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ORIGINAL PAPER

Olfactory discrimination between litter mates by mothers and alien adult cats: lump or split?

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Abstract

Mother cats can discriminate between their own and alien kittens using kittens' body odour. Here we ask whether they can also distinguish between body odours of kittens from the same litter. We conducted three experiments using the habituation–dishabituation technique with the odour of 1- and 7-week-old kittens of both sexes. In Experiment 1, we found no evidence that mothers discriminated among their own kittens of either age when presented three times with the odour of one individual (habituation trials) and then with the odour of a different individual (dishabituation or discrimination trial), even when the donor kittens were of different sex. In Experiment 2, alien adults of both sexes distinguished between 7 but not between 1-week-old litter mates. In Experiment 3, mothers distinguished between unknown litter mates in a similar and age-dependent manner to the animals of Experiment 2. We conclude that litter mates possess individual odour signatures that can be discriminated by adult cats, that these cues take some time to develop, but are not discriminated by their own mother, at least not during the pre-weaning period. Mothers possibly perceive and respond to a learned "nest"/litter odour shared by all litter mates or categorize the individual odours of their kittens as belonging to an "own kitten" category. That mothers did not discriminate between the odours of their own kittens but did so between individual kittens of alien litters suggests that different levels of processing olfactory information exist in mothers' ability to cognitively partition and differentially respond to such odours.

Keywords Domestic cat · *Felis silvestris catus* · Habituation–dishabituation technique · Individual recognition · Odour discrimination · Olfaction

Introduction

For many mammals, olfaction undoubtedly plays an important part in the regulation of mother–young relations. This has been shown in numerous studies across a range of taxa and functional contexts (Arteaga et al. 2013; Corona and Lévy 2015; Lévy and Nowak 2017). One of the best studied of these contexts is the ability of mothers to discriminate between own and alien young using olfactory cues—along with other cues—enabling them to allocate costly maternal care preferentially to their own offspring (Hamilton 1964). In many cases mothers appear able to distinguish between own and alien young by scent soon after birth, demonstrating both their ability to rapidly learn the distinctive odour of their own offspring and that the young possess distinctive odour signatures enabling such discrimination from an early age; e.g. in ungulates (review in Poindron et al. 2007), rodents (Yamazaki et al. 2000; Jesseau et al. 2008), bats (Gustin and McCracken

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1987), carnivores (Hepper 1994; Bánszegi et al. 2017), and humans (Porter and Moore 1981; Porter et al. 1983a; Kaitz et al. 1987; Roberts and Eryaman 2017).

However, less attention has been given to the question whether in polytocous species bearing litters of altricial young, mothers discriminate among members of the same litter using olfactory cues. This could function to allow mothers to allocate care preferentially to particular individuals or categories of individuals. One indication of this is evidence that in several rodent species mothers discriminate between male and female young and allocate more care such as anogenital licking to males (Moore 1981; Moore and Samonte 1986; Clark et al. 1989; Koskela et al. 2009). In ground squirrels (*Spermophilus beldingi*), using chromatography and behavioural sniffing tests by conspecifics, it has been found that juvenile litter mates possess distinctive odour signatures by the time they emerge from the burrow (around postnatal day 25; Mateo 2006). Thus, if individual young, even from the same litter, possess unique odour types, mothers are possibly able to discriminate among them using such cues, at least at some period during development.

The domestic cat (*Felis silvestris catus*) provides a good opportunity to investigate this further. Adult cats use chemical communication in the regulation of various aspects of their social lives; they possess a variety of odiferous skin glands, they display various marking behaviours associated with depositing the products of these as well as urine and faeces in their environment (Verberne and de Boer 1976; Wolski 1982; Feldman 1994; Crowell-Davis et al. 2004; Overall 2013), and they can discriminate between individual conspecifics based on the odours of the secretions of such glands (e.g. Miyazaki et al. 2018). Furthermore, in a previous study we found that mother cats can distinguish between the odours of their own and alien kittens, although this ability is not necessarily reflected in selective maternal care since we found that cat mothers retrieve own and alien kittens into their nest with the same frequency and latency (Bánszegi et al. 2017).

