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ORIGINAL PAPER

Can but don't: olfactory discrimination between own and alien offspring in the domestic cat

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Abstract Mammalian maternal care usually comes at a large energetic cost. To maximize their fitness, mothers should preferentially care for their own offspring. However, the majority of studies of mother–offspring recognition have focused on herd- or colony-living species and there is little information on maternal discrimination in more solitary-living species. Olfaction has been found to play a major role in mother–offspring recognition across various taxa. Therefore, our aim was to study this in a species evolved from a solitary-living ancestor, the domestic cat. We asked whether cat mothers distinguish between their own and alien offspring when providing maternal care, and whether cat mothers use olfactory cues in the offspring discrimination process. Results of Experiment 1 showed that cat mothers do not discriminate between own and alien young when retrieving them to the nest. They treated own and alien young similarly with respect to latency and order of retrieval. However, the results of Experiments 2 and 3, where we used an olfactory habituation-discrimination technique, showed that mothers were able to distinguish between the odours of their own and alien kittens. We discuss what ecological and/or behavioural factors might influence a mother's decision when faced with discriminating between own and alien young, and why mothers might not discriminate between them when they are able to do so. Our findings support the view that maternal care alone should not be used as a measure of offspring recognition, and equal maternal care of own and alien young should not be immediately interpreted as an inability to discriminate between them.

Keywords Domestic cat · *Felis silvestris catus* · Habituation-discrimination technique · Mother–offspring discrimination · Olfactory communication · Retrieval test

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Introduction

For mammalian mothers, maternal care comes at a large energetic cost; lactation in particular can nearly triple a mother's caloric requirements (Gittleman and Thompson 1988). Therefore, evolutionary theory suggests that to maximize their fitness, mothers should preferentially care for their own offspring (Hamilton 1964b) and thus should be able to recognize them. If a mother indiscriminately cares for both her own and unrelated offspring, this could elevate even further her energetic requirements, exposing her to greater risks of debilitation, injury or even death and thereby reducing her fitness and future fecundity (König et al. 1988; Clutton-Brock et al. 1989; Neuhaus and Pelletier 2001; Koivula et al. 2003). Also for the mother's own offspring, it can be costly for maternal care to be diverted to alien offspring, if as a result they do not receive the resources (e.g. milk or protection) needed for adequate growth and development (Fleming and Rauscher 1978; Horrell and Bennett 1981; Mappes et al. 1995; Andersen et al. 2011).

Olfactory cues have been found to play an important role in mother–offspring recognition in a variety of mammals. The majority of these studies have focused on herd- or colony-living species which are usually synchronized, seasonal breeders, e.g. bats (Gustin and McCracken 1987), goats and sheep (review in Poindron et al. 2007), degus (Jesseau et al. 2008), pigs (Maletínská et al. 2002), dogs (Hepper 1994) and also humans (Porter et al. 1983; Kaitz et al. 1987), and where for mothers identifying their own young among the group is a daily, recurring task. In contrast, to our knowledge there is almost no study or available information on mother–offspring olfactory recognition in solitary-living species. This is understandable since mothers of solitary species are unlikely to encounter alien young and thus should rarely have to distinguish them from their own. We found only one study in the literature on the domestic cat. Ohkawa and Hidaka (1987) reported that it seems the mothers of this species do not have the ability to discriminate their own kittens from alien ones. However, this study was conducted under artificial laboratory conditions of extremely high animal density. Nevertheless, even in solitary species the ability to recognize kin can be important at later life stages, e.g. to avoid inbreeding (Bateson 1983; Pusey and Wolf 1996) and/or to be more tolerant during a reencounter or even to participate in cooperative behaviour (Hamilton 1964a, b; West et al. 2002). However, as mentioned above, it is rather difficult—almost impossible—to observe and compare a solitary mother's behaviour with her own and with alien young under natural conditions.

