we expected to see significantly more intensive use of the central enclosure areas, which are equipped with trees and climbing structures, compared to the peripheral areas, which are poor in structure, as these provide less incentive for the animals to visit them.

Capuchin monkey groups are composed of several adult males and females and their common offspring and are organized matrilineally (Robinson & Janson, 1986; MacKinnon & Bezanson, 2023). Capuchins have hierarchies that are differentiated by age and sex (Fragaszy et al., 2004) and reflected in access to food and reproduction, among other things (Robinson & Janson, 1986; MacKinnon & Bezanson, 2023). The spatial position of an individual within the group is primarily related to the amount of aggression it experiences from the dominant male of the group, but is also influenced by its sex (Janson, 1990). Location selection varies with changes in an individual's social status, but not with seasonal differences in food availability, which means that individuals compete for preferred spatial positions (Janson, 1990). Subordinate animals direct more visual attention to dominant animals than vice versa, and likewise to the animals that most frequently attack them and others, what means that social monitoring behavior within a group of capuchin monkeys is driven largely by conflict avoidance (Pannozzo et al., 2007). Beyond this background, we also attempted to determine whether the social hierarchy in the capuchin monkey group at Allwetterzoo Münster affects enclosure use by individual group members. To do so, we examined possible individual differences in (4.) space usage intensity and (5.) evenness by quantifying and comparing these aspects for single focal animals. Further, we investigated (6.) what behaviors the capuchins exhibit in the outdoor enclosure, the proportions of different behaviors, and which locations in the outdoor enclosure are visited more often for specific actions to draw conclusions about the motivation behind preferring or avoiding certain parts of the enclosure.

Studies on gorillas have come to different conclusions regarding the effects of social rank on enclosure use. Unlike in juvenile gorillas, no consistent relationship was found between dominance rank and constraints on individual space use in adults (Hedeen, 1983). This means, at least, that an enclosure may not have the same effective quality for all its inhabitants. This aspect has not received much attention in capuchins but is of great importance for zoo animal management to ensure the welfare of each individual group member and to make population management decisions. For these reasons, we (7.) paid special attention to whether or not individual space utilization restrictions could be detected in the capuchins in Münster. The possible indicators we focused on are differences in intensity of outdoor enclosure use, different preferences for parts of the outdoor enclosure and different proportions of behavioral categories exhibited outside between group members of high and low social rank. Especially the behavior of the lowest-ranking group members was of great interest from an animal welfare perspective.

Enclosure description

The housing complex of the capuchin exhibit at Allwetterzoo Münster includes three indoor cages (one with 20 m², the two others with 15 m² each), two outdoor cages of 60 m² and 80 m², respectively, and a large outdoor enclosure (hereafter abbreviated as OE) of 500 m² (Fig. 1). Walkways with a total area of an estimated 24 m² connect the different cages and the OE. Altogether, the housing complex has approximately 714 m² of accessible space for the animals. While the OE was added to the exhibit in 2012, the remaining parts of the capuchin housing complex date back to the 1970s and only received some smaller upgrades over the years. Therefore, they lack the design of modern zoo buildings and are not very naturalistic, but still are adapted to the needs of the animals.

Study subjects

At the time of our studies, the group of YBC at Münster Zoo consisted of 27 (17.10) animals, including three offspring each from 2019 and 2021 (3.3), whose sex had not yet been determined at the time. This group size grew through regular breeding success from an initial group of six animals (2.4). The group of YBC at Allwetterzoo Münster was therefore similar in size, origin, composition, age structure, and social dynamics to a group in the wild and hence offered good opportunities to observe natural behaviors. Although the species is highly endangered (Kierulff et al., 2020), capacity at Allwetterzoo was reached and placement of offspring in other zoos is difficult. Reproduction had to be managed in accordance with the EAZA ex situ programme (EEP). Therefore, the former breeding male has been vasectomized and hormonal contraception was in use in all adult females. The four oldest male offspring had been castrated.

The YBC received several feedings per day and were managed as follows: At 9 a.m., they received various kinds of salad as well as a pap containing chopped apples and shredded turnips in the outdoor cages, which had already been cleaned before, and also in the indoor enclosures, which were cleaned shortly after the feeding. To prevent tensions in the group and to ensure that all animals had access to enough food, the animals were split into five subgroups for this feeding event. There were no feedings in the OE at any time. At 10 a.m., the OE was opened. At 3 p.m., the YBC were fed vegetables and other food items, such as germinated wheat, cooked potatoes, or cooked rice (depending on the day of the week), in the inside enclosures and in the outdoor cages. For this feeding the group was divided into subgroups as before. Access to the OE was closed at this time until the next morning at 10 a.m., meaning the animals could not use it overnight. This was changed shortly after the study. The last regular feeding took place at 4 p.m., when pellets were scattered in all indoor enclosures and both outdoor cages. For enrichment purposes different food items like nuts or finely chopped carrots were offered irregularly, but never during the observation times for data collection. They were either scattered, or sometimes placed in enrichment objects like cardboard tubes. Except for the OE or if separated during

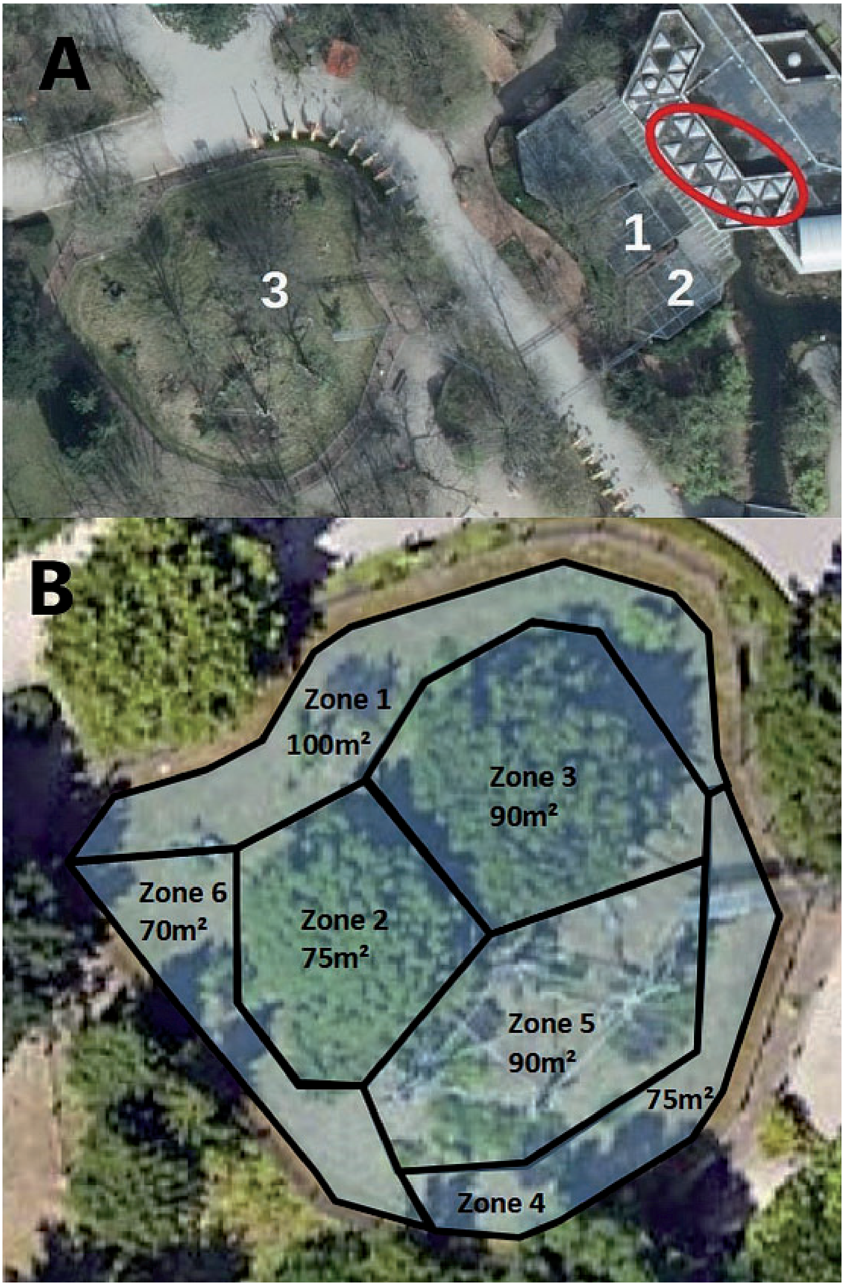

Fig. 1: Study site. **A:** Overview of the enclosure complex yellow-breasted capuchin monkeys at Allwetterzoo Münster. Outlined in red: Location of the three indoor cages in the monkey house; 1 and 2: outdoor cages; 3: main outdoor enclosure (accessible via grid walkway from outdoor cage 2); Source of photograph: City of Münster (2021); own markings and labeling. **B:** Zoning of the outdoor enclosure with sizes. Own production. Aerial photo from Google Maps.

feeding and cleaning (for about 20-30 minutes), all YBC had access to all enclosures. This means that during all observation hours, all animals had access to the entire enclosure complex without any restrictions. No food was offered during times of data collection, but leftovers from previous feeding may have been available.

Methods

Data collection

Data collection took place on 20 days between the 5th and the 30th of July 2021 at Allwetterzoo Münster and in two shifts of 96 minutes (morning and afternoon) per day. We combined instantaneous scan sampling and focal animal sampling (Martin & Bateson, 2021). To be able to investigate the questions in relation to individual animals, 12 (6.6) focal animals were selected in advance of the study (Tab. 1). Unfortunately, one focal male (KAHLO) had to be euthanized after the first eight days of observation due to severe injuries caused by group members.

Tab. 1: Overview of focus animals with information on sex, year of birth and social rank (according to zookeepers).

Name	Sex	Year of birth	Social rank	Name	Sex	Year of birth	Social rank
ALFREDO	male	2016	medium	CASSY	female	2005	high
CUCO	male	2002	high	FREEDA	female	2009	high
IGUACU	male	2008	low	JAQUI	female	2006	high
KAHLO	male	2013	low	JESS	female	2004	medium
SALVADOR	male	2015	medium	MAYA	female	2013	low
TIAGO	male	2014	medium	WANJA	female	2014	low

We used instantaneous scan sampling (Martin & Bateson, 2021) to examine the use of the OE by the entire group. For this purpose, we virtually divided the OE into six zones with rather homogeneous characteristics (Tabs 2, 3, Fig, 1B, 2A-D) and recorded the number of individuals present in each zone every 12 minutes. The indoor area and the two outdoor cages (Fig. 1A) together formed a seventh zone. This procedure resulted in 18 data points per day (9 each in the morning and afternoon) for each enclosure area, making 360 scans for 20 observation days. With eight observation days of 27 animals and twelve of 26 animals, the sample included a total of 9,504 animal localizations.

Between two scan samplings, we observed a preselected focal animal for 8 min and recorded its location (i.e., zone of the OE) and activity (behavior) or absence from the enclosure instantaneously at 20-second intervals. Behavior was recorded as one of four categories: movement, resting, social interaction, and foraging. The focal animal for each time slot was selected in

Tab. 2: Area shares of the zones to the total area of the outdoor enclosure for YBC at Allwetterzoo Münster.

Zone	1	2	3	4	5	6	Other	Sum
Area (estimated)	100 m²	75 m²	90 m²	75 m²	90 m²	70 m²	214 m²	714 m²
Share of area to the outdoor enclosure	20 %	15 %	18 %	15 %	18 %	14 %	0 %	100 %
Share of area to the whole enclosure complex	14 %	10,5 %	12,6 %	10,5 %	12,6 %	9,8 %	30 %	100 %

Tab. 3: Description of the zones.

Zone	Description
1	Predominantly exposed to the sun, periphery of the capuchin monkey exhibit, close to visitors, oriented towards the penguin exhibit, which is highly frequented by zoo visitors, poor in structure (single low bushes and large stones)
2	Almost completely shaded, central area of the outdoor enclosure, far from visitors, rich in structure (densely branched chestnut tree)
3	Almost completely shaded, central area, far from visitors, rich in structure (large hornbeam), close to the animals' entrance to the enclosure
4	Almost completely sun-exposed, periphery, close to visitors, poor in structure (single low bushes and large stones)
5	Predominantly sun-exposed, central area, far from visitors, rich in structures (climbing frame), animals' access to the enclosure opens here, own outdoor cages visible for the animals (= visual contact to conspecifics)
6	Mostly shaded, peripheral area, far from visitors, rather poor in structure (bushes and some large stones), quiet and low disturbance, little overview of the rest of the area (bushes act as a visual barrier)

Fig. 2: Pictures of the main outdoor enclosure of the YBC at Allwetterzoo Münster. **A** Zone 1 (foreground left side), zone 6 (foreground right side), zone 2 (area around front tree), zone 3 (area around back tree). **B** Zone 6 (foreground), zone 2 (area around front tree), zone 3 (area around back tree). **C** Zone 4 (foreground), zone 3 (tree in the center of the picture), zone 5 (background left half of the picture). **D** Zone 4 (foreground), zone 3 (tree at right image border), zone 5 (background image center). Photos: J. Overberg

advance and independently of the individual's actual presence on the OE by following a recurrent sweep through the focal animals in an order that was determined once randomly. This left the possibility that an animal is not present in the OE during its observation time slot, meaning that we were able to measure the proportion of time the individual spent outdoors. Over the total duration of the study, an equal frequency of observations of all animals was ensured by the recurring sweeping through all individuals to be recorded. This also had the advantage that individual animals took their turn at alternating times, eliminating the influence of individual daily schedules among animals. Each focal animal was observed 30 times over the 20 days, providing 750 data points. For KAHLO, 250 data points (10 sessions) had been collected by the time of his death. Since the data for this animal were of good and assured quality, we considered them robust and scaled them up by a factor of 3 to achieve homogeneous sample sizes for further analysis.

Data analysis

Data analysis was performed using the statistics software R version 4.0.3 (R Core Team, 2020).

1. Overall intensity of enclosure use: We used chi-squared tests to compare the "intensity" of use (i.e., the number of individuals present) of the OE with the other areas of the housing complex. Expected values were calculated based on the proportion of area corresponding to the OE (70 %) and to the remaining enclosures of the capuchins (30 %).

2. Differences between morning and afternoon outdoor enclosure use: We used chi-squared tests to compare the intensity of OE use in the morning and in the afternoon.

3. Overall evenness of enclosure use and location preferences: To examine whether the different zones of the OE were used uniformly in relation to the size (area) of the zones, we calculated Plowman's adjusted spread-of-participation index (SPI; Plowman, 2003) as a quantifier for evenness of enclosure use. Since for this calculation only presence data is used, the index is independent of the overall intensity of OE use. The SPI compares the observed distribution of visits over a given set of zones (enclosure use) to a distribution assuming random location, meaning that the zones' share of all visits is equal to their size share of the total area. SPI values of 0.3 and below are usually considered to define relatively uniform enclosure use, while values above 0.7 are considered to indicate uneven enclosure use (Daoudi et al., 2017). We checked the significance of the deviance from uniformity of the enclosure utilization we observed by using again a chi-squared test. The test compared the observed spatial distribution with the case of animals' distribution over the zones that is perfectly in relation to their size, as if complete evenness of enclosure use was given.

To identify preferred or avoided areas of the OE, the percentage deviation of the observed frequency of animal localizations from the expected value was calculated for each zone. Subsequently, two zones were compared in a chi-squared test if the pairing was of interest. By combining the values of the three central zones (2, 3, and 5) and the three zones (1, 4, and 6) in the periphery of the site, a comparison between the intensity of use of the central and peripheral zones was also performed in another chi-squared test.

4. Individual intensity of enclosure use: For examining individually different patterns of enclosure use, first the intensity of use of the OE by the focal animals was considered. For each focal animal, we calculated the balance of presence and absence in the OE and the share of the six zones on its OE use. Analogous to examining the intensity of use with respect to the entire group, we tested a distribution consisting of the sum of all data points that documented an individual's presence and absence on the OE against a distribution formed by the two associated expected values in a chi-squared test for each focal animal. In addition, we also contrasted the observations with adjusted expected values in the same way. These were determined to be expected values regarding to the information already obtained based on the observed balance between presence and absence at the OE by the whole group. They derive from information on time spent outdoors combined (multiplied) with area share (Tab. 2). This allowed the identification of individuals that showed particularly intensive or low use of the OE.

5. Individual evenness of enclosure use: The assessment of the evenness of OE use on an individual level was once again based on the SPI, which we calculated for each focal animal. Then, for each focal animal, we performed a one-sample t-test of its SPI value against the SPI values of all other focal animals to identify animals with noticeably uneven enclosure use. Prior to this, we checked all distributions from the other SPI values, against which a focal animal's SPI value was tested, for normal distribution using a Shapiro-Wilk test (5 % significance level). All tests suggested a normal distribution (smallest p-value for $W = 0.912$, $p > 0.05$).

6. Behavior in the OE: We compared the frequencies of the four behavioral categories we defined (moving, resting, social interaction, foraging) shown by all focal animals together in relation to the enclosure part (defined zones) in which they were located in while acting. Since zones 1, 4, and 6 as well as 2, 3, and 5 showed very similar proportions between the frequencies of the behavioral patterns at first glance, we subjected them to a chi-squared test combined into these two groups.

7. Influence of social rank: We used chi-squared tests to determine whether there were differences in the use of the OE between socially higher-ranking and lower-ranking group members. For this purpose, we summarized the data of the highest-ranking animals and the lowest-ranking animals (Tab. 1). Information on the social rank of our focal individuals was given by zookeepers, who know the social structure of the group very well due to the daily work with the capuchins. Tests followed between the summed presences and absences in the OE of individuals with high and low social rank as well as between the distributions of their stays among the six zones. The same procedure was performed for the behavioral categories to learn whether animals visit the OE for different reasons based on their status in the group. In addition, we tested intensity of utilization of the central area of the OE and its peripheral areas for differences between high- and low-ranking group members. We repeated the whole procedure for the comparison between the four lowest-ranking focal animals and the eight others (high- and medium-ranking) as a whole remainder, as we assumed the lowest-ranking to be most susceptible to remarkably different patterns of enclosure use and of particular interest with regard to aspects of animal welfare. We also calculated the mean SPI values for these groupings.

Results

1. Overall intensity of enclosure use: The capuchin monkeys used the OE less intensively than expected, assuming utilization were proportional to the size of its area ($X^2 = 3901.4$, df = 1, $p < 0.001$). On average, the number of animals present was only about one-quarter (24.75 %) of the group members, which is approximately one-third of the expected number.

2. Differences between morning and afternoon outdoor enclosure use: The animals used the OE more intensively in the morning compared to the afternoon (Tab. 4). The intensity of enclosure use in the afternoon scattered significantly more than the morning data, with a coefficient of variation (relative standard deviation) of 43.3 % against 20.3 %. More intensive use of the OE over the mornings was highly significant ($X^2 = 233.6$, df = 1, $p < 0.001$).

Tab. 4: Mean count and range of the number of capuchin monkeys in the outdoor enclosure per session and per scan.

Time	Mean sum of counts per session (range of sums)	Mean count per scan (range of daily mean counts per scan)	Range of animals counted at single scans
All day	117.6 (38 - 160)	6.5 (2.1 - 8.9)	0 - 15
Morning	74.9 (33 - 100)	8.3 (3.7 - 11.1)	0 - 15
Afternoon	42.7 (5 - 75)	4.7 (0.6 - 8.3)	0 - 14

3. Overall evenness of enclosure use and location preferences: The OE was not only used less, but also more unevenly than expected, if one assumes that the animals do not show any preferences for certain areas. The adjusted spread-of-participation index took a value of 0.366 for the whole group's space usage over the duration of the study, which corresponds to a slightly unevenly distributed usage. The frequency of use of the six defined zones differed highly significantly ($X^2 = 570.3$, df = 5, $p < 0.001$) from the expected distribution of animals over the OE (Fig. 3A). The expected value here already refers to the observed total intensity of enclosure use by the group. For three zones (1, 4, and 6), the observations deviated downward from the expected value. For the other three (2, 3, and 5), they exceeded it; in the case of zone 3, even by double (Fig. 3B). The preference for zone 3 was highly significant ($X^2 = 21.9$, df = 1, $p < 0.001$) compared to zone 2, which had the second highest intensity of use, and thus to all other zones. Zone 2 was not significantly favored over zone 5 ($X^2 = 1.34$, df = 1, $p >= 0.05$), but highly significantly (for all: $X^2 >= 105.99$, df = 1, $p < 0.001$) over zones 1, 6, and 4, as was the case for zone 5 (for all: $X^2 >= 90.8$, df = 1, $p < 0.001$). Among the peripheral zones, the intensity of use of zone 1 was significantly higher than that of zone 6 and zone 4 ($X^2 >= 6.29$, df = 1, $p < 0.05$). Overall, the centrally located zones were highly significantly preferred ($X^2 = 522.1$, df = 1, $p < 0.001$) over the peripheral zones.

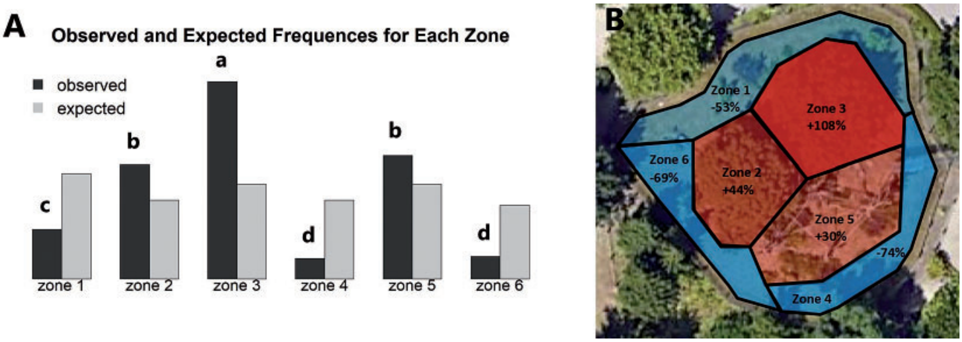

Fig. 3: Intensity of use of the different parts of the outdoor enclosure. **A** Observed and expected intensity of use of each zone as the sum of observed respectively expected to be observed animals after 360 scans. The expected values here already refer to the actual observed intensity of enclosure use overall (adjusted expected value). Letters (a/b/c/d) form groups of zones with significant preference over others. For example: Pairwise comparison of zone 3 (a) with any other shows significant preference of zone 3 over the other (b/c/d). Among the others b indicates significant preference over zones with c and d; c is preferred over ones with d. **B** Heat map of the frequency of use of the six defined zones as a relative deviation from the expected value for the area proportions corresponding to the distribution of all the animals over the outdoor enclosure. The expected values for zones 1 to 6 already refer to the actually observed intensity of enclosure use in total. Blue color indicates less intensity of use than expected by random distribution of animals; red color shows areas with more intensive utilization than expected. The transparency of the fill color indicates the degree of deviation from the expected value.

4. Individual intensity of enclosure use: The intensity of OE use varied considerably between individuals. With 1.0 CUCO (the alpha male), there was one among the focal animals that never entered the OE. This was already known before the beginning of our study. Therefore, it was treated as a non-representative outlier and excluded from further analysis. The individual that spent the highest amount of time in the OE was there more than seven times as long as the animals with the fewest observed residences in the OE. Only this one animal exceeded the unadjusted expected value of 70 % (based on 500/714 m²) with 86.8 % presence time in the OE. The mean value among the focal animals (already without CUCO) was 32.35 %, which was highly significantly ($X^2 = 126.6$, df = 1, $p < 0.001$) higher than the value of the whole group, which spent on average only 24.75 % of the time in the OE. Five of the eleven animals analyzed, predominantly very low-ranking ones, had individual presence times outside above the focal animal mean. Among the individuals with presence time outside lower than the focal animals' mean were the three females with young. The deviation of the intensity of OE use from the actual expected value of 70 % was highly significant for all focal animals – highly significantly higher for 1.0 KAHLO ($X^2 = 61.5$, df = 1, $p < 0.001$) and highly significantly lower for all others (for all: $X^2 >= 22.4$, df = 1, $p < 0.001$). If, instead of the 70 % of the observation time, which is to be assumed on the basis of the area share of the OE on the whole exhibit space accessible for the capuchins, the share of 24.75 % of time spent outdoors actually observed in the animals is taken as the expected value, this adjusted value was exceeded by the same five individuals that exceeded the mean value among the focus animals. One castrated male and the four breeding females also clearly missed the adjusted expected value of presence time outside.

