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**COMUNICACIÓN VOCAL MADRE-CRÍA EN EL
GATO DOMÉSTICO:
LAS CRÍAS RECONOCEN LOS LLAMADOS DE SU
MADRE**

T E S I S

QUE PARA OBTENER EL TÍTULO DE:

BIÓLOGA

P R E S E N T A:

ANDREA CITLALLI URRUTIA SCHROEDER



**DIRECTOR DE TESIS:
DRA. OXÁNA BÁNSZEGI
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CIUDAD UNIVERSITARIA, D. F.



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Hoja de datos del jurado

1. Datos del alumno

Urrutia
Schroeder
Andrea Citlalli
21574333
Universidad Nacional Autónoma de México
Facultad de Ciencias
Biología
308329113

2. Datos del tutor

Dra.
Oxána
Bánszegi

3. Datos del sinodal 1

Dr.
Hugh Michael
Drummond
Durey

4. Datos del sinodal 2

Dra.
María de Lourdes
Arteaga
Castañeda

5. Datos del sinodal 3

Dr.
Carlos Rafael
Cordero
Macedo

6. Datos del sinodal 4

Mae.
José Carlos
Sánchez
Ferrer

7. Datos del trabajo escrito

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Table of contents

Abstract	5
Introduction	6
<i>Recognition</i>	6
<i>Mother-offspring recognition</i>	7
<i>Vocal recognition</i>	8
<i>The domestic cat</i>	9
<i>Kitten development</i>	10
<i>Vocal communication in domestic cats</i>	13
<i>Aim of the study</i>	14
Methods	15
<i>Study site and animals</i>	15
<i>Ethics note</i>	16
<i>Recording of vocalizations</i>	17
<i>Playback stimuli</i>	20
<i>Experimental procedure</i>	21
<i>Video recording and analysis</i>	23
<i>Acoustic analysis of own mothers' versus alien mothers' vocalizations</i>	24
<i>Data treatment and statistical analysis</i>	24
Results	26
<i>Behavioural response of kittens to mothers' vocalizations</i>	26
<i>Acoustic analysis of the mothers' vocalizations</i>	32
Discussion	33
References	37
Annexes	43
<i>Annex 1</i>	43
<i>Annex 2</i>	46

Abstract

Many mammalian young depend for their early survival on the ability to recognize their mother and to distinguish her from potentially dangerous conspecifics. Acoustic communication can play an important part in this process. This, however, has still only been investigated in a small range of typically herd- or colony-living species. Here we report on the response of kittens of the domestic cat *Felis silvestris catus*, a typically solitary carnivore species, to playbacks at the nest of two kinds of vocalizations from their own versus alien mothers. We used 7 mixed-breed litters (29 kittens/3 mothers) from a colony kept under free-ranging conditions. Experiments started when kittens began to leave the nest at around 4 weeks of age. In a balanced design kittens were presented with playbacks of their own and alien mothers' greeting chirps, and with their own and alien mothers' meows. On all measures – duration of alertness, latency to approach and to remain near the speaker, percentage of kittens in each litter to approach the speaker, and the first kitten in each litter to show alertness and to approach the speaker – we found significantly stronger responses to the chirps from kittens' own mother than to her meows or to the chirps or meows of alien mothers. For both chirps and meows, acoustic analysis revealed greater variation between vocalizations from different mothers than for vocalizations from the same mother. We conclude that chirps emitted by mother cats at the nest represent a specific form of vocal communication with their young, and that kittens learn and respond positively to these and distinguish them from chirps of other mothers and from other cat vocalizations while still in the nest.

Introduction

Recognition

Recognition among conspecifics can be defined as the process of becoming familiar with other individuals to later remember and treat them accordingly (Mateo, 2004).

