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Meerkats (*Suricata suricatta*) are able to detect hidden food using olfactory cues alone

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ABSTRACT

Meerkats (*Suricata suricatta*) are known to strongly rely on chemical signals for social communication. However, little is known about their use of the sense of smell in foraging and food detection. The aim of the present study was therefore to assess whether captive meerkats are able to (1) detect hidden food using olfactory cues alone, (2) discriminate between the odor of real food and a single food odor component, and (3) build an association between the odor of real food and a novel odor. We employed the buried food test, widely used with rodents to assess basic olfactory abilities and designed to take advantage of the propensity of certain species to dig. We found that the meerkats were clearly able to find all four food types tested (mouse, chicken, mealworm, banana) using olfactory cues alone and that they successfully discriminated between the odor of real food (banana) and a food odor component (*iso*-pentyl acetate). In both tasks, the animals dug in the food-bearing corner of the test arena as the first one significantly more often than in the other three corners. No significant association-building between a food odor and a novel odor was found within the 60 trials performed per animal. We conclude that meerkats are able to use olfactory cues when foraging for hidden food. Further, we conclude that the buried food test, employed for the first time with a non-rodent species, is a useful means of assessing basic olfactory capabilities in meerkats.

1. Introduction

Meerkats (*Suricata suricatta*) are small-bodied mammalian carnivores belonging to the mongoose family, Herpestidae [37]. They live in cooperatively breeding social groups of up to 25 individuals and inhabit the arid areas of southern Africa [8]. It is well-established that meerkats strongly rely on olfactory signals in the context of social communication. They have been shown to use scent signals for territorial and mate defence [18], for advertising and maintaining social dominance [17], and for suppressing subordinate reproduction [10]. Their anal sac secretions have been shown to contain chemical information about sex, age, and social group membership [20,21,23] and allow them to discriminate between kin and non-kin [22]. In addition to different forms of scent-marking [24], they also display flehmen [13], suggesting a functional vomeronasal system. Similarly, it has been reported that both wild and captive meerkats are able to recognize predators using olfactory cues and accordingly to perform adaptive behavioral responses based on this chemical information [39,42,43].

The strong reliance upon their sense of smell should not be surprising considering that meerkats have well-developed olfactory brain structures [5,15,38]. However, in contrast to the wealth of knowledge about the role of olfaction in meerkat social communication, much less is known about their use of the sense of smell in foraging and food detection. A recent study reported that meerkats bit on cotton-buds impregnated with a prey odor significantly more often than on blank control cotton-buds, suggesting that they are able to detect and recognize prey odors [19].

The diet of meerkats is primarily based on arthropods, but includes up to 20% of small-bodied mammals and other vertebrates such as birds, lizards, and snakes as well as eggs and plant material such as seeds, roots and tubers [11,37]. Animal prey may be caught on top of the ground but is often mobile in the ground which has led to the propensity of meerkats to dig or rake at the location of potential underground food [11,13]. Meerkats have been reported to constantly sniff during foraging [13], suggesting that they may also use olfactory cues for detecting and locating hidden food.

It was therefore the aim of the present study to assess the role of the sense of smell in foraging and food detection by meerkats. More specifically, we assessed whether captive meerkats are able to (1) detect hidden food using olfactory cues alone, (2) discriminate between the

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odor of real food and a single food odor component, and (3) build an association between the odor of real food and a novel odor.

At the same time, we assessed the suitability of two behavioral methods for testing olfactory capabilities in the meerkats: the buried food test, widely used with rodents to assess basic olfactory abilities and designed to take advantage of the propensity of certain species to dig [41], and olfactory associative learning, which forms the basis of operant conditioning procedures which are less dependent on motivational factors compared to procedures based on spontaneous behavior such as the buried food test [14].

2. Materials and methods

2.1. Ethics statement

The experiments reported here comply with the *European Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU)* and also with current Swedish Animal Welfare laws. They were performed according to a protocol approved by the ethical board of the Swedish Board of Agriculture (Jordbruksverket, protocol # 31–2647/10).

2.2. Animals

Four adult male meerkats (*Suricata suricatta*) that were part of a group of 11 meerkats (ten males plus one female) were used. The animals weighed between 600 and 800 g and were between 24 and 28 cm long (head plus body). The meerkats were maintained at Kolmården Wildlife Park (Sweden) and were housed in an enclosure that consisted of an indoor exhibit of 50 m^2 and an outdoor exhibit of 100 m^2, connected by a sliding door. The indoor exhibit had a ground substrate of sand and contained bushes, tree stumps and various hiding places, such as wooden boxes and an artificial termite nest with tunnels. The outdoor exhibit had a ground substrate of natural soil and grass and contained bushes, tree stumps, coniferous trees and rocks. The sliding door connecting the two exhibits was open during the study period, allowing the animals to freely move between them. The meerkats were fed three times a day (approximately at 08:00, 13:00 and 16:00) with whole dead mice (one per individual), whole dead newly-hatched chicks (one per individual) or a chunk of meat (from different ungulate species) and had access to water *ad libitum*. The animals were also regularly fed live crickets, live mealworms, pelleted cat food, boiled eggs as well as fruits such as bananas and apples. The four animals that participated in the study were selected based on their willingness to voluntarily and singly enter the test arena described below. In order to reliably identify these four animals they were color-marked. During all parts of the study, participation by the animals was strictly voluntary and the animals were never food-deprived.

2.3. Experimental set-up

To assess the ability of the meerkats to detect hidden food using olfactory cues alone, we employed the buried food test [41]. This test, developed for and widely used with laboratory rodents to assess basic olfactory capabilities, takes advantage of the propensity of species such as mice and rats to dig. The test arena was made of 6 mm plywood and consisted of two assembled wooden boxes, each 50 × 50 × 30 cm (W × L × H), with hinged transparent acrylic glass lids on top. Both boxes had an opening of 15 × 15 cm in the center of the connecting side, with a sliding door between them to allow an animal to pass from one box to the other. The box into which an animal entered the arena ("Entrance box") had a 15 × 15 cm entrance opening with a sliding door. The entrance opening was extended with a 30 cm long tunnel to make it easier to allow only one animal to enter at a time. The entrance box also had a hinged flap door of 15 × 15 cm that could be opened by an animal from the inside by a light press with its head. The flap door

