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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",

[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.

*"Head swinging": 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.

[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 & Ganslosser, 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 & Ganslosser, 2021) or squats (“Squatting”, Höft & Ganslosser, 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 & Ganslosser, 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 & Ganslo ß er, 2021) or sit close together with physical contact. On their backs or hindquarters, juveniles[3] (more rarely adults[4]) squat ("Squatting", Höft & Ganslo ß er, 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 & Ganslo ß er, 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 & Ganslo ß er, 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

[3]Sale (1965c) thinks that this will prevent the young from being trampled by conspecifi cs 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

[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 & Ganslоßer, 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.

[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 prestretching".

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).

[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

[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.

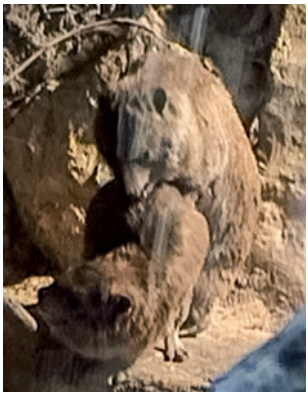

Fig. 51: "Turning hindquarters towards head away". Photo: S. Höft

Fig. 52: "Turning sideways". Photo: S. Höft

"Turning sideways" (62): 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)

"Walking away" (61): 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.

Legend for Figs 53-55: / 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"

[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.

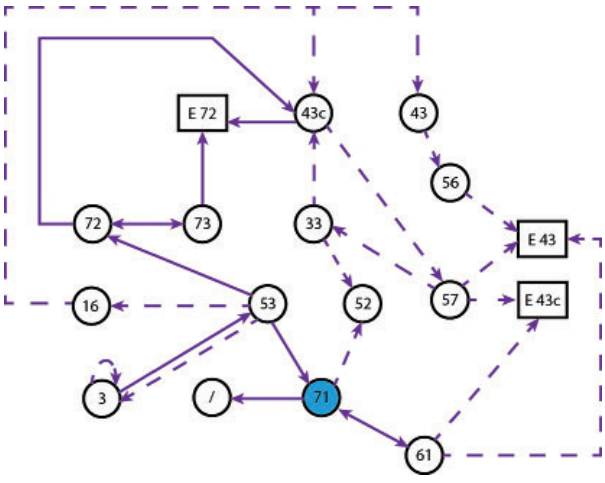

Fig. 53: Sequential analysis of sexual behaviour.