Here we propose the domestic cat (*Felis silvestris catus*) as a model species to study mother–young olfactory communication in a carnivore evolved from a solitary-living ancestor (*Felis silvestris lybica*). Cats can be kept and experimented with under semi-natural free-ranging conditions, and mothers readily permit the handling and manipulation of newborn young by familiar caretakers (Hudson et al. 2009; Szenczi et al. 2016), thereby providing an exception to the difficulties in observing and conducting research with solitary carnivores. Although cats do not construct nests or dens, they are adept at hiding their kittens in refuges (referred to here as "nests") providing protection from weather, predators and potentially infanticidal males (MacDonald et al. 1987; Pontier and Natoli 1999). The domestic cat is a seasonal breeder; females give birth synchronously to their litters in spring and sometimes to a second one at the end of summer. Litter size usually varies from 3 to 5 (Hall and Pierce 1934; Mellen 1993; Schmidt et al. 2007), although 1–10 kittens have also been reported (Jemmett and Evans 1977; Deag et al. 1987). The domestic cat is generally considered a facultatively solitary species; in low-density populations, adult females usually live alone (Spotte 2014). However, under high density or laboratory conditions, nest sharing and communal rearing of kittens may also occur (Lawrence 1980; Feldman 1993), although under such conditions high rates of abortion and kitten mortality have been reported (Ohkawa and Hidaka 1987).

Even for a less social mammal like the cat, chemical cues are an important means of conspecific communication (Verberne and de Boer 1976; Wolski 1982). Cats have a variety of scent glands distributed over their body (cheeks, abdomen, paws, above the tail and near the anus; Feldman 1994; Ellis et al. 2013), and with these they frequently mark objects in their surroundings (Overall 2013). During conspecific encounters, cats routinely sniff each other's faces and especially each other's anogenital area (own observation). Cat mothers also sniff and lick their kittens upon entering the nest, focusing particularly on their anogenital area, at least in part to help them to eliminate (Rosenblatt 2010; Hart and Hart 2013). It therefore seems that chemical cues play an important role in the cats' daily life and in the development of the mother–offspring relationship.

Here we studied two aspects of maternal discrimination in the domestic cat: firstly, whether cat mothers distinguish between their own and alien kittens, and second, whether cat mothers use olfactory cues in the discrimination process. Since it is known that in several species maternal selectivity develops rapidly—even within hours of giving birth (Porter et al. 1973; Hudson and Mullord 1977; Poindron et al. 2007)—we carried out our experiments at an early lactational age.

General methods

Study sites and animals

The 19 domestic cat mothers (12 mix breed, 4 Persian, 2 Bengal, 1 British short hair, age from 1 to 4 years) participating in this study were kept as pets in private homes in Mexico City and had recently given birth to their litters. We worked with mothers which had a litter size of at least 3 kittens (mean litter size: 4.3 ± 0.28 SEM range from 3 to 7). All mothers had access to separate rooms within their homes to raise their offspring. Ten of them were free to leave the house and the garden at will, and the other 9 were kept indoors. Seventeen of them lived with other conspecifics in the same home. They were fed daily with commercial canned cat food and received regular treatment against parasites. Water, milk, dried cat food and sand boxes were always available. Owners were asked to provide the mothers with a commercial foam cat bed (oval, 68×57 cm) placed within a large cardboard box ($60 \times 80 \times 70$ cm) with a small floor-level opening ($22 \times$

27 cm) as a nest. Kittens were weighed at birth and daily thereafter to check for normal growth. We performed 3 experiments as reported below. In all experiments, we tried to use same-age own and alien kittens, but as this was not always possible we set the maximum acceptable age difference between the two types of kittens at 3 days. Since not all the owners consented to all the tests, the sample sizes differed between the experiments. All the experiments were conducted in the mother's room, near her nest, by an experimenter who the mothers were familiar with.

All experimental trials were video recorded using a static high-definition wide-angle camera (GoPro 4 Session, GoPro Inc., CA, USA) for further analysis. Behavioural variables were coded using Solomon Coder (Péter 2015).

Experiment 1: retrieval to the nest

Methods

We conducted retrieval tests with 12 mothers (5 multiparous, 5 primiparous and 2 of unknown reproductive history). Each mother was used only once in a retrieval test. We used 2 of the mothers' own and 2 alien kittens in all trials. The test was performed when the older litter was 7 days old. When choosing the test kittens from the litters, we tried to match their sex and colour whenever possible. Alien kittens were transported together in a plastic container lined and covered with cloth from their own nest. Since cat mothers spend considerable time away from their offspring even at this age, and the kittens were kept warm and in the company of their sibling, they did not show apparent distress during transportation such as vocalizing (Hudson et al. 2015). Kittens were never transported for more than 15 min. The brief experimental separation of mothers and young did not appear to adversely affect the mothers' behaviour or the kittens' development.