Recognition, or the lack thereof, has a role in shaping most animal social interactions and thus is central to the behaviour and ecology of any animal species (Insley, Phillips, & Charrier, 2003). The ability to recognize individuals can be expected to have evolved whenever there are repeated interactions among multiple individuals of a species with differing intentions, such that discriminating between individuals is beneficial. Most of the research on the subject of individual recognition has focused on three main situations: territoriality, aggressive competition and parental care (Mateo, 2004; Tibbetts & Dale, 2007).

Recognition of an individual may be carried out through different mechanisms. One such mechanism is context-based recognition, where discrimination is based on indirect, contextual (particularly spatial) cues rather than those of an individual; another recognition mechanism is familiarity by prior association, wherein an animal learns the direct, phenotypic cues of an individual and later remembers and discriminates these (Mateo, 2004). Individual recognition is often carried out by relying on a combination of these two mechanisms; for example, bats rely on a combination of spatial memory, acoustic, olfactory, tactile and/or visual cues to communicate with conspecifics and to identify their young (Kunz & Hood, 2000).

Mother-offspring recognition

For mammalian mothers, maternal care is an investment which comes at a large energetic cost (Gittleman & Thompson, 1988; Trivers, 1972). Lactation alone can increase the demand of caloric intake for a mother by up to 188%, and energy levels may increase five-fold (Gittleman & Thompson, 1988). Under natural conditions this increased food requirement may expose the mother to greater risks of debilitation, injury or death. Thus, for a mammalian mother it is important to ensure that her parental investment is being allocated appropriately in her own offspring and is contributing to her reproductive success, so recognition of her own offspring can be important in ecological contexts in which a mother may erroneously administer care to offspring which are not her own (Roulin, 2002).

On the other hand, it is important for the early survival of young mammals that they learn to recognize their own mother and to distinguish her from other conspecifics, since these offspring depend entirely upon her as their only food source during early developmental stages. However, the young are not simply passive receptors of maternal care; even altricial offspring, who are generally born in a very immature state – relatively immobile, and unable to see nor hear – actively influence the caregiving behaviour of their mother; for example, by searching for nipples and sucking (Kristal, 2009; Nowak, Porter, Lévy, Orgeur, & Schaal, 2000).

The benefit of maternal recognition for offspring also extends to the avoidance of dangerous situations. In various herd-living ungulates and colony-living mammals, the attempt by new-born young to suckle from an alien mother may result not only in rejection but also in serious injury or even death (Harcourt, 1992; Le Boeuf, Whiting, & Gantt, 1972;

Trillmich, 1981; Wolski, Houpt, & Aronson, 1980). Also for the young of more solitary species hidden away in nests or dens, it can be vital for their early survival that they remain quiet at the approach of predators or potentially infanticidal conspecifics (Sieber, 1985; Torriani, Vannoni, & McElligott, 2006; Vaňková, Bartos, & Málek, 1997), and only respond positively with approach to their mother.

Vocal recognition

Acoustic communication has been found to play an important part in the recognition by newborns of their mother in a variety of mammals (Balcombe & McCracken, 1992; Barfield, Tang-Martinez, & Trainer, 1994; Briefer & McElligott, 2011; Charrier, Pitcher, & Harcourt, 2009; Jin et al., 2015; Sèbe, Nowak, Poindron, & Aubin, 2007; Trillmich, 1981; Walser, 1986). However, much of this work has been done in herd- or colony-living species, with less information available on other taxonomic groups. This is understandable given the difficulty of observing the behaviour of mothers and young of solitary, more secretive species, and to the difficulty, exemplified by carnivores, of experimentally manipulating young often defended by well-armed mothers or other caretakers.

Evidence gathered through observation, vocal analysis and playback experiments in mammals shows that mother–offspring vocal recognition may be uni- or bidirectional. Mutual vocal recognition has been found in a variety of species (e.g., goats: Briefer & McElligott, 2011; sheep: Searby & Jouventin, 2003; Sèbe, Aubin, Boué, & Poindron, 2008; pinnipeds: Insley, 2001; mongoose: Müller & Manser, 2008; reindeer: Espmark, 1971), while in others species only the mother recognizes the voice of her young (e.g., bats: Balcombe, 1990; Knörnschild & von Helversen, 2008) or only the young recognize the

mother's voice (e.g., red deer: Vaňková et al., 1997; fallow deer: Torriani et al., 2006; raccoon: Sieber, 1985).