Play behaviour

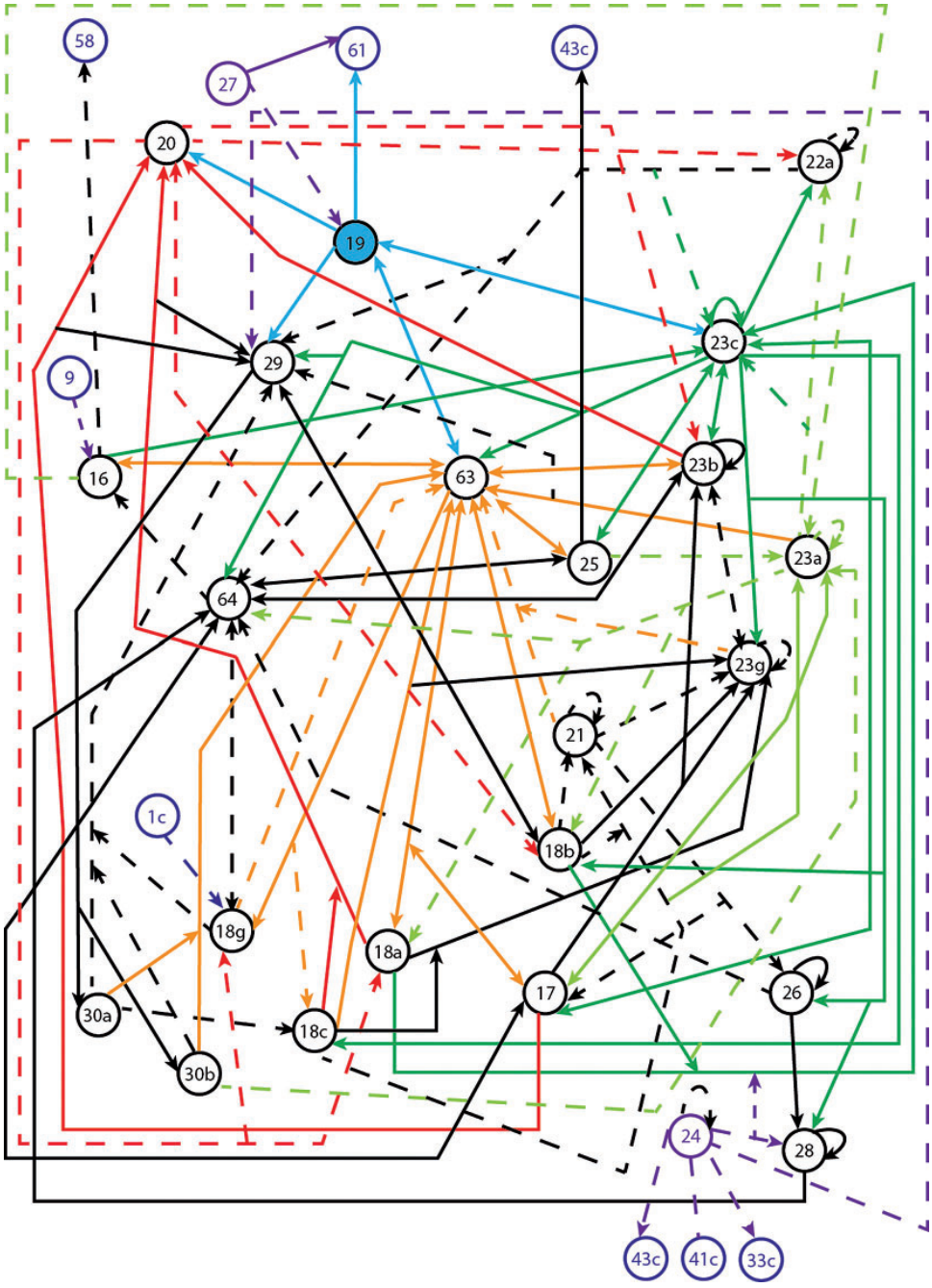

Fig. 54: Play behaviour: The dark blue elements are not part of the play behaviour.