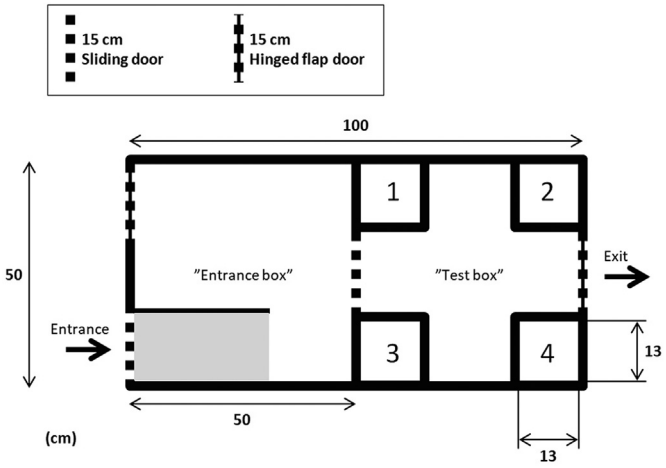

Fig. 1. Test arena used for assessing the olfactory abilities of meerkats. All dimensions are given in cm. Labels 1–4 refer to the four test compartments in which food and/or odors were presented, hidden under woodchip bedding.

was placed on the entrance side of the box and was intended to work as an "emergency exit" for the animals in case of distress. The second box, in which the tests took place ("Test box"), contained four 13 × 13 × 7 cm compartments (labelled 1–4) that were open on the top and that were placed one in each corner of the box. The "Test box" also had a 15 × 15 cm hinged flap door on the opposite side of the middle sliding door, allowing an animal to exit the arena (Fig. 1).

For presenting food items and odorants, small petri dishes (3.5 cm diameter, Sarstedt, Nümbrecht, Germany) were used. For food items, one piece of either banana, or mouse, or chicken, or 5–7 mealworms were placed directly into the petri dish. For odorants, a filter paper (3 cm diameter, Munktell, Stockholm, Sweden) was placed on the bottom of the petri dish and 100 µl of an odorant was pipetted onto the filter paper. For both empty and food- or odor-containing petri dishes, one half of a ball-shaped metal tea net (5 cm diameter) was placed over the petri dish in order to avoid direct contact with and thus contamination of the woodchips covering the metal tea nets while still allowing the odors of the food or the odor-impregnated filter papers to emanate through the nets and bedding. In all tests, at least one petri dish covered by a metal tea net was placed in each of the four compartments in the "Test box" of the arena, either with a food item or an odor-impregnated filter paper inside, or empty. All four compartments were then filled to the brim with poplar woodchips (Lignocel select, Rettenmaier & Söhne, Rosenberg, Germany) so that the petri dishes and the metal tea nets were completely covered and thus invisible to the animals.

For data collection, a digital video camera (Canon Legria HF M52, Solna, Sweden) was used. The video camera was attached to a horizontal aluminium bar that was mounted on a tripod so that the camera was placed centrally above the "Test box". Videos were analyzed for the occurrence of five behaviors (Table 1) as well as for the location where (compartments 1–4 of the "Test box") and the sequence in which they occurred.

2.4. Experimental procedure

The experiments described below were preceded by a habituation phase during which the meerkats were allowed to freely explore the test arena which was occasionally baited with pieces of food while all doors were open (2 weeks). The animals were then habituated to the presence of the experimenter (2 weeks), to the sliding doors being closed while being inside the test arena (3 weeks), and to the petri dishes bearing food, the metal tea nets covering the petri dishes, and to the woodchips (3 weeks). The habituation phase also served to identify those

Table 1
The behaviors recorded during the tests.

Behavior	Description
Sniffing	Using the nose to smell with face directed towards the woodchips of a test compartment at a distance < 5 cm.
Scratching	Using one paw to scratch the top layer of woodchips, without uncovering the metal tea net and petri dish.
Digging	Using one or two paws to dig deeply into the woodchips, uncovering the whole metal tea net and petri dish.
Eating	Exposing the food item by removing the metal tea net from the petri dish. Counted as *eating* only after the animal had also consumed the food item.
Exiting	Leaving the test box by pressing the forehead against the exit flap door.

individuals which were most willing and eager to voluntarily and singly enter the test arena.

2.4.1. Experiment 1: Olfactory detection of real food

To assess the meerkats' ability to detect hidden food using olfactory cues alone, a petri dish containing a food item and covered with a metal tea net was placed in one of the four compartments of the "Test box". Empty petri dishes, also covered with metal tea nets, were placed in each of the remaining three compartments. All four compartments were then filled to the brim with woodchips so that the petri dishes and the metal tea nets were completely covered and thus invisible to the animals. The type of food used (banana, chicken, mouse, and mealworm) was alternated between days. Approximately five trials were performed per animal and day until each of the four animals had performed 30 trials with each of the four food types.

2.4.2. Experiment 2: Olfactory discrimination between real food and a monomolecular odorant

To assess the meerkats' ability to discriminate between the odor of real food and a monomolecular odorant, a petri dish containing a food item and covered with a metal tea net was placed in one of the four compartments of the "Test box". A petri dish containing either a food odor component (*iso*-pentyl acetate) or a control odor (cyclamen aldehyde), and covered with a metal tea net, was placed in another compartment of the "Test box". Empty petri dishes, also covered with metal tea nets, were placed in each of the remaining two compartments of the "Test box". All four compartments were then filled to the brim with woodchips so that the petri dishes and the metal tea nets were completely covered and thus invisible to the animals. The following three combinations of food type and odor were tested:

(A) banana *vs.* *iso*-pentyl acetate.

iso-pentyl acetate is known to be the quantitatively and qualitatively predominant component of banana odor [6] and humans describe its odor quality as banana-like [7]. Therefore, this odor combination assessed, firstly, whether the meerkats are able to discriminate between the odor of real food and a food odor component, and secondly, whether the monomolecular odorant *iso*-pentyl acetate might have the property of a "key" or "character impact" compound [12]. If that was the case, the animals should dig in the corner bearing the monomolecular odorant as the first one in at least some of the trials.

(B) mouse *vs.* *iso*-pentyl acetate.

As the tests with odor pair (A) showed that the meerkats dug at least in some cases in the corner bearing *iso*-pentyl acetate as the first one, we tentatively concluded that this monomolecular odorant may have at least some property as a "key" or "character impact" compound of banana odor for the meerkats. Therefore, this odor combination assessed whether the assumed property of *iso*-pentyl acetate as a "key" or "character impact" compound might also lead the meerkats to dig in the corresponding corner when the alternative stimulus was the odor of a different type of real food.