The aim of the present study was therefore to investigate whether mother cats are able to distinguish between the body odour of individual kittens from the same litter. Since our previous work showed that mothers' true discriminative abilities can be masked or overridden by the kittens' behaviour (e.g. vocalization) and/or by mothers' motivational state (Bánszegi et al. 2017), in the present study we used only olfactory cues from the kittens to test mothers' discriminatory abilities and behaviour. Additionally, we tested the response of alien adult male and female cats to see whether they would discriminate between body odour of kittens from the same litter so as to exclude possibly confounding motivational factors of the mothers.

General methods

Study sites and animals

Adults and kittens were mixed breed domestic cats except for one adult Maine Coon and three adult British Shorthair. Details of sample sizes, reproductive status and age of adults, and the number of odour-donor kittens are given for each of the three experiments below. All were pets kept in private homes in Mexico City. Adult responders were tested in their home environment in a room that was familiar to them, and with informed consent of their owners. All tests were conducted when the kittens were 1- and 7-weeks old; the latter is during the weaning period, just before the kittens were given away as pets. We chose to test the cats' response to 1-week-old kitten odours because in our previous study we found that even at this early age the mothers were able to distinguish between odours of own and alien kittens. We included the later age to maximize the possibility that kittens had acquired individual body odours (olfactory "signatures"), that mothers could have learned to discriminate these, and even alien cats with no prior contact with the kittens might also be able to do so.

Olfactory testing

To test adult cats' response to the body odour of individual litter mates we used the olfactory habituation–dishabituation technique, a well-established method to test olfactory discrimination ability in mammals [reviews in Halpin (1986), Todrank and Heth (2003); see also Jesseau et al. (2008)] and as we previously used (Bánszegi et al. 2017). In this procedure the test animal is presented with an odour (habituation odour) for either an extended period or across repeated trials. During this phase the subject's attention to the odour, e.g. typically time spent sniffing it, should decrease due to habituation. Next, a different odour (dishabituation odour) is presented in the same way to the same test animal. If the subject is able to distinguish between the two types of odour stimuli, the time spent sniffing the new (dishabituation) odour will be greater compared to the previous presentation of the habituation odour. Thus, in the present study the subjects, either the kittens' own mother or alien adult cats, were presented 3 times with 3 samples of whole body odour from the same kitten collected on 3 different 15-cm-long dry, sterile cotton swabs (Deltalab S.L., Spain), and then with an odour sample from a different but same ("same-sex" condition), or opposite-sex ("different-sex" condition) kitten from the same litter (see details for each experiment below). Since to our knowledge no information is available on the

development of scent glands in young kittens, we collected whole body odour assuming at least some parts of a kitten's body might produce individual, biologically relevant odours. Separate swabs were used for each trial from each donor kitten. Odour samples were collected by rubbing swabs in a standardized manner each 5 times across both sides of the donor kitten's face, back, axilla, ventrum and anogenital area. The swabs were then returned to their airtight plastic covers. In Experiment 1 in which mothers were tested with odours of their own kittens the swabs were used within 10 min of odour collection. In Experiments 2 and 3 in which adult cats were tested with the odour of alien kittens the swabs were usually used within 30 min of collection but not later than 1 h. During transport the swabs were placed in an insulated bag containing an ice-pack.

The tests were performed by an experimenter familiar to the cats and in the presence of an assistant who filmed the procedure in a standardized manner holding a video camera approximately 150 cm from the animal's head. The cats were presented with the swabs while unrestrained on a table or on the floor, with each swab held immediately in front of, but not touching, their nostrils. The animals were unrestrained to avoid struggling behaviour from affecting olfactory inspection of the swabs as well as possible influence of the handler.