5. *Individual evenness of enclosure use:* Differences in the distribution of their duration of presence in the OE across the six zones were extreme among the focal animals. The SPI took a value between 0.234 and 0.534 for the eleven focal animals, with a mean of 0.376. Values were distributed evenly around the mean value without notable extremes. All values were well below the threshold of 0.7, but, except for two, most animals exceeded the threshold of 0.3, which implies no noticeably equal enclosure use anymore. Only two individuals reached a value above 0.5, which then was due to a high number of observations in zone 3.

6. *Behavior in the OE:* The intensity of use of an enclosure part is related to the purpose for which the animals spend time there (Ross et al., 2009). In respect to this, the six zones could be divided into two groups based on our observations (Fig. 4). The peripheral zones and central zones had quite similar proportions of behavioral categories among themselves, but completely different proportions compared to the other group. Border zones 1, 4, and 6 were used by animals almost exclusively for foraging. Foraging accounted for at least 70 % of all observations in each of the three zones, with zone 1 accounting for the most at 85 % (Fig. 4). This was almost entirely foraging for insects in the grass or feeding on bushes growing in the enclosure, where berries or live insects would be the most likely food items consumed. There was no direct feeding of the animals in the OE during observation hours. Other behaviors exhibited in these zones were also mostly related to foraging. Observations of "movement" and "resting" in these

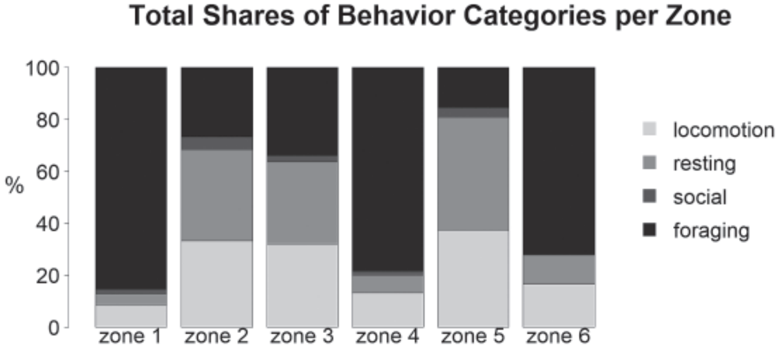

Fig. 4: Proportions of each behavior category in the behavior exhibited by the selected focal animals among the yellow-breasted capuchin monkeys at Allwetterzoo Münster in each zone.

zones, which accounted for the remainder of behavior there in about a 2:1 balance (Fig. 4), were to be strictly speaking short-term and small-range changes of position or pauses in which insects were not searched for for a few seconds. Instead, for example, the surroundings were observed. Despite that, there were exceptions, i. e. animals that predominantly showed other behaviors in these zones, such as movement and especially resting. They were staying on the ground like the others, but not searching for food. The central zones also were partially used for foraging – zone 3 even to almost 34 % – but resting and movement made up the majority here. These two together took up almost 65 % of the behavior in zones 2 and 3 and about 80 % in zone 5 having roughly equal shares (Fig. 4). In general, the recorded resting behavior was hardly true resting behavior in the sense of lying down or sleeping, which was observed only sporadically in the OE, but rather temporary sitting stationary, observing the surroundings or watching events outside the enclosure. Social interactions were generally observed to an extremely low extent. They took place almost entirely indoors and in the outdoor cages and had the highest share in the OE with 5 % in zone 2 (Fig. 4). All these differences between outer zones and center area together were highly significant ($X^2 = 109.9$, df = 3, $p < 0.001$).

7. Influence of social rank: We found notable differences in the intensity of OE use by animals of different level in the social hierarchy (Fig. 5A). On average, the lowest-ranking animals spent about three times as much time in the OE as the other focal animals did (highly significant, $X^2 = 1094.8$, df = 1, $p < 0.001$) and even about five times as much as the highest-ranking ones (highly significant, $X^2 = 1604.5$, df = 1, $p < 0.001$). The distribution of presence time across the zones also differed clearly depending on the rank of the animals (Fig. 5B). For example, the lowest-ranking animals used zone 1 noticeably less than the rest of the focal animals did and only one third as much as the highest-ranking animals. On the other hand, zone 2 was visited about three times as often by the lowest-ranking animals as by the highest-ranking animals (Fig. 5B). Zones

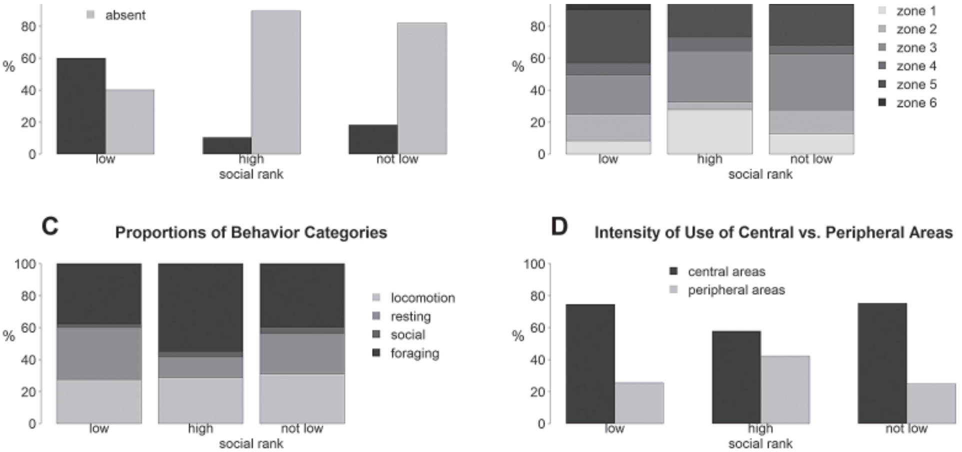

Fig. 5: Outdoor enclosure use with respect to social rank. "Not low" includes individuals of medium and high rank, what means it excludes only the four lowest ranking of the twelve focal animals. **A:** Intensity of outdoor enclosure use and non-use by animals of different social rank. **B:** Percentage distribution of presence in the outdoor enclosure among the zones for individuals of different social rank. **C:** Average proportions of different behavioral categories in the behavior of individuals of different social rank in the outdoor enclosure. **D:** Differences in the ratio of intensity of use of central and peripheral enclosure areas in individuals of different social rank.

5 and 6 also were more popular with the lowest-ranking animals than with the others, especially when compared with the highest-ranking individuals only (Fig. 5B). Overall, the comparison of the lowest-ranking animals with the highest-ranking ones was highly significant ($X^2 = 67.03$, df = 5, $p < 0.001$) and the comparison of the lowest-ranking animals with the remaining focal animals of high and intermediate social rank all together was still significant ($X^2 = 15.57$, df = 5, $p < 0.01$). The SPI averaged 0.320 for the lowest-ranking animals and was neither significantly different (t = 0.35, df = 4.3912, $p \geq 0.05$) from the mean value of 0.341 for the highest-ranking ones, nor from the one of all remaining focal animals together (0.408; t = -1.367, df = 5.6528, $p \geq 0.05$). The distribution of time spent in the OE between central and peripheral enclosure areas was virtually indistinguishable between the lowest-ranking animals and all others combined ($X^2 = 0.011$, df = 1, $p \geq 0.05$), but the central area of the OE was less favored by the highest-ranking individuals with about 60 % compared to about 75 % with the lowest-ranking specimens (Fig. 5C). This difference was highly significant ($X^2 = 18.99$, df = 1, $p < 0.001$).

The proportions of the four behavioral categories in the observations were similarly distributed for the lowest-ranking animals and all others combined (Fig. 5D) and therefore not significantly different between these two groups ($X^2 = 6.31$, df = 3, $p \geq 0.05$). Only slightly fewer social interactions and foraging behavior were recorded in the lowest-ranking animals, which instead showed a slightly higher proportion of resting periods. Compared with the highest-ranking specimens exclusively, differences were much larger. Although the percentages of movement and social behavior were about the same, the highest-ranking group members did not show resting behavior even half as often as the lowest-ranking ones. These spent less of their time searching for food. The result of the chi-squared test between highest- and lowest-ranking focal animals is highly significant ($X^2 = 38.45$, df = 3, $p < 0.001$). Overall, enclosure use did not differ between animals of different levels in the social hierarchy of the group with respect to evenness, but did differ in intensity, manner, and intent behind the visits there.

Discussion

General trends in the enclosure use of the whole group of capuchins

Our results show that a random distribution of the YBC over the space available to them can be ruled out. Instead, the observed intensity of OE use indicates the existence of preferences and purposeful decisions in the animals' choice of their location. Non-random choice of location and resulting preferences were to be expected, as they are common for animals and well documented for a range of species (Hosey, 2005; Rose & Robert, 2013; Beaudin-Judd et al., 2019; Fernandez & Harvey, 2021; Galardi et al., 2021; Rose, 2022), including various primates (Hornshaw, 1975; Hedeen, 1983; Ogden et al., 1993; Bettinger et al., 1994; Stoinski et al., 2001; Hosey, 2005; Mallapur et al., 2005; Ross et al., 2009). The attractiveness of the individual areas in relation to intentions to act, as well as social interactions, seem to determine the spatial distribution of group members (Hedeen, 1983; Ross et al., 2009). Especially the second aspect appears to play a crucial role. The capuchins appeared eager to distribute themselves in harmonious subgroups over the whole housing complex and to consider their enclosure less as one single area, but as a sum of several functional units.

Social reasons as explanation for observed enclosure use patterns

Throughout the observations, there were animals present in all parts of the housing complex (OE, outdoor cages, indoor enclosure) at almost every point of time. In most cases, the same individuals were present together in one part of the housing complex. The splitting of a group into subgroups for short periods of time is often observed in wild primate groups as well (Puschmann et al., 2009; Schröpel, 2010; Mittermeier et al., 2013). Females with young often stayed together near the highest-ranking male, what aligns with the observations of Ross & Giller (1988) on wild capuchins. Younger males, born in recent years, formed their own groups, while the lowest-ranking animals tended to roam alone at some distance from other group members. In a smaller group or in a differently structured housing complex, this splitting into subgroups probably would not have been observed the way it was.

Studies on other primates came to the conclusion that crowding may increase aggressive behavior and frequency of fights, but normally primates also show the aim and ability to prevent or reduce such situations through different behaviors, such as avoiding proximity or visual contact (Waterhouse & Waterhouse, 1971; Kummer, 1982; Nieuwenhuijsen & de Waal, 1982; de Waal, 1989; de Waal et al., 2000; Hosey, 2005). A study conducted by van Wolkenten et al. (2006) on tufted capuchins (*Sapajus apella* Linnaeus, 1758) found the animals to keep social stress caused by crowding at a low level mainly by avoiding social encounters.

By a widespread distribution to all parts of the exhibit, the YBC in Münster seemed to avoid conflicts and to be able to relax the social situation, which was tense due to the high density of animals in the exhibit and the surplus of males in the group. For this, visual barriers and the availability of several spatially independent enclosures were more important than the overall size of area. This assumption is also supported by the fact that during the entire observation hours, i.e. during a period in which the animals had permanent access to the OE, no aggressive confrontations were observed outdoors. Probably, the large area and ample structuring (visual barriers, enlargement of the usable area) allowed the animals to avoid social encounters. In contrast, in the evenings and at night, when the animals had only the indoor facility and outdoor cages available, leading to fewer opportunities to avoid each other, repeated conflicts occurred, sometimes resulting in injuries for the lower-ranking animals. In one case injuries caused by conspecifics necessitated euthanasia.

In general, more complex habitats with more visual barriers can decrease the number of social interactions, and through this, may reduce aggression and competition for resources (Fieschi-Meric et al., 2022; de Azevedo et al., 2023). The OE of the YBC at Allwetterzoo Münster offers many visual barriers that seem to fulfill this purpose. From this point of view, the OE plays a key role in relaxing the group dynamics and ensuring the well-being of all group members. This also means that, due to social interactions, the OE – and equally the housing complex as a whole – cannot provide a habitat of equal quality for each group member. It also means that it is not possible for each animal to select its location solely based on individual spatial preferences or on intentions to act (Hedeen, 1983; EAZA, 2021). There is no need for the OE to be frequented according to its area share in the total housing complex, since the identity of the animals around it is more important for an individual than their number (Pannozzo et al., 2007).

Nevertheless, social aspects certainly are not the only reason for the unexpectedly low intensity of use of the OE. Another factor could be that there were no feedings or engagement activities in this enclosure during observations, which, if they take place at other times, immediately increase the number of animals present outside. Finally, the fact that the outdoor cages are almost completely shaded could also play a role. They are also partially roofed and can easily be completely overlooked by an animal, which should help its sense of security and make them more attractive places to stay than the OE is for some purposes, despite their lack of natural features (Jennings et al., 2009; Ross et al., 2009; EAZA, 2021).

Signs of daily routine

The group displayed a relatively consistent daily routine. In the mornings, the animals were more active than in the afternoons and, for example, were busy foraging, while they spent the afternoons mainly with resting or social interactions such as grooming and playing (in the younger animals). It is normal and to be expected that animals have a regular daily routine with recurring times of activity and resting to a certain extent. This has been investigated and proven for various species in zoos (Weller & Bennett, 2001; Rose & Robert, 2013; Rose, 2022; Friedmann et al., 2023). Capuchin monkeys have been found to develop a daily routine, for example adapted to the schedule of feeding times (Ulyan et al., 2006; Di Polizzi Sorrentino et al., 2009). Wild capuchins also show clear activity patterns and travel routines (Robinson, 1984; Presotto & Izar, 2010). A pronounced search for food shown by at least some individuals, which were mainly low-ranking ones, made the animals' daily routine similar to that of their conspecifics in the wild (Fragaszy et al., 2004; de Oliveira et al., 2014). This behavior was possible in this form only due to the natural design (meadow, fruiting plants) of the enclosure, what underlines the importance of this aspect for appropriate captive environments.

Space utilization related to behavioral purposes and spatial preferences

For resting and socializing the YBC chose the indoor areas and outdoor cages rather than the OE. True resting and social behaviors were rarely observed in the OE at all. The presumable reason for this is that the OE likely offers the animals less (perceived) security, which could be decisive for their choice of location, especially for activities associated with limited vigilance. However, it is also possible that the animals simply had no reason to visit the OE for these behaviors because the remaining areas are equally or even better suited for them. Not only the intensity, but also the evenness of enclosure use was lower than would be expected under the premise of no electoral choices. Specifically, the peripheral areas (zones 1, 6, and 4) were less frequented than the central zones 2, 3, and 5. The reason for this could be that the peripheral areas are less attractive to arboreal animals, because they must be free of tall structures in view of escape safety of the enclosure. Ross et al. (2009) demonstrated a reluctance for great apes to reside in open, low-structure areas, which seems to be present in the capuchin monkeys as well. However, such areas are still well suited for foraging by the capuchins. The short-mown grass facilitates the hunt for insects and there are specially planted raspberry and blackberry bushes in parts of these zones. Accordingly, the zones in question were predominantly used for searching for additional food to what is provided by the zookeepers and otherwise tended to be avoided. In contrast, the areas in the center of the site, which with natural trees and climbing branches better resemble the natural habitat of the animals, were visited much more frequently and used in a more varied manner. According to Mallapur et al. (2005), the poor utilization of the peripheral areas suggests that the rest of the enclosure is sufficiently attractive and rich in structure.

Evenness of enclosure use

The values for the adjusted Spread-of-Participation Index do not suggest strikingly uneven patterns in the utilization of the OE, but do not suggest true evenness either. As all areas of the site are visited by the YBC on a regular basis, utilization of the entire OE is given. Attractiveness-enhancing actions such as the planting of fruiting shrubs certainly play a part in this completeness of space utilization, making them a good example of a low-cost and effective measure to encourage the animals to visit certain areas more frequently. The evenness of enclosure use was in the satisfactory range, as the existence of certain spatial preferences is natural (Hosey, 2005; Rose, 2022). In the context of a zoo enclosure, we regard regular visits of all parts of it as an indication of good functionality of the space. This is the case with the YBC in Münster.

Importance of social reasons for differences in enclosure use between individuals

On an individual level, differences in the degree and pattern of OE use were pronounced. Lower-ranking animals spent more time outside than did the higher-ranking individuals. However, it remains unclear to what extent this result is influenced by the highest-ranking male never visiting the OE.

The females with young offspring, which were among the focal animals of high social rank, spent most of their time in close physical proximity to the highest-ranking male and showed regular (positive) social interactions with it. This was presumably because his presence affords protection to the young. Ross & Giller (1988) studied the social interactions in a captive group of another *Sapajus* species and reported that the dominant individuals of both sexes were found in close proximity to each other most of the time and even shared shelter during cold or rainy conditions. Accordingly, it is likely that these females visited the OE less frequently, because they had to leave the male's protection when doing so. This idea is supported by the high-ranking females almost exclusively engaging in foraging during their short time in the OE. Foraging is the only one of the defined behaviors that they can engage in exclusively in the OE. Thus, their visits to the OE are purpose-bound and limited in time to the fulfillment of a predetermined task. However, the connection with the dominant male's aversion to the OE cannot be proven by these observations.

The lowest-ranking animals spent a lower proportion of their time foraging in the OE than the other individuals we observed, but as they spent most of their time outside, they still spent more time foraging in the OE in absolute terms. Thus, they presumably consumed a larger amount of food while doing so. We did not investigate the total amount of food the YBC consumed. Still, we assume that the lowest-ranking individuals utilized the OE for additional food intake because of their low competitive power against other group members and therefore limited choices for preferred foods during regular feedings. All group members always had the opportunity to consume enough food since there were leftovers of the previous day's feedings every morning. Nevertheless, the food available in the OE was likely preferred by the monkeys due to higher sugar (berries) and protein (insects) content. Likewise, primarily the low-ranking females were observed feeding outside. This supports the conclusion that access to the OE is important, especially for the lowest-ranking animals, and is a relief to their situation. During their residence in the OE, the social pressure on them was probably much lower and the overall situation in the group more relaxed for the reasons we explained.

Social rank is not only the most obvious explanation for individual behavior related to foraging, but also for other trends in the choice of location that were evident in animals of different hierarchical positions. For example, the lowest-ranking animals spent less time in zone 3, where several other individuals were always present, and more time in zone 6, where they usually were on their own. In this way, they took advantage of the size and complexity of the OE to avoid the rest of the group. Zone 6 is separated from the rest of the enclosure by a row of plants, so there was even a visual barrier giving individuals the opportunity of temporary isolation from the others. Real resting behavior was hardly ever observed in the OE and was almost exclusively exhibited by the lowest-ranking males. Despite limited vigilance and a theoretical risk of predation, it was probably more favorable for them to rest in the OE than in the indoor area or the outdoor cages, where they would have experienced social pressure and competition for resting places. The high-ranking individuals, on the other hand, never exhibited true resting behavior outside, but spent large parts of their afternoons resting somewhere else. Again, access to the OE allows the animals to improve their situation on their own through avoidance behavior.

Conclusion

The main outdoor enclosure for capuchin monkeys at Allwetterzoo Münster proved to be well designed to meet the behavioral needs of the animals, as demonstrated by their exhibition of natural behavior there. This was supported by natural structures like shrubs serving multiple purposes (foraging sites, visual barriers, climbing structures).

The size of the group and its naturally grown structure resemble the situation of YBC in the wild. However, due to limited enclosure space, group size and maturity of the oldest male offspring entailed tensions between the animals and a more difficult animal management. Our results indicate that the YBC seem to consider their enclosure to be the combination of several somewhat independent parts that it is. They use existing barriers to separate themselves spatially and thus minimize conflicts. Therefore, the six sections of the enclosure, that are optionally separable and mostly visually parted, play a crucial role in managing social tensions between individuals. Although the group had to be split shortly after data collection for this study due to escalating social conflicts, the enclosure had successfully housed the largest group of YBC in Europe for several years.

Our findings suggest that the social structure of capuchin monkey groups significantly influences how they utilize the space available to them. Access to an enclosure of sufficient size and a complex, thoroughly designed structure, can be of particular importance. Especially low-ranking animals seem to profit from enclosure complexity as it gives them opportunity to escape social pressure and thus reduce their stress levels. Based on the insights from this study and the long-term experience gained in Münster, we recommend aiming for complex structures including visual barriers and creation of several well-equipped compartments rather than one continuous space. Additionally, options for temporary separation of individuals or subgroups are important to manage social tensions at any time, but especially when group size increases.

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Author Contributions

This paper is based on the BSc thesis of J.O. from the year 2021. J.O., M.G. and E.W.H. designed and planned the study. J.O. performed the data collection as well as the statistical analyses and production of the figures. J.O. wrote the manuscript. M.G. and E.W.H. revised the manuscript.

Zusammenfassung

Die Untersuchung der Gehegenutzung ist ein Ansatz, der in der jüngeren Vergangenheit Popularität erlangt hat und bereits auf eine Reihe von Tierarten angewendet wurde, darunter verschiedene Primaten. Die Bewertung der Raumnutzung von Tieren in menschlicher Obhut kann als Anhaltspunkt für die Qualität der Haltungsbedingungen dienen und Informationen über das Wohlbefinden der Tiere liefern. Durch die Untersuchung der möglichen Gründe für die Bevorzugung von bestimmten Gehegebereichen können Verantwortliche eine Vorstellung davon bekommen, wie die Tierhaltung verbessert werden kann. In dieser Studie untersuchten wir die Nutzung des Außengeheges durch eine Gruppe von 27 Gelbbrust-Kapuzineraffen (*Sapajus xanthosternos* Wied, 1826) im Allwetterzoo Münster, Deutschland. Neben dem Innengehege und zwei Außenkäfigen hatte die Gruppe Zugang zu einer großen Außenanlage. Die Intensität der Nutzung dieser Außenanlage und die Verhaltensweisen, die dort gezeigt wurden, wurden mit Hilfe von Momentaufnahmen der gesamten Gruppe (instantaneous scan sampling) und der kontinuierlichen Beobachtung von ausgewählten Fokustieren erfasst.

Wir stellten fest, dass die Affen die verschiedenen Teile der Außenanlage nicht wahllos aufsuchten, sondern Orte bevorzugten, die für bestimmte Verhaltensweisen gut geeignet waren. Die Affen zeigten im Außengehege zumeist wenige spezifische Verhaltensweisen und folgten einer ausgeprägten täglichen Routine. Sie hielten sich draußen bevorzugt in den strukturreichen Bereichen in der Mitte der Anlage auf und nutzten die strukturarmen Randzonen nur zum Zwecke der Nahrungssuche.

Die Tiere scheinen ihren Gehegekomplex aus Innengehegen, Außenkäfigen und der großen Außenanlage als mehrere funktionale Bereiche zu interpretieren, die unterschiedlich stark frequentiert werden und jeweils für unterschiedliche Verhaltensmuster von Bedeutung sind. Der soziale Rang der Tiere beeinflusste ihre Nutzung der Außenanlage. Vor allem rangniedrige Individuen verbrachten dort einen großen Teil ihrer Zeit. Dies deutet darauf hin, dass die Außenanlage als Rückzugsort fungieren kann und es Tieren, die unter sozialem Stress stehen, erlaubt, diesen zeitweilig zu mindern. Es bedeutet aber auch, dass der Gehegekomplex insgesamt nicht für jedes Gruppenmitglied die gleiche Lebensraumqualität bietet und dass einige Individuen ihren Standort möglicherweise aus Gründen wählen, die nicht auf Verhaltensabsichten oder persönlichen Vorlieben beruhen, sondern auf sozialem Druck. Insgesamt bietet die naturnahe Gestaltung des Außengeheges den Tieren die Möglichkeit, natürliche Verhaltensweisen auszuüben, und scheint eine entscheidende Rolle bei der Verringerung sozialer Spannungen zu spielen, indem Wahl- und Handlungsmöglichkeiten bestehen, die sich wahrscheinlich positiv auf das Wohlbefinden aller, insbesondere aber der rangniedrigen Tiere, auswirken.