Tests were performed at a time when the mother had spontaneously left the nest site and the room. One experimenter—with whom the mother was familiar—entered the room and placed in alternating order 2 alien and 2 own kittens approximately 1 m from the entrance of the nest in separated plastic containers (16 × 27 cm), leaving 25 cm between kittens (Fig. 1a). The containers were necessary to restrain the kittens since even at such an early age they are quite mobile and can crawl on flat surfaces. The rest of the test mother's own kittens were left in the nest. After the experimenter positioned the kittens in the containers, she walked to the farthest corner of the room and stayed there motionless. Within seconds, the kittens started emitting separation cries, which prompted the mothers to return quickly to the room. The test lasted until the mother retrieved all the kittens back to the nest, or for 5 min after the last retrieval, or for 5 min after the mother entered the room but retrieved no kittens. After the test, the kittens were returned to their proper nest.

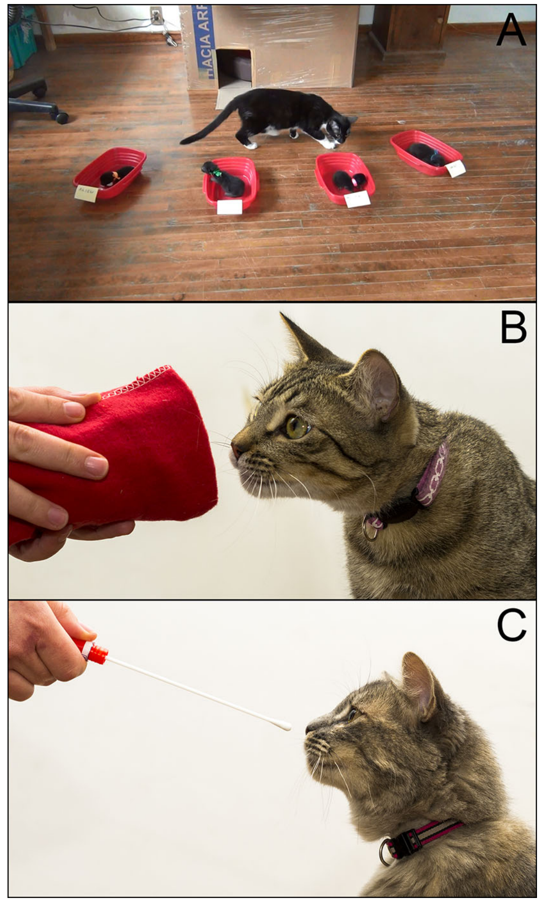

Fig. 1 The three experimental situations. **a** Retrieval test setup. **b** Presentation of kittens' anogenital area. **c** Presentation of general kitten body odour on a cotton swab

We measured the latency, frequency and duration of the mothers investigating (sniffing) each kitten and the latency and order of retrieving kittens into the nest. Normally distributed data were analysed using linear mixed models (LMM) with mothers' identity as a random factor. Non-normally distributed and count data were analysed with generalized linear mixed models (GLMM) with Poisson error distribution and with mothers' identity as a random factor. *P* values were extracted by Wald Chi-square tests (type II). All statistical analyses were done using the program R, version 3.3.1 (R Core Team 2016), and all linear models were performed using the package *lme4* (Bates et al. 2015).

Results and discussion

Kittens started to vocalize within seconds when placed individually in the plastic test containers. After entering the room, the mothers almost immediately started sniffing the kittens (mean latency to sniff the first kitten: 1.58 s ± 0.26 SEM, mean latency to sniff all kittens: 20.2 s ± 5.4 SEM) and continued to investigate them (mean duration of sniffing: 6.53 s ± 0.95 SEM), even returning to each kitten several times (mean frequency of sniffing a kitten: 3.36 s ± 0.40 SEM). However, we found no difference in mothers' behaviour toward own and alien kittens except mothers tended to investigate alien kittens earlier and longer (Table 1). These slight, yet significant differences in the latency and duration of the first examination of the two types of kittens suggest that upon entering the room, mothers noticed (perhaps by olfactory or vocal cues) there were unfamiliar kittens present and so they investigated those first.

However, 7 of the 12 mothers retrieved all 4 kittens, 2 only retrieved 2 kittens (in both cases 1 own and 1 alien kitten), and the other 3 mothers did not retrieve any. Thus, only the data for the 9 mothers retrieving kittens are given in Table 1. We found no significant difference in the latency to retrieve own and alien young (mean latency to retrieve a kitten: 168.2 s ± 25.7 SEM) nor in the order to retrieve them (Table 1).