Behavioural analysis

For each trial the duration of sniffing was defined as the cat having its nose within 1 cm of the tip of the swab accompanied by movement of the nostrils and often with whiskers directed forward [see Fig. 1 in Bánszegi et al. (2017)]. The trial ended when the cat turned its head away. Approximately 5 s elapsed between trials while the swabs were changed. All trials were video recorded with a high-definition camera (Sony HDR-CX405) for further analysis. Behavioural variables were coded using Solomon Coder (Péter 2015). To assess inter-rater reliability, 128 of the total 644 trials (20%) were randomly chosen and analysed by two of the experimenters, blind to the type of trial. We calculated the intraclass correlation coefficient (ICC) using the R package *irr* (Gamer et al. 2012) and obtained $R_{ICC} = 0.836$ which is considered very good agreement.

Data treatment and statistical analysis

Responder cats sometimes became distracted, did not respond to the odour stimuli in any visible manner, or walked away from the setting of the experiment, resulting in unequal numbers of subjects across conditions and age classes. Statistical analyses were performed using the software Statsoft STATISTICA 10.0 (IBM Corp. 2011). All data were log-transformed and tested for normality of distribution using Shapiro–Wilk tests and with Levene's test for homoscedasticity. We performed repeated measures-analyses of variance (RM ANOVA) followed by Tukey HSD post hoc tests in the case of significance. An alpha of < 0.05 was taken as the level of significance.

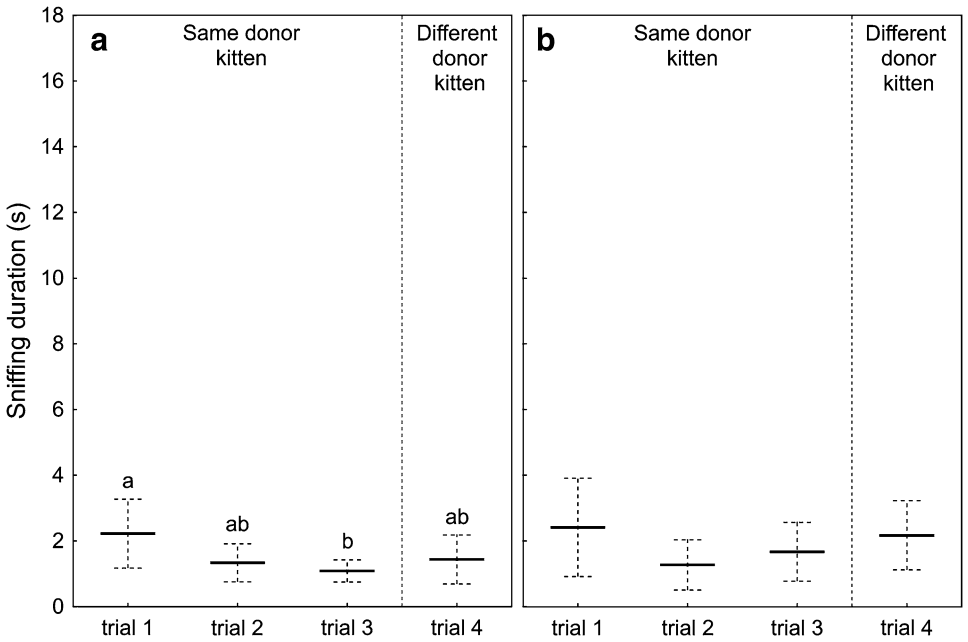

Fig. 1 Time spent by cat mothers sniffing cotton swabs with odours from two kittens from their own litter (trials 1–3 with swabs from the same kitten, trial 4 with a swab from a different kitten): **a** when the donor kittens were of the same sex ($n = 16$ mothers), and **b** when the different kitten was of the opposite sex ($n = 14$ mothers). Means ± 0.95 CI. Different letters indicate significant differences among trials ($P < 0.05$) as reported by Tukey HSD post hoc tests following application of a repeated-measures ANOVA

Experiment 1: olfactory discrimination by mothers between kittens of their own litter

Since in a previous study (Bánszegi et al. 2017) we found that mothers could discriminate between own and alien kittens using only olfactory cues, here we asked whether they could also distinguish between odours of individual members of their own neonatal and weanling litters.