(C) banana *vs.* cyclamen aldehyde.

Cyclamen aldehyde has been described as having a lily-of-the-valley-like odor quality [3]. It does not occur in nature, and none of the foods commonly consumed by meerkats has an odor quality which is similar to that of cyclamen aldehyde. Thus, this monomolecular odorant is unlikely to have any properties as a "key" or "character impact" compound for the meerkats. Therefore, this odor combination assessed whether the meerkats might dig in the corner bearing an odorant which is unfamilar to them and presumably has no behavioral relevance for them as the first one in at least some of the trials. This would indicate that the meerkats might respond with explorative behavior towards a novel odor stimulus, even when a food odor was the alternative stimulus.

Approximately five trials were performed per animal and day until each of the four animals had performed 20 trials with each of the three stimulus combinations.

2.4.3. Experiment 3: Olfactory association between real food and a novel odor

To assess the meerkats' ability to learn to associate a food type (banana) with a novel odor (eugenol), a petri dish containing banana was placed in one of the four compartments of the "Test box", together with another petri dish containing eugenol, both covered with metal tea nets (Fig. 2, lower left panel). Empty petri dishes, also covered with metal tea nets, were placed in each of the remaining three compartments of the "Test box". This set-up was alternated every third trial by removing the petri dish containing banana, leaving only the petri dish containing eugenol in one of the four compartments (Fig. 2, lower right panel). Approximately five trials were performed per animal and day until each of the four animals had performed 60 trials with both banana *plus* eugenol and 20 trials with eugenol *only*. Fig. 2 summarizes the set-ups in Experiments 1–3.

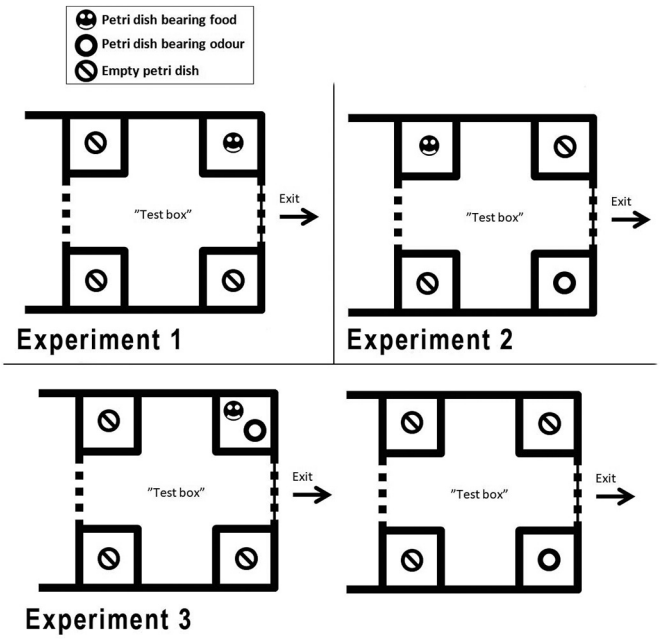

Fig. 2. Examples of the experimental set-ups in Experiment 1 (Olfactory detection of real food, upper left panel), Experiment 2 (Olfactory discrimination between real food and a monomolecular odorant, upper right panel), and Experiment 3 (Olfactory association between real food and a novel odor, lower panels).

In all three experiments, individual trials were performed as follows: after preparing the four compartments of the "Test box", the entrance sliding door of the "Entrance box" was opened and one animal was allowed inside. After closing the entrance sliding door, the video camera was started, the middle sliding door was opened and the animal was allowed into the "Test box" and its behavior was recorded. When the animal exited the "Test box" through the exit flap door, the video camera was stopped and the four compartments of the "Test box" were prepared for the next trial. With all three experiments, care was taken that the position of the hidden stimulus or stimuli was pseudorandomized between the four compartments of the "Test box" as well as between animals and trials. Similarly, the sequence in which the animals performed their approximately five trials per day was pseudorandomized. At the end of each testing day, the metal tea nets were washed with detergent and hot water and allowed to dry. Used petri dishes were replaced daily. Woodchips were replaced at every change of food presented as stimulus, and otherwise refilled when needed. In the rare cases when woodchips got contaminated by a food or odor stimulus *via* direct contact they were replaced immediately. All tests took place between 09:00 and 12:00 on 5 days per week.

2.5. Odor stimuli

The following food items were used as odor stimuli:

Banana (*Musa paradisiaca*). Ripe bananas were peeled and prepared by cutting 1 cm thick slices and cutting each slice twice to create four equally sized pieces of which one was used per trial.

Mouse (*Mus musculus*). Frozen adult mice were defrosted and prepared by removing the tail, inner organs and intestines and then cutting the body into 6–8 pieces of which one was used per trial.

Chicken (*Gallus gallus domesticus*). Frozen 2–3 day old chicks were defrosted and prepared by removing legs, inner organs and intestines and then cutting the body into 8–10 pieces of which one was used per trial.

Mealworm (larvae of the mealworm beetle, *Tenebrio molitor*). Frozen mealworms were defrosted and used without further preparation. Five to seven mealworms were used per trial.

The rationale for choosing banana, mouse, chicken, and mealworm was to use food items that were highly attractive to the animals as determined by pilot testing with a variety of different foods. Care was taken that all food items were presented at room temperature to prevent the meerkats from using thermal cues for finding the hidden food.

The following monomolecular odorants were used as odor stimuli:

iso-pentyl acetate (CAS# 123–92-2). This odorant has been reported to be the quantitatively predominant component in banana odor [6] and has been described as having a typical fruity, banana-like odor quality [7].

Cyclamen aldehyde (CAS# 103–95-7). This odorant is not naturally occurring and is synthesized for use in the perfume and fragrance industry. It has been described as having a lily-of-the-valley-like odor quality [3].

Eugenol (CAS# 97–53-0). This odorant has been reported to be the quantitatively predominant component in clove (*Syzygium aromaticum*) oil [4] and has been described as having a typical spicy, clove-like odor quality [7].

The rationale for choosing these odor stimuli was that one of them (*iso*-pentyl acetate) should resemble the odor of one of the chosen food items (banana), and the other two (cyclamen aldehyde and eugenol) should not resemble the odor of any food item, be novel to the animals, and not be part of their natural diet. All three monomolecular odorants were diluted using near-odorless diethyl phthalate (CAS# 84–66-2). The dilutions (1:1000 with *iso*-pentyl acetate, 1:100 with cyclamen aldehyde, and 1:18 with eugenol) were chosen based on intensity matching against the odor of a piece of ripe banana. An additional experiment, performed after the experiments described above, verified that the meerkats were clearly able to detect the three monomolecular odorants used in Experiments 2 and 3. All odorants and the solvent were obtained from Sigma-Aldrich (Stockholm, Sweden) and were of the highest available purity (> 99.5%).