These results are consistent with the previous findings of Ohkawa and Hidaka (1987) that cat mothers do not discriminate between own and alien offspring; they retrieve them equally. Several studies have shown that mammalian mothers—including humans—allonurse and provide maternal care to offspring other than their own (Packer et al. 1992; reviews in Hayes 2000; König 2006; Hewlett and Winn 2014) and that this phenomenon is more common in litter-bearing mammals and carnivores compared to other taxonomic groups (Packer et al. 1992; MacLeod and Lukas 2014). Our findings on the domestic cat confirm these observations, as a generally solitary, litter-bearing carnivore.

This nevertheless raises the question whether mothers who provide nondiscriminative maternal care are in fact able to distinguish between their own and alien offspring? Several studies have shown that although in some mammalian species mothers have the ability from an early lactational age to discriminate between own and alien young using olfactory cues, they do not do so when providing maternal care, e.g. in degus (Ebensperger et al. 2006; Jesseau et al. 2008), mice (Ostermeyer and Elwood 1983) and pigs (Maletínská et al. 2002). Therefore, in a second experiment we were interested to know whether cat mothers show similar behaviour, namely, are able to discriminate between own and alien offspring, and if yes, do they use olfactory cues to do so?

Table 1 Results of statistical tests for behavioural variables in Experiment I: response of mothers to own versus alien kittens

Variable	Own	Alien	χ^2	*P*
Sniff—latency	29.5 ± 10.2	10.9 ± 3.14	3.91	0.048*
Sniff—frequency	3.2 ± 0.59	3.5 ± 0.54	0.21	0.65
Sniff—duration	5.5 ± 1.27	7.6 ± 1.44	4.25	0.039*
Retrieve—latency	152.4 ± 40.0	199.8 ± 42.3	0.29	0.59
Retrieve—order	2.2 ± 0.24	2.7 ± 0.26	1.13	0.29

Response of mothers ($n = 9$) to own and alien kittens (mean ± SEM). *P* values were extracted by Wald Chi-square tests (type II) following linear mixed models. Detailed information on the statistical methods is given in the text

* Statistically significant differences ($\alpha = 0.05$).

Experiment 2: anogenital inspection

Methods

Habituation-discrimination technique

In the second and third experiments, we used the olfactory habituation-discrimination technique, which was first used by Schultze-Westrum (1969) and subsequently by many others to test olfactory discrimination abilities in mammals (reviews in Halpin 1986; Todrank and Heth 2003) including human infants (Houston-Price and Nakai 2004). In the habituation-discrimination procedure, the test animal is presented with an odour (habituation odour) for either an extended period or over repeated trials. During this phase, the subject's interest in the odour should decrease due to habituation. Next, a different odour (test odour) is presented in the same way to the same test animal. If the subject is able to differentiate between the two types of odour, the time spent investigating the test odour increases compared to the previous habituation odour.

Test procedure

Thirteen cat mothers participated in this study (7 multiparous, 5 primiparous and 1 of unknown reproductive history). Eight of them had also participated in the first study. In each test, we presented 3 different kittens from the mother's own litter (habituation trials), followed by presentation of an alien kitten. During this second experiment, we presented kittens to the mothers which they were not able to see apart from the kittens' anogenital region, and which they were only allowed to sniff. The kittens were presented in the following way: the experimenter gently wrapped them individually in clean, unscented cloth in such a way that only their anogenital region was exposed (Fig. 1b). The experimenter presented each kitten's anogenital region to the mother, allowing her to sniff it. Each trial lasted until the mother turned her head away.

Approximately 10 s elapsed between the trials to allow for changing the kittens. Sniffing was defined as the mother having her nose within 1 cm of the stimulus, with nostrils moving and whiskers directed forward towards the kitten. Each mother was used only once in this experiment.

As in Experiment 1, we tried to match the sex and colour of the own and alien kittens whenever possible. The test was performed when the older litter was 8 days old. All kittens remained silent to the human ear during the tests. If the mother also participated in the previous or the following experiment (see below), we tried to use different own and alien kittens during the present experiment inasmuch as the litter sizes allowed.

Close-up videos of the mothers' faces were recorded using high-definition cameras (GoPro 4 Session) in narrow field-of-view settings placed approximately 50 cm from the animals' heads. We analysed the time the mothers sniffed in each trial, that is, how long the mothers investigated each stimulus kitten. Data were tested for normality with the Shapiro–Wilk test and with Levene's test for homoscedasticity. Data were analysed using repeated-measures analysis of variance (RM ANOVA) followed by Tukey HSD post hoc tests.