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

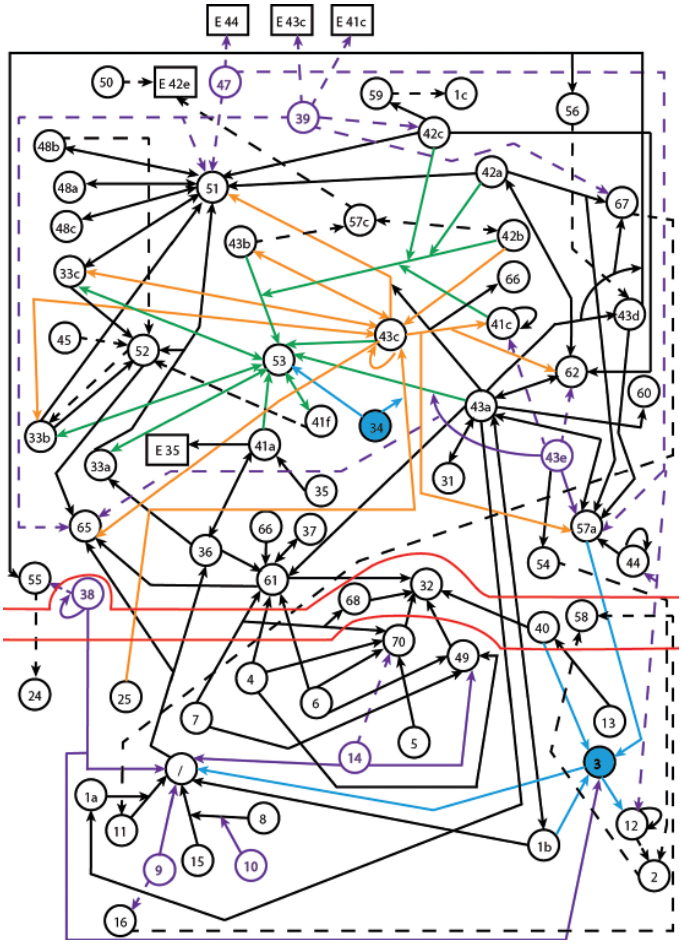

Fig. 55: Sequential analysis of social behaviour: Above the red line is the category “Agonistic behaviour” and below the red line is “Sociopositive behaviour”. Between the two lines are behaviour patterns that could not be definitively assigned to one of these categories.

"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)

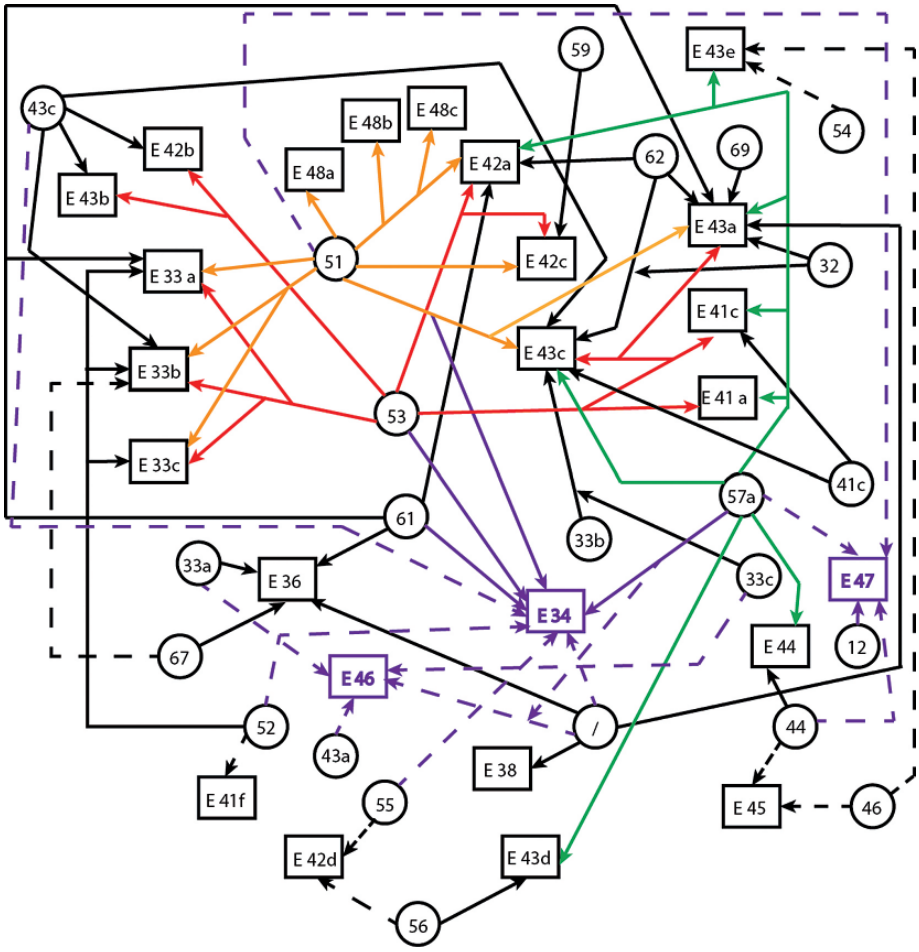

Fig. 56: Termination of aggressive behavioural patterns.

"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 fi ve 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

[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 & Ganslоßer, 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