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Die Zucht von Nagelrochen (*Raja clavata* Linnaeus, 1758) im Zoo am Meer Bremerhaven

Breeding of thornback rays (*Raja clavata* Linnaeus, 1758) at Zoo am Meer Bremerhaven, Germany

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Zusammenfassung

Nagelrochen *Raja clavata* lebten Anfang des 20. Jahrhundert noch in großer Zahl in der Nordsee. Aufgrund von übermäßiger Fischerei mit Grundschleppnetzen und Beifang sind sie in der Deutschen Nordsee vom Aussterben bedroht, sodass eine Wiederansiedlung Sinn ergeben könnte. Die Ergebnisse werden im Kontext einer möglichen Optimierung der Zucht in Zoo-Aquarien und damit Erhöhung der Anzahl an Jungtieren für eine mögliche Auswilderung diskutiert. Zu diesem Zweck wurden die Parameter zur Nachzucht im Zoo am Meer überprüft und die Entwicklung der Eier und Jungtiere analysiert. Im Zoo am Meer werden 2,2 Nagelrochen bei 13 °C im Winter und 16 °C im Sommer gehalten. Die Gesamtzahl an Eiern ist höher als in Vergleichsstudien, die Befruchtungsrate geringer im Vergleich zu Studien, wenn die Haltung von ganzjährig 10 °C oder von im Winter 4 °C und im Sommer 16 °C erfolgt. Viele Eier waren durch zahlreiche Mitbewohner im Schaubecken beschädigt, in einigen Fällen war der Dotter herausgelutscht. Daher sollten die abgelegten Eier umgehend aus dem Becken entfernt werden. Die Jungtiere schlüpfen bei Temperaturen zwischen 12 und 16 °C nach durchschnittlich 119 Tagen, haben aber mit 11,2 g im Vergleich zu einer Inkubation bei 10 °C und Schlupf nach 308 Tagen ein geringeres Gewicht. Eine Befruchtung kann nach drei Wochen durch das sichtbare Schlagen des Schwanzes festgestellt werden. Beim Handling der Eier unter Licht stellen die Jungtiere die Schwanzbewegung ein. An verschiedenen Merkmalen konnten die Entwicklungsstufen der Embryonen festgemacht werden. Die Gewichtszunahme der Jungtiere erfolgte nicht linear; nach 30 Tagen wuchsen sie deutlich schneller und erreichten nach sechs Monaten ein durchschnittliches Gewicht von 88 g.

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Schlüsselwörter: *Raja clavata*, Zucht unter Zoo-Aquarienbedingungen, bedrohte Tierart, mögliche Wiederauswilderung

Einleitung

Der Nagelrochen *Raja clavata* ist in ganz Europa im Mittelmeer, der Nord- und Ostsee sowie im Nordatlantik und dem Schwarzen Meer verbreitet. Er lebt benthisch in Küstennähe und bevorzugt sandiges oder schlammiges Substrat in 10 bis 300 m Tiefe (Ebert & Stehmann, 2013; Ferragut-Perello et al., 2023). Es handelt sich beim Nagelrochen um eine ovipare Art, welche Eier legt, die von einer festen Hülle umgeben sind (Holden et al., 1971). Anfang des 20. Jahrhunderts gab es sie noch in großer Zahl; das Wattenmeer war die Kinderstube. Durch Bodenfischerei und Beifang gilt die Art in der IUCN Red List als potenziell gefährdet, in der Roten Liste für Deutschland als „Vom Aussterben bedroht". Daher könnte eine Stärkung der Bestände durch Wiederansiedlung in der Deutschen Nordsee eine Option sein. In anderen Regionen, wie z.B. dem Mittelmeer, konnte eine Zunahme des Bestandes dokumentiert werden (Finucci et al., 2024).

Ziel der Untersuchungen im Zoo am Meer Bremerhaven war es, die aktuellen Zuchtbedingungen zu erfassen und auf ihren Erfolg hin zu überprüfen. Daneben sollten Möglichkeiten zur Erfassung der Embryonalentwicklung untersucht werden. Die Voraussetzung für einen Zuchterfolg ist eine möglichst große Anzahl an unbeschädigten und befruchteten Rocheneiern. Hierfür soll die Eiablage der Elterntiere im Schaubecken dokumentiert und die Befruchtungsrate der Eier sowie die Entwicklungsdauer der Embryonen bis zum Schlupfzeitpunkt bestimmt werden. Für ein besseres Verständnis der Embryonalentwicklung ist es von Interesse, den aktuellen Entwicklungsstand der Embryonen festzustellen. Ebenfalls sollen Merkmale definiert werden, welche auf einen abgestorbenen Embryo oder ein unbefruchtetes Ei hindeuten.

Eine Arbeit, welche ganzheitlich die Zucht von *R. clavata* in menschlicher Obhut untersucht, das Handling der Tiere sowie der Rocheneier betrachtet und zusätzlich Angaben zum zeitlichen Verlauf der Embryonalentwicklung macht, könnte einen Teil dazu beitragen, die Zuchterfolge zu verbessern und damit eine ausreichende Anzahl an Jungtieren zu generieren. Dafür sollen Lösungsansätze gefunden werden, die ohne größeren Aufwand innerhalb der vorhandenen Infrastruktur einer zoologischen Einrichtung durchgeführt werden könnten.

Material und Methoden

Versuchsablauf

Die komplette Versuchsdurchführung fand im Zoo am Meer Bremerhaven statt. Für die Versuchsdurchführung erfolgte eine fortlaufende Entnahme der Rocheneier aus dem Elterntierbecken, welche in Quarantäne in ein Aufzuchtbecken überführt wurden und dort bis zum Zeitpunkt des Schlupfes inkubiert wurden. Die Jungtiere wurden nach dem Schlupf in ein weiteres Aufzuchtbecken überführt. Die einzelnen Untersuchungen können in Beobachtungen und einer Datenerfassung eingeteilt werden. Der Untersuchungszeitraum war Januar – Dezember 2023.

Zuchtgruppe

Bei den vier adulten Tieren handelt es sich um zwei Weibchen und zwei Männchen. Es handelt sich um Wildfänge aus der Nordsee, die zuvor im Aquarium des „Nationalpark-Zentrum

Multimar Wattforum“ in Tönning gehältert wurden. Das exakte Alter dieser Tiere ist nicht bekannt. Ein weibliches Tier ist zum Zeitpunkt der Untersuchungen mindestens 10 Jahre alt und 74 cm lang; die übrigen Tiere sind mindestens fünf Jahre alt. Die beiden männlichen Tiere sind je 67/69 cm groß, das zweite Weibchen 73 cm.

Hälterungsbedingungen

Das Schaubecken, welches ebenfalls als Zuchtbecken diente, hat ein Gesamtvolumen von 100.000 Litern sowie eine Flächenausdehnung von 41 Quadratmetern. Die Wassertiefe beträgt 1,70 m bzw. 2,40 m (Abbildung 1).

Abb. 1: Schaubecken für die Hälterung der Elterntiere: Links der flache Bereich, rechts der tiefere Bereich. Foto: Archiv Zoo am Meer Bremerhaven

Fig. 1: Tank for keeping the parent animals: the shallow area on the left, the deeper area on the right. Photo: Archive Zoo am Meer Bremerhaven

Gefiltert wird das Wasser über Rieselfilter und Abschäumer mit Ozon sowie einer UV-C-Anlage. Es erfolgte eine Beleuchtung mittels HQI-Strahler (1.000 Watt/ 15.000 Kelvin) und Leuchtstoffröhren (Lumilux T5, 54 Watt). Die Temperierung erfolgt über eine Kühlanlage und liegt von November bis Februar zwischen 13 °C, März/Oktober bei 14 °C, zwischen April und September bei 15 °C – 16 °C.

Bei dem Becken handelt es sich um ein Gemeinschaftsbecken mit weiteren typischen Nordseebewohnern. Neben den Rochen leben auch Katzenhaie (*Scyliorhinus canicula*), Streifenbarben (*Mullus surmuletus*), Meeräschen (*Chelon labrosus),* Doraden (*Sparus aurata,)* Graue und Rote Knurrhähne (*Eutrigla gurnadus, Chelidonichthys lucerna*), verschiedene Lippfischarten (*Ctenolabrus rupestris, Labrus bergylta, Labrus mixtus)*, Europäische Hummer (*Homarus gammarus*), Taschenkrebse (*Cancer pagurus*) und verschiedene Seesternarten (*Marthasterias glacialis, Asterias rubens*) im Gemeinschaftsbecken. Die Fütterung erfolgte täglich mit Seelachs, Muscheln, Tintenfisch, Krill und Nordseegarnelen (tiefgekühlte Futtermittel). Das Becken bietet verschiedenartige Strukturen. Kunstfelsen formieren sich zu Halbinseln, Überhängen und Höhlen. Kunstalgen bieten Deckung und Schutz. Der Bodengrund ist von feinem Sand bedeckt. Auf dem Kunstfelsen sind lebende Miesmuscheln *(Mytilus edulis*) angesiedelt.

Die Aufzuchtbecken für die überführten Rocheneier und Jungtiere befinden sich in dem Quarantänebereich (Abb. 2), der über eine separate Kühlung und Filterung mit Abschäumer und Ozon, Rieselfilter sowie eine UV-C-Anlage verfügt.

Abb. 2: Aufzuchtbecken mit den für die Dauer der gesamten Inkubation aus dem Elterntierbecken überführten und fixierten Rocheneiern. Foto: Finn Wendt

Fig. 2: Rearing tank with the skate eggs transferred from the parent tank and fixed for the duration of the entire incubation. Photo: Finn Wendt

Handling der Rocheneier

Die Entnahme der Rocheneier aus dem Elterntierbecken erfolgte durch Taucher in regelmäßigen sieben- bis zehntägigen Intervallen. Es folgte eine direkte Überführung in das Aufzuchtbecken. Die Rocheneier wurden mit Hilfe von Kabelbindern und einer eingeschweißten Nummer zur Identifikation an einer Stange oder dem Plastikgitter befestigt. Die Befestigung erfolgte an den Haftfäden oder an einer der vier Eispitzen (Abb. 3).

Mögliche Luftblasen in der Eihülle wurden durch vorsichtiges Drücken entfernt, sodass diese an den Eispitzen entweichen konnten. Handling und Transport derEier erfolgten jedoch stets unter Vermeidung einer direkten Luftexposition.

Die geschlüpften Jungtiere wurden nach 12-24 Stunden in ein Aufzuchtbecken überführt. Die ersten Tage wurden sie mit lebenden Mysis gefüttert, nach einer Woche mit aufgetauten Mysis und Krill und später je nach Größe der Tiere mit passenden Futterstückchen von Seelachs, Tintenfisch, Muscheln und Nordseegarnelen.

Dokumentation der Embryonalentwicklung

Die Beurteilung einer Befruchtung und der Entwicklungsstadien erfolgte über die gesamte Entwicklungsdauer. Mit einem Skalpell wurden Reste der Haftfäden sowie Algen an der Oberfläche der Eihülle entfernt. Für eine optische Untersuchung des Embryos erfolgte ein Durchleuchten der Eier mit einer Unterwassertaschenlampe oder es wurde ein Leuchttisch verwendet. Für eine Größenmessung wurde ein Glasaquarium auf Millimeterpapier genutzt. Bei der Wiegung wurden die Eier kurzzeitig aus dem Wasser entnommen, waren aber bei der Überführung stets von Wasser benetzt. Von Interesse waren strukturelle Veränderungen, Adern oder identifizierbare Bewegungen eines möglichen Embryos (Luer et al., 2007). Für

Abbildung 11 wurde mit einem Skalpell in ein dreiwöchiges Ei zur Entwicklungsdokumentation eine Öffnung geschnitten und mit Folie verklebt. 14 Tage später verendete dieser Embryo.

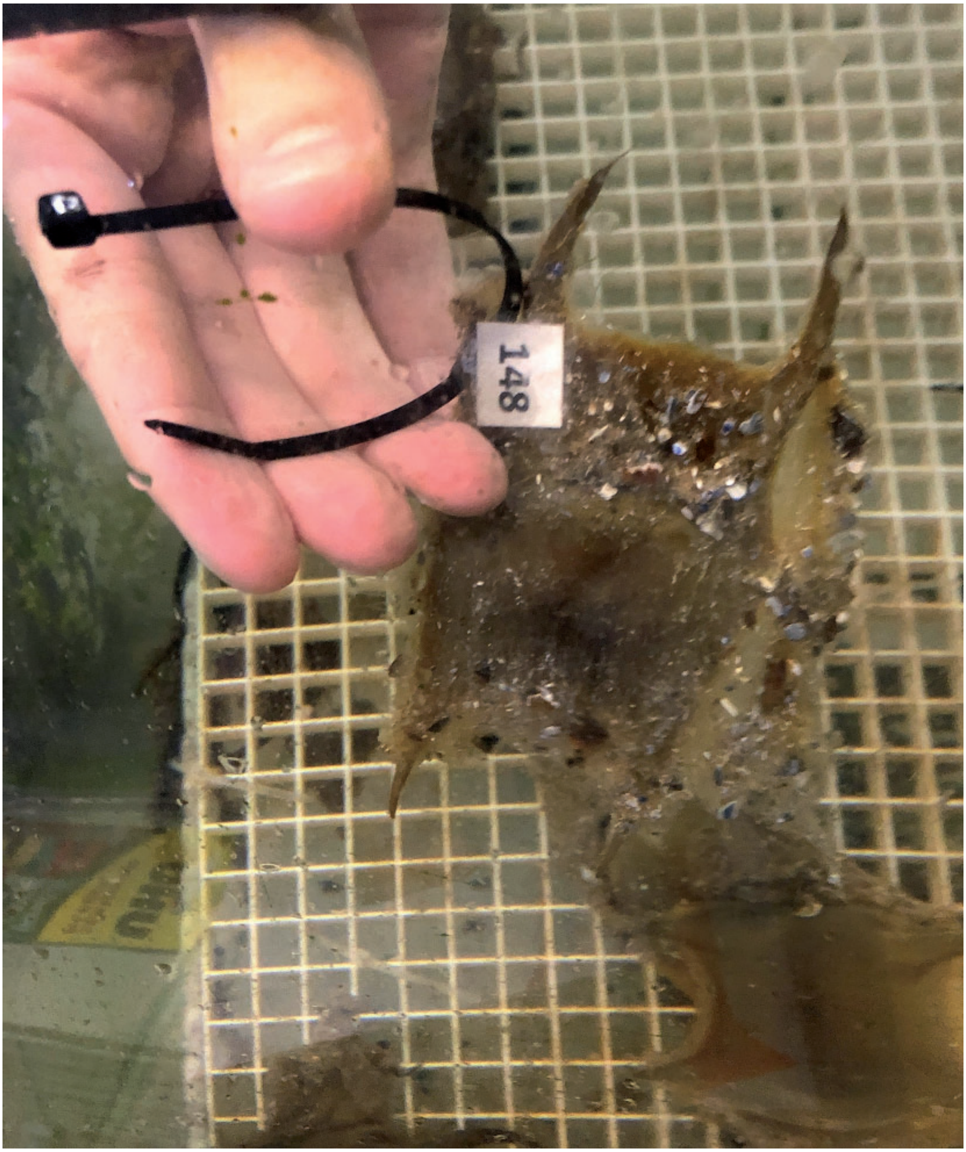


Abb. 3: Handling eines der überführten Rocheneier. Kabelbinder für lockere Fixierung am Gitter. Der Kabelbinder wurde zwischen Eihülle und Haftfäden fixiert. Ein laminiertes Nummernschild dient der Identifikation. Foto: Finn Wendt

Fig. 3: Handling one of the transferred skate eggs. Cable tie for loose fixation on the grid. The cable tie was fixed between the egg shell and the adhesive threads. A laminated plate is used for identification. Photo: Finn Wendt

Ergebnisse und Diskussion

Auswertung von den Orten der Eiablage und der Befruchtungsrate

Es konnten Eier an den Felsstrukturen, an den Wänden, in den Kunstalgen und auf dem Sandboden nachgewiesen werden. Viele Eier wurden durch Tiere oder Strömung von ihrer eigentlichen Position gelöst. Es ist naheliegend, dass die Weibchen durch Überschwimmen von Strukturen die Chance zur Befestigung der Eier erhöhen. Bei der Ablage auf dem Sandboden besteht die Gefahr, dass die Eier von Sand bedeckt werden und sich nicht entwickeln können. In der Natur nutzen Nagelrochen ein breites Spektrum an Strukturen (Maia et al., 2015).

Die aus dem Elterntierbecken überführten Rocheneier wurden auf ihren Befruchtungszustand untersucht (Abb. 4). Die Feststellung einer Befruchtung erfolgte optisch durch die Identifizierung einer Bewegung des Embryos (Abb. 5).

Bei der Betrachtung der Datenlage konnten sowohl in der Anzahl der gelegten Eier als auch in den Befruchtungsraten große Schwankungen zwischen den Monaten festgestellt werden. Im gesamten Untersuchungszeitraum wurden insgesamt 217 Eier gelegt, was unter der Annahme einer gleichmäßigen Verteilung zwischen beiden Weibchen etwa 108 Eiern pro Tier entspricht. Zu beachten ist, dass keine Zuordnung der Eier zu dem jeweiligen Muttertier erfolgen konnte. Es ist nicht auszuschließen, dass die Weibchen individuell jeweils eine unterschiedliche Anzahl an Eiern legten. Bei beiden adulten weiblichen Tieren konnten Eier in der Kloake identifiziert werden, jedoch ist nicht nachgewiesen, ob beide Weibchen auch befruchtete Eier legen können. Bekannt ist, dass eine Abhängigkeit zwischen der Größe der Elterntiere und der zu erwartenden Anzahl an gelegten Eiern besteht (Holden, 1975).

Im Januar waren zwei von insgesamt 17 Rocheneiern befruchtet, im Februar vier von insgesamt 20 und im März zwei von insgesamt 32 Eiern. Von April bis August wurden keine befruchteten Eier gelegt. Im April wurden die meisten Eier gelegt (41), gefolgt von Juni (37), Juli (24) und Mai (22). Im September wurden elf Eier gefunden, von denen vier befruchtet waren. Im November und Dezember wurden keine Eier gelegt. Die beiden weiblichen Tiere haben im Untersuchungszeitraum insgesamt 217 Eier gelegt.

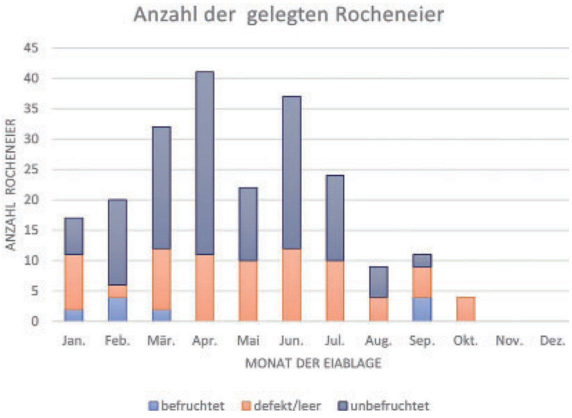


Abb. 4: Gesamtzahl an gelegten Eiern im jahreszeitlichen Verlauf sowie Differenzierung zwischen befruchteten, unbefruchteten sowie beschädigten/leeren Rocheneiern.

Fig. 4: Total number of eggs laid over the course of the season and differentiation between fertilized, unfertilized and damaged/empty skate eggs.

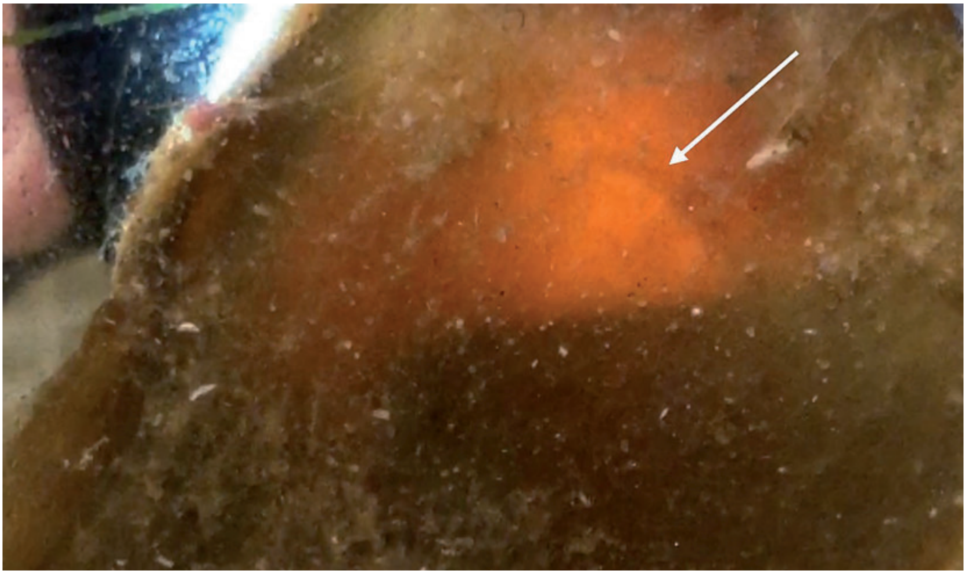


Abb. 5: Embryo in einer frühen Entwicklungsphase (Alter: 24 Tage); Bewegung einer feinen, länglichen Struktur (s. Markierung). Foto: Finn Wendt

Fig. 5: Embryo in an early stage of development (age: 24 days); movement of a fine, elongated structure (see marking). Photo: Finn Wendt

Vergleichende Untersuchungen mit Populationen vor der englischen Küste geben eine Anzahl von 141,6 Rocheneiern pro Individuum an, wobei in dieser Untersuchung ausschließlich Eier zwischen Februar und September gelegt wurden. Die maximale Anzahl wurde demnach im Juni gelegt (30), gefolgt von Mai (26) und Juli (25) (Holden, 1975). Eine weitere Untersuchung aus Südfrankreich (Languedoc) nennt eine durchschnittliche Anzahl von 215 Eiern (108-262) im Jahr pro Weibchen (Capapé et al., 2007).

Die höchste Befruchtungsrate mit 36,4 % konnte bei einer durchschnittlichen Temperatur von 15,92 °C im September nachgewiesen werden (Abb. 6). Die geringste Befruchtungsrate lag im

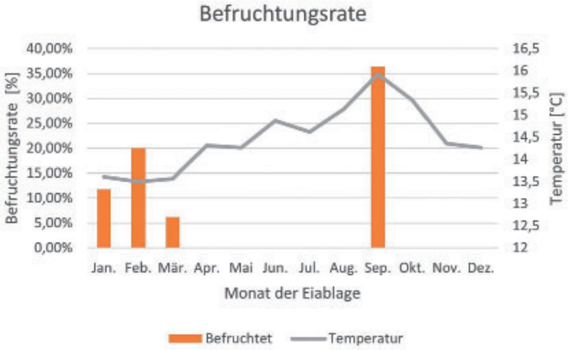


Abb. 6: Befruchtungsrate der gelegten Eier im jahreszeitlichen Verlauf mit der dazugehörigen durchschnittlichen Temperatur im Elterntierbecken.

Fig. 6: Fertilization rate of the eggs laid over the course of the season with the corresponding average temperature in the parent animal tank.

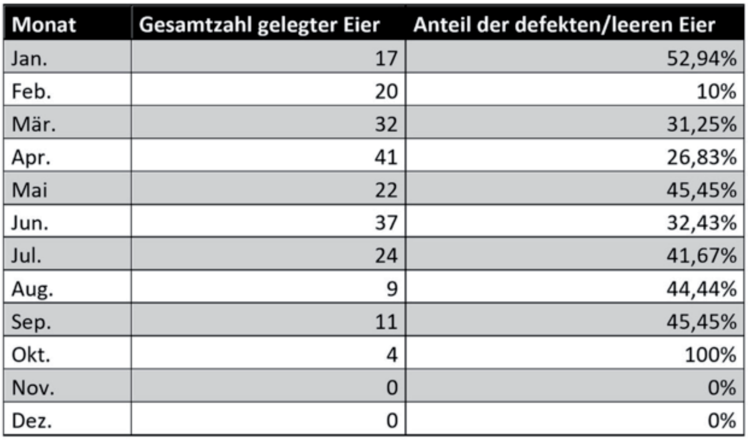
März mit 6,25 % bei durchschnittlich 13,56 °C. Im Januar lag die Rate bei 11,76 % (13,6 °C) und im Februar bei 20 % (13,5 °C). Auffällig ist auch hier die hohe Varianz zwischen den Monaten. Die maximale Befruchtungsrate trat in der Bremerhavener Untersuchung im September mit 36 % auf. Zu beachten ist hierbei die geringe Gesamtzahl an Eiern (11).

Ellis & Shackley (1995) nennen eine Befruchtungsrate von 73 % bei Untersuchungen an vor Wales gefangenen Nagelrochen. Ein variabler Parameter beim Vergleich verschiedener Untersuchungsgruppen ist die Temperatur, welcher die Elterntiere ausgesetzt waren. Die zum Vergleich herangezogenen Untersuchungen weisen entweder eine konstante und niedrigere Temperatur auf (Henard et al., 2020), oder orientieren sich an den lokalen Gegebenheiten im Untersuchungsgebiet. Verglichen mit der Temperatur in der Bremerhavener Studie war die Temperatur während der Wintermonate in sämtlichen Vergleichsuntersuchungen geringer. Der offensichtlich positive Einfluss der niedrigen Temperatur auf die Befruchtungsrate sollte in folgenden Zuchtbemühungen berücksichtigt werden. Die Anzahl der Eier war ähnlich wie im Freiland, daher ist sie offenbar unabhängig von der Temperatur. Für die Beurteilung der Daten sollten weitere Faktoren in Betracht gezogen werden, da z.B. die Anzahl an gelegten Eiern auch abhängig von der Größe und dem Alter der Tiere ist, wobei die Gesamtzahl an Eiern positiv mit der Größenzunahme korreliert (Holden, 1975; Saglam & Ak, 2012). In der Studie wurden männliche und weibliche Tiere beprobt und auf ihre Fruchtbarkeit untersucht. Die Auswertung ergab, dass die Weibchen 720 mm bis 930 mm lang waren und die Männchen 680 mm bis 920 mm. Die minimale Größe, bei welcher 50% der weiblichen Tiere geschlechtsreif waren, wurde in britischen Gewässern mit 720 mm und in den irischen Gewässern mit 718 mm angegeben (Gallagher et al., 2004; Holden, 1975).