It bears noting, however, that lack of vocal recognition by one or both parties does not necessarily imply a lack of recognition altogether, as acoustic communication is only one of several modalities available to animals. The types of cues used for recognition on both sides may change as the offspring grow older, their sensory and cognitive abilities develop, and their behaviour and behavioural context changes (Mateo, 2004), while the mother's hormonal and motivational state changes across the lactation phase.

The domestic cat

The domestic cat (*Felis silvestris catus*) is an interesting and good model species, as it provides an exception to the difficulties in observing and conducting research with solitary carnivores. Cats can be kept and experimented with under semi-natural free-ranging conditions, and mothers readily permit the handling and manipulation of new-born young by familiar caretakers (Hudson, Raihani, González, Bautista, & Distel, 2009; Raihani, González, Arteaga, & Hudson, 2009).

The cat is a carnivorous species, sociable to some degree but generally considered a solitary animal. Feral cats tend to live alone or, if there is a concentrated, abundant food source (Deag, Manning, & Lawrence, 1988). The mating system tends towards polygyny, although one female may mate with, and bear offspring from, several males in one litter. Mothers usually have two litters per year with an average of 4 to 5 kittens per litter (Bateson, 2000). Male cats do not form a permanent pair bond nor do they remain with a

female whom they have mated with, and so do not play any part in raising the kittens (Deag et al., 1988).

As solitary-living obligate carnivores, cat mothers must spend considerable time hunting away from their young (Bradshaw, Goodwin, Legrand-Defréтин, & Nott, 1996; Martin, 1986). Although they do not construct dens, they are adept at hiding their kittens, already well-furred at birth, in refuges (referred to in this text as “nests”) providing protection from weather, predators and infanticidal males (Feldman, 1993; MacDonald, Apps, Carr, & Kerby, 1987; Pontier & Natoli, 1999). Cat mothers initially spend up to 83% of their time in their nest, grooming, nursing and resting with their kittens. However, between 4 and 6 weeks post partum, mothers drastically diminish their time spent in the nest, which remains low thereafter (Martin, 1986). The young typically remain still and silent when the mother is absent or at the approach of animals other than their mother (Haskins, 1977, own observations).

Kitten development

The cat is an altricial species; kittens are born with closed eyes and ears, and with poor motor control (Fig. 1) (Levine, Hull, & Buchwald, 1980; Villablanca & Olmstead, 1979). Locomotor activity increases markedly during the fourth and fifth postnatal weeks and, with the development of the visual and auditory systems, it represents maturation of the neural systems (Levine et al., 1980). At this time the kittens also start to eat solid food, which marks the onset of the weaning period (Bateson, 2000; Martin, 1986). They start to leave the nest for short periods and by the sixth week they use all of the gaits found in adult locomotion (Peters, 1983).

Even as blind and effectively deaf neonates, within 12 hours after birth, kittens develop a preferential use of certain nipples and begin to establish a ‘nipple order’. This order is maintained throughout the nursing period, showing that kittens are able to learn from a very early age (Hudson et al., 2009).



Figure 1. Development of a kitten. Kitten at A) 1 day of age, B) 2 weeks of age, C) 3 weeks of age, and D) 5 weeks of age.

The hearing of new-born kittens is limited; the external auditory canals reach their maximum depth around the end of the second postnatal week (Fig. 2) (Olmstead & Villablanca, 1980). Starting from around the third postnatal week, kittens show greater

responsiveness to biologically relevant sounds, such as the recorded voices of their mother and siblings, than to other sounds (e.g., hand claps, pure tones) (Olmstead & Villablanca, 1980; Villablanca & Olmstead, 1979). By the end of the fourth week they reach the adult threshold of absolute auditory frequency range and spatial sound localization (Ehret & Romand, 1981; Olmstead & Villablanca, 1980; Villablanca & Olmstead, 1979).