2.6. Data analysis

Two-tailed binomial tests were performed to assess whether the number of correct first digs, that is, an animal digging in the corner bearing the hidden food (in Experiments 1–3) or the hidden odor (in Experiment 3) as the first one, differed from chance. The Chi-square test with Bonferroni correction was used to assess whether the number of correct first digs differed between success rates, tasks and conditions.

Preliminary analysis of the data showed that among the five behaviors that we recorded during the tests (see Table 1) only the behavior "digging" was relevant as an outcome measure as the animals always "sniffed", "ate", and "exited" the arena in all trials of all three experiments, and hardly ever "scratched". Accordingly, only the parameter "digging in the correct corner as the first one" is reported.

3. Results

3.1. Olfactory detection of real food

Fig. 3 shows the performance of the four meerkats in the olfactory detection test using real food as odor stimulus. With banana (Panel A), chicken (Panel B), and mouse (Panel C), all four animals performed significantly above chance level (binomial test, $p < .01$) and dug in the corner bearing the hidden food as the first one in at least 16/30 and up to 27/30 trials, corresponding to success rates of 53% to 90%. With mealworms (Panel D), three out of four animals performed significantly above chance level (binomial test, $p < .01$ with one individual, and $p < .05$ with two individuals) and dug in the corner bearing the hidden food as the first one in at least 13/30 and up to 19/30 trials, corresponding to success rates of 43% to 63%. Only one animal failed to perform above chance level with the mealworms (11/30 correct first digs, corresponding to a success rate of 37%).

A comparison between the four food types showed that the success rate with the mealworms (57/120) was significantly lower than with the other three food types (Chi-square test, $p < .01$ with all three comparisons). The success rates with banana (83/120), chicken (92/120), and mouse (96/120) did not significantly differ from each other (Chi-square test, $p > .05$ with all three comparisons) (Fig. 4).

A comparison between the four individuals showed that none of the meerkats performed significantly better or significantly poorer than any of the other three meerkats, with success rates of 75/120 (animal A), 88/120 (animal B), 73/120 (animal C), and 92/120 (animal D) summed across the four food types tested (Chi-square test, $p > .05$).

3.2. Olfactory discrimination between real food and a monomolecular odorant

Fig. 5 shows the performance of the four meerkats in the olfactory discrimination test using real food and a monomolecular odorant as stimuli. With all three stimulus combinations, banana *versus iso*-pentyl acetate (Panel A), mouse *versus iso*-pentyl acetate (Panel B), and banana *versus* cyclamen aldehyde (Panel C), all four animals performed significantly above chance level (binomial test, $p < .01$) and dug in the corner bearing the hidden real food as the first one in at least 13/20 and up to 19/20 trials, corresponding to success rates of 65% to 95%. With all three stimulus combinations, there were only very few cases in which the animals dug in the corner bearing the food odor component (*iso*-pentyl acetate) or the control odor (cyclamen aldehyde) as the first one.

A comparison between the three discrimination tasks showed that the success rates with banana *versus iso*-pentyl acetate (64/80), mouse *versus iso*-pentyl acetate (67/80), and banana *versus* cyclamen aldehyde

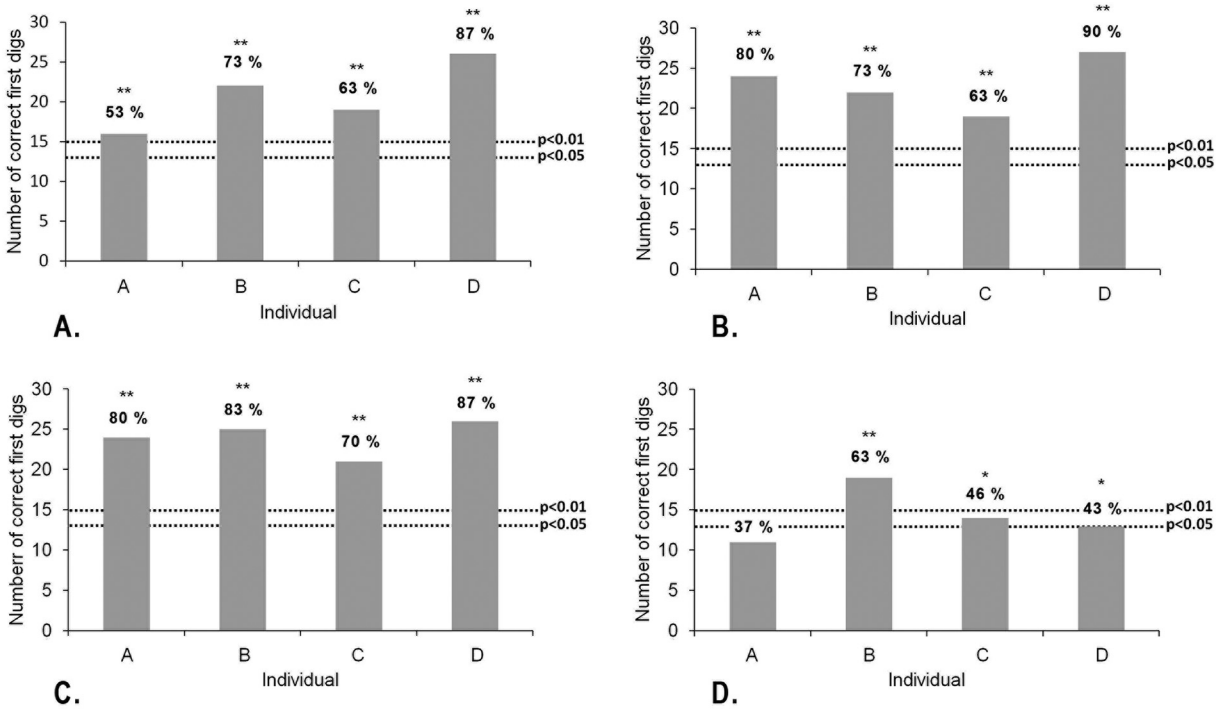

Fig. 3. Number of correct first digs in the food detection test for all four individuals, with banana (Panel A), chicken (Panel B), mouse (Panel C), and mealworms (Panel D) as food item. Asterisks indicate a significant deviation from chance (two-tailed binomial test, * $p < .05$, and ** $p < .01$, respectively).