Mit 100 % war im Oktober bei insgesamt vier gelegten Eiern der größte Anteil defekt, gefolgt vom Januar mit 53 %. Der geringste Anteil an defekten Eiern lag mit 10 % im Februar vor. Die übrigen Monate wiesen Raten zwischen 27 % (April) und 45 % (September) auf (Tab. 1).

Tab. 1: Gesamtzahl der gelegten Eier und dem jeweiligen prozentualen Anteil an defekten Eiern im jahreszeitlichen Verlauf.

Tab. 1: Total number of eggs laid and the respective percentage of defective eggs over the course of the season.



Monat	Gesamtzahl gelegter Eier	Anteil der defekten/leeren Eier
Jan.	17	52,94%
Feb.	20	10%
Mär.	32	31,25%
Apr.	41	26,83%
Mai	22	45,45%
Jun.	37	32,43%
Jul.	24	41,67%
Aug.	9	44,44%
Sep.	11	45,45%
Okt.	4	100%
Nov.	0	0%
Dez.	0	0%

Abhängig vom Ablage- bzw. Entnahmeort der Rocheneier konnten verschiedene mechanische Beschädigungen der Eihülle festgestellt werden. Untersuchungen von angespülten Nagelrocheneiern vor der niederländischen Küste ergaben, dass 29 % der vorgefundenen Eier Spuren einer mechanischen Beschädigung aufwiesen oder komplett beschädigt waren, wobei diese

Schäden auf Prädatoren zurückzuführen waren (Schröder et al., 2021). Das gehäufte Auftreten von Deformierungen und das Fehlen von Bestandteilen der Eihülle im Aquarium lässt auf einen Zusammenhang mit dem Entnahmeort schließen. Im Becken gibt es eine Vielzahl an lebenden Organismen. Neben den Nagelrochen leben in dem Aquarium Kleingefleckte Katzenhaie, Doraden, Meeräschen, verschieden Arten von Lippfischen, Streifenbarben, Graue und Rote Knurrhähne, Hummer, Taschenkrebse und Seesterne. Diese Arten könnten aufgrund ihrer z.T. benthischen Lebensweise für die Beschädigungen verantwortlich sein. Die Benetzung der Eihülle mit Eigelee lässt auf grundsätzlich intakte Eier schließen, welche vermutlich erst nach der Ablage beschädigt wurden. Das Aussaugen der Dotter durch Rochen konnte beobachtet werden (pers. Mit. Rune Kristiansen, Kattegatcenter, DK). Unter Annahme dieser Zusammenhänge könnte der Zuchterfolg durch eine Verringerung von Einflüssen, welche zu einer Beschädigung der Eier führen, erhöht werden.

Es ist zu beachten, dass die festgestellte Befruchtungsrate aufgrund des signifikanten Anteils an beschädigten Eiern von der reellen Befruchtungsrate abweichen könnte.

Entwicklungsdauer der Eier

Die durchschnittliche Entwicklungsdauer lag bei 117,8 Tagen (± 12,2 Tage, n = 8), wobei die maximale Dauer 138 Tage und die geringste 96 Tage betrug (Abb. 7).

Die in der Untersuchung betrachteten Eier wurden im Zeitraum zwischen dem 25. Januar und dem 25. Februar 2023 gelegt. In vergleichenden Untersuchungen im französischen Aquarium Nausicaá wurde bei einer Temperatur von 10 °C eine durchschnittliche Entwicklungsdauer von 308 Tagen ermittelt (Henard et al., 2020).

Die Temperatur im Elternbecken und auch im Aufzuchtbecken in der Bremerhavener Untersuchung scheint eine verkürzende Wirkung auf die Entwicklungsdauer zu bewirken. Vergleichende Ergebnisse konnten (Ellis & Shackley, 1995) gewonnen werden, welche ebenfalls eine kürzere Entwicklungszeit bei steigender Temperatur beobachtet haben. So wurde bei einer Temperatur von 9,3 °C eine Entwicklungszeit von 18 bis 20,5 Wochen dokumentiert, wohingegen bei den bei einer Temperatur von 15,2 °C bis 16,3 °C gehälterten Eiern eine Entwicklungsdauer von 16 bis 17,5 Wochen dokumentiert wurde (Ellis & Shackley, 1995).

Im Zusammenhang mit der Inkubationsdauer war die Größe (Länge und Gewicht) der Jungtiere zum Zeitpunkt der Geburt von Interesse. Nach dem Schlupf der Jungtiere aus der Eihülle erfolgte bei der Überführung in das Aufzuchtbecken eine erste Wiegung und Messung. Das

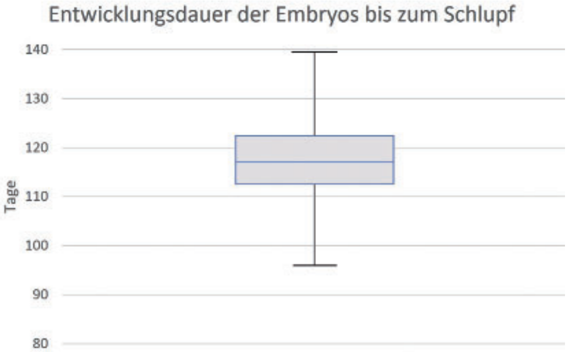


Abb. 7: Durchschnittliche Entwicklungsdauer der Rocheneier bis zum Schlupfzeitpunkt der Jungtiere.
Fig. 7: Average development time of the skate eggs until the hatching of the young animals.

durchschnittliche Gewicht nach dem Schlupf lag bei 11,2 g (± 1,4 g, n = 8). Das maximale Gewicht lag bei 14,36 g, das geringste bei 9,34 g.

Die Längenbestimmung (Schwanz bis Rostrum) ergab eine Länge von 12,94 cm (± 0,3 cm, n = 8) nach dem Schlupf mit einer maximalen Länge von 13,5 cm und einer minimalen von 12,7 cm. Nach einem Monat lag die durchschnittliche Länge bei 18,01 cm (± 2,8 cm, n = 8).

Verglichen mit den Untersuchungen in der SUMARiS-Studie (Henard et al., 2020) in welcher ebenfalls die Reproduktion von Nagelrochen in menschlicher Obhut untersucht wurde, ist das durchschnittliche Gewicht der Jungtiere bei der Geburt um 0,8 g geringer (Henard et al., 2020). Die durchschnittliche Länge der Jungtiere bei der Geburt war um 0,2 cm geringer. Die Rocheneier in der SUMARiS-Studie wurden bei einer geringeren Temperatur (10 °C) inkubiert und hatten eine längere Entwicklungsdauer. Der Effekt einer geringeren Größe der Jungtiere beim Schlupf bei zunehmender Temperatur konnte bei *Raja microocellata* nachgewiesen werden (Hume, 2019). Eine identische Auswirkung auf *R. clavata* scheint denkbar. Ein Merkmal unmittelbar nach dem Schlupf der Rochen war ein nahezu komplett aufgenommener äußerer Dotter bei allen Jungtieren. Der innere Dotter war im Vergleich deutlich ausgeprägter. Innerhalb der ersten Wochen wurde auch der innere Dotter komplett aufgenommen und war nicht mehr zu erkennen (Abb. 8).

Nach dem Schlupf konnten die jungen Rochen problemlos mit zunächst lebenden *Mysis*, später mit kleingeschnittenem Frostfutter aufgezogen werden. Bei einer Hälterung von 16 °C nahmen sie bis zu einem Alter von einem Monat linear zu, danach deutlich schneller bis zu einem Gewicht von 88 g und einer Länge von 26,5 cm nach sechs Monaten. Das ist für eine mögliche Auswilderung interessant, wenn man die Frage stellt, in welchem Stadium die Auswilderung vorgenommen sollte. Als Ei, zur besseren Adaptation an die regionalen Gegebenheiten oder vor dem Hintergrund, dass adulte Weibchen den Platz des eigenen Schlupfes zur Eiab-

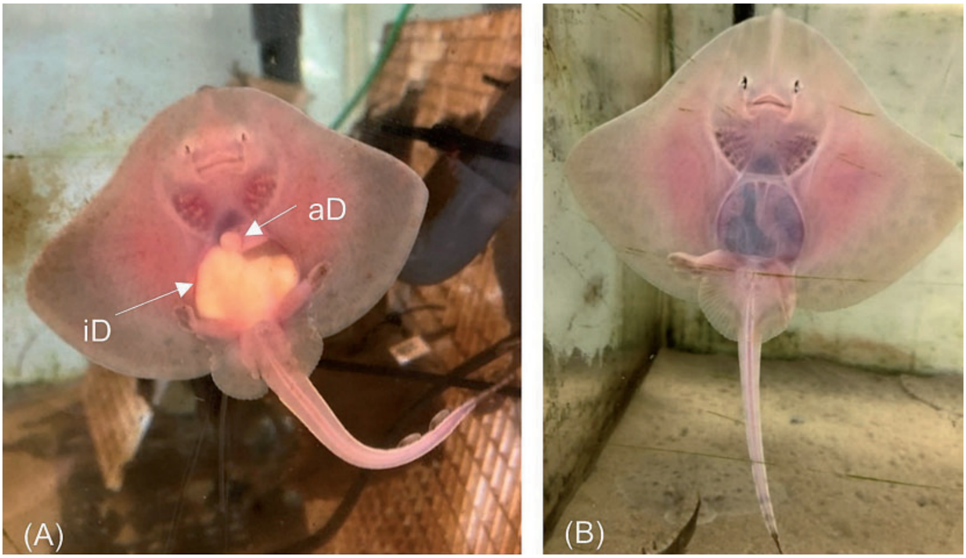


Abb. 8: Jungtiere zu verschiedenen Zeitpunkten nach dem Schlupf. **A:** Jungtier 24 h nach Geburt mit innerem Dotter (iD) und äußerem Dotter (aD). **B:** Jungtier nach vier Wochen ohne erkennbaren inneren/äußeren Dotter. Fotos: Finn Wendt

Fig. 8: Hatchlings at different times after hatching. **A:** Hatchling 24 h after birth with inner yolk (iD) and outer yolk (aD). **B:** Hatchling after four weeks without recognizable inner/outer yolk. Photos: Finn Wendt

lage aufsuchen könnten, als frisch geschlüpftes Jungtier oder in einem Alter von sechs Monaten, da dann der Verlust durch Prädatoren deutlich geringer sein sollte. In Vorversuchen hatte bei zwei Nachwuchsrochen im Alter von einem Monat die Reduktion der Temperatur von 15 °C auf 11 °C zu einer Abnahme der Gewichte geführt (Kück, pers. Mit.). Bei der langsamen Erhöhung auf 15 °C nahmen die Tiere wieder zu.

Dokumentation der Embryonalentwicklung

Zu Beginn der Inkubation war eine klare Erkennbarkeit der inneren Strukturen gegeben. Es konnte in diesem Stadium eindeutig zwischen komplett leeren Eiern und solchen mit Dotter unterschieden werden (Abb. 9). In den unbefruchteten Rocheneiern konnte im weiteren Verlauf der Zersetzungsprozess des Dotters festgestellt werden.

Größe, Gewicht und Optik der Rocheneier konnten keine Rückschlüsse auf eine erfolgreiche Befruchtung liefern.

Nach drei Wochen (20 Tage ± 10 Tage, n = 4) konnten erste Bewegungen eines Embryos festgestellt werden. Dabei war ein etwa 1 Millimeter breiter, länglicher Embryo zu erkennen, wobei dieser sich in Schwanzteil und Kopf differenzieren ließ (Abb. 5).

Im weiteren Wachstumsverlauf war, abhängig von der Positionierung des Embryos, ein Kopfbereich mit Augen identifizierbar (Abb. 10). Der Embryo schien sich oftmals frei oberhalb des Dotters zu bewegen. Dabei konnten von dem Schwanzteil schlagende, wellenförmige Bewe-

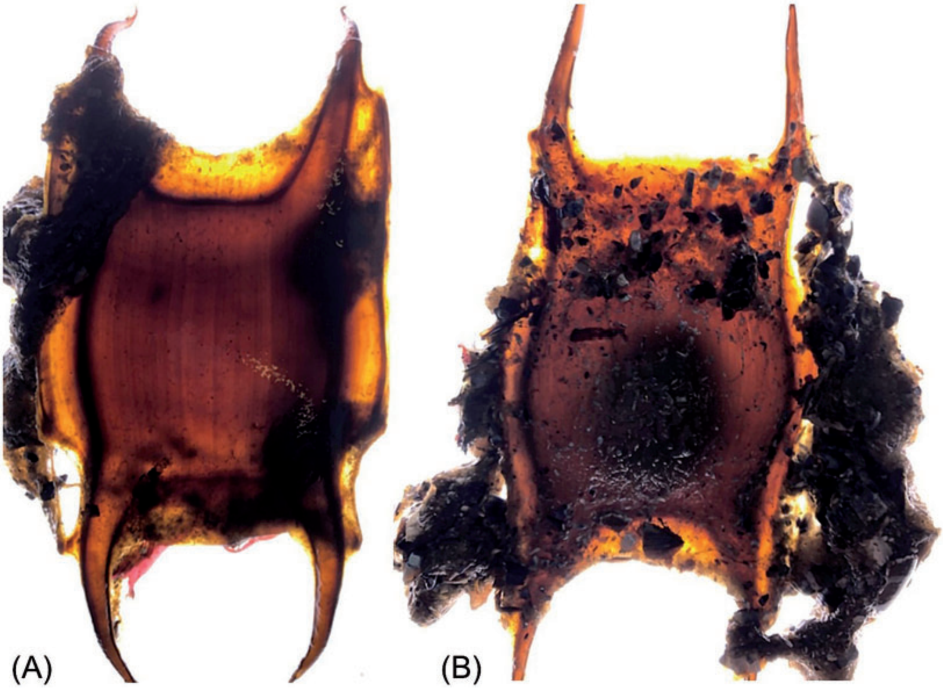


Abb. 9: Rocheneier zu Beginn der Inkubation. **A:** leere Eikapsel. **B:** Eikapsel mit Dotter. Fotos: Finn Wendt

Fig. 9: Skate eggs at the beginning of incubation. **A:** empty egg capsule. **B:** egg capsule with yolk. Photos: Finn Wendt

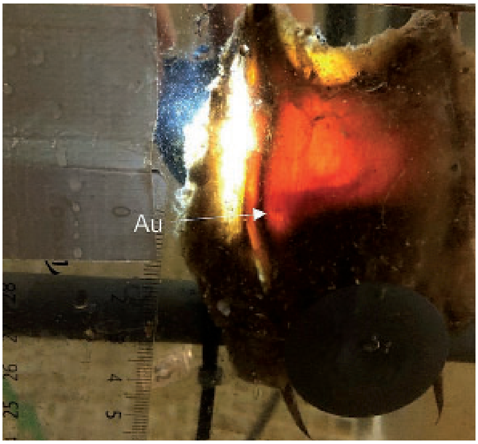


Abb.10: Embryo im Alter von vier Wochen auf Dotter liegend mit Verdickung im Kopfbereich und identifizierbaren Augen (Au). Ohne erkennbare Ausdifferenzierungen der Brustflossen. Foto: Finn Wendt
Fig.10: Embryo at the age of 4 weeks lying on yolk with thickening in the head area and identifiable eyes (Au). Without recognizable differentiation of the pectoral fins. Photo: Finn Wendt

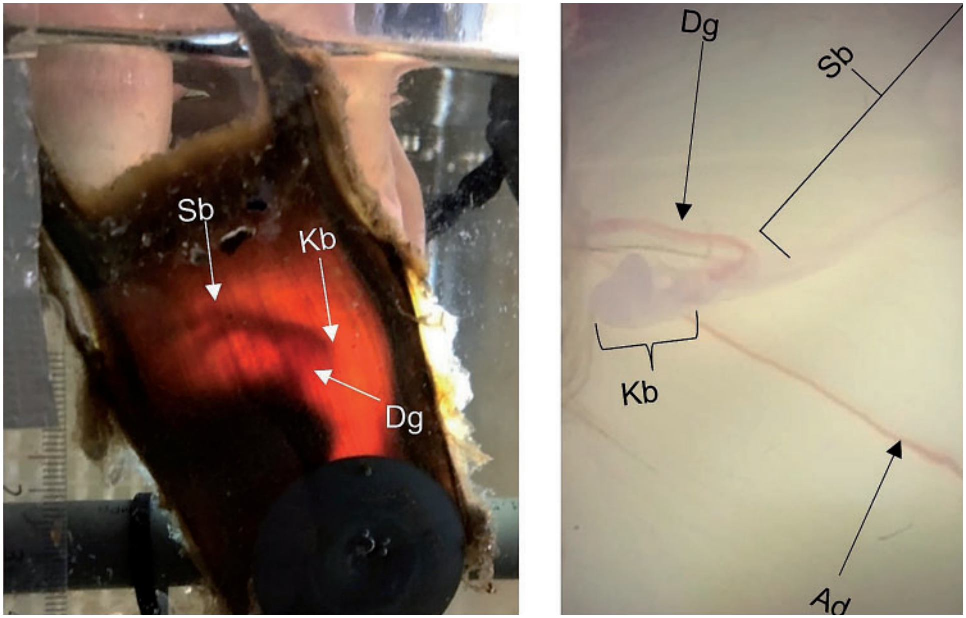


Abb. 11: Embryonen nach 6-wöchiger Inkubation der Eier. **A:** Embryo mit Dottergang (Dg) zwischen Embryo und Dottersack, Kopf (Kb) und Schwanzbereich (Sb). **B:** Embryo im frühen Entwicklungsstadium mit Kopf (Kb) und Schwanzbereich (Sb) mit einem Dottergang als Verbindung zum Dottersack mit feinen Adern (Ad). Fotos: Finn Wendt
Fig. 11: Embryos after 6 weeks of egg incubation. **A:** Embryo with yolk duct (Dg) between embryo and yolk sac, head (Kb) and tail area (Sb). **B:** Embryo in the early stage of development with head (Kb) and tail area (Sb) with a yolk duct as a connection to the yolk sac with fine veins (Ad). Photos: Finn Wendt

gungen beobachtet werden, die für die Versorgung des Embryos mit Sauerstoff notwendig sind (Leonard et al. 1999).

Mit zunehmendem Wachstum war nach sechs Wochen der Dottergang zwischen Embryo und Dottersack zu erkennen (Abb. 11).

Ab der 8. Woche konnten, abhängig von der exakten Lokalisation des Embryos, die entwickelten Brustflossen dokumentiert werden (Abb. 12). Ebenfalls war es möglich das Rostrum und die Augen der Tiere zu identifizieren. Der Embryo befand sich in diesem Entwicklungsstadium oftmals liegend auf dem Dotter. Der Rochenschwanz war wahlweise in Ruheposition um den Körper geschlungen oder es konnte eine raumfüllende, schlagende Bewegung im Ei festgestellt werden.

Ein Schlagen des Schwanzes konnte während der gesamten Entwicklung festgestellt werden. Die Bewegung wurde aber nach 30 Sek. der Lichtexposition eingestellt. Nach einer Unterbrechung von mehreren Minuten konnte oftmals eine erneute Bewegung festgestellt werden. Es

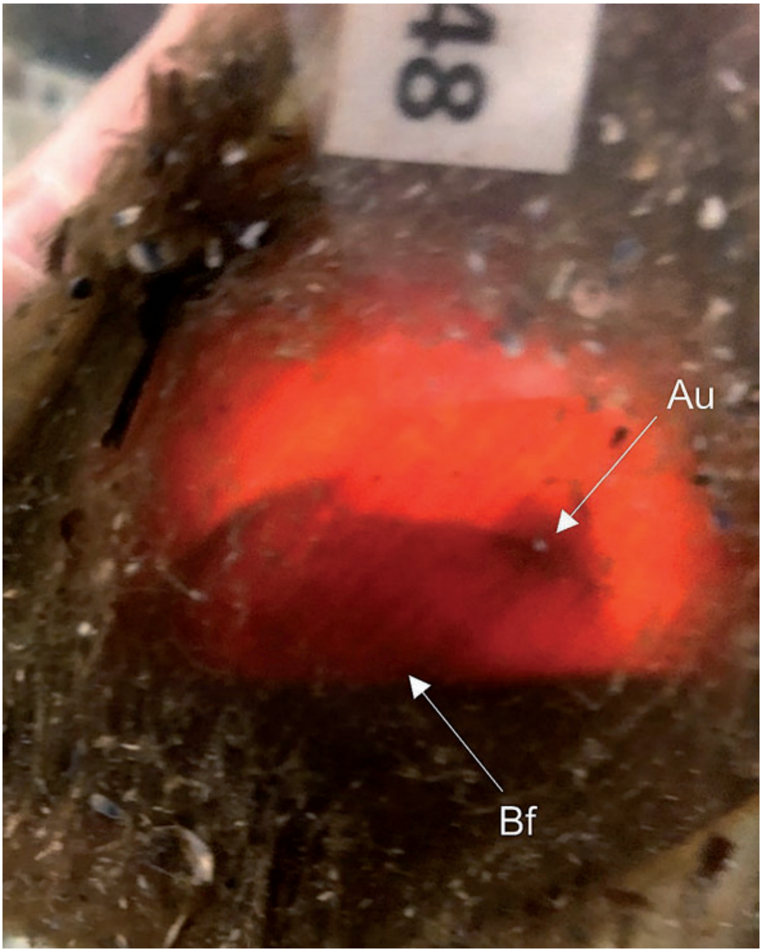


Abb. 12: Embryo im Alter zwischen 8-10 Wochen auf dem Dotter liegend mit Augen (Au) und Brustflosse (Bf). Foto: Finn Wendt

Fig. 12: Embryo between 8-10 weeks old lying on the yolk with eyes (Au) and pectoral fin (Bf). Photo: Finn Wendt

ist bekannt, dass elektromagnetische Wellen zu einem Erstarren der Embryonen bei *R. clavata* führen können und die Regenerationsfähigkeit von diesem Zustand auch abhängig vom Alter der Embryonen ist (Ball et al., 2016). Die Beobachtungen könnten Hinweise liefern, dass die direkte Exposition mit Licht zu einer ähnlichen Reaktion führen könnte. Die Bewegung des Rochenschwanzes eignet sich zur Vitalitätskontrolle des Embryos. Abhängig von der exakten Positionierung des Embryos war der restliche Körper nicht zu erkennen.

Auffällig war die Positionierung der Brustflossen. Wie in Abbildung 13 dargestellt, überschlugen diese den restlichen Körper. Dies führte dazu, dass nur kleine Ausschnitte des Kopfbereiches, zum Beispiel das Rostrum oder ein Teil der Brustflossen, erkennbar waren. Weitere Körperregionen, inklusive des Dotters, waren nicht sichtbar. Morphologisch waren bis zum Schlupf keine weiteren Veränderungen feststellbar. Der erkennbare Entwicklungszustand ist ähnlich zum Zustand der frisch geschlüpften Rochen.