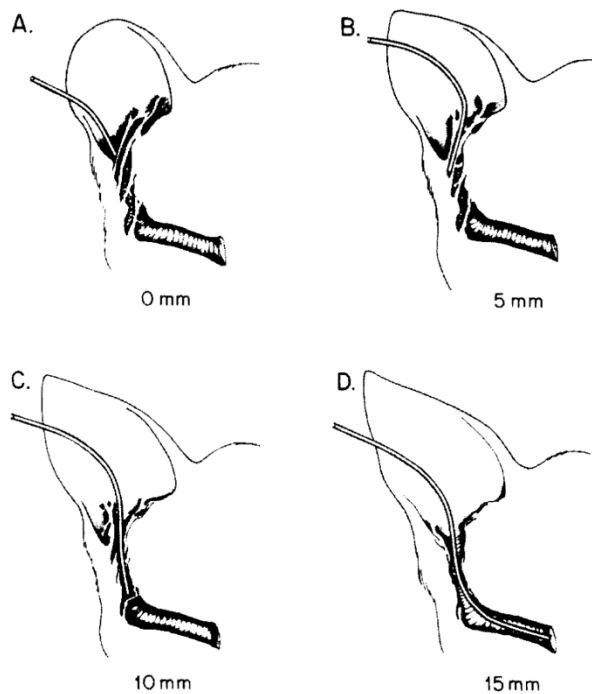


Figure 2. A representation of the maturation of the external auditory canal and the pinna in the kitten. Maturation at 0 (A), 7 (B), 9 (C) and 12 (D) days of age. The number under each schema represents the depth of the external auditory canal, as gaged by probing the canal with a piece of polyethylene tubing (From Olmstead & Villablanca, 1980).

Vocal communication in domestic cats

Domestic cats have a broad and complex vocal repertoire, consisting of at least a dozen different types of calls (see Bradshaw & Cameron-Beaumont, 2000 for a review). Perhaps the most notable vocalization is the meow, of which there are many sub-types, each with different connotation; however, these remain understudied. Meows are most often heard in cat-human interactions rather than cat-cat interactions, and are emitted in amicable social encounters (Bradshaw & Cameron-Beaumont, 2000).

Cats employ other vocalizations in communicating with their young (Brown, Buchwald, Johnson, & Mikolich, 1978; Farley, Barlow, Netsell, & Chmelka, 1992; Moelk, 1944; Scheumann et al., 2012; Yeon et al., 2011): when mothers approach the “nest” and while nursing, they emit a particular soft call referred to in the literature as a “chirp” or “^{l̥ə}mhrn” (Martin, 1986; Moelk, 1944). Apparently, chirps and purrs are the only vocalizations emitted by mothers at the nest (own observation).

Despite being a highly vocal animal, there have been few studies of mother-young vocal communication in the domestic cat (Haskins, 1977; Scheumann et al., 2012) and, to our knowledge, only one of kittens’ behavioural responses to mothers’ vocalizations (Luschekin & Shuleikina, 1989). However, in this study there was not always a clear experimental separation between the kittens’ use of any type of acoustic or other sensory modalities to orient to the nest, or if the acoustic stimuli were from their own or alien mothers. No studies exist, to our knowledge, of mother-offspring communication (vocal or otherwise) in other feline species.

Aim of the study

It was our aim to investigate whether kittens distinguish between their own and alien mothers' vocalizations at around postnatal week 4, the age at which they start to leave the nest. We predicted: 1) that kittens would respond more strongly with positive behaviours such as approach to their mother's chirps than to a presumably unknown stimulus, her meows; 2) that they would respond more strongly and positively to the chirps of their own mother compared to the chirps of an alien mother; and 3) that acoustic analysis would reveal greater variation between the chirps of different mothers than between chirps from the same mother.