Methods

Nine primiparous and eight multiparous mothers from 1 to 5 years of age were tested in this experiment. One week after their kittens were born, 15 mothers were successfully tested in the "same-sex" condition and 13 in the "different-sex" condition. Similarly, on the 7th week after the kittens were born, 16 mothers were tested in the "same-sex" condition and 14 in the "different-sex" condition. Approximately equal numbers of male and female kittens were used in each of the conditions and the order of presenting the two conditions was balanced across mothers.

Results and discussion

When testing the odours of 1-week-old kittens, analysis of the data from the "same-sex" condition showed a significant difference in the mothers' sniffing duration across the 4 trials (RM ANOVA: $F(3, 42) = 6.71$, $P = 0.0008$). Tukey post hoc tests reported significant habituation across the 3 trials from the same kitten, but no dishabituation in response to the odour from a different kitten. In the "different-sex" condition the results were similar. Although we found a significant difference in sniffing time across the 4 swabs ($F(3, 36) = 4.11$, $P = 0.013$), the post hoc tests reported a significant decrease in sniffing time indicating habituation only between the first and the remaining three trials and thus no indication of dishabituation in the fourth trial.

The same pattern was seen in the mothers' response to their 7-week-old kittens' odours. In the "same-sex" condition, RM ANOVA reported a significant difference in sniffing duration across the 4 trials ($F(3, 45) = 3.84$, $P = 0.016$), and Tukey post hoc tests reported a significant decrease in sniffing time between the first and third swab indicating habituation to these same-kitten stimuli. However, as before, no significant difference was found between the sniffing duration of the third swab and the fourth swab from a different kitten contrary to the expected effect of dishabituation in response to the odour of a different kitten (Fig. 1a). In the "different-sex" condition no significant difference in the duration of sniffing was found across the four trials ($F(3,39) = 2.34$, $P = 0.09$; Fig. 1b).

In summary, the results of this experiment did not provide evidence that mother cats distinguish among their kittens from the same litter using olfactory cues, and even when the kittens were close to weaning age and were of different sex; that is, following the third trial habituation phase we did not observe a significant increase in the duration of sniffing in response to the new, "dishabituation" odour from a different litter mate.

There are at least five explanations for this result. First, kittens at the young ages tested here may not yet have developed distinctive individual odours enabling mothers to discriminate among them, perhaps because the various skin glands used by the cat for chemical communication had not yet matured (cf. Feldman 1994; Miyazaki et al. 2018). Second, the kittens may have acquired a common "nest" or litter odour with which the mothers were familiar and to which to some extent they were already habituated before the start of testing. Thus, any distinction in the odour of the different kitten presented on the fourth trial was possibly "masked" by the overall litter odour and provided no new information of relevance to the mothers. Third, it could have been a form of phenotype matching in which mothers perceived some correspondence between their own odour and that of their kittens (Halpin 1991). Fourth, mothers might have learned the individual odours of each of their kittens but grouped these together into one category of "own kittens", resulting in reduced interest in distinguishing between them (cf. Porter and Moore 1981). And finally, there is the possibility that the method of testing was not sufficiently sensitive to detect mothers' ability to distinguish between their individual kittens.

To begin to investigate these possibilities we conducted a second experiment in which we tested the response of alien, non-maternal cats to the odours of litter mates, using the same habituation–dishabituation paradigm.

Experiment 2: olfactory discrimination between litter mates by alien adults

By testing alien adults with no prior contact with the donor kittens we aimed to examine the possibility that the kittens indeed have individually distinct odour signatures when not masked by the possible maternal behaviour mentioned above. If the case, it would mean whereas mothers lump the odours of their own kittens—by whatever mechanism—into one "own kitten" category, alien cats should distinguish between the odours of individual litter mates.