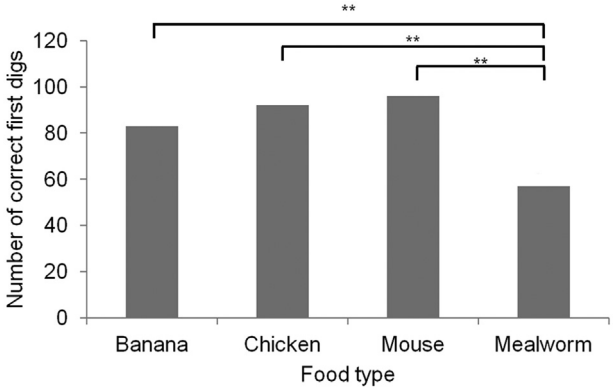

Fig. 4. Number of correct first digs in the food detection test for all four individuals combined across the four food types. Asterisks indicate a significant deviation from chance (two-tailed binomial test, * $p < .05$, and ** $p < .01$, respectively).

(65/80) did not significantly differ from each other (Chi-square test, $p > .05$ with all three comparisons).

A comparison between the four individuals showed that none of the meerkats performed significantly better or significantly poorer than any of the other three meerkats, with success rates of 44/60 (animal A), 54/60 (animal B), 42/60 (animal C), and 56/60 (animal D) summed across the three stimulus combinations tested (Chi-square test, $p > .05$).

3.3. Olfactory association between real food and a novel odor

Fig. 6 shows the performance of the four meerkats in the olfactory association test using real food and a novel odor as stimuli. When the real food (banana) was presented together with (that is: in the same compartment as) the novel odor (eugenol), all four animals performed significantly above chance level (binomial test, $p < .01$) and dug in the corner bearing the hidden real food (plus the novel odor) as the first one in at least 50/60 and up to 54/60 trials, corresponding to success rates of 83% to 90% (Panel A). In contrast, when the novel odor (eugenol) was presented alone, all four animals failed to perform significantly above chance level (binomial test, $p > .05$) and dug in the corner bearing the novel odor as the first one in only between 2/20 and up to 9/20 trials, corresponding to success rates of 10% to 45% (Panel B).

A comparison between the two tasks showed that the success rate with the banana *plus* eugenol condition (211/240) was significantly higher than with the eugenol *alone* condition (20/80) (Chi-square test, $p < .01$).

A comparison between the four individuals showed that all four meerkats performed significantly above chance level in the banana *plus* eugenol condition and that none of them performed significantly better or significantly poorer than any of the other three meerkats, with success rates of 53/60 (animal A), 54/60 (animal B), 50/60 (animal C), and 54/60 (animal D) (Chi-square test, $p > .05$). All four meerkats failed to perform significantly above chance level in the eugenol *only* condition and none of them performed significantly better or significantly poorer than any of the other three meerkats, with success rates of 9/20 (animal A), 3/20 (animal B), 2/20 (animal C), and 6/20 (animal D) (Chi-square test, $p > .05$).

4. Discussion

The results of the present study demonstrate that the meerkats were clearly able to find buried food using olfactory cues alone and that they successfully discriminated between the odor of real food and a main odor component of this food. Within the limited number of trials performed ($n = 60$ per animal), the meerkats did not succeed in building an association between a food odor and a novel odor. Further, the results demonstrate that the buried food test is a useful means of assessing basic olfactory capabilities in meerkats.

4.1. Olfactory detection of real food

Our finding that the meerkats were clearly able to find buried food using olfactory cues alone is not trivial considering that they are known

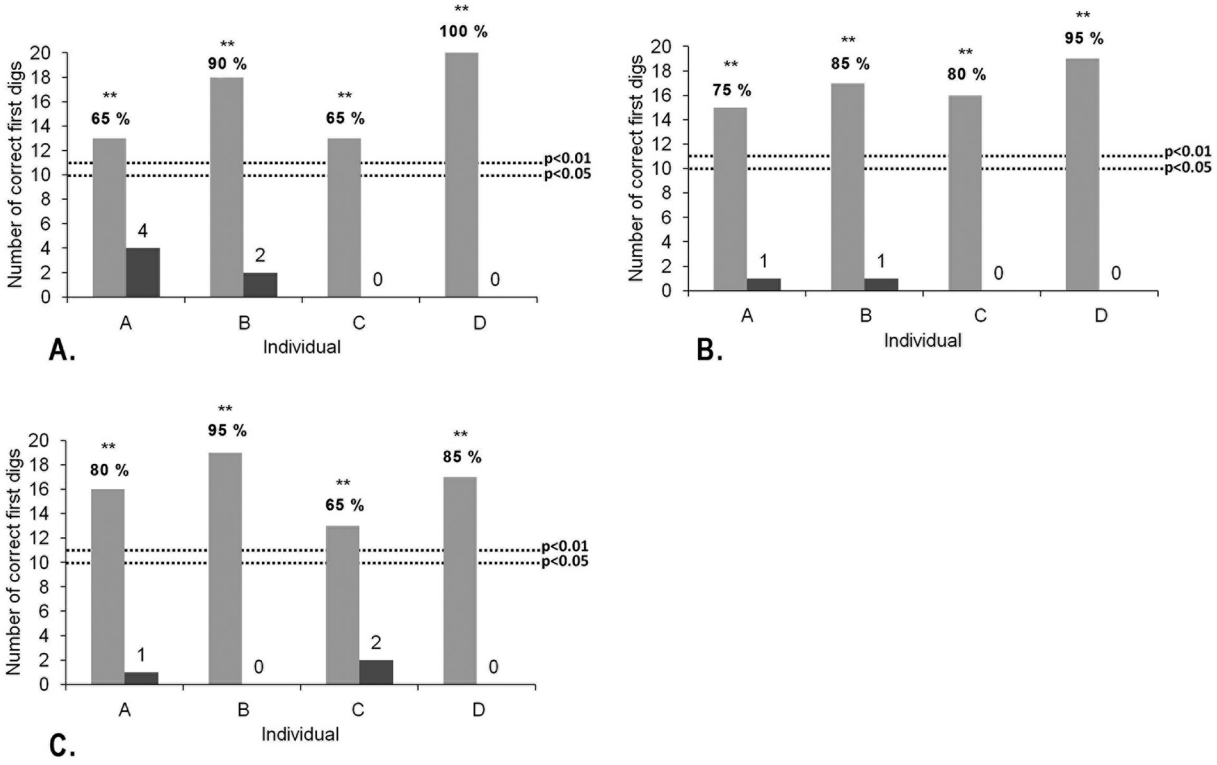

Fig. 5. Number of correct first digs in the olfactory discrimination test for all four individuals, with banana *versus iso*-pentyl acetate (Panel A), mouse *versus iso*-pentyl acetate (Panel B), and banana *versus* cyclamen aldehyde (Panel C) as stimulus combinations. Light grey bars indicate the number of first digs in the compartment bearing the hidden food item, and dark grey bars indicate the number of first digs in the compartment bearing the hidden monomolecular odorant. Asterisks indicate a significant deviation from chance (two-tailed binomial test, * $p < .05$, and ** $p < .01$, respectively).