Methods

Study site and animals

We collected data from 29 kittens of seven litters from three mixed-breed multiparous females belonging to an established breeding colony of cats (four adult females, three of which mated during the present study, and two adult males plus other visiting males). With the intention of studying animals in semi-natural conditions, the cats were kept in a private house with a garden, which they were free to leave at will. They were fed daily with commercial canned cat food and fresh meat, and received regular treatment against parasites. Water, milk, dried cat food and litter trays were always available. There was sufficient space in the house for each adult animal to have its own resting place, and for mothers to raise their litters in separate rooms, apart from other mothers and their young. The doors of the rooms were remodelled to 1.2 m in height, so that all the adult cats were free to jump in or out, but the kittens were not able to leave. Mothers showed little interest in the litters of other females and communal nursing did not occur.

Mothers always gave birth in the house. A day or so after delivery, the litters with their mothers were moved to one of the rooms in a quiet, undisturbed part of the house. Within the rooms nest sites were provided: a commercial foam cat bed (oval, 68 × 57 cm) was placed inside a large cardboard box (60 × 80 × 70 cm). The top of the box was open, but covered with a blanket, and a small floor-level opening (22 × 27 cm) was cut for the mother (Fig. 3). The box was removed when litters were 28 days old and began leaving it.

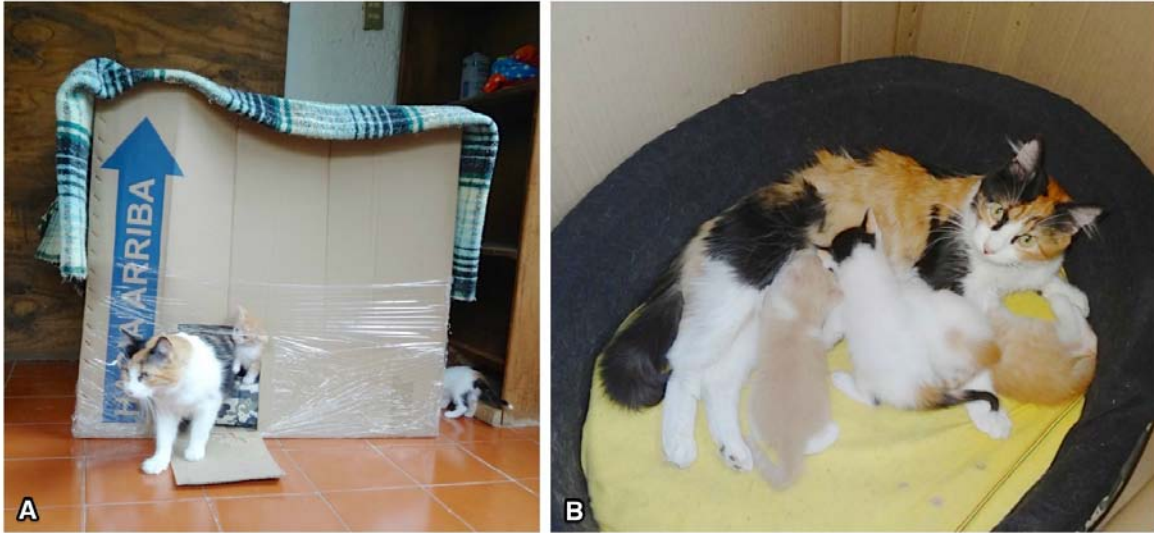


Figure 3. Example of a nest-box used to house the mother and kittens. A) A blanket was used to cover the top of the box and a floor-level opening was cut for the mother and kittens. B) Inside view of the nest-box, showing the commercial cat bed and a cat mother nursing her young.

Kittens were weighed at birth and daily thereafter to measure growth and to habituate them to human presence and handling. Each kitten was fitted at birth with a coloured neck ribbon for individual identification. The ribbons were adjusted to the appropriate size as kittens grew. From the 4th week onward, kittens were fed daily with commercial canned cat food and ad libitum dry cat food. Water and a litter tray were also provided.