Methods

A total of 33 adult cats from 1 to 9 years of age (18 females, one sexually intact, and 15 males, two sexually intact) were tested using donor kittens from four litters. The paradigm was the same as for Experiment 1; that is, when the kittens were 1-week-old body odour was collected from them, and unfamiliar adult cats were tested in the "same-sex" condition ($n = 19$) and "different-sex" condition ($n = 17$). The procedure was repeated when the kittens were 7 weeks old and 23 adult cats were tested in both conditions. Approximately equal numbers of male and female kittens were used as scent donors in each of the conditions and the order of presenting the two conditions was balanced across the adult responders.

Results and discussion

As for the mothers in Experiment 1, when alien adults were presented with swabs from 1-week-old kittens they sniffed these briefly for several seconds and showed a significant difference in duration of sniffing across the four swabs in both the "same-sex" and "different-sex" conditions ($F(3, 54) = 3.14$, $P = 0.032$ and $F(3, 48) = 4.45$, $P = 0.008$, respectively). Tukey post hoc tests reported a significant decrease in the duration of sniffing of the first swab compared to the subsequent swabs, indicating habituation. However, in neither of the conditions was a significant difference in the duration of sniffing between the third and fourth (different kitten) trials observed, that is, no evidence was found for discrimination between the odour of litter mates at this early age.

In contrast, the adult cats' behaviour was different in response to swabs from 7-week-old kittens. As shown in Fig. 2, in both the "same-" and "different-sex" conditions the adult responders sniffed the swabs in general for around 6–8 s, and so considerably longer than the mothers in Experiment 1 in response to kittens of the same age, although with greater variance. In the "same-sex" and "different-sex" condition RM ANOVAs reported a significant difference in sniffing duration across the four trials ($F(3, 66) = 4.26$, $P = 0.008$ and $F(3,66) = 12.2$, $P = 0.0001$, respectively), with Tukey post hoc tests reporting a significant decline in the duration of sniffing indicating habituation across trials 1 and 3. However, and in contrast to the results from week 1, for both conditions Tukey post hoc tests reported a significant increase in sniffing duration between trials 3 and 4, indicating dishabituation and thus discrimination between the odours of litter mates (Fig. 2).

In summary, the results of the two conditions provide evidence that adult cats with no experience of the body odour of kittens (other than of their own siblings during early development) can discriminate among individual litter mates, at least when these have reached 7 weeks of age. This was the case despite the heterogeneity of the responding adults in terms of sex, age, and reproductive status (gonadally intact or neutered).

Based on the findings of the present experiments we can tentatively conclude that adult cats can distinguish between the body odours of alien litter mates, although apparently not when these are 1 week old, and that they do not need previous experience of the kittens to do so. This suggests that with the approach of weaning, kittens have developed individual odour signatures and that the