to also possess well-developed visual and auditory systems [13,37] and considering that animals tend to use a combination of their senses rather than to rely on a single sense for foraging and food detection whenever possible [9]. Although this may also be the case with meerkats, the present findings suggest that their sense of smell is at least critically involved in finding food that is not readily detectable visually and/or acoustically and fully sufficient for efficient foraging. Thus, our findings are in agreement with a recent study which reported that meerkats displayed differential behavior towards visually identical cotton buds impregnated with either a prey odor or a blank control, suggesting that they are able to detect and recognize prey odors [19]. Further, they are consistent with reports of well-developed olfactory brain structures in meerkats [5,15,38] which are the neuroanatomical prerequisite for this olfactory capability.

Our finding that the meerkats detected hidden mealworms at a lower success rate compared to mouse, chicken and banana may at first seem surprising as arthropods comprise up to 80% of the meerkats' diet in the wild [11,37]. However, several aspects should be considered with regard to this finding: Although we cannot completely exclude the possibility that differences in familiarity with the food types tested might account for our results as mouse and chicken were fed daily to the meerkats whereas mealworms or other arthropods (*e.g.* larvae of the darkling beetle, *Zophobas morio* and imagos of field crickets, *Gryllus campestris*) were fed only occasionally, this seems rather unlikely as banana, too, was fed only occasionally but was nevertheless detected by the meerkats at the same high degree as mouse and chicken (*cf.*Fig. 3). Differences in attractivity of the four food types tested are also unlikely to explain this finding as both pilot tests with a variety of foods that we performed during the habituation phase of the present study as well as an earlier study on food preferences in captive *Suricata suricatta* [32] both showed that the meerkats are highly attracted to arthropods such as mealworms, *Zophobas* larvae and adult crickets and even prefer those over simultaneously presented food types such as eggs and banana. Differences in odor intensity of the four food types used in the present

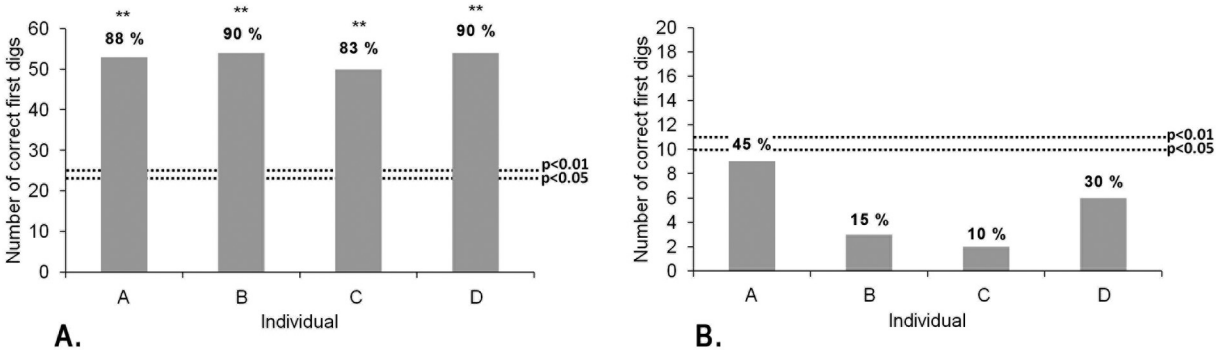

Fig. 6. Number of correct first digs in the olfactory association test for all four individuals, with the banana *plus* eugenol condition (Panel A) and the eugenol *alone* condition (Panel B). Asterisks indicate a significant deviation from chance (two-tailed binomial test, * $p < .05$, and ** $p < .01$, respectively).

study are therefore the most likely explanation for our finding that the mealworms were detected at a lower success rate - although still above chance level - compared to the other three food types. This possibility is supported by the fact that mealworms are considerably less smelly than mouse, chicken and banana for human noses.

4.2. Olfactory discrimination between real food and a monomolecular odorant

Naturally occurring odor stimuli are, with very few exceptions, highly complex mixtures composed of dozens or even hundreds of volatile compounds [27,34]. Olfactory systems have therefore to deal with the problem to recognize the identity of an odor stimulus despite perpetual changes in its composition or intensity which are caused by changes in the odor source itself (*e.g.* the ripening of a fruit) or in the environment (*e.g.* the convection of odor molecules in air currents) [31]. In order to reliably recognize a complex odor mixture animals may adopt the strategy to rely on only one "key" or "character impact" compound which determines its odor identity [12]. Such a strategy requires that this compound is reliably present in the odor mixture and that the animal is able to detect it against the background of the other compounds. Behavioral studies on the ability of animals to use "key" or "character impact" compounds to recognize behaviorally relevant odors yieded inconsistent results: single compounds of predator odors, for example, have been reported to be as efficient as the full odor mixture, or less efficient, or completely inefficient in eliciting avoidance responses in prey species, depending on the species and the compound tested [1,35]. Frugivorous mammals have been reported to rely on the relative abundance of several compounds rather than on the presence of a single compound for food selection [16,25]. Carnivorous mammalian top predators such as Siberian tigers and Eurasian wolves, in contrast, have been shown to be as attracted to a single blood odor component named *trans*-4,5-epoxy-(E)-2-decenal as they are to the complex odor of real blood [2,26]. A recent study showed that this is also true for meerkats despite the fact that they are small-bodied mesopredators rather than top predators [29].