Results and discussion

Mothers spent a decreasing amount of time sniffing their own kittens' anogenital region, but then sniffed significantly longer when we presented them with an alien kitten (RM ANOVA followed by Tukey HSD post hoc tests, $F(3, 36) = 17.4$, $P < 0.0001$; Fig. 2).

Results of Experiment 2 showed that the cat mothers could discriminate between own and alien kittens even though the kittens were apparently silent (at least for the human ear) and the mothers were only allowed to examine the kittens' anogenital region; the mothers sniffed an alien kitten's anogenital region significantly longer than their own kittens' anogenital region, suggesting that the alien kitten's scent was distinct from that of their own kittens. A further notable result of Experiment 2 was that during the first phase (habituation), the mothers sniffed their own 3 kittens for decreasing, but almost equal amounts of time. Perhaps this was because mothers have a general olfactory concept of their own litter as a whole, rather than of each kitten individually (see in mice: Ostermeyer and Elwood 1983). Since the current experiments were not designed to investigate the mechanism by which cat mothers discriminate between own and alien offspring, this question remains open for future research.

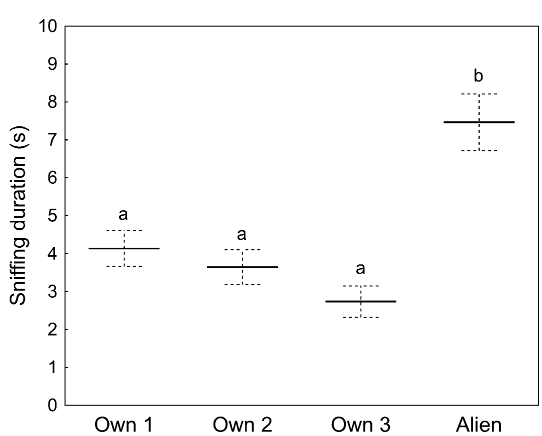

Fig. 2 Time spent by cat mothers investigating kittens. Mean ± SEM of the time (s) mothers ($n = 13$) spent in olfactory investigation of own and alien kittens' anogenital region. *Letters* indicate significant differences ($P < 0.05$) as reported by Tukey HSD post hoc tests following application of a repeated-measures ANOVA

As in Experiment 2 we used live kittens, we cannot rule out the possibility that the mothers used cues other than smell to discriminate between own and alien kittens (e.g. visual: mothers might have recognized the anogenital regions of their own kittens, or have used ultrasonic vocalizations; Härtel 1975). We therefore conducted a third experiment in which we presented mothers only with (possible) kitten olfactory cues.

Experiment 3: general body odour

Methods

Eleven cat mothers participated in this experiment (7 multiparous, 3 primiparous and 1 of unknown reproductive history). Five of them had also participated in both previous experiments, and 3 had also participated in Experiment 2. Since no information is available on the development of the scent glands of young kittens, we collected whole body odour assuming that at least some parts of the kitten produce biologically relevant odours. The test was performed when the older litter was 9 days old. Each kitten was rubbed with a dry, sterile cotton swab stick (15 cm long; Deltalab S.L., Spain; Fig. 2c) 5 times on its back, stomach, axilla, anogenital area and on both sides of the face. The swab was then sealed in its cover and used within 10 min. As in the previous experiments, we tried to match kittens' age and sex whenever possible.

Similarly to Experiment 2, the experimenter presented one by one the first three swabs that had been rubbed on the mother's own but different kittens, followed by a swab that had been rubbed on an alien kitten, and allowed her to sniff each one (Fig. 1c). A trial lasted until the mother turned her head away. Approximately 5 s elapsed between the trials to allow changing the swabs. Each mother was used only once in this experiment. Video recordings and data analysis were similar to the previous experiment.

Results and discussion

Mothers spent a decreasing amount of time sniffing swabs that had been rubbed on their own kittens, but then sniffed significantly longer at the swab that had been rubbed on an alien kitten (RM ANOVA followed by Tukey HSD post hoc tests $F(3, 30) = 8.67$, $P < 0.001$; Fig. 3).