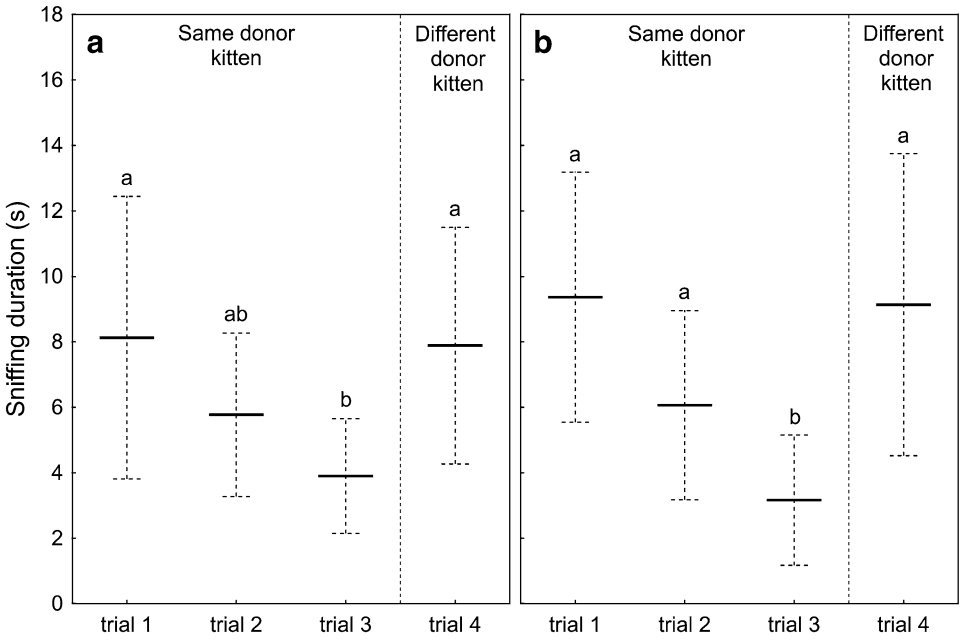

Fig. 2 Time spent by male and female adult cats sniffing cotton swabs with odour from two kittens from alien litters (trials 1–3 with swabs from the same kitten, trial 4 with a swab from a different kitten from the same litter): **a** when the donor kittens were of the same sex ($n = 23$ adults), and **b** when the different kitten was of the opposite sex ($n = 23$ adults). Means ± 0.95 CI. Different letters indicate significant differences among trials ($P < 0.05$) as reported by Tukey HSD post hoc tests following application of a repeated-measures ANOVA

habituation–dishabituation technique used here is adequate to demonstrate this. In addition, the present results suggest the lack of discrimination among individual kitten odours by the mothers in Experiment 1 may indeed have been because (1) of the mothers' familiarity with a common nest or litter odour and this deflecting their attention from individual differences, or similarly (2) by mothers perceiving a correspondence between their own and their kittens' odour, or (3) mothers having learned the individual odours of each of their kittens and grouped these together into one category of "own kitten".

Experiment 3: olfactory discrimination by mothers between kittens from alien litters

To further investigate these possibilities, that is, that mothers' familiarity with some form of common litter odour, phenotype matching, or categorization of individuals' odours as "own kittens" reduced mothers' motivation to discriminate among their kittens, we conducted a third experiment using alien litter mates as odour donors.

Methods

We tested 12 mothers from 1 to 3 years of age, 6 primiparous, 6 multiparous, using kittens from 8 litters. Using the same paradigm as in Experiments 1 and 2, we tested the response of mothers to the body odours of individual kittens from alien litters, but only used the "same-sex" condition ($n=10$ with 1-week-old kittens' odour, $n=11$ with 7-week-old kittens' odour). Approximately equal numbers of male and female kittens were tested. We used only one condition after finding in Experiment 2 that the sex of the different individuals in trial 4 had little apparent effect on the outcome and because of the difficulty in obtaining parallel mothers and alien litters of similar age and sex composition to implement both the "same-sex" and "different-sex" conditions. We tried to collect scent from kittens which were of the same age as the mothers' own kittens, but as this was not always possible we set the maximum acceptable age difference between the kittens to 3 days.

Results and discussion

When mothers were presented with swabs from 1-week-old alien kittens they sniffed them for several seconds but showed no significant difference in the duration of sniffing between any of the swabs ($F(3,27)=1.76$, $P=0.18$). However, as shown in Fig. 3, when the mothers were presented with swabs from 7-week-old alien litter mates, they sniffed the swabs for around 4–10 s, and so considerably longer than the mothers in Experiment 1, although with large variance. Furthermore, a RM ANOVA reported a significant difference in sniffing duration across the four trials ($F(3, 30)=11.7$, $P=0.0001$) and with Tukey post hoc tests reporting significant differences between trials 1 versus 2 and 3 (indicating habituation) and between trials 3 and 4 (indicating discrimination).