Our finding that the meerkats successfully discriminated between the odor of real banana and its quantitatively and qualitatively predominant component *iso*-pentyl acetate [6,7] and only rarely dug in the corner bearing *iso*-pentyl acetate as the first one could, at least theoretically, be due to an inability of the animals to detect this monomolecular odorant. Similarly, it could be the case that the successful discrimination between mouse odor and *iso*-pentyl acetate as well as between banana odor and cyclamen aldehyde was based on a specific anosmia to these two monomolecular odorants. To address this issue we performed an additional experiment in which we simultaneously presented four non-hidden, but freely accessible ball-shaped tea nets in the enclosure of the meerkats. (Please note that this additional experiment did not employ the test apparatus used in Experiments 1–3, and that not only the four experimental animals, but all 11 meerkats participated.) Each of these four tea nets held a filter paper which was impregnated with one of the three monomolecular odorants used in Experiments 2 and 3 (*iso*-pentyl acetate, cyclamen aldehyde, and eugenol) or with the near-odorless solvent diethyl phthalate. We found that the meerkats sniffed significantly more often and significantly longer at the three tea nets bearing the three monomolecular odorants than at the tea net bearing the solvent. From this we conclude that a) the meerkats were clearly able to detect the three monomolecular odorants, and b) that the discrimination performance that they displayed in Experiment 2 was not based on detection of banana odor or mouse odor alone.

These findings may, at first glance, appear to contradict the finding of a previous study that meerkats found a single blood odor component as attractive as the odor of real blood [29]. However, at least two reasons might explain this discrepancy: firstly, considering the complexity of naturally occurring odors it is difficult to determine the existence of "key" or "character impact" compounds in species other than humans due to the vast number of compounds that would need to be tested behaviorally. Thus, it might be that a banana odor compound other than the isopentyl acetate used in the present study serves in this function for meerkats. Secondly, and perhaps more importantly, it may well be that the olfactory system of a given species employs more than one strategy or neural mechanism for odor recognition, with relying on "key" or "character impact" compounds for certain odor stimuli, and relying on mixture patterns for other odor stimuli. Human psychophysical studies on the perception of odor mixtures support this idea [36].

4.3. Olfactory association between real food and a novel odor

The ability to build an association between a novel sensory stimulus and a certain event or consequence is almost ubiquitous in the animal kingdom [40]. This ability allows an animal to learn to either seek the novel stimulus, in case that it is accompanied by a positive consequence, or to avoid the novel stimulus, in case of a negative consequence. At the same time, this ability is the basis of all operant or instrumental conditioning procedures which are widely used in assessments of animal cognition and sensory performance [30].

Our finding that the meerkats failed to build an association between a novel odor and a real food within the 60 trials performed per animal may seem surprising. However, our failure to find a significant association-building between a novel odor and a food in the meerkats does not suggest a general inability of this species for this type of learning, but can be plausibly explained by a too low number of trials performed. Additionally, it should be considered that seemingly small differences in the methods used in different studies on associative learning may have a strong impact on learning speed in terms of number of trials needed to reach a pre-set learning criterion. It could therefore well be that the experimental set-up based on the buried food test employed in Experiments 1 and 2 might have been suboptimal for the purpose of olfactory associative learning. Unfortunately, it was not possible for us to perform more trials due to time constraints. Future studies should therefore explore how many trials meerkats need in order to succeed in olfactory associative learning and whether modifications to the current experimental set-up might facilitate this type of learning.

4.4. The buried food test as a means of assessing olfactory capabilities in meerkats

To the best of our knowledge, the present study is the first one which successfully employed the buried food test with a non-rodent species. This paradigm takes advantage of the propensity of certain species to dig and therefore it has been and is widely used with rodent species such as mice and rats (*e.g.* [28,33]). The buried food test reliably excludes the possibility of using sensory cues other than olfactory ones for finding hidden food and thus provides a relatively simple and ethologically-based means of assessing basic olfactory capabilities [41]. The ease with which the meerkats acquired this paradigm suggests that it should also be applicable with other carnivore species digging for food such as badgers, coatis, and mustelids, and with members of other mammalian orders that dig for food such as aardvarks (order Tubulidentata), shrews, hedgehogs and moles (order Eulipotyphla), and tenrecs (order Afrosoricida), to name but a few.

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References

[1] R. Apfelbach, M.H. Parsons, A.H. Soini, M.V. Novotny, Are single odorous components of a predator sufficient to elicit defensive behaviors in prey species? Front.