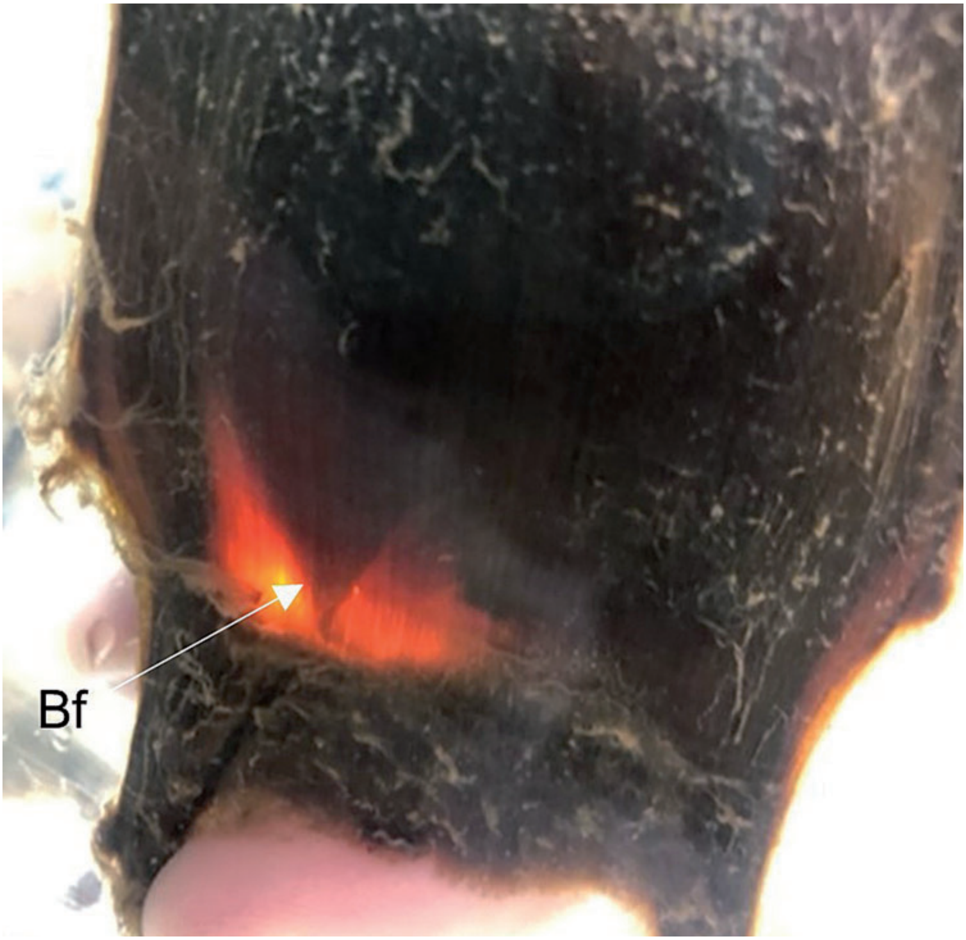


Abb. 13: Mindestens 15 Wochen alter Embryo mit erkennbarem Teilbereich der aufgerollten Brustflossen (Bf). Foto: Finn Wendt

Fig. 13: At least 15-week-old embryo with recognizable part of the rolled-up pectoral fins (Bf). Photo: Finn Wendt

Die äußerliche Begutachtung der Rocheneier während der Inkubation ergab einige Auffälligkeiten. Auf der Oberfläche der Eihülle konnten mykologische Kontaminationen und verschiedene Polychaeta-Arten nachgewiesen werden. Diese siedelten sich überwiegend an den Haftfäden und zu einem geringeren Anteil direkt auf der Eihülle an. Diese wurden meist an beschädigten und leeren Rocheneiern gefunden. Unabhängig vom Befruchtungszustand konnte mit zunehmender Inkubationsdauer auf den Haftfäden die Entstehung mikrobieller Kolonien festgestellt werden. Es konnten jeweils keine negativen Einflüsse auf die Entwicklung der Embryonen festgestellt werden.

Fazit

Die durchgeführten Untersuchungen konnten hilfreiche Erkenntnisse für eine erfolgreiche Zucht von *R. clavata* liefern. Das Durchleuchten der Rocheneier zur Dokumentation der Embryonalentwicklung und zur Identifikation von befruchteten Eiern hat sich als geeignete Methode herausgestellt. Dabei konnte festgestellt werden, dass die Embryonalentwicklung während des kompletten Entwicklungszeitraumes beobachtbar war. Es konnte effizient zwischen befruchteten und unbefruchteten Rocheneiern differenziert werden und es war eine Zuordnung des Entwicklungsstadiums möglich. Ebenfalls war es möglich, abgestorbene Embryonen zu identifizieren. Es wurde im Untersuchungszeitraum eine Gesamtzahl an Eiern gelegt, welche bei Betrachtung der vergleichenden Literatur den Erwartungswerten entsprach und diese zum Teil auch übertraf.

Entscheidend für einen Zuchterfolg scheint eine Erhöhung der Befruchtungsrate. Eine schnellstmögliche Entnahme der Rocheneier aus dem Zuchtbecken, um eine nachträgliche mechanische Beschädigung zu verhindern, kann als ein relevanter Faktor betrachtet werden. Die Untersuchungen zeigen, dass die Temperatur von besonderer Relevanz ist. Es könnte für Zuchtbedingungen sinnvoll sein, sich möglichst nah an den natürlichen Gegebenheiten zu orientieren und die jahreszeitliche Variabilität der Temperatur nachzubilden. Speziell die niedrige Temperatur im Winter sollte umgesetzt werden. Die Temperatur während der Inkubation der Rocheneier scheint sowohl Einfluss auf die Entwicklungsdauer der Embryonen als auch auf Größe und Gewicht der Jungtiere zum Zeitpunkt des Schlupfes zu haben. Ein vorsichtiges Bewegen der Eier beim Durchleuchten sowie ein Entfernen der Haftfäden und der Pilzkolonien schien keine Auswirkungen auf die Entwicklung zu haben.

Aufgrund der aktuellen Bestandssituation von *R. clavata* in der Deutschen Nordsee könnten die Zuchtbemühungen mit einem Fokus auf eine mögliche Auswilderung liegen. Neben der notwendigen Markierung der Tiere sollte daher das genetische Profil der Eltern- und Jungtiere bestimmt werden, um eine maximale genetische Diversität zu erhalten und sie mit lokalen Populationen im Auswilderungsgebiet vergleichen zu können. Wenn eine Auswilderung in Zusammenarbeit mit den zuständigen Behörden in Betracht gezogen wird, hat sie nach den „Guidelines for Reintroductions and other Conservation Translocations (2013) zu erfolgen. Nur eine Auswilderung in Schutzgebieten ohne Grundnetzbefischung und das Monitoring von markierten Tieren könnten weitere Daten liefern, z.B. auch zu Wanderungsbewegungen, um wieder eine stabile Population in der Deutschen Nordsee zu etablieren.

Danksagung

Die Autoren danken Frau Prof. Dr. Laurie Hofmann für hilfreiche Diskussionen, dem Aquarienteam des Zoo am Meer, Herrn Philipp Kleppe, Herrn Olaf Mertes und Herrn Tim Troegel für

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Summary

Thornback rays *Raja clavata* lived in large numbers in the North Sea at the beginning of the 20th century. Due to excessive fishing with bottom trawls and bycatch, they are threatened with extinction in the German North Sea, so that a possible reintroduction could make sense. The results are discussed in the context of a possible optimization of breeding in zoo aquariums and thus increasing the number of young animals for a possible release into the wild.

To this end, the parameters for breeding at Zoo am Meer were reviewed and the development of the eggs and juveniles were analyzed. At Zoo am Meer, 2.2 thornback rays are kept at 13 °C in winter and 16 °C in summer. The total number of eggs is higher than in comparative studies, while the fertilization rate is lower than in studies where the animals are kept at 10 °C all year round or at 4 °C in winter and 16 °C in summer. Many eggs were damaged by numerous co-inhabitants in the display tank; in some cases the yolk was sucked out. The eggs should therefore be removed from the tank immediately. The young hatch at temperatures between 12 and 16 °C after an average of 119 days, but with 11.2 g they have a lower weight as in comparative studies with incubation at 10 °C and hatching after 308 days.

Fertilization can be determined after three weeks by the visible beating of the tail. When handling the eggs under light, the young animals stop moving their tails. The stages of development of the embryos could be determined by various characteristics. The weight gain of the hatchlings was not linear; after 30 days they grew significantly faster and reached an average weight of 88 g after 6 months.

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Creation of an Ethogram for Rock Hyrax (Procavia capensis) Based on a Group in Osnabrück Zoo (Germany): Social Behaviour

Erstellung eines Ethogramms für Klippschliefer (*Procavia capensis*) anhand einer Gruppe im Zoo Osnabrück: Sozialverhalten

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Abstract

The following study aims to establish an ethogram for social behaviour of rock hyraxes (*Procavia capensis*). The study's object was a group of rock hyraxes living in the Osnabrück Zoo. The group consisted of one adult male, five adult females (only four as of 2 April 2010) and four juveniles (2.2). The qualitative data collection was carried out from the 2 December 2009 until 27 April 2010. The individual behaviour was described in Höft & Gansloßer (2021).

The patterns of social behaviour were arranged into the categories of "sexual behaviour", "sociopositive behaviour", "play behaviour" and "agonistic behaviour" (with the classes "attack and threat behaviour" and "defensive behaviour") by using sequential analysis following Gerber (1976, according to Wilhelm & Gansloßer, 1989) and a binomial test. Therefore, actions and reactions of observed individuals, which were involved in dyadic interactions, were recorded from 13 January to 27 April 2010. In total, 334 hours were observed for the quantitative analysis, at which N = 75,647 (number of action-reactions pairs) was obtained.

Introduction

Rock hyraxes (*Procavia capensis*) are marmot-like or guinea-pig-like mammals. They weigh between 1.8 and 5.4 kg, with an average weight of 3.6 kg for females and 4.0 kg for males (Olds

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& Shoshani, 1982; Thenius & Hoeck, 1987). Their length varies between 30 and 58 cm (Olds & Shoshani, 1982). Hyraxes form a separate order within the class of mammals: Hyracoidea. Rock hyraxes are present in large parts of Africa and in parts of the Sinai and Arabian Peninsula (Rahm, 1964; Sale, 1966a; Taylor & Sale, 1969; Fourie, 1977; Olds & Shoshani, 1982; Estes, 1991; Butynski, 2015). They inhabit steppes, deserts and the edges of rainforests (Hahn, 1934; Coe, 1962; Fourie, 1977; Estes, 1991). They are very good climbers and jumpers (Coe, 1962). Their good climbing ability is due to adhesive forces: When they climb, they powerfully press their soles, which are moist due to the numerous sweat glands, against the substrate (e.g. rock) (Fischer, 1986). This enables the animals to climb even on "[…] stark geneigten bis senkrechten Flächen […]" (strongly inclined to vertical surfaces); Fischer, 1986, p. 49). Rock hyraxes have a dorsal organ that serves for visual and olfactory signalling (Sale, 1970b) (Fig. 1). It is located between the 14th and 18th thoracic vertebrae (Fischer, 2004). The dorsal organ is a glandular field (dorsal gland) surrounded by a ring of hair (dorsal patch) that is lighter or darker in colour than the surrounding fur (Fox, 1933; Rahm, 1964). When the rock hyrax is excited, the anterior and lateral hairs of the hair ring are erected, exposing the dorsal gland below (Sale, 1970b; Estes, 1991). Different signals can be attributed to defined set-up angles of the hairs of the dorsal patch. Thus, piloerection up to 45° means alarm, 90° threat and 180° appears during mate choice. In addition to the visual signal created by the erection of the differently coloured hairs, the glandular field is also exposed, thus intensifying the olfactory signal. The erection of the glandular hair is often supplemented by the erection of the hairs on the head and neck (Sale, 1970b).

Fig. 1: "Dorsal organ". Photo: S. Höft

The incisors are elongated in rock hyrax and between them is a diastema (Fischer, 1992, 2004; Fig. 2). The upper ones serve for defence, and the lower ones for grooming (Sale, 1966b). Rock hyraxes cannot maintain their body temperature as well as other mammals (Turner & Watson, 1965; Sale, 1970a; Hoeck, 1976d) and have a low heat tolerance (Louw et al., 1972). Regulation of their body temperature is mainly controlled by their sunbathing behaviour, by lying next to conspecifics in body contact or by frequenting shadowy areas under plants or in their caves (with a relatively constant microclimate; Mendelssohn, 1965; Sale, 1966a, 1970a; Louw et al., 1973). Rock hyraxes live in polygynous family groups with variable group sizes (Hoeck et al., 1982; Fourie & Perrin, 1987). A group consists of several adult females (older than 24 months), subadult animals (between 13 and 24 months old) and young animals (0 to 12 months old) of both sexes and a territorial male (Coe, 1962; Hoeck, 1982a; Hoeck et al., 1982; Fourie & Perrin, 1987). The IUCN status of the rock hyrax is "Least concern", because of the wide distribution, the wide range of habitats and the absence of major threats (Butynski et al., 2015).

Fig. 2: “Incisor”. Photo: S. Höft

There are some publications on social behaviour of rock hyraxes (Sale, 1970a, 1970b; Hoeck, 1976c, 1976d, 1978; Hoeck et al. 1982; Fourie & Perrin, 1987). Hoeck described the mating behaviour (Hoeck, 1976c, 1980) and the playing behaviour of free-ranging rock hyraxes (Hoeck, 1978, 1980). Only a few behavioural patterns were defined and described by him. Sale (1970a) described the thermoregulatory behaviour in social contexts. The meaning of the dorsal gland and patch in social contexts was described by Sale (1970b) but no behavioural patterns were defined. Studies about the acoustic communication were done by Fourie (1977), Koren & Geffen (2009b) and Weissman et al. (2019). However, in this study it was not possible to record sounds. Modern zoos have four main goals: conservation, education, research and entertainment (WAZA, 2005). To realise these goals, zoos have to establish self-sustaining ex-situ populations of animals which are preferably genetically diverse, and have to maintain high standards of animal keeping. Studbooks are the basis for the zoos’ ex-situ management of a species according to demographic and genetic criteria. The EAZA Small Mammal TAG recommend in their RCP (Regional Collecting Plan) the keeping of rock hyraxes and a monitoring level in the form of an ESB (European studbook). Recommendation criteria are educational reasons, for research purposes and that the species shall serve as a husbandry model for the future conservation of related, endangered species (Meike et al., 2012). The ESB for rock hyrax was managed by the Osnabrück Zoo from 2008 until 2012 and is currently managed by the Zoological Garden of Zagreb (Croatia). In recent years, rock hyraxes can be increasingly found in zoological facilities. According to the studbook, the number of zoos keeping rock hyraxes has increased from 14 (in 2006) to 27 (in 2009). Consequently, the number of animals increased from 101 to 265 (U. Magiera, personal communication). In 2019, 327 individuals were kept in 48 institutions (Beneta, 2019). In order to manage a particular species successfully, gathering extensive behavioural knowledge is a necessity (Eisenberg & Kleiman, 1977). For example, knowledge about the natural behaviour is important to build up stable breeding groups.

Keeping animals in species-appropriate exhibits, supplying them with species-appropriate feeding and a high level of animal welfare (Barber, 2009; Hill & Broom, 2009; Barongi et al., 2015; Mellor et al., 2015; EAZA, 2019) are important parts of good animal husbandry. In 2015, WAZA launched their animal welfare strategy, which shows the importance the zoo community places on animal welfare (Mellor et al., 2015). Measuring animal welfare is not easy (Mason & Mendl, 1993; Barber, 2009). The expression of natural behaviour is often seen as one important welfare indicator (Carlstead, 1996; Melfi & Feistner, 2002; Barber, 2009; Hill & Broom, 2009; Maple & Perdue, 2013), while exhibiting abnormal behaviour is considered a signal of poor well-being (Manteca et al., 2016). The World Organisation for Animal Health recognises the "Five Freedoms" as one of the guiding principles for animal welfare (World Organisation for Animal Health, 2019). The concept of the "Five Freedoms", formalised in 1979 in a press statement by the UK Farm Animal Welfare Council, defined one freedom as "[…] freedom to display most normal patterns of behaviour […]". Mellor & Beausoleil (2015) developed the concept further into the „Five Domains" which is part of the WAZA Animal Welfare Strategy (Mellor et al., 2015) and the EAZA Welfare policy (see "How to develop your animal welfare assessment programme", EAZA, 2024). Behaviour is one of the Five Domains. The EU Zoos Directive Good Practices Document also sees the display of natural behaviour as an important welfare indicator (European Union, 2015). Even though this approach is not without criticism (see Veasey et al., 1996), it is also used in legislation. The German Animal Protection Act, for example, requires behaviourally appropriate keeping of animals. Zoos are therefore also legally obligated to have knowledge about the natural behaviour of the animals they keep in order to ensure species-appropriate keeping and animal welfare. Knowledge about the behaviour of a species is necessary to design their exhibit in a species-appropriate fashion. Knowledge about social behaviour enables, among other things, the assessment of group compositions. Do the individuals harmonise with each other or do animals have to be removed from the group? The assessment of social behaviour is crucial for the breeding and welfare of the animals. In order to be able to make an assessment, the behaviour of an animal species must first be precisely described.

Play behaviour in particular is considered important in measuring animal welfare, as animals do not play when they are sick or stressed (Manteca et al., 2016). However, this is not unproblematic, because adult animals usually play less and play behaviour has been described almost exclusively in mammals and birds (Oliveira, 2010; Manteca et al., 2016). To know which behaviour patterns are considered play, one has to describe the entire behavioural repertoire.

Listing and describing every behavioural pattern of a species is done in an ethogram (Immelmann, 1982; Grier & Burk, 1992, Kappeler, 2006). Behavioural patterns are "[…] clearly defined, from each other distinguishable behavioural units" (Naguib, 2006, p. 70). A description of these has to be objective and without any appraising or interpretive comments. It is important that the described behavioural patterns are discrete units which have biological relevance and can be recognised by others (Naguib, 2006). After they are described, the behavioural patterns can be subsumed into categories (Grier & Burk, 1992). If such categories include behaviours with the same or similar objective and effect, they can be termed functional systems ("Funktionskreise" in German; Tembrock, 1974; Immelmann, 1982).

To define natural or normal behaviour and to determine behavioural diversity, an ethogram is necessary. In conclusion, an ethogram is helpful to judge animal welfare and is an important part in the definition of species-appropriate keeping. Furthermore, an ethogram is the basis for any behavioural study (Grier & Burk, 1992; Lehner, 1996) and therefore very important. Rock hyraxes are among the species for which no ethogram exists.

The observation period was outside the mating season, which is why only a few elements of "Sexual behaviour" could be observed. The young of the group (born April 2009) were already quite independent, so that birth and rearing behaviour patterns could also not be observed.

For the classification of the behavioural patterns into the categories "Sociopositive behaviour" and "Agonistic behaviour", the following hypotheses were established for the statistical analysis:

H_0: Whether behavioural element Y follows behavioural element X is random.

H_1: Whether behavioural element Y follows behavioural element X is not random, but there is a coupling between the two.

For the classification of the behavioural patterns of "Agonistic behaviour" into the categories "Attack and threat behaviour" and "Defence behaviour" the following hypotheses were formulated:

H_0: Behaviour X generates and terminates agonistic behaviours with equal frequency, i.e. the event under consideration occurs as often as expected.

H_1: Behaviour X frequently generates agonistic behaviour or frequently terminates agonistic behaviour, i.e. the event under consideration occurs frequently or less frequently than expected.

Materials and Methods

When creating the ethogram for social behaviour, no distinction was made between "attacking behaviour" and "threatening behaviour". Instead, the category "attacking and threatening behaviour" was formed. Together with the "Defensive behaviour" (behaviours that protect and defend), it forms the category "Agonistic behaviour" (Scott & Fredericson, 1951). "Agonistic behaviour" is opposed to the category "Sociopositive behaviour".

Data collection

At the time of observation at Osnabrück Zoo, the group of rock hyraxes consisted of one adult male, five adult females (four since 2 April 2010) and four adolescents (2.2). The indoor enclosure measured 17 m^2 and the outdoor enclosure 50 m^2. Only when the temperature was lower than 0 °C on consecutive days, the slide to the outdoor enclosure was closed.

The behaviours were observed by S. Höft from the visitor hall or from the visitor path in front of the outdoor enclosure and only during times when the visitor hall was open. For the qualitative description of behavioural patterns, data were collected using the ad libitum-method (Altmann, 1974) from 2 to 19 December 2009 (43.5 observation hours) and new patterns or new characteristics of already recorded behavioural patterns were collected until 27 April 2010. To record these observations, a camcorder ("Sony Handycam DCR-HC37E") was used. The recorded video material was examined and analysed using the programme Picture Motion Browser, version 2.0.01, which allowed an analysis of detailed screens of the motion sequences.

To arrange the social behaviour into the classes of "Sociopositive behaviour" and "Agonistic behaviour", a sequence analysis according to Gerber (1976 according to Wilhelm & Gansloßer, 1989) was used. Data were collected for this purpose using the ad libitum method (Altmann, 1974) from 13 January 2010 until 27 April 2010 (334 observation hours). Action and reaction of the involved animals were recorded. Only dyadic interactions were analysed because otherwise it cannot be judged which action results in which reaction. Behavioural patterns that occurred simultaneously were defined as a new behavioural pattern (e.g. "Turning head towards with Squawking") for the quantitative analysis. Behavioural patterns that transitioned smoothly into each other were assessed as separate behavioural patterns. For example, animal A showed "Biting" towards animal B. In reaction, animal B showed "Turning hindquarters towards" and "Turning head towards". Noted was then "Turning hindquarters towards" and "Turning head towards" in reaction to "Biting" . In such smooth transitions, it is not possible to assess which of the responses ended the action. Therefore, in such cases, all response elements were scored as discontinuing the behavioural pattern of the action. The discontinuation of a behaviour was considered to be the termination of that behaviour. It did not matter whether this was done by showing another behaviour from the social behaviour category (e.g. "Pouncing on conspecifics") or by a behaviour from another category/functional system (e.g. "Eating"). Only if there was a pause of at least one second between the individual behavioural elements, the first reaction was evaluated as the trigger of the action.

For the behavioural pattern "Play chasing", no distinction was made whether this took place with or without "Playful mouthing", as this could not always be seen on the video recordings. "Walking away" and "Jumping away" were treated as one behavioural element ("Walking and Jumping away").

The recorded video material (qualitative as well as quantitative data) was examined and analysed on a PC with a programme which allows single-frame analysis of the motion sequences ("Picture Motion Browser, Version 2.0.01").

Data analysis

Sequential analysis by Markov Analysis according to Gerber (1976 according to in Wilhelm & Gansloßer, 1989) can be used to statistically test whether the sequence of behavioural elements is random or indicates a biological linkage, i.e. the action X has a communicative meaning for the conspecific and triggers in it the reaction Y. For this purpose, two significance levels (C-values) are determined as follows (Gerber, 1976 according to Wilhelm & Gansloßer, 1989):

$$C2 = \frac{OV}{EV+2*\sqrt{EV}}$$

$$C3 = \frac{OV}{EV+10*\sqrt{EV}}$$

OV: Observed value

EV: Expected value; $EV = \frac{Sum\ of\ rows * sum\ of\ columns}{N}$

N: sample size

The expected values result from the representation of the behavioural elements in a matrix (rows = action of animal A; columns = reaction of animal B).

If C_2 or $C_3 > 1$, the null hypothesis H_0 can be rejected, i.e. the coupling between the two behavioural elements is not random. The larger the C values, the stronger the coupling. The calculation was made using Excel ("Microsoft Office Excel 2007").

For the classification of the behavioural patterns into the categories "Sociopositive behaviour" and "Agonistic behaviour", a diagram was drawn using the C_3 values. The C_3 values were used because they are the stricter criterion and therefore more reliable statements can be made.

First, a behavioural pattern was assigned to each category: "Biting" for agonistic behaviour, "Sniffing at conspecifics" for sociopositive behaviour, "Sexual mounting" for sexual behaviour and "Playful mounting" for play behaviour. These defined elements were connected with behavioural elements for which the C_3 value is > 1. In the second step, these newly inserted elements are also linked to behavioural patterns with a C_3 value > 1, and so on, until all linkages have been worked through. Some behavioural patterns could not be inserted into the diagram based on the C_3 values (C_3 value < 1). For these elements, the weaker C_2 value was then used for classification.

Behavioural elements associated with "Biting" (directly or indirectly via other behavioural elements) are considered agonistic, while those associated with "Sniffing at conspecifics" (directly or indirectly via other behavioural elements), are considered sociopositive. Behaviour patterns which are associated with "Sexual mounting" (directly or indirectly via other behavioural elements) are classified as sexual behaviour and those which are associated with "Playful mounting" as play behaviour.

Behavioural patterns which were observed less than five times were excluded from the analysis (prerequisite of the chi-square test related to the sequence analysis) (see Appendix). The sample size contains N = 75,647 action-reaction pairs. Combined behavioural patterns (for example "Pouncing on conspecific with Squawking") were summarised in their basic element, when $n < 15$. The body's general movement was defined as basic element (for example "Pouncing on conspecific"). A list with the enumeration of the combined behavioural patterns can be taken from the appendix.

The class of "Agonistic behaviour" contains all behavioural patterns which deal with threat, attack, defence and flight. Thereby behavioural patterns with different functions are summarised. For this reason, the "Agonistic behaviour" should be divided into "Attack and threat behaviour" and "Defence behaviour". For the behavioural patterns from the class "Agonistic behaviour", it was noted how many elements from this class they ended (summation ending) or induced (summation inducing). Only the behavioural patterns with a $C_3 > 1$ were included, unless the total sum (summation ending plus summation inducing) was less than five. Then the agonistic behavioural patterns with a C_2-value > 1 were added to the single summations.