The results of Experiment 3 confirmed that cat mothers are indeed able to distinguish own from alien young using only olfactory cues. However, and perhaps surprisingly, in the habituation phase of Experiment 3 the mothers spent significantly longer sniffing the first cotton swab presented to them with their own kitten's smell than they did smelling their first kitten itself in the habituation phase of Experiment 2. We think that this might have been because the cotton swab itself was a novel object for them, or had a particular smell, and its novelty caused an increase in investigation time.

General discussion

The results of Experiment 1 clearly show the cat mothers did not differentiate between own and alien young when retrieving them to the nest (consistent with Ohkawa and Hidaka 1987). However, this does not necessarily mean cat mothers cannot distinguish between own and alien young (Experiment 2) or that they may use olfactory cues to do so (Experiment 3; in contradiction to the conclusion of Ohkawa and Hidaka 1987). Our findings are consistent with previous reports on other mammalian species where mothers did not discriminate between own and alien offspring when providing maternal care, but did discriminate when presented only with odour cues of the young (Ostermeyer and Elwood 1983; Maletínská et al. 2002; Ebensperger et al. 2006; Jesseau et al. 2008). In summary, our findings suggest cat mothers have the ability from an early lactational age to distinguish between the scent of their own and alien offspring, but in practice treat them equally.

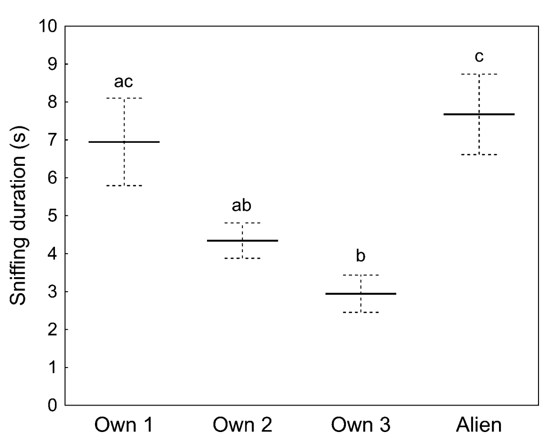

Fig. 3 Time spent by cat mothers investigating the cotton swabs. Mean ± SEM of the time (s) mothers ($n = 11$) spent in olfactory investigation of own and alien kitten-scented cotton swabs. *Letters* indicate significant differences ($P < 0.05$) as reported by Tukey HSD post hoc tests following application of a repeated-measures ANOVA

So if mother cats have the ability, why didn't they distinguish between own and alien young in Experiment 1? Lack of differentiation could have been due to the vocalization of the kittens outside the nest, which would have several implications for a mother. The basic function of separation cries is to elicit attentiveness and trigger caregiving behaviour (Murray 1979; Newman 2007). Similarly to other species, in the domestic cat, kittens' vocalizations increase the probability of the mother returning to and retrieving the young into the nest (Haskins 1977, 1979; also in our experiment). Even in humans an infant's cry is such a strong stimulus that it can immediately activate certain regions of a mother's brain (Lorberbaum et al. 2002; Seifritz et al. 2003; Sander et al. 2007; De Pisapia et al. 2013) and cause physiological changes such as a rise in temperature of the mammary glands (Vuorenkoski et al. 1969). Therefore, the presence of a kitten crying near the nest might have had such a strong motivational effect on the mothers that it overrode other sensory cues and the mother's need to discriminate (Maletínská et al. 2002).

Here we would like to add a note. To explore further the effect a vocalizing kitten outside the nest has on cat mothers, we performed a preliminary test with 3 of the mothers several months later (when they had new litters) using a dummy "kitten" (an IKEA soft toy mouse, GOSIG MUS) in which we implanted a small wireless speaker. The dummy was placed inside the nest when the mothers gave birth to imbue it with the scent of the nest, and on postnatal day 7, at a time when the mother had voluntarily left the nest, we placed the dummy next to the nest and began a playback of pre-recorded kitten separation cries. All mothers ran to the nest site within seconds and sniffed the dummy. One mother immediately retrieved the dummy into the nest, another attempted to pick it up (although failed to retrieve it), and the third became very agitated, entered the nest and growled until we stopped the playback. Although anecdotal, these observations suggest that kittens' cries are such powerful stimuli for mother cats that they can trigger a retrieval response, even of an inanimate object.