Ethics note

All kittens survived to weaning at approximately 8 weeks of age, when they were given away as pets with the help of local veterinarians. Throughout the study, animals were

kept and treated according to the guidelines for the care and use of animals in research of the ASAB/ABS (Rollin & Kessel, 1998), the Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, and according to the National Guide for the Production, Care and Use of Laboratory Animals, Mexico (Norma Oficial Mexicana NOM-062-200-1999).

Recording of vocalizations

For each litter, two kinds of playback stimuli were used: “chirps” and “meows” either from kittens’ own mother or from alien mothers (both of the other mothers participating in the study) at the same lactational phase (see Fig. 4 for sample spectrograms of each of these vocalization types).

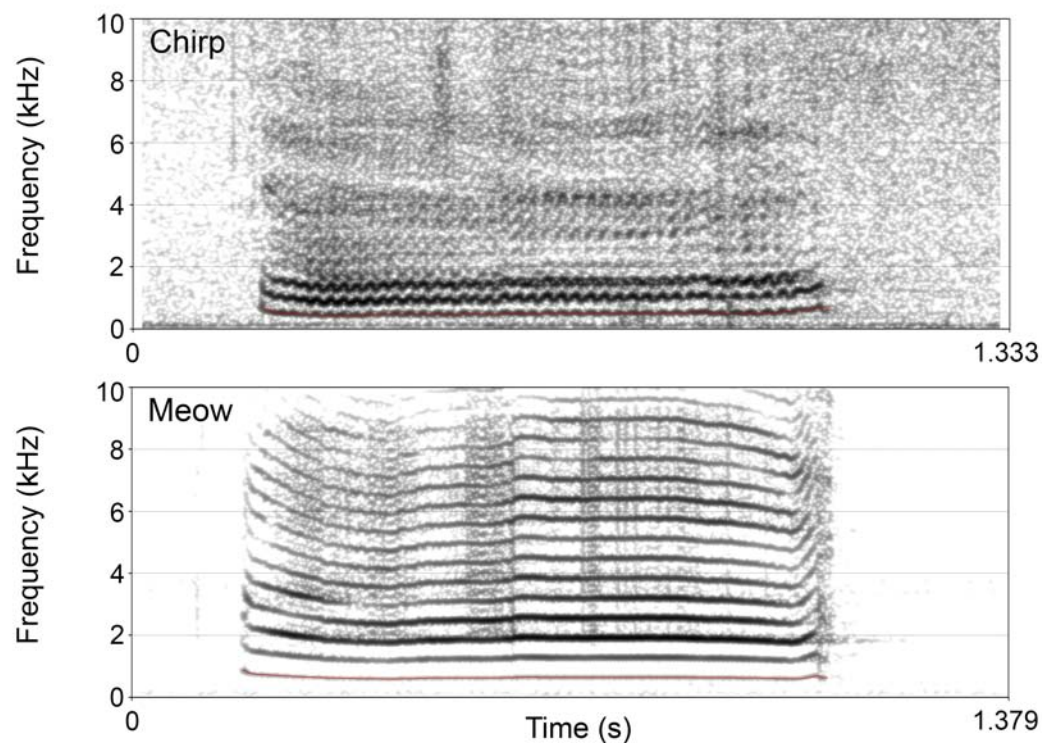


Figure 4. Spectrograms of the vocalization types used from a single mother. Frequency range 0 – 10 000 Hz, window length: 0.01 s, dynamic range 50 dB. The fundamental frequency is highlighted with red.

Recordings were made in WAV format, using a unidirectional microphone (Sennheiser ME66, Wedemark, Germany; frequency range: 40 – 20 000 Hz) on a stand, connected to a recorder (Tascam DR-40, Montebello CA, USA; 96 kHz / 24 bit). Editing was carried out in Audacity 1.2.6, and stimuli were saved in lossless AIFF format.