Using a test for binomial distribution[1], it was tested whether the deviations from the expected value are significant.

The expected value was a distribution of 50% each for "generation of agonistic behaviour" and "ending of agonistic behaviour" (under these circumstances, the behaviour would not be assigned to either category).

The significance level was set at $a = 0.05$. If the determined p-value (probability of error) is below ($p < a = 0.05$), the null hypothesis (H_0) can be rejected. The tests were carried out using the programme "IBM® SPSS® Statistics 18 for Windows Version 18.0.0».

Behavioural patterns which significantly more often ended agonistic behaviour were classified as "Defensive behaviour" and which significantly more often induced agonistic behaviour as "Attack and threat behaviour".

With the help of the results from the sequential analysis and from the binomial test, social behaviours were arranged in the ethogram.

Results: Ethogram social behaviour

Behavioural patterns which are marked with a "*" could not be attached to a category by the sequential analysis. They were attached by logic and compare with similar behavioural patterns. Behavioural patterns marked with a "#" are attached to one category based on the C_2-value. Behavioural patterns marked with a "!" are sorted against the results of the sequence analysis (see Discussion). The bracketed numbers behind the behavioural patterns declare the numeration in the graphics of the sequence analysis.

"Territorial call" (= Territorialruf) (Hoeck, 1976c): The forelegs are placed in an elevated position and the head is tilted back into the nape (tip of the snout pointing obliquely upwards). The mouth is opened and the corners of the mouth point downwards (similarity to "Squawking",

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[1] Data are ordinal data and non-parametric: Kolmogorov-Smirnov goodness-of-fit test, $p < 0.001$

but the mouth is opened wider). The hairs around the dorsal gland are erected. The rock hyrax emits a nagging sound while contracting its entire belly. This behavioural pattern could only be observed once. According to Hoeck, the call is emitted more frequently during the mating season (1976c) and is used to signal supremacy over the females as well as marking of the territory (1980). (Figs 3, 4)

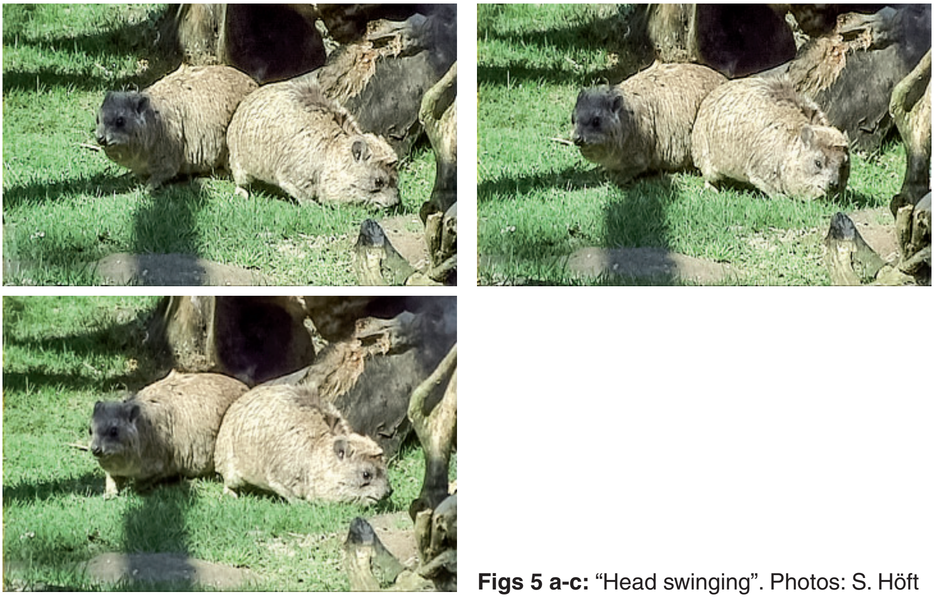
Fig. 3: "Territorial call, animal from the side". Photo: S. Höft

Fig. 4: "Territorial call, animal from the front". Photo: S. Höft

Sexual behaviour

The observation period was outside the mating season. Therefore, only a few elements of sexual behaviour could be observed. The male of the group and one of the pregnant females were involved. During sexual behaviour, the hairs around the dorsal gland are erected by both sexes.

*<u>"Head swinging":</u> The male lowers its head and moves it slowly from one side to the other. (Figs 5 a-c)



Figs 5 a-c: "Head swinging". Photos: S. Höft

*"Lowering the head" (56): The head is moved ventrally below the dorsal line. In doing so, the rock hyrax may carry out nodding movements (up and down movements of the head). These are elements of defensive behaviour as well as mating behaviour.

"Mating bite" (72): The male clasps the female's skin/fur (preferring that of the hindquarters) with its mouth. (Figs 6 a, b)

Figs 6 a, b: "Mating bite". Photo: S. Höft

"Quiver" (73): The female pulls her rump jerkily towards her body or the ground. Twitching continues through the body. "Quiver" was shown in response to "Mating bite".

"Sexual mounting" (71): The male clasps the female's lumbar region with its forelegs and presses its genital region against the female's. It performs thrusting movements with its hindquarters. Alternating mounts from female and male are possible. Before the "Sexual mounting", the female may sniff at the male's genital region and then the male may sniff at the female's genital region[2]. (Figs 7, 8)

Fig. 7: "Sexual mounting: male on female". Photo: S. Höft

Fig. 8: "Sexual mounting: female on male". Photo S. Höft

Sociopositive behaviour

The category of sociopositive behaviour includes all behavioural patterns that lead to a tolerance of the conspecific's presence.

Social approach

"Approach" (1): An animal approaches a conspecific forwards or backwards.

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[2] Fourie & Perrin (1987): The receptive female approaches the dominant male with the hair of the dorsal gland erected. It smells the male's genital region and then presents its own hindquarters. The male next smells the genital region of the female and then mounts.

“Climbing on conspecific” (4): The forepaws are placed on the conspecific’s back and the animal tries to get its hind legs onto the back of the other.

“Follow” (10): The animal moves behind a conspecific in the same direction.

“Jumping on conspecific” (6): The rock hyrax jumps (“Jumping”, Höft & Gansloßer, 2021) onto the back of a conspecific. The animal may slide off the conspecific’s back again, especially if the conspecific moves in response. This behavioural pattern is also shown when the animal is unable to jump all the way across one or more conspecifics, and uses them as stepping stones to reach its destination.

“Licking conspecific” (2): The rock hyrax touches a conspecific with its tongue (Fig. 9). The conspecific may also be bitten with low intensity (Fig. 10).

Fig. 9: “Licking conspecific”. Photo: S. Höft

Fig. 10: “Licking conspecific with biting”. Photo: S. Höft

*“Laying a leg onto”: The animal puts one foreleg or hind leg on a lying conspecific. This could be observed during “huddling” (Sale, 1970a).

“Laying chin onto” (11): The head is placed with the chin on the conspecific’s body (for example, nape or back). (Fig. 11)

Fig. 11: “Laying chin onto”. Photo: S. Höft

“Laying on conspecific” (5): The rock hyrax lays itself onto the conspecific, either a part of its body (during “huddling”) or the entire body (during “heaping”). The hyrax may also push itself onto the conspecific by first placing only the head onto the conspecific and then following with the body by walking forward with physical contact. Another option to reach the position “Lying on conspecific” for the rock hyrax is by falling over onto one of its sides from the position “Placing itself on conspecific”. (Figs 12, 13)

Fig. 12: “Lying on conspecific”. Photo: S. Höft

Fig. 13: “Lying on conspecific”. Photo: S. Höft

*“Nudging the corner of the mouth”: The tip of the snout is pressed against the corner of the conspecific’s mouth. This may push the conspecific’s lips upwards.

“Nibbling on conspecific” (16): Incisors nibble on the conspecific’s fur/skin through quick opening and closing movements of the lower jaw. The mouth is opened only a little bit. (Fig. 14)

Fig. 14: “Nibbling on conspecific”. Photo: S. Höft

“Placing itself on conspecific” (7): One or both forepaws or hind paws are placed on the conspecific’s body. The other pair of extremities stands on the ground. This causes the back line to slope downwards. The head may be placed with the chin on the conspecific’s back (“Lying chin onto”).

!“Pressing towards” (37): The rock hyrax’s hindquarters or side touch the conspecific. The rock hyrax walks backwards or sidewards and thereby pushes the conspecific partly away, but then searches for physical contact so that “huddling” results. “Pressing towards” is also possible with the head.

“Sniffing at conspecific” (3): The nose is held over or onto a conspecific (with physical contact) and the conspecific is sniffed. Preference is given to the areas around the dorsal gland, the snout and the anal and genital region. (Figs 15, 16)

“Snouts in contact” (12): Each of the rock hyraxes moves its snout to toward that of the conspecific and sniffs at it. In doing so, physical contact is possible. (Fig. 17)

Fig. 15: “Sniffing at conspecific: head”. Photo: S. Höft

Fig. 16: “Sniffing at conspecific: anal and genital region”. Photo: S. Höft

Fig. 17: “Snouts in contact”. Photo: S. Höft

!“Squeezing in between” (66): The rock hyrax places itself with its hindquarters between the heads of two conspecifics or with its head between the hindquarters of two conspecifics. By walking backwards or forwards, it places all or part of its body between the conspecifics. More rarely “Squeezing in between” occurs from a head-to-head position. “Squeezing in between” can occur from a “heaping” (Sale, 1970a) position, where the extremities may be pressed against the conspecific (e.g. flank or back). In doing so, the conspecific is shoved aside. By “Jumping” (Höft & Ganslоßer, 2021) between conspecifics, “Squeezing in between” is also possible. Additionally, the possibility exists of “Squeezing in between” between a wall and a conspecific. (Fig. 18)

“Standing on the back”: The rock hyrax stands (“Standing”, Höft & Ganslоßer, 2021) or squats (“Squatting”, Höft & Ganslоßer, 2021) with all four extremities on the back of one or several conspecifics. The behavioural pattern could be observed during “heaping” (Sale, 1970a) and “Eating” (Höft & Ganslоßer, 2021).

“Sticking snout into conspecific’s fur” (9): The snout is stuck into the conspecific’s fur.

Fig. 18: "Squeezing in between". Photo: S. Höft

"Taking food from conspecific": The rock hyrax eats the food that hangs off another conspecific's mouth. At this time, it may bite off a piece of the food or tear off pieces of it by pulling (the head and body are pulled backwards while the extremities remain still).

"Touching" (8): The snout or another body part is held on the conspecific's fur with physical contact. (Fig. 19)

Fig. 19: "Touching". Photo: S. Höft

"Walking under the chin" (13): The animal walks with bent extremities – causing the belly to touch the ground – under the conspecific's head. In doing so, physical contact is possible.

Thermoregulatory behaviour in social context

"Heaping" (14) (Sale, 1970a): Some rock hyraxes squat ("Squatting", Höft & Gansloßer, 2021) or sit close together with physical contact. On their backs or hindquarters, juveniles[3] (more rarely adults[4]) squat ("Squatting", Höft & Gansloßer, 2021), sit (Serruya & Eilam, 1996), lie (with the whole body; Serruya & Eilam, 1996) or stand (Serruya & Eilam, 1996). While "heaping" (Sale, 1970a), the animal may change its position by "Turning" (Höft & Gansloßer, 2021) or walking a bit. For formations see "huddling" (Sale, 1970a). (Figs 20,21)

"Huddling" (15) (Sale, 1970a): The animals sit, lie (Serruya & Eilam, 1996) or squat ("Squatting", Höft & Gansloßer, 2021) on the ground. Thereby the rock hyraxes have close physical contact with each other. In doing so, the animals are not on the backs of conspecifics with the

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[3] Sale (1965c) thinks that this will prevent the young from being trampled by conspecifics as well as protect them from extreme temperatures of the substrate (cold in the cave, heat of the sun-exposed rocks).

[4] Corresponding observations were made by Sale (1970a).

Fig. 20: “Heaping by juvenile”. Photo: S. Höft

Fig. 21: “Heaping by adult”. Photo: S. Höft

Fig. 22: “Huddling”. Photo: S. Höft

exception of the forepaws and hind paws or only part of the body. While "huddling", an animal may change its position by "Turning" (Höft & Gansloßer, 2021) or walking a bit. When "huddling" (Sale, 1970a), rock hyraxes can form different formations: a star-shaped formation with the heads pointing outwards; hindquarters of one animal adjoining the side of another; "Lying chin onto", in which several heads can be piled upon each other[5]; frontal head to head[6]; parallel with the head on the conspecific's hindquarters. (Fig. 22)

Play behaviour

In play behaviour, elements from other functional systems of social behaviour are used, but they lack the seriousness and apparently are without immediate function (Immelmann, 1982; Burghardt, 2014). The behaviour elements can be freely combined and are often characterised by role changes and frequent repetitions or exaggerated execution (Immelmann, 1982). According to Graham & Burghardt (2010), play is defined by the following five criteria: 1. the behaviour is "[…] incompletely functional in the context in which it appears"; 2. the behaviour is "[…] spontaneous, pleasurable, rewarding, or voluntary"; 3. the behaviour "[…] differs from other more serious behaviours in form (e.g., exaggerated) or timing (e.g., occur early in life, before the more serious version is needed)"; 4. the behaviour is "[…] repeated, but not in abnormal and unvarying stereotypic form (e.g., rocking or pacing)" and 5. the behaviour is "[…] initiated in the absence of severe stress".

Moreover, when playing, the rock hyraxes emit no sounds, as is possible with the corresponding behaviour from the agonistic category. Erection of the hairs around the dorsal gland does not take place, either. Play behaviour of the rock hyrax is commonly restricted to juveniles (Hoeck, 1978). Only in the first six weeks of life do rock hyrax dams invite their young to play with them or with each other (Fischer, 1992), although occasionally other adults also play with young (Hoeck, 1978).

In the rock hyrax group at Osnabrück Zoo, play between juveniles and adults could rarely be observed. The adults were the youngest adult female and the pregnant females. Play between adults was not observed.

"Fur nipping" (17) (Hoeck, 1978): The mouth is opened wide and then clasps the fur (for example, in the region of the hindquarters or the shoulder). In doing so, the rock hyrax may pull at the fur or carry out shaking motions. According to Hoeck (1978), this behaviour serves to initialise play. (Fig. 23)

Fig. 23: "Fur nipping". Photo: S. Höft

"Nibbling on conspecific" (16): Incisors nibble on the conspecific's fur/skin through quick opening and closing movements of the lower jaw. The mouth is opened only a little bit. This behavioural pattern could be observed during "Playful mounting", for example, but also appeared in a non-playing context. (Fig. 14)

[5, 6] Sale (1970a) described that rock hyrax avoid contact lying between head and head.

“Playful chasing” (30)[7]: Rock hyrax runs by “Galloping” (Höft & Gansloßer, 2021) behind a conspecific, who flees from it (“Playful fleeing”). In doing so, the rock hyrax can show “Playful opening of the mouth”. The roles can be reversed (chaser becomes the hunted and vice versa). (Fig. 24)

Fig. 24: “Playful chasing and fleeing”. Photo: S. Höft

“Playful craning of the neck” (25): The neck is elongated forward with high speed whereby the head is moved away from the body and towards the conspecific.

#“Playful crowding” (27): The rock hyrax touches the conspecific with its hindquarters. By mowing backwards, the conspecific is pushed aside. In doing so, the rock hyrax may show “Playful head shaking”.

“Playful fleeing” (29): The animal runs away from the conspecific by “Galloping” (Höft & Gansloßer, 2021). If the conspecific follows, it can result in “Playful chasing”. (Fig. 24)

“Playful head tossing” (24): The head is hurled from one side to the other with a high frequency. Thereby the forelegs may throw the upper part of the body a little bit up from the ground. (Fig. 25)

Fig. 25: “Playful head tossing”. Photo: S. Höft

“Playful head up” (22): The head is raised over the dorsal line. The forelegs may be extended, causing the upper part of the body to be erected. In doing so, the upper part of the body may additionally or alternatively be stretched.

“Playful turning hindquarters away” (20): The hindquarters are turned away from the conspecific. This was shown as response to “fur nipping” (Hoeck, 1978) in the hindquarters, for example.

“Playful turning hindquarters towards” (63): The rock hyrax turns its hindquarters towards the conspecific. In doing so, the hindquarters may additionally be pushed upwards

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[7] The behaviour pattern corresponds to “chasing” mentioned by Fourie & Perrin (1987).

by stretching of the hind legs and positioning of the toes. Thereby the conspecific can be touched with the hindquarters. This was observed in response to "Playful jumping onto", for example.

"Playful jumping onto" (18): The rock hyrax jumps (forelegs throw up the front body) with its forepaws onto the conspecific's hindquarters or jumps towards the conspecific. In doing so, the rock hyrax can show "Playful head shaking" or "Playful opening of the mouth" for example. (Fig. 26)

Fig. 26: "Playful jumping on". Photo: S. Höft

"Playful mounting" (19) (= mounting; Hoeck, 1978)[8]: The rock hyrax clasps the conspecific's lumbar region with its forelegs and presses its genital region against that of the conspecific. It may carry out thrusting movements with its hindquarters. Thereby "fur nipping" (Hoeck, 1978) at the nape is possible. In male juveniles, the penis may be erected[9]. (Fig. 27)

Fig. 27: "Playful mounting". Photo: S. Höft

"Playful mouth opening" (26): The mouth is opened wide, but the upper lip is not pulled upwards (as is possible with "Mouth opening"). If the incisors are seen at all, its only their tips. The head may swing from one side to the other.

*"Playful rolling over the back": The animal rolls from the position "Lying on the side" (Höft & Gansloßer, 2021) onto the back and then to the other side. The extremities provide the push. (Fig. 28)

*"Playful squirming": The animal rotates around its own axis or raises the upper part of the body.

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[8] Due to also using the term "mounting" for mating behaviour, the term "Playful mounting" is suggested to prevent confusion. The behavioural pattern conforms to "mock mating", mentioned by Fourie & Perrin (1987).

[9] Hoeck (1978) also observed this.

Fig. 28: "Playful rolling over the back". Photo S. Höft

"Playful standing up" (21): The animal stands up on its hind legs. "Playful standing up" may be accompanied by "Playful mouth opening".

"Playful turning head away" (64): The head is turned sideways away from the conspecific and is moved upward or downward.

"Playful turning head towards" (23): In play, the head is turned toward the conspecific. In doing so, the upper part of the body may be lifted. The head may swing from one side to the other. "Playful turning head towards" can be combined with "Playful mouth opening", "fur nipping" (Hoeck, 1978) or "Nibbling on conspecific". This was observed in response to "Playful jumping on", for example. (Fig. 29)

Fig. 29: "Playful turning head towards". Photo: S. Höft

"Playful mouth wrestling" (28): Rock hyraxes move their heads towards each other. Their heads are then rotated around the longitudinal axis with wide opened mouths or swung from one side to the other. In doing so, the tips of the rock hyraxes' mouths are at the same height as the corners of the conspecific's mouths. (Fig. 30)

Fig. 30: "Playful wrestling with the mouth". Photo: S. Höft

Termination of physical contact

“Head raising” (40): The head is lifted and sometimes put back in the nape. In addition, a hollow back may be made. “Head raising” was shown as response to “Placing itself on conspecific”, for example.

“Jumping away” (61): The animal departs from the conspecific by “Jumping” (Höft & Gansloßer, 2021).

*“Pulling away the paw” (58): The paw is moved away from the conspecific. This was observed in response to “Licking conspecific” on the paw.

!“Raising the upper part of the body” (49): Forelegs are placed at an elevated position or they push the upper part of the body off the ground by extending (upper part of the body is moved upward). This could be observed in response to “Jumping on conspecific” or “Placing itself on conspecific”, for example. (Fig. 31)

Fig. 31: “Raising the upper part of the body”. Photo: S. Höft

“Slipping off” (32): The rock hyrax slips or moves away from the conspecific’s back. This could be observed in response to “Walking away”, for example.

!“Social standing up” (70): The rock hyrax changes from the position “Squatting” (Höft & Gansloßer, 2021), “sit” (Serruya & Eilam, 1996), “lie” (Serruya & Eilam, 1996) or “Lying on the side” (Höft & Gansloßer, 2021) to a “stand” (Serruya & Eilam, 1996) position within a social behaviour context.

“Walking away” (61): The rock hyrax departs from the conspecific by walking or turning away. This was observed in response to “Placing itself on conspecific”, for example.

Agonistic behaviour

Agonistic behaviour includes aggressive behaviour and flight. Aggressive behaviour is a “collective name for all elements of the attack, submissive and threat behaviour” (Immelmann, 1982, p. 18). Agonistic behaviour leads to an increasing of the distance between individuals involved.

Agonistic behavioural patterns of rock hyraxes may be accompanied by erection of the back's hairs, especially of the hairs around the dorsal gland (Fig. 32). Slightly erected hairs (especially of the dorsal spot) signal alarm and more greatly erected hairs of the dorsal spot and of the nape are a signal of threatening (Sale 1970a, b). Through a combination of wrinkling the bridge of the nose (skin of the nose bridge is tightened so that it wrinkles) (Fig. 33), lifting of lips (Figs 34a, b) and varying degrees of opening the mouth, the incisors are exposed to a greater or lesser degree. According to Sale (1970a, b), submissive behaviour is signalled by a lack of hair erection and by backward ears. Laying the ears against the head could not be observed in the rock hyrax group at Osnabrück Zoo.

Fig. 32: "Erected hair of dorsal gland". Photo: S. Höft

Fig. 33: "Nose bridge wrinkling". Photo: S. Höft

Fig. 34 a: "Lifting of the flews". Photo: S. Höft

Fig. 34 b: "Lifting of the flews". Photo: S. Höft

Behavioural patterns marked with a "+" were added to either the category "attacking and threatening behaviour" or the category "defensive behaviour" based on the C2 value.

The following behavioural patterns could not be definitely attributed to the "Attacking and threatening behaviour" or "Defensive behaviour" (binomial analysis yields no significant results). Preliminary statements on probable categorisation were made that require verification by following studies.

"Empty chewing" (38): Mouth is slightly opened and closed again (by moving the lower jaw). While closing, one side of the upper lip is pulled upwards, so that the upper incisor of the same side is visible. The next time the mouth is closed, the other side of the upper lip is pulled upwards, and so on. In between, the tongue is stuck out. (Fig. 35).

Fig. 35: "Empty chewing". Photo: S. Höft

In the movie "Ethologie von Busch- und Klippschliefern" by Hoeck (1980), two territorial males who meet each other in a non-territorial region are shown. He describes that the males make chewing movements to threaten each other (Hoeck, 1980). Possibly "Attacking and threatening behaviour".

"Head shaking" (55): The head is turned around the longitudinal axis with a high frequency. The movement resembles the shaking of the head in comfort behaviour ("Shaking" Höft & Gansloßer, 2021). "Head shaking" may appear along with other defensive behaviours like "Turning head away".

Possibly "Defensive behaviour".

*"Head tossing": The head is hurled from one side to the other with a high frequency. Thereby the forelegs may push the upper part of the body a little bit up from the ground.

Perhaps "Attacking and threatening behaviour".

"Lowering the head" (56): The head is moved ventrally below the dorsal line. Thereby it may perform nodding movements (upward and downward movements of the head). (Fig. 36)

Possibly "Defensive behaviour" and "mating behaviour".

Fig. 36: "Lowering the head: animal in the middle". Photo: S. Höft

"Pulling head to body" (54): The head is moved slowly or jerkily towards the body.

Possibly "Defensive behaviour".

"Snapping" (47): The mouth is opened and quickly closed again. In doing so, the conspecific is not touched. This is shown together with "Turning head towards" or "Head pre-stretching".

Possibly "Attacking and threatening behaviour".

"Squawking" (46): The mouth is opened slightly. The corners of the mouth are pulled backwards and sometimes additionally downwards. Thus the corners of the mouth appear pointed. The bridge of the nose may be puckered. Depending on the degree of the mouth's opening and the upward movements of the lips, the incisors are more or less exposed. Optical signals may be accompanied by a squawking sound. (Fig. 37)

Possibly "Defensive behaviour" with mixed motivation.

Fig. 37: "Squawking". Photo: S. Höft

"Standing up" (39): Animal stands on its hind legs. This may be accompanied by "Mouth opening" or "Biting".

Possibly "Attacking and threatening behaviour".

#"Walking backwards" (59): The rock hyrax retreats from the conspecific by walking backwards with the hindquarters first. This was shown in answer to "Mouth opening", for example.

Possibly "Defensive behaviour".