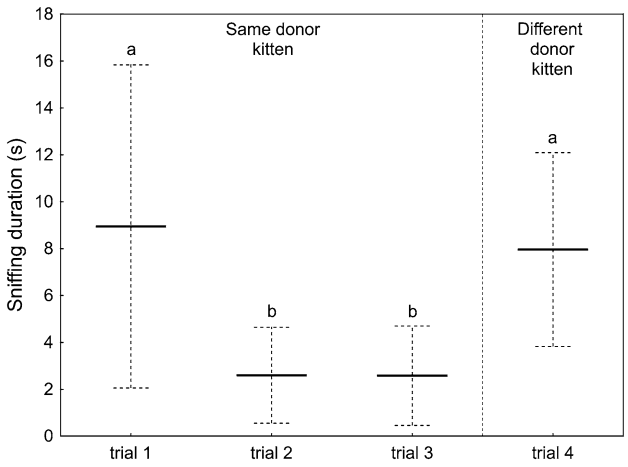

Fig. 3 Time spent by cat mothers sniffing cotton swabs with odour from two siblings from alien litters (trials 1–3 with swabs from the same kitten, trial 4 with a swab from a different kitten from the same litter). Donor kittens were males and females but of the same sex across the four trials ($n=11$ mothers), means ± 0.95 CI. Different letters indicate significant differences among trials ($P<0.05$) as reported by Tukey HSD post hoc tests following application of a repeated-measures ANOVA

The results confirm those of Experiment 2 showing that adult cats can discriminate among weanling litter mates using individuals' body odour alone. Since this was the case for mothers when presented with body odour of alien kittens of the same age as their own litters, the results also support the interpretation of the negative finding of Experiment 1 that mothers did not distinguish among their own young possibly because these shared common odour cues familiar to the mother or that mothers had learned the odours of the individuals and categorized all as "own kittens". These results also confirm that possibly kittens do not have individually distinct odours at an early age (1 week) or that these are so weak a shared litter odour masks them. To produce a sufficiently distinct odour signature may take time during early development possibly, for example, associated with the development of scent glands.

General discussion

Returning to the main aim of the study, to investigate whether mother cats can distinguish between the body odour of litter mates, the present results suggest they can, at least

when the kittens are several weeks of age and are not their own. Thus, in Experiment 1 mothers did not distinguish between the odours of their own kittens and even when the odour stimuli were from kittens of different sex, but did so in Experiment 3 when the stimuli were from individuals of alien litters. These results, together with previous findings (Bánszegi et al. 2017), suggest that kittens from the same litter share a general litter odour but also have individually distinct odours both of which are probably used in chemical communication between conspecifics.

As mentioned above (Experiment 1, results and discussion), there are several possible explanations for the intuitively puzzling result of mothers not distinguishing among their own kittens, while they do so among alien litter mates. With this series of experiments we were able to exclude some explanations, but still three possibilities remain. One is that mothers might have learned a general "nest" or litter odour carried by all their kittens Familiarity with such a shared odour (cf. O'Riain and Jarvis 1997; Bradshaw and Cameron-Beaumont 2000; Safi and Kerth 2003; Crowell-Davis et al. 2004) might also explain the generally shorter duration of sniffing the odour stimuli from own kittens in Experiment 1 than sniffing equivalent but novel stimuli from alien kittens in Experiment 3. Of course, this implies that alien litter mates also carry a general litter odour, but which is probably not relevant to an alien cat and is distinct from their individual scent. A second mechanism could be a form of phenotype matching (cf. Porter et al. 1983b; Holmes 1986; Main and Bull 1996; Sun and Müller-Schwarze 1997; Heth et al. 1998). And a third, perhaps less likely possibility is that kittens do not have a shared litter odour, but mothers learn the individual odours of their kittens and group these into a general "own kitten" category not requiring a differential behavioural response. Although the present study does not allow us to decide between these explanations and further investigation is needed, the first possibility seems the most parsimonious.

Furthermore, the results of Experiments 2 show that at least by postnatal week 7 individual litter mates possess odour signatures that are sufficiently distinct even alien non-maternal male and female adults, with no prior experience of the stimulus kittens, could discriminate between them, including when the donor kittens were the same sex. This was the case even though the majority of the adult cats to our knowledge had no prior experience of kittens (at least since they were weaned).