Recordings were obtained as follows:

“*Chirps*”: Continuous recordings were made at the nest when litters reached 3 weeks of age. Recording was carried out overnight (approx. 23:00 – 06:00) to minimize background household and street noise. The microphone was placed inside the box, 30 cm above the nest and pointing towards it (Fig. 5).



Figure 5. Outside view of the setup used to record mothers' chirps in the nest.

A unidirectional microphone (Sennheiser ME66, Wedemark, Germany) was placed inside the box, pointing at the nest, to make an overnight recording.

“*Meows*”. Recordings were made from each mother when a highly preferred food (raw beef) was held above her. The microphone was held on a boom pole 30 cm away from the mother (Fig. 6).

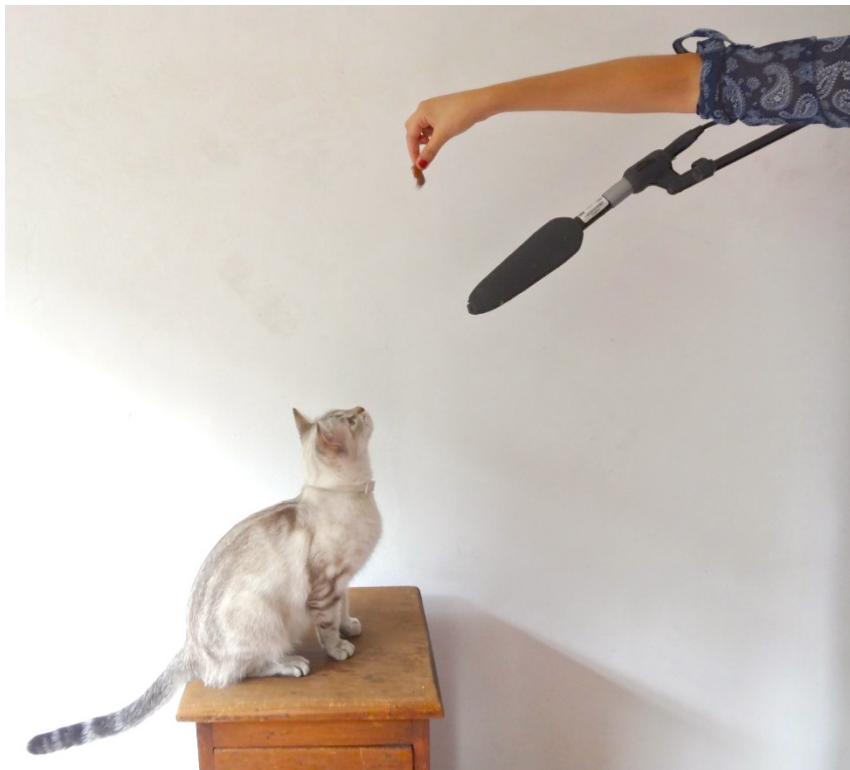


Figure 6. Method for obtaining recordings of mothers' meows. A unidirectional microphone (Sennheiser ME66, Wedemark, Germany) was pointed at the mother, while a highly preferred food (raw beef) was held above her.

Playback stimuli

Individual chirps and meows, when clear and free of background noise, were cut from the recordings. Stimuli were prepared by editing together a train of seven chirps or seven meows, separated from each other by 2 s of silence and repeated twice ($\bar{X} \pm SE = 36.5 \pm 1.7$ s, $N = 14$ different trains for each vocalization type) (Fig. 7). All of the chirps or meows in one stimulus train belonged to the same mother. Sound pressure of all stimuli was normalized to 60 dB measured from 1 meter distance with a sound pressure meter (General DSM402SD, New York, NY USA). To ensure that all the kittens were in the nest and were engaged in some neutral behaviour (play, grooming), at the beginning of the playback we included one minute of pre-playback observation. Additionally, we continued the observation one minute after the playback ended. To avoid pseudoreplication, each individual vocalization was used in one prepared stimulus only, and each stimulus was presented to a litter only once.