Attacking and threatening behaviour

"Biting" (34): The mouth is opened and an attempt is made to clasp the conspecific's fur/skin with the incisors. The bite can vary in intensity. The tock hyrax may perform shaking movements with the head and/or emit squeaking sounds. The rock hyrax may bite into the conspecific, i.e. the conspecific is held tight with the incisors even while it flees. (Fig. 38)

Fig. 38: "Biting". Photo: S. Höft

"Chasing" (48)[10]: The animal gallops ("Galloping", Höft & Gansloßer, 2021) behind a fleeing conspecific. The conspecific can be caught up to, then "Biting" can follow. (Fig. 39 right animal)

"Hassling" (35): The rock hyrax turns its hindquarters towards the conspecific and then walks backwards towards the conspecific, or the hindquarters are repeatedly turned to the conspecific, which causes them to move in a circle. This behavioural pattern was observed during "Eating" (Höft & Gansloßer, 2021).

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[10] This behavioural pattern is likely to correspond to the agonistic "chasing" mentioned by Fourie & Perrin (1987).

Fig. 39: Left animal “Fleeing from conspecific”, right animal “Chasing”. Photo: S. Höft

“Head pre-stretching” (42): The neck is stretched forward with a high frequency, causing the head is moved away from the body and towards the conspecific. In doing so, the upper part of the body may move forward, too, with or without a step towards the conspecific. If the rock hyrax is at a higher position than its conspecific, the head will be stretched downwards towards the conspecific. “Mouth opening”, “Snapping” or “Biting” may be observed as accompanying behaviours. (Figs 40, 41)

Fig. 40: “Head pre-stretching”. Photo: S. Höft

Fig. 41: “Head pre-stretching with biting”. Photo: S. Höft

“Head up” (41): The head is raised above the dorsal line. The view is directed towards the conspecific. The forelegs may be extended, whereby the upper part of the body is straightened up. This may be stretched additionally or alternatively or the forelegs are placed onto an elevated position. (Fig. 42)

Fig. 42: “Head up”. Photo: S. Höft

“Jostling” (36): The rock hyrax’s hindquarters or side touch the conspecific. The rock hyrax walks backwards or sideways and in doing so, sometimes pushes the conspecific aside. “Jostling” is also possible with the head. “Jostling” was shown during “Eating” (Höft & Gansloßer, 2021). (Fig. 43)

Fig. 43: “Jostling: animal in the back”. Photo: S. Höft

+“Laying paw on conspecific” (45): The rock hyrax places one forepaw onto the conspecific’s back or hindquarters. (Fig. 44)

Fig. 44: “Laying paw on conspecific.” Photo: S. Höft

“Mouth opening” (44): The mouth is opened. In addition, the upper lip may be pulled upwards, revealing the incisors. By combining the opening width of the mouth and different intensities of raising the upper lip, the incisors are exposed to different degrees. The head is directed towards the conspecific and may swing from side to side, and thereby can be turned backwards over the shoulder. Squeaking noises may be emitted during “Mouth opening”. (Fig. 45)

Fig. 45: “Mouth opening”. Photo: S. Höft

Fig. 46: "Pouncing on conspecific". Photo: S. Höft

"Pouncing on conspecific" (33): The animal jumps onto the conspecific's hindquarters or back with its forepaws or does a jump towards it. The head may be placed onto the conspecific and the animal can try to bite it ("Biting"). (Fig. 46)

"Standing still" (31): The rock hyrax remains still in response to a conspecific's aggressive actions. "Standing still" was assigned to "Attacking and threatening behaviour" because it produced more aggressive behaviour than would be expected (it was observed 91 times and produced aggressive behaviour in 64 cases).

"Turning head towards" (43): The head is turned to the conspecific, or sometimes also backwards when the conspecific is behind the animal or on its back. In doing so, the upper part of the body may be lifted or turned around with the head. The view is directed towards the conspecific. The head may swing from one side to the other. During "Turning head towards", the rock hyrax may show "Mouth opening". (Figs 47, 48)

Fig. 47: "Turning head towards: right animal". Photo: S. Höft

Fig. 48: "Turning head towards with biting". Photo: S. Höft

Submissive behaviour and flight

Submissive behaviour conduces to protection and defence

"Fleeing from conspecific" (51): The animal turns away from the conspecific and moves away from it in a gallop ("Galloping", Höft & Gansloßer, 2021). In the gallop, large jumps (body is extremely lengthened) may be performed. This was shown as a response to "Biting", "Snapping" or "Pouncing on conspecific", for example. (Fig. 39 left animal)

"Jumping away" (61): The animal moves away from the conspecific through a jump ("Jumping", Höft & Gansloßer, 2021).

+ "Jumping over conspecific" (60): The animal jumps ("Jumping", Höft & Gansloßer, 2021) over the conspecific. This could be observed as response to "Turning head towards", for example. (Fig. 49)

Fig. 49: "Jumping over conspecific". Photo: S. Höft

"Squirming" (67): The animal turns around its own longitudinal axis. This could be observed in response to "Biting", for example.

"Turning head away" (57)[11]: The head is turned aside away from the conspecific, moved up or down. In doing so, the mouth may be opened or the head may be shaken. This was shown in response to "Snapping", "Biting" or "Mouth opening", for example. (Figs 50a, b)

Figs 50a, b: "Turning head away". Photo: S. Höft

"Turning hindquarters away" (52): The hindquarters are turned away from the conspecific. The rock hyrax may show "Mouth opening" or "Biting". "Turning hindquarters away" could be observed in response to "Sexual mounting", for example.

"Turning hindquarters towards" (53)[12]: The rock hyrax turns its hindquarters towards its conspecific or presents them by turning away the upper part of the body. The hindquarters may additionally be pushed upwards by extending the hind legs and standing on the toes. In doing so, the conspecific can be touched with the hindquarters[13]. The head may be turned aside or lowered[14]. (Fig. 51)

+"Turning jump" (50): The forelegs push the upper part of the body upwards. Then the hind legs push the hindquarters off the ground. Thereby the head and upper part of the body are

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[11] According to Sale (1970a), this behavioural pattern conduces to the prevention of aggression, too.

[12] According to Sale (1970a, b), this behaviour is characteristic of situations in which agonistic behaviour could arise and conduces therefore to the prevention of aggression.

[13] Hoeck (1976c) describes the pressing of the hindquarters on a conspecific as an appeasement gesture.

[14] According to Sale (1970b), the turning of the head conduces to keeping the aggressor in view from the side.

turned to one side, forming an arch. The hindquarters may turn to the other side. The forelegs are stretched forward for landing. “Turning jump” could observed with “Playful fleeing” and in response to aggressive behaviour of conspecifics.

Fig. 51: “Turning hindquarters towards head away”. Photo: S. Höft

Fig. 52: “Turning sideways”. Photo: S. Höft

<u>“Turning sideways” (62):</u> The forelegs throw the upper part of the body up and it is turned sideways in the air or the forelegs are moved sideways, so that the upper part of the body is moved away from the conspecific. In this way, the head is moved away from the conspecific. “Turning sideways” could be observed in response to “Biting”, for example. (Fig. 52)

<u>“Walking away” (61):</u> The rock hyrax moves away from the conspecific by walking (“Walking”, Höft & Gansloßer, 2021) or turning around. This was shown in response to “Turning head to”, for example.

Results: sequential analysis

Due to the large number of behavioural elements, it was sometimes not possible to present the results of the sequence analysis legibly in one graph. Therefore, the “ending of aggressive behavioural patterns” from the category “Agonistic behaviour” was illustrated in separate graphics. The line lengths as well the exact position of the behavioural patterns within the functional system/category are of no significance, but were only intended to achieve a comprehensible representation. Unless otherwise noted, the numbers correspond to the same behavioural patterns as in the ethogram. Behavioural patterns which were defined for one functional system/category are marked in light blue. The violet colouring indicates elements that are grouped by the C_2-value. The other colours have no meaning unless otherwise indicated, but are only intended to increase the readability of the graphics. Dashed lines connect behavioural patterns where the C_3 or C_2-value > 1, but these combinations occur less than five times. Square boxes indicate behavioural elements which end behavioural patterns.

<u>Legend for Figs 53-55:</u> / No visible reaction by the conspecific; **1a** An fn (approach[15] with the head toward the conspecific’s body); **1b** approach ff (with the head towards the conspecific’s head); **1c** approach with the backside otherwise: a basic behavioural pattern; b basic behavioural pattern with “Biting” (playing behaviour: with fur nipping); c basic behavioural pattern with “Mouth opening”

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[15] The approach towards a conspecific was only considered as “Approach” if the distance between the animals was a hyrax’s body length or less after the approach.

(playing behaviour: with “Playful mouth opening”); d basic behavioural pattern with “Squawking”; e basic behavioural pattern with “Snapping”; f basic behavioural pattern with “Laying paw on conspecific”; g basic behavioural pattern with “Nibbling on conspecific”; **2** “Licking conspecific”; **3** “Sniffing at conspecific”; **4** “Climbing on conspecific”; **5** “Laying on conspecific”; **6** “Jumping on conspecific”; **7** “Placing itself on conspecific”; **8** “Touch”; **9** “Sticking snout into conspecific’s fur”; **10** “Follow”;**11** “Lying chin onto”; **12** “Snouts contact”; **13** “Walking under the chin”; **14** “heaping”; **15** ”huddling”;**16** “Nibbling on conspecific”; **17** “fur nipping”; **18** Playful jumping onto; **19** Playful mounting; **20 “**Playful turning hindquarters away”; **21** “Playful standing up”; **22** “Playful head up”; **23** “Playful turning head towards”; **24** “Playful head tossing”; **25** “Playful craning of the neck”; **26** “Playful mouth opening”; **27** “Playful crowding”; **28** “Playful mouth wrestling”; **29** “Playful fleeing”; **30** “Playful chasing”; **31** ”Standing still”; **32** “Slipping off”; **33** “Pouncing on conspecific”; **34** “Biting”; **35** “Hassling”; **36** “Jostling”; **37** “Pressing towards”; **38** “Empty chewing”; **39** “Standing up”; **40** “Head raising”; **41** “Head up”; **42** “Head pre-stretching”; **43** “Turning head towards”; **44** “Mouth opening”; **45** “Laying paw on conspecific”;**46** “Squawking; **47** “Snapping”; **48** “Chasing”; **49** “Raising the upper part of the body”; **50** “Turning jump”; **51** “Fleeing from conspecific”; **52** “Turning hindquarters away”; **53**” Turning hindquarters towards”; **54** “Pulling head to body”; **55** “Head shaking”; **56** “Lowering the head”; **57** “Turning head away”; **58** “Pulling away the paw”; **59** “Walking backwards”; **60** “Jumping over conspecific”; **61** “Walking away and jumping away”; **62** “Turning sideways”; **63** “Playful turning hindquarters towards”; **64** “Playful turning head away”; **65** stopped playing; **66** “Squeezing in between”; **67** “Squirming”; **68** “comfort behaviour”; **69** stopped approach (approach is stopped completely without any reaction from the category of social behaviour (like “Sitting down” (Höft & Gansloßer, 2021)); **70** “Social standing up”; **71** “Sexual mounting”; **72** “Mating bite”; **73** “Quiver”

Sexual behaviour

The observation period was outside the mating season. Therefore, the quantity of observed behavioural elements from mating behaviour was low. The C_3-values were all < 1. So the elements were grouped on the basis of the C_2-values.

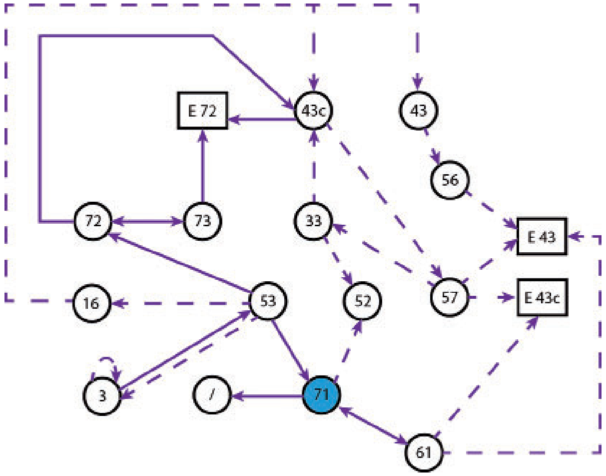

Fig. 53: Sequential analysis of sexual behaviour.

Play behaviour

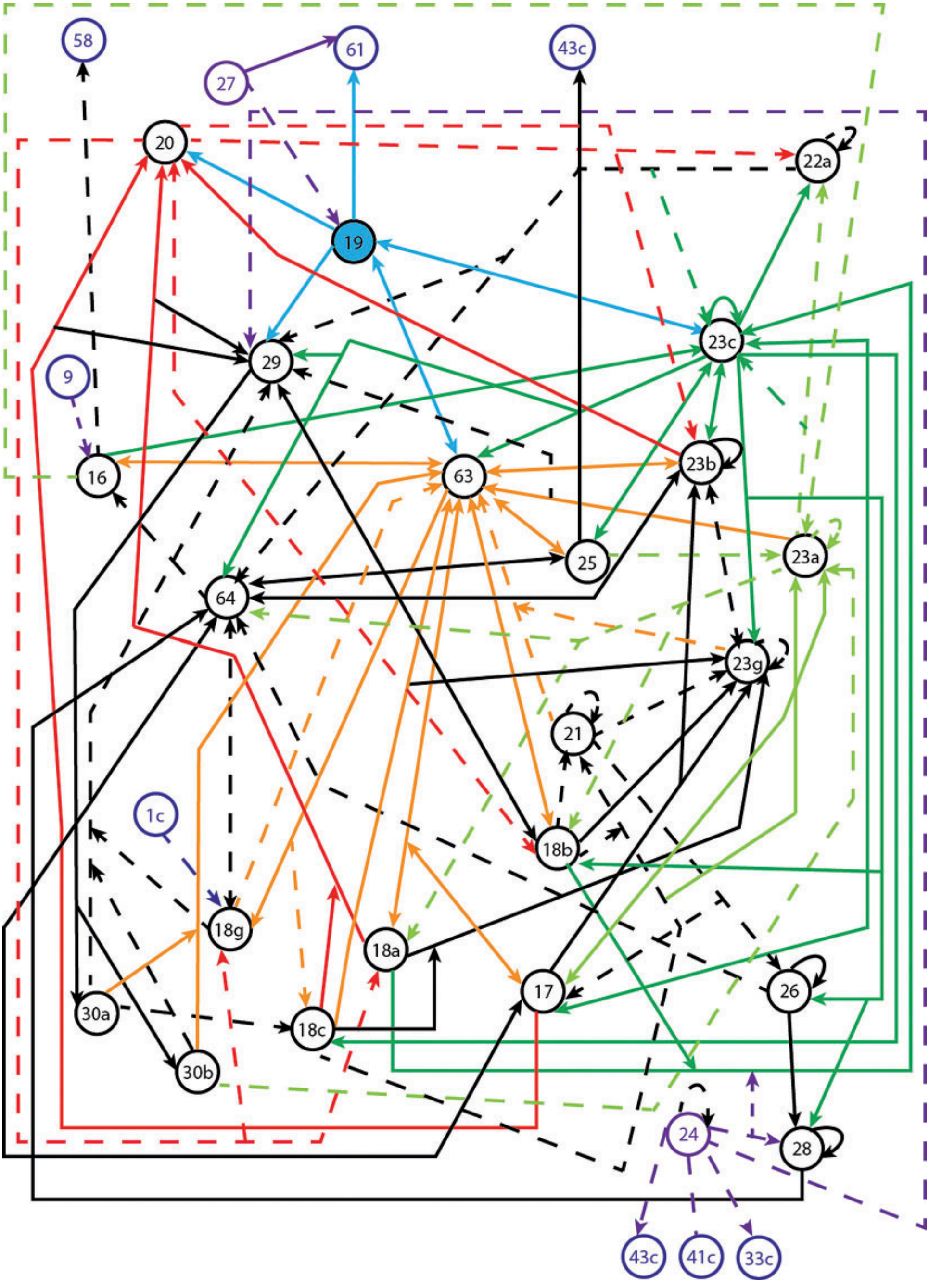

Fig. 54: Play behaviour: The dark blue elements are not part of the play behaviour.

Central behaviour elements of play behaviour are “Playful turning hindquarters towards” (63) and “Playful turning hindquarters towards with playful mouth opening” (63c). Both elements occurred both as an action and as a reaction to the playing behaviour. “Nibbling on conspecific” (16), “Playful mounting” (19), “Playful head tossing” (24) and “Playful craning of the neck” (25) led to agonistic behaviour.

“Playful turning hindquarters towards” (63) occurred in response to all variations of “Playful turning head towards” (64), “Playful jumping onto” (18) and “Playful chasing” (30). In the variants of “Playful jumping onto” (18), additional “Playful fleeing” (29) occurred as reaction. “Playful fleeing” (29) led to “Playful chasing” (30). “Playful turning head away” (64) occurred in response to “Playful turning head towards” (23), “Playful turning head towards with fur nipping” (23b) and “Playful turning head towards with Playful mouth opening (23c)”. (Fig. 54)

Social behaviour

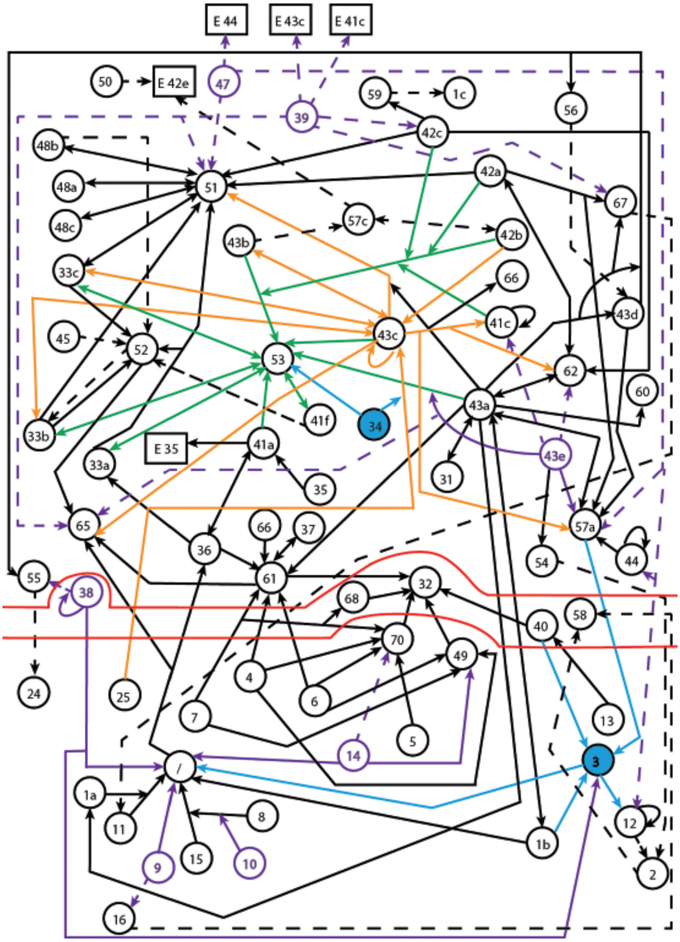

Fig. 55: Sequential analysis of social behaviour: Above the red line is the category “Agonistic behaviour” and below the red line is “Sociopositive behaviour”. Between the two lines are behaviour patterns that could not be definitively assigned to one of these categories.

"Walking away and jumping away" (61) connects the sociopositive part and the agonistic part, being more often associated with agonistic behaviours and therefore placed under "agonistic behaviour". The central element of sociopositive behaviour is "no reaction" (/) which was shown often as a reaction to sociopositive behaviour. Central elements of agonistic behaviour are "Fleeing from conspecific" (51), "Turning hindquarters to" (53) and "Turning head towards with mouth opening" (43c). All three elements occurred as actions as well as reactions towards agonistic behaviour.

The variants of "Chasing" (48a-c) led to "Fleeing from conspecific" (51) and vice versa.

Except for "Turning head towards with Squawking", the other variants of "Turning head towards" (43) led to "Turning hindquarters towards" (53). "Turning hindquarters towards" was also the reaction to all combinations with "Head pre-stretching" (42). "Climbing on conspecific" (4) and "Jumping on conspecific" (6) led to "Social standing up" (70) and "Raising the upper part of the body" (49). The reaction to "Laying on conspecific" (5) was "Social standing up" (70) and the reaction to "Placing itself on conspecific" (7) was "Raising the upper part of the body (49)". (Fig. 56)

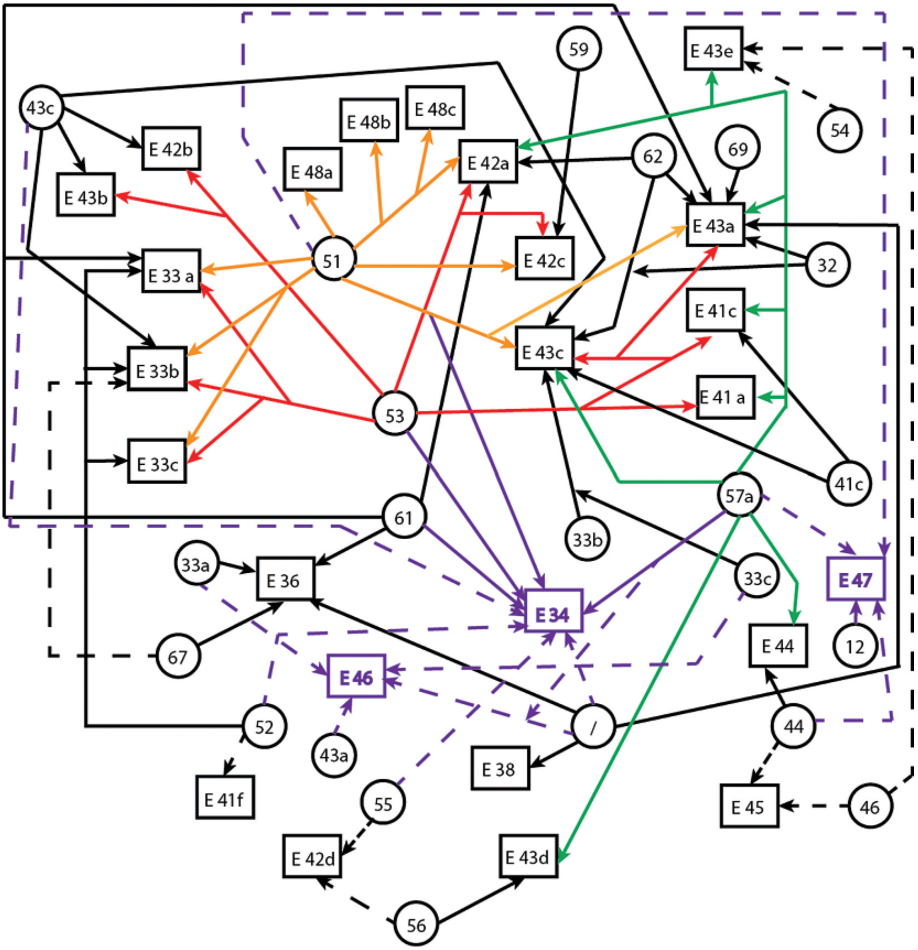

Fig. 56: Termination of aggressive behavioural patterns.

"Turning head away" (57), "Turning hindquarters towards" (53) and "Fleeing from conspecific" (51) are the central elements in termination of aggressive behaviours. These behaviours therewith often led to the stopping of aggressive behaviours. The forms of "Chasing" (48) were terminated by "Fleeing from conspecific" (51), and that of "Pouncing on conspecific" (33) by "Fleeing from conspecific" (51) and "Turning hindquarters away" (52). "Turning head away" (57) and "Turning hindquarters away" (52) ended all variants of "Head up" (41). With the exception of "Head pre-stretching with Squawking (42d)", the other types of "Head pre-stretching" (42) were ended by "Turning hindquarters to" (53) (Fig. 56).

Discussion

For discussion about the influence of the observer and the transferability of zoo observations to wild living rock hyraxes, please see Höft & Gansloßer (2021).

Sequential analysis

Sequential analysis enabled most behaviour patterns of the social behaviour to be categorized as "Sociopositive Behaviour" or "Agonistic Behaviour" and thus be placed in a behavioural context and interpreted. Between the categories of "Sociopositive behaviour" and "Agonistic behaviour" stand the behavioural patterns "Slipping off" (32), "Head raising" (40) and "Pulling away the paw" (58). This is because these behaviours are the end of body contact and are therefore neither socio-positive nor agonistically motivated. These behaviours were therefore categorised as "Stopping body contact". "Comfort behaviour" (68) is probably a displacement activity, as Hoeck (1976a) also described for scratching in communication situations. The rock hyraxes often did not react at all to socio-positive behaviour, which could be interpreted as toleration. As an agonistic element, "Walking away and jumping away" (62) has some connections to socio-positive behavioural elements, as it occurred as a reaction in the case of body contact which was not tolerated. For this reason, it was also classified as "stopping body contact". The central element of "agonistic behaviour" is "Turning head towards with Mouth opening" (43c), which according to binomial test belongs to "Attack and threat behaviour". "Turning head away" (58), "Turning hindquarters towards" (53) and "Fleeing from conspecific" (51) often led to the ending of aggressive behaviour and are defensive according to the binomial test. Sale (1970a, b) also interprets the former as behavioural elements that avoid aggression. "Fleeing from conspecific" (51) enlarges the distance between the individuals involved and thus often prevents attacking behaviour.