Together the results of the three experiments raise two main but interrelated questions: what are the sources of both the sibling kittens' individual and possibly shared body odours, and how do maternal and non-maternal adult cats process and categorize these? Considering the possible origin of kittens' body odours, as mentioned in the Introduction, there are several, not mutually exclusive, possibilities. One might be differences in the maturation and activity of odiferous skin glands. There could also be a genetic contribution to such differences, increased by the promiscuous mating system of the female cat and the frequency of multiple paternity of litters (Natoli and De Vito 1991; Say et al. 1999; Ishida et al. 2001). This was very likely in the present study given that most litters were the result of uncontrolled matings by unconfined females and where in several cases matings by the same female with several free-ranging males were observed. Additionally, a source of general body odour likely to be shared by all kittens and conferring a general litter odour are the various common sources of odours within the nest. These could include contact of kittens with each other, with the mother and her saliva via her frequent licking of them, and possibly originating from their common diet, including indirectly the diet of their mother which via her milk or ventral body odour might also contribute to a common litter odour (Doane and Porter 1978; Hepper 1988; Bilkó et al. 1994; Coureaud et al. 2002).

Presently unknown is the significance, if any, of such individual odour signatures for the kittens at this early (pre-weaning) age. First, can they themselves learn and distinguish between the odours of individual litter mates? Certainly, they would seem to be capable of this at both a sensory and cognitive level. Within a few hours of birth kittens establish a "teat order" in which each individual learns to identify its "own" nipple(s), almost certainly using olfactory cues (Hudson et al. 2009; Raihani et al. 2009). They can also distinguish their mother's greeting or "chirp" calls from those of other mothers by the time they start to leave the nest around postnatal week five (Szenczi et al. 2016). But then if kittens can discriminate between their litter mates by smell, how early does this develop and for how long might it endure beyond weaning once the kittens have gone their separate ways? This is currently under investigation. More difficult is the question what might be the adaptive function of any such early and longer-term olfactory discrimination (recognition) among litter mates? For example, might this permit greater tolerance among related individuals (since cats do not defend territories but rather avoid or tolerate conspecifics in overlapping home ranges), or permit or facilitate allo-nursing (Izawa and Ono 1986; MacDonald et al. 1987; Feldman 1993), or reduce inbreeding (Ishida et al. 2001)?

Whatever the case, the results echo the results of our previous study in which we found that although mothers did not discriminate between own and alien kittens in retrieval tests they could discriminate between them by smell (Bánszegi et al. 2017); that is, because an animal does not appear to perceive differences between stimuli in spontaneous (untrained) contexts does not necessarily mean it cannot. For a cat mother the matter of main importance is likely to be whether a kitten is hers or not, with any of the three more general possible mechanisms mentioned above (Experiment

2, Results and discussion) overriding attention to individual body odours.

Finally, perhaps the most interesting immediate outcome of this study is what it seems to suggest about the multilevel, complex nature of olfactory mother–young communication and the processing of olfactory signals in the cat. Thus, at one level mother cats appear able to lump the odours of their own kittens into a single general category signifying litter identity, something they might use to distinguish own from alien kittens as shown previously (Bánszegi et al. 2017). At the same time, they also appear able to split the odours of alien litter mates according to the kittens' individual odour signatures. This suggests a high level of cognitive processing of olfactory information in the cat that deserves further investigation.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Throughout the study, animals were kept and treated according to the Guide for the Production, Care and Use of Laboratory Animals Mexico (Norma Oficial Mexicana NOM-062-200-1999), and with approval by the Institutional Committee for the Care and Use of Experimental Animals (SICUAE, permission number DC-2017/1–4) of the Faculty of Veterinary Medicine and Animal Science of the UNAM. This article does not contain any studies with human participants performed by any of the authors.

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