From an ecological perspective, a kitten crying outside the nest might pose a threat to the whole litter by attracting predators or potentially infanticidal conspecifics and hence requires rapid intervention by the mother. As a solitary animal, if a cat mother encounters a kitten outside her nest, it is most likely her own. Even if the mother detects that a kitten is not hers, it could be advantageous for her to rapidly retrieve—and therefore silence—any crying kitten outside her nest (Beecher 1991; Sherman et al. 1997). Mothers can perhaps also tolerate a certain level of error (misdirected feedings)—which seems to be the case particularly in polytocous mammals (Packer et al. 1992; Pusey and Packer 1994)—as long as their own progeny receive adequate maternal care (Beecher 1991). Finally, there is no negative feedback (Muul 1970) when a cat mother retrieves a kitten that is not her own, but only positive reinforcement—namely, the kitten becoming silent.

Horrell and Hodgson (1992) found sows spent twice as long sniffing alien piglets compared to their own and proposed this could have an adaptive function if spending more time to gather information could help an uncertain sow decide whether a piglet is hers. In the present study, the results of Experiments 2 and 3 showed that the mothers sniffed an alien kitten's anogenital region or whole body odour significantly longer than their own kittens', suggesting the alien kitten's odour was distinct from that of their own kittens. Even in Experiment 1, mothers were quicker to sniff alien kittens and sniffed them longer than their own kittens although this had no apparent effect on their retrieval behaviour.

The possible source of the odours which makes the kittens distinguishable could be intrinsic and/or extrinsic. One probable intrinsic source could be one or more of the kittens' scent glands. As we mentioned in the Introduction, cats have a variety of scent glands distributed over their body and they use these glands to mark objects in their environment, probably as a means of conspecific communication. However, beyond this almost nothing is known about the development or function of these scent glands, including to what extent they are involved in the mother–young recognition process. Since mothers did not differentiate between their own kittens' scents (Experiments 2 and 3), it suggests that the whole litter has a general scent rather than each kitten being individually distinguishable. Perhaps their scent glands do not even function (or do not fully function) at this early age, though in adults they might be used for individual recognition. An extrinsic source of such odours could be the mother herself. Since she licks the kittens frequently, perhaps she recognizes the scent of her own saliva on her kittens and discriminates it from an alien mother's scent on an alien kitten. Another possible source of extrinsic scent is that the kittens carry particles from their environment (nest site) which result in them smelling similar to each other as a litter, but different from alien litters from a different site.

To our knowledge, this is the first study to examine the existence of maternal offspring discrimination by means of olfactory cues in a solitary carnivore. Other, highly social members of the carnivore family such as lions (Pusey and Packer 1994), seals (Fogden 1971) and domestic dogs (Hepper 1994) have already been studied in this respect, and it has been found that mothers in these species are able to distinguish between own and alien young, probably using olfactory cues. Since the domestic cat is considered a solitary species, in nature mothers will rarely find themselves in a situation where they must discriminate between own and alien young. Yet from an evolutionary perspective, it could be interesting to investigate whether this failure is a result of domestication or a general characteristic shared with the domestic cat's presumed wild ancestors (*F. silvestris lybica, F. silvestris silvestris*). Perhaps functionally relevant discrimination between own and alien young only occurs at a later age when offspring emerge from the nest (Holmes 1984), and the costs and benefits of discriminating have changed (Hayes et al. 2004). Even if mothers don't need to apply this ability during the lactational phase, it might be important at a later stage when they might reencounter their offspring, e.g. to avoid inbreeding (Pusey and Wolf 1996).

In conclusion, if a mammalian mother nurses and cares for her own and alien young in the same manner, this should not be immediately interpreted as an inability to discriminate between them (Holmes and Mateo 2007). We would also like to draw attention to the idea that maternal care (e.g. nursing or retrieval) alone should not be used as a measure of maternal recognition or discrimination of offspring (Jesseau et al. 2008, 2009). For a better understanding of the mother–offspring relationship, it is important to take into account in test design and the interpretation of the results of past and future studies that mothers can care for alien offspring even when they are capable of distinguishing them from their own.

Ethics approval: All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Throughout the study, animals were kept and treated according to the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health, USA, and the National Guide for the Production, Care and Use of Laboratory Animals, Mexico (Norma Official Mexicana NOM-062-200-1999), and with approval by the Institutional Committee for the Care and Use of Experimental Animals (CICUAE) of the Faculty of Veterinary Medicine and Animal Science of the UNAM. In addition, the animals were under regular supervision by two qualified veterinarians from the Veterinary Faculty, National University of Mexico, associated with our cat program. This article does not contain any studies with human participants performed by any of the authors.

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