Some playing behaviours ("Nibble a Conspecific" (16), "Playful Mounting" (19), "Playful craning of the neck" (25)) provoked not only playing behaviour but also agonistic behaviour and could stop playing behaviour. Hoeck (1978) also mentions that "Playful Mounting" (= mounting) often ends in agonistic behaviour. In the case of "Nibble a Conspecific" (16) and "Playful Mounting" (19), however, the reactions are defensive ("Walking away and jumping away" (62) in the case of "Playful Mounting" (19)) or are elements that end body contact (in the case of "Nibble a Conspecific" (16)). For both play elements, the body contact is maintained for longer, which is only tolerated for a short time by the playmate, whereby the defensive reaction does not have to end the play. However, defensive behaviour occurred only three times in the case of "Nibble a Conspecific" (16), so that this coupling is to be considered critically. "Playful craning of the neck" (25) triggered not only playing behaviour but also "Turning head towards with Mouth opening" (43c), which is an "Aggression and threatening behaviour". One possible cause could be that "Playful craning of the neck" (25) was misinterpreted by the conspecific, and not recognised as playful, as it resembles the aggressive "Head pre-stretching" (42).

A few behaviour patterns[16] were so rare that they had to be excluded from sequence analysis in advance, while others[17] could not be assigned to any category of the social behaviour because of their low frequencies. The behavioural elements of the "Sexual behaviour" could be assigned of the basis of the C_2-value, but most of these behaviour patterns occurred less than five times. Sexual behaviour could only be observed on eleven days[18]. This was also to be expected, as the observation months were outside of the rock hyrax's mating period. Sexual behaviour could only be observed between the pregnant females and the male, where sexual behaviour ("Sexual mounting") with the rock hyrax named "Fuzzy" was registered only once. An explanation for the appearance of mating elements outside mating time could be related to sex hormone status [e.g. oestrogen; progesterone does not seem to play a role in the pregnancy of rock hyraxes (Heap et al. 1975)] at the end of the pregnancy of the rock hyrax named "Alpha-Weibchen" (parturition on 2010/06/03) and of "Fuzzy" (parturition on 2010/06/16), especially as the longer sequences occurred only towards the end of the period of observation, two to three months before the birth term[19]. Mating behaviour during pregnancy can also be observed in other animal species (e.g. Rhesus monkey, *Macaca mulatta*; Bielert et al., 1976).

The observations gave the impression that besides the "Playful head tossing" (24), there is an agonistic "Head tossing". However, this could not be clearly confirmed by the sequence analysis. "Playful head tossing" (24) also led significantly to agonistic behaviour[20], which would support a differentiation between head swinging in playful and agonistic context. The significance, however, lies only at the C_2 level and with individual frequency <5, which makes a distinction rather critical. Further studies are needed in order to find a significant separation or to delete a non-occurring behaviour.

According to sequential analysis, "Pressing towards" (37) and "Squeezing in between" (66) are part of the "Agonistic behaviour" (due to the use of "Walking away and jumping away" (62) in response). However, these behavioural elements both cause and maintain body contact. The conspecifics had no reaction to these behaviours much more often than that they distanced themselves from the conspecific. Because of the numerous other behavioural elements that generated "no reaction" (/) very frequently (("huddling" led, for example, 9,803 times to "no reaction" (/), while "Pressing towards" (37) occurred only 872 times (of which "no reaction" (/) was generated 611 times)), the expected value for the action-response pairs "Pressing towards" (37) – "no reaction" (/) and "Squeezing in between" (66) – "no reaction" (/) is high. The combination of the high expected value and low observed value does not produce significant C_3 values. The C_2 value is, at least for "Pressing towards" (37), significant for the response "no reaction" (/), which would indicate a possible coupling. Another reason to place both behavioural elements in the functional category "Sociopositive behaviour" is the definition of the behavioural element "Walking away and jumping away" (62). Thus, "Walking away and jumping away" was also noted when the conspecific in response moved away only a little bit and body contact was maintained. In subsequent studies, it is recommended to make a distinction between "Walking and jumping with maintenance of body contact" and "Walking and jumping with termination of body contact". For the same reason, in the future, "no reaction" (conspecific does not react and there is no body contact) and "tolerance of body contact" (conspecific does not react, but there is body contact) should be distinguished.

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[16] "Head swinging", "Nudging the corner of the mouth", "Playful squirming", "territorial call".

[17] "Laying a leg onto", "Head tossing".

[18] Total on eleven days in 2010: 28/01, 03/03, 05/03, 13/03, 19/03, 23/03, 29/03, 06/04, 15/04, 20/04, 25/04.

[19] 13/03, 16/03, 19/03, 24/03, 06/04, 15/04, 25/04.

[20] Seven times; playing behaviour occurred only five time as response.

In summary, with a few exceptions, social behaviour could certainly be assigned to the behavioural contexts ("sexual behaviour", "play behaviour", sociopositive behaviour" or "agonistic behaviour"). However, especially concerning the sexual behaviour, there is a need for further research, as well as for the verification of the existence of "Head tossing" in playful and agonistic contexts.

Subdivision of the "Agonistic behaviour"

The agonistic behaviour patterns were classified into the categories "Attack and threatening behaviour" as well as "Defensive behaviour" with the help of the binomial test and thus placed in a behavioural context. In "Agonistic behaviour", some behaviours[21] could be assigned to one of the two categories ("Attack and threatening behaviour" and "Defensive behaviour") based only on the C_2 value. Further studies are needed to verify the classification. Other behavioural elements[22] could not be uniquely assigned to either category. There is a possibility that these elements are mixed-motivation behaviours[23]. The bigger problem, however, may again be that the behaviours occurred only rarely or in combination with other elements and were thus investigated as a combination. Thus, "Squawking" (46) could not be attributed to either "Attack and threatening behaviour" nor "Defensive behaviour", but "Turning head towards with Squawking" (43d) is a behavioural element of the category "attack and threatening behaviour". However, this may also be due to the fact that only in combination with the "Turning head towards" (43) does the behaviour acquire a definite meaning as "Attack and threatening behaviour". It remains to be seen what subsequent investigations will reveal.

The behaviour patterns which could not be assigned clearly to one of the categories of agonistic behaviour were assigned hypothetically to these, which must be verified by subsequent studies. For the assessment, the signals which occurred with these behavioural patterns (e.g. baring the upper incisors) were compared with those which occurred in the attributable behavioural patterns and the ones described in the literature. Furthermore, the combination with other behavioural patterns was considered. Signals of "Attack and threatening behaviour" are the showing of the upper incisors serving as weapons as well as the alignment of the head on the conspecific (Sale 1970b; own observation). Defensive behaviours are those which lead to a turning of the head from the conspecific or to a presentation of the hindquarters (Sale 1970a, b; own observation). "Snapping" (47) appeared in part with behaviour patterns of "attack and threatening behaviour" ("Turning head towards" (43), "Head pre-stretching" (42)) and exposing the upper incisors, so a possible classification was made as "attack and threatening behaviour". "Standing up" (39) can also occur in combination with elements of "attack and threatening behaviour" ("Mouth opening" (44)) and was therefore also hypothetically classified in the category "attack and threatening behaviour". "Pulling head to body" (54) and "Lower the Head" (56) both lead to the removal of the head from the conspecific and were therefore classified as potentially "Defensive behaviour". In addition, "Lower the Head" (56) also occurred in the "Sexual behaviour" category. "Head shaking" (55) occurred sometimes in combination with "defensive behaviour" ("Turning head away" (57)) and was therefore hypothetically assigned to this category. By "Walking backwards" (59), the rock hyrax distances itself from the conspecific, so this is therefore likely to be a defensive behaviour. At the same time, the animal can

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[21] "Turning jump" (50), "Laying paw on conspecific" (45), "Jumping over conspecific" (60).

[22] "Head shaking" (55), "Head tossing", "Lowering the head" (56), "Pulling head to body" (54), "Snapping" (47), "Squawking" (46), "Standing up" (39), "Empty chewing" (38), "Walking backwards"(59).

[23] "[…] designation for the fact [that] some behaviour patterns do not appear to be just formed by the basis of a single motivation, but [that] different motivations are involved in there." (Immelmann, 1982, p. 156)

keep an eye on its conspecific, which is not possible if it turns around and then distances itself. "Head tossing" could not be separated from the "Playful head tossing" (24) (see Discussion section "Sequence analysis"). Due to the fact that "Playful head tossing" (24) is also used in the non-playing context and then behavioural elements of the "Attack and threatening behaviour" occurred in response, the possible attack and threatening behaviour element "Head tossing" was created. Its existence must be verified by further investigation.

"Empty chewing" (38) is not attributable to a category of agonistic behaviour, but this is probably not due to the small sample size. It occurred relatively frequently (105 times), but usually led to "no reaction" (/) among the conspecific (91 times). Either a reaction was not recognisable to the observer or the behaviour has no signal quality to conspecifics.

The latter would be supported by the fact that during the "Empty chewing" (38), the head was often not directed at a conspecific as in the other elements of "Attack and threatening behaviour". "Empty chewing" (38) was also most often shown by the breeding male and this often in the presence of humans (animal keepers, (personal communication with them); television team; graduate on the first observation days in December). "Empty chewing" (38) could therefore be a threatening signal for potential enemies, because in the "Empty chewing" (38), the extended upper incisors are exposed, which serve as weapons (Sale, 1966b). Males defend their group from danger (Coe, 1962; Sale 1965a), which could be an explanation for the fact that "Askari" showed "Empty chewing" (38) more often than the other group members. Males golden-bellied mangabeys (*Cercocebus chrysogaster*) (Mitchel et al., 1991) and mandrills (*Mandrillus sphinx*) (Chamove et al., 1988) showed more threatening signals to zoo visitors than females. Keepers or visitors can be perceived as a threat (Hosey, 2008; Hosey et al., 2009; Sherwen & Hemsworth, 2019) and threatened by the animals (Chamove et al., 1988; Mitchell et al., 1991) or even attacked (Fa, 1992). The presence of visitors (Chamove et al., 1988; Hosey & Druck, 1987; Mitchell et al., 1992; Lacey & Pankhurst, 2001; Mitchell & Hosey, 2005; Hosey et al., 2009; Sherwen & Hemsworth, 2019) or keepers (Del Thompson, 1989; Sherwen & Hemsworth, 2019) can influence the behaviour of the animals. When visitors influence behaviour, both the number of people (Chamove et al., 1988; Fa, 1992; Mitchell et al., 1992; Lacey & Pankhurst, 2001; Hosey et al., 2009; Sherwen & Hemsworth, 2019) as well as their behaviour (e.g., annoying the animals, active groups) (Hosey & Druck, 1987; Chamove et al., 1988; Mitchell et al., 1992; Lacey & Pankhurst, 2001; Hosey et al., 2009; Sherwen & Hemsworth, 2019) plays a role. However, the influence of visitors on the behaviour of zoo animals is rarely researched (Hosey, 2005; Mitchell & Hosey, 2005; Sherwen & Hemsworth, 2019). Zoo animals are to some extent habituated to the presence of visitors (Hosey et al., 2009). However, rare events in connection with visitors or large and noisy gatherings of people can cause a reaction in the animals. Such a special event was the presence of a television team on 11/03/2010, which caused a clear reaction in the animals. The large camera with lighting was held directly onto the rock hyrax (behind the window where the animals were), after which the breeding male showed "Empty chewing" (38) in a short sequence. The breeding male may have considered the television team as a potential threat and the "Empty chewing" (38) thus either served as a defensive action or was ambivalent conflict behaviour. Hoeck (1980) describes it as threatening behaviour between two equally strong territorial males. To confirm the signal as threatening behaviour, further investigations would have to review the connection. It would be interesting to compare the observed defence mechanisms with those from rock hyraxes living in the wild (e.g. against humans, predators).

In addition to the appearance in the agonistic context, "Walking away and jumping away" (61) also served to end the body contact with a conspecific. For this reason, it was also classified in the category "Ending of physical contact". From this the critical question arises to what extent "Walking away and jumping away" (61) may be used to define agonistic behaviour or whether only "Fleeing from conspecific" (51) is suitable for this. Comparing the appearance of both behavioural elements in reaction to “Attack and threatening behaviour” (C_3 value), “Walking away and jumping away” (61) occurred more frequently (659 times compared to 514 times). Especially in response to “Turning head towards” (43), it has a special meaning, since it is the third most common reaction shown. This shows that “Walking away and jumping away” (61) is a defensive behaviour in rock hyraxes and can therefore also be used to define agonistic behaviour.

In conclusion, most agonistic behaviours can be categorised as either “Attack and threatening behaviour” or “Defensive behaviour”. Some behavioural elements could only be assigned to one of these two categories based on the C_2 value or not at all. Further research is needed here.

Selected additional observations

In the rock hyrax group in Osnabrück Zoo, occasional playing behaviour between adults and young animals could be observed, some of which was initiated by the adults. In zoos it is more common that adults also play, while their conspecifics in nature do not (Hughes & Plowman, 2005). However, field observations have also shown play behaviour between adults and young animals (Hoeck, 1978; Fischer, 1992). In the rock hyrax group in Osnabrück Zoo, a total of three adult females played. They played only with young animals and not with other adults. Hoeck (1978) already described that in free-ranging rock hyraxes, young females (born in the previous year) in particular often played with the current young animals and invited them to play. The age difference between one female and the young animals was one year, so this observation is consistent with those of Hoeck. Apart from young females, mothers in particular play with their offspring in the wild (Hoeck, 1978; Fischer, 1992). Both pregnant animals were at the end of their pregnancies at this time (parturition of the “Alpha-Weibchen” on 03/06/2010 and of “Fuzzy” on 16/06/2010). It is therefore possible that the willingness to play with young animals (maternal behaviour) was already present due to an appropriate hormone status. In rats (*Rattus norvegicus* forma *domestica*), maternal behaviour can be triggered towards the end of pregnancy by the presentation of young animals (Nelson, 2000). “Alpha-Weibchen” had partially erected glandular hair during “Playful mounting”, which actually only occurs during “Sexual mounting”. This could have been a mixed motivation triggered by the hormone balance during pregnancy or it could have been sexually motivated and due to the lack of alternative reactions, the young animal in question then initiated a game.

Sale (1970a) describes that rock hyraxes avoid lying head-to-head with their conspecifics in order to avoid agonistic conflicts. This could not be confirmed with the group in Osnabrück Zoo. On the contrary, it often happened that the animals were lying head-to-head (see Fig. 57). Whether this is a general behavioural peculiarity of captive rock hyraxes or just typical for the group at Osnabrück Zoo would have to be reviewed by comparison with other zoo groups.

Hoeck (1978) mentions mounting in an agonistic context and ascribes to it a significance for the establishment of a hierarchy. Mounting in an agonistic context could not be observed in the present study. However, this would be expected if this behaviour is used to clarify the hierarchy or if it would be a gesture of dominance.

Fig. 57: Laying head-to-head during “huddling”. Photo: S. Höft

However, it is also possible that due to the established group structure, mounting in an agonistic context was not necessary in the rock hyrax group at Osnabrück Zoo. This requires further investigations.

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Zusammenfassung

Für Klippschliefer (*Procavia capensis*) existiert bisher kein Ethogramm. Ziel der vorliegenden Studie war es unter anderem, ein Ethogramm zu erstellen. Dazu wurde im Zoo Osnabrück eine Gruppe von Klippschliefern im Zeitraum vom 2. Dezember 2009 bis 27. April 2010 beobachtet. Die Gruppe bestand aus einem adulten Männchen und fünf adulten Weibchen (ab dem 4. Februar nur noch vier) sowie vier juvenilen (2,2) Tieren. Die vorliegende Publikation bezieht sich nur auf das Sozialverhalten. Das Individualverhalten wurde bereits publiziert (Höft & Gansloßer, 2021).

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Appendix I: List of summarised behavioural elements

- Approach backwards (1c) = Approach backwards-frontal (approach with the hindquarters towards the conspecific's head) + Approach backwards-non frontal (approach with the hindquarters towards conspecific's body

- Ending of Head up (E 41) = Ending of Head up + Ending of Head up with Biting + Ending of Head up with Snapping + Ending of Head up with Squawking + Ending of Head up with Empty chewing

- Ending of Head up with Laying paw on conspecific (E 41f) = Ending of Head up with Laying paw on conspecific + Ending of Head up with Laying paw on conspecific with Mouth opening + Ending of Head up with Laying paw on conspecific with Squawking

- Ending of Pouncing on conspecific (E 33) = Ending of Pouncing on conspecific + Ending of Pouncing on conspecific with Nibbling on conspecific + Ending of Pouncing on conspecific with Squawking

- Ending of Turning head towards (E 43) = Ending of Turning head towards + Ending of Turning head towards with Nibbling on conspecific + Ending of Turning head towards with Empty chewing

- Head pre-stretching (42) = Head pre-stretching + Head pre-stretching with Squawking + Head pre-stretching with Snapping

- Head shaking (55) = Head shaking + Head shaking with Mouth opening

- Head up (41) = Head up + Head up with Biting + Head up with Empty chewing + Head up with Snapping + Head up with Squawking

- Head up with Laying paw on conspecific (41f) = Head up with Laying paw on conspecific + Head up with Laying paw on conspecific with Mouth opening + Head up with Laying paw on conspecific with Squawking

- Lowering the head (56) = Lowering the head + Lowering the head with Squawking

- Playful craning of the neck (25) = Playful craning of the neck + Playful craning of the neck with fur nipping + Playful craning of the neck with Playful mouth opening

- Playful head up (22) = Playful head up + Playful head up with Playful mouth opening

- Playful head tossing = Playful head tossing + Playful head tossing with Playful mouth opening + Playful head tossing with Playful fleeing

- Playful mounting (19) = Playful mounting + Playful mounting with Nibbling on conspecific + Playful mounting with fur nipping + Playful mounting with Playful mouth opening

- Playful standing up (21) = Playful standing up + Playful standing up with fur nipping + Playful standing up with Playful mouth opening Playful mouth opening

- Playful turning head away (64) = Playful turning head away + Playful turning head away with Playful mouth opening
- Pouncing on conspecific (33) = Pouncing on conspecific + Pouncing on conspecific with Nibbling on conspecific + Pouncing on conspecific with Squawking + Pouncing on conspecific with Snapping
- Pulling head to body (54) = Pulling head to body + Pulling head to body with Mouth opening + Pulling head to body with Squawking
- Standing up (39) = Standing up + Standing up with Mouth opening
- Turning head away (57) = Turning head away + Turning head away with Squawking
- Turning head towards (43) = Turning head towards + Turning head towards with Biting and licking + Turning head towards with Nibbling on conspecific + Turning head towards with Threatening chewing
- Turning hindquarters away (57) = Turning hindquarters away + Turning hindquarters away with Mouth opening
- Turning hindquarters to (53) = Turning hindquarters to + Turning hindquarters to with Mouth opening + Turning hindquarters to with Squawking
- Turning jump (50) = Turning jump + Turning jump with Head shaking + Turning jump with Mouth opening
- Turning sideways (62) = Turning sideways + Turning sideways with Mouth opening + Turning sideways with Squawking

Appendix II: Behavioural patterns which were excluded

Behavioural patterns that occurred less than five times (also after summarisation, if possible) were excluded from the sequential analysis.

Excluded actions

- Nudging the corner of the mouth
- Playful rolling over the back
- Playful squirming
- Pulling away the paw

Excluded reactions

- Ending of Standing up
- Ending of Standing up with Mouth opening
- Nudging the corner of the mouth
- Jumping on conspecific
- Playful crowding
- Playful rolling over the back
- Playful rolling over the back with fur nipping
- Playful squirming
- Quiver
- Standing up
- Standing up with Mouth opening
- Stopped approach frontal-non frontal (approach with the head towards conspecific's body)
- Touching
- Turning jump with Head shaking

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DER
ZOOLOGISCHE
GARTEN
THE ZOOLOGICAL GARDEN

In Memoriam

VR Dr. Klaus Teuchner

Klaus Teuchner auf der Löwenfeier 2015. Foto: Privat

Im 4. Oktober 2023 ist Herr Veterinärrat Dr. Klaus Teuchner im 101. Lebensjahr nach einem erfüllten und arbeitsreichen Leben nach kurzer Krankheit verstorben. Mit Dr. Teuchner verliert die Tiroler Tierärzteschaft nicht nur einen hoch angesehenen und verdienten Kollegen, sondern eine prägende Persönlichkeit und einen Lehrmeister für viele Generationen von Tierärzten.

Dr. Teuchner wurde am 27. Juli 1923 in Innsbruck geboren. Er wollte bereits seit Kindheitsjahren Tierarzt werden, musste aber unmittelbar nach seiner Matura 1942 zum Wehrdienst einrücken. Mehrere Verwundungen in den Kriegsjahren hinderten ihn nicht daran, ab 1945 in Innsbruck Human- und ab 1946 in Wien Veterinärmedizin zu studieren. 1947, nach Abschluss der Vorklinik, musste er vor der russischen Besatzungsmacht flüchten und konnte sein Studium an der Universität Bern fortsetzen. 1949 folgten Studienabschluss, Promotion und Assistententätigkeit an der Universität Bern. Dr. Teuchner praktizierte noch zwei Jahre im Schweizer Kanton Appenzell und absolvierte eine chirurgische und infektiologische Ausbildung in Stockholm und München. Zwischendurch erwarb er 1951 in Wien die Nostrifikation. 1953 eröffnete er seine tierärztliche Großtierpraxis im Tiroler Wipptal und seine Kleintierpraxis in Innsbruck. Seine Kunden waren von seinem außerordentlichen Fachwissen, seinem unermüdlichen Ein-

Klaus Teuchner. Foto: Privat

satz zu jeder Tages- und Nachtzeit und zugleich auch seiner Ehrlichkeit begeistert – und bei unklaren Befunden bekannte er: „Da muss ich erst nachlesen“. 1960 legte Dr. Teuchner die Physikatsprüfung in Wien ab, bevor er 1964 zum Sprengeltierarzt für das Tiroler Wipptal ernannt wurde. Diese Tätigkeit übte er bis 1991 aus. Seit der Eröffnung des Innsbrucker Alpenzoo 1962 war Dr. Teuchner über 50 Jahre als Zootierarzt tätig. 2013 übergab er 90-jährig diese Aufgabe seinem Nachfolger und stand ihm auch anschließend mit Rat und Tat zur Seite. In dieser langen Zeit im Alpenzoo nutzte Klaus Teuchner seine unzähligen Kontakte und Freundschaften zu europäischen Kollegen, um sich fortzubilden und auch den Alpenzoo sukzessive auf ein internationales Niveau zu heben. Die Verbesserungen in der Hygiene, von Diätplänen, der medizinischen Prophylaxen, der Behandlungsräume, die Betreuung von Fundtieren aus dem Freiland, die zahlreichen Immobilisationen und Operationen, die vielen geglückten Auswilderungen von Steinwild wären ohne ihn nicht denkbar gewesen. Der Alpenzoo als heutiges Kompetenzzentrum in der Haltung alpiner Tiere ist zu einem Großteil sein Verdienst. Sein enormes Fachwissen und sein immenser Erfahrungsschatz wurden nur noch von seinem großen Fleiß und seinem ständigen Wissensdurst übertroffen. Seine Bereitschaft, sein Wissen zu teilen, führte dazu, dass Dr. Teuchner in den vielen Jahren seiner Tätigkeit zum Lehrmeister zahlreicher Tierärzte und Tierärztinnen wurde. Im Jahr 1980 wurde Dr. Teuchner aufgrund seiner Verdienste der Ehrentitel Veterinärrat verliehen; es folgten zahlreiche weitere Ehrungen von Bund, Land, Stadt Innsbruck und dem Alpenzoo. Auch nach der Beendigung seiner praktizierenden tierärztlichen Tätigkeit im Jahr 2006 im Alter von 83 Jahren war Dr. Teuchner für viele Tierärzte und Tierärztinnen, Tierhalter und Tierhalterinnen und Freunde sowie Freundinnen ein wichtiger Ratgeber und wertvolle Ansprechperson.

Wir betrauern den Verlust eines höchst kompetenten, wunderbaren, hilfsbereiten und humorvollen Menschen und werden ihm ein ehrendes Andenken bewahren. Möge er in Frieden ruhen!

VR Dr. Helmut Pechlaner, Direktor a.D. Alpenzoo Innsbruck, Direktor a.D. Tiergarten Schönbrunn

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