Neurosci. 9 (2017) 263.
[2] A. Arshamian, M. Laska, A.R. Gordon, M. Norberg, C. Lahger, D.K. Porada, N. Jelvez Serra, E. Johansson, M. Schaefer, M. Amundin, H. Melin, A. Olsson, M.J. Olsson, M. Stensmyr, J.N. Lundström, A mammalian blood odor component serves as an approach-avoidance cue across phylum border – from flies to humans, Sci. Rep. 7 (2017) 13635.
[3] K. Bauer, D. Garbe, H. Surburg, Common Fragrance and Flavor Materials, Wiley, New York, 2003.
[4] N.I. Bhuiyan, J. Begum, N.C. Nandi, F. Akter, Constituents of the essential oil from leaves and buds of clove (*Syzygium caryophyllatum* (L.) Alston), African J. Plant Sci. 4 (2010) 451–454.
[5] D.J. Bird, A. Amirkhanian, B. Pang, B. Van Valkenburgh, Quantifying the cribriform plate: influences of allometry, function, and phylogeny in carnivora, Anat. Rec. 297 (2014) 2080–2092.
[6] N. Boudhrioua, P. Giampaoli, C. Bonazzi, Changes in aromatic components of banana during ripening and air-drying, Food Sci. Technol. 36 (2003) 633–642.
[7] G.A. Burdock, Fenaroli's Handbook of Flavor Ingredients, 6th Edition, CRC Press, Boca Raton, FL, 2009.
[8] T.H. Clutton-Brock, P.N.M. Brotherton, A.F. Russell, M.J. O'Riain, D. Gaynor, R. Kansky, A. Griffin, M. Manser, L. Sharpe, G.M. McIlrath, T. Small, A. Moss, S. Monfort, Cooperation, control, and concession in meerkat groups, Science 291 (2001) 478–481.
[9] M.R. Conover, Predator-Prey Dynamics – The Role of Olfaction, CRC Press, Boca Raton, FL, 2007.
[10] H.A. Coombes, P. Stockley, J.L. Hurst, Female chemical signalling underlying reproduction in mammals, J. Chem. Ecol. (2018), https://doi.org/10.1007/s10886-018-0981-x in press.
[11] S.P. Doolan, D.W. Macdonald, Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari, J. Zool. (Lond.) 239 (1996) 697–716.
[12] A. Dunkel, M. Steinhaus, M. Kotthoff, B. Nowak, D. Krautwurst, P. Schieberle, T. Hofmann, Nature's chemical signatures in human olfaction: a foodborne perspective for future biotechnology, Angew. Chem. Int. Ed. Eng. 53 (2014) 7124–7143.
[13] R.F. Ewer, The behaviour of the meerkat, *Suricata suricatta* (Schreber), Ethology 20 (1963) 570–607.
[14] M. Fendt, R. Apfelbach, B. Slotnick, Behavioural tests of olfaction, in: B. Nielsen (Ed.), Olfaction in Animal Behaviour and Welfare, CABI, Wallingford, UK, 2017, pp. 39–60.
[15] J.L. Gittleman, Carnivore olfactory bulb size: allometry, phylogeny and ecology, J. Zool. 225 (1991) 253–272.
[16] R. Hodgkison, M. Ayasse, C. Häberlein, S. Schulz, A. Zubaid, W.A.W. Mustapha, T.H. Kunz, E.K.V. Kalko, Fruit bats and bat fruits: the evolution of fruit scent in relation to the foraging behaviour of bats in the New and Old World tropics, Funct. Ecol. 27 (2013) 1075–1084.
[17] N.R. Jordan, Scent-marking investment is determined by sex and breeding status in meerkats, Anim. Behav. 74 (2007) 531–540.
[18] N.R. Jordan, M.I. Cherry, M.B. Manser, Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence, Anim. Behav. 73 (2007) 613–622.
[19] S. Leclaire, Recognition of prey odor in wild meerkats, Chemoecology 27 (2017) 85–90.
[20] S. Leclaire, S. Jacob, L.K. Greene, G.R. Dubay, C.M. Drea, Social odours covary with bacterial community in the anal secretions of wild meerkats, Sci. Rep. 7 (2017) 3240.
[21] S. Leclaire, J.F. Nielsen, C.M. Drea, Bacterial communities in meerkat anal scent secretions vary with host sex, age, and group membership, Behav. Ecol. 25 (2014) 996–1004.
[22] S. Leclaire, J.F. Nielsen, N.K. Thavarajah, M. Manser, T.H. Clutton-Brock, Odour-based kin discrimination in the cooperatively breeding meerkat, Biol. Lett. 9 (2013) 20121054.
[23] R. Mares, A.J. Young, D.L. Levesque, N. Harrison, T.H. Clutton-Brock, Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation, Behav. Ecol. 22 (2011) 594–600.
[24] G. Moran, L. Sorensen, Scent marking behavior in a captive group of meerkats (*Suricata suricatta*), J. Mammal. 67 (1986) 120–132.
[25] O. Nevo, R. Orts Garri, L.T. Hernandez Salazar, S. Schulz, E.W. Heymann, M. Ayasse, M. Laska, Chemical recognition of fruit ripeness in spider monkeys (Ateles geoffroyi), Sci. Rep. 5 (2015) 14895.
[26] S. Nilsson, J. Sjöberg, M. Amundin, C. Hartmann, A. Buettner, M. Laska, Behavioral responses to mammalian blood and a blood odor component in four species of large carnivores, PLoS One 9 (2014) e112694.
[27] G. Ohloff, Scent and Fragrances: The Fascination of Odors and their Chemical Perspectives, Springer, Berlin, 1994.
[28] T. Peña, R.C. Pitts, M. Galizio, Identity matching-to-sample with olfactory stimuli in rats, J. Exp. Anal. Behav. 85 (2006) 203–221.
[29] H. Pettersson, M. Amundin, M. Laska, Attractant or repellent? Behavioral responses to mammalian blood and to a blood odor component in a mesopredator, the meerkat (*Suricata suricatta*), Front. Behav. Neurosci. 12 (2018) 152.
[30] W.D. Pierce, C.D. Cheney, Behavior Analysis and Learning, Lawrence Erlbaum Associates, Mahwah, NJ, 2004.
[31] J.A. Riffell, H. Lei, T.A. Christensen, J.G. Hildebrand, Characterization and coding of behaviorally significant odor mixtures, Curr. Biol. 19 (2009) 335–340.
[32] C. Salomonsson, Food Preferences in Captive Meerkats (*Suricata suricatta*), M.Sc. Thesis University of Linköping, 2011.
[33] H.M. Schellinck, C.A. Forestell, V.M. LoLordo, A simple and reliable test of olfactory learning and memory in mice, Chem. Senses 26 (2001) 663–672.
[34] C.S. Sell, Chemistry and the Sense of Smell, Wiley, Hoboken, NJ, 2014.
[35] T. Sievert, M. Laska, Behavioral responses of CD-1 mice to six predator odor components, Chem. Senses 41 (2016) 399–406.
[36] T. Thomas-Danguin, C. Sinding, S. Romagny, F. El Mountassir, B. Atanasova, E. Le Berre, A.M. Le Bon, G. Coureaud, The perception of odor objects in everyday life: a review on the processing of odor mixtures, Front. Psychol. 5 (2014) 504.
[37] M.J. van Staaden, Suricata suricatta, Mamm. Species (483) (1994) 1–8.
[38] B. Van Valkenburgh, B. Pang, D. Bird, A. Curtis, K. Yee, C. Wysocki, B.A. Craven, Respiratory and olfactory turbinals in feliform and caniform carnivorans: the influence of snout length, Anat. Rec. 297 (2014) 2065–2079.
[39] P. Wadewitz, Olfactory Discrimination of Predators and Conspecifics in Meerkats (*Suricata suricatta*), M.Sc. Thesis University of Zurich, 2010.
[40] E.A. Wasserman, T.R. Zentall, Comparative Cognition. Experimental Explorations of Animal Intelligence, Oxford University Press, Oxford, 2006.
[41] M. Yang, J.N. Crawley, Simple behavioral assessment of mouse olfaction, Curr. Prot. Neurosci. 48 (2009) (8.24.1–8.24.12).
[42] M. Zöttl, R. Lienert, T. Clutton-Brock, E. Millesi, M.B. Manser, The effects of recruitment to direct predator cues on predator responses in meerkats, Behav. Ecol. 24 (2013) 198–204.
[43] L.I. Hollén, M.B. Manser, Persistence of alarm-call behaviour in the absence of predators: a comparison between wild and captive-born meerkats (Suricata suricatta), Ethology 113 (2007) 1038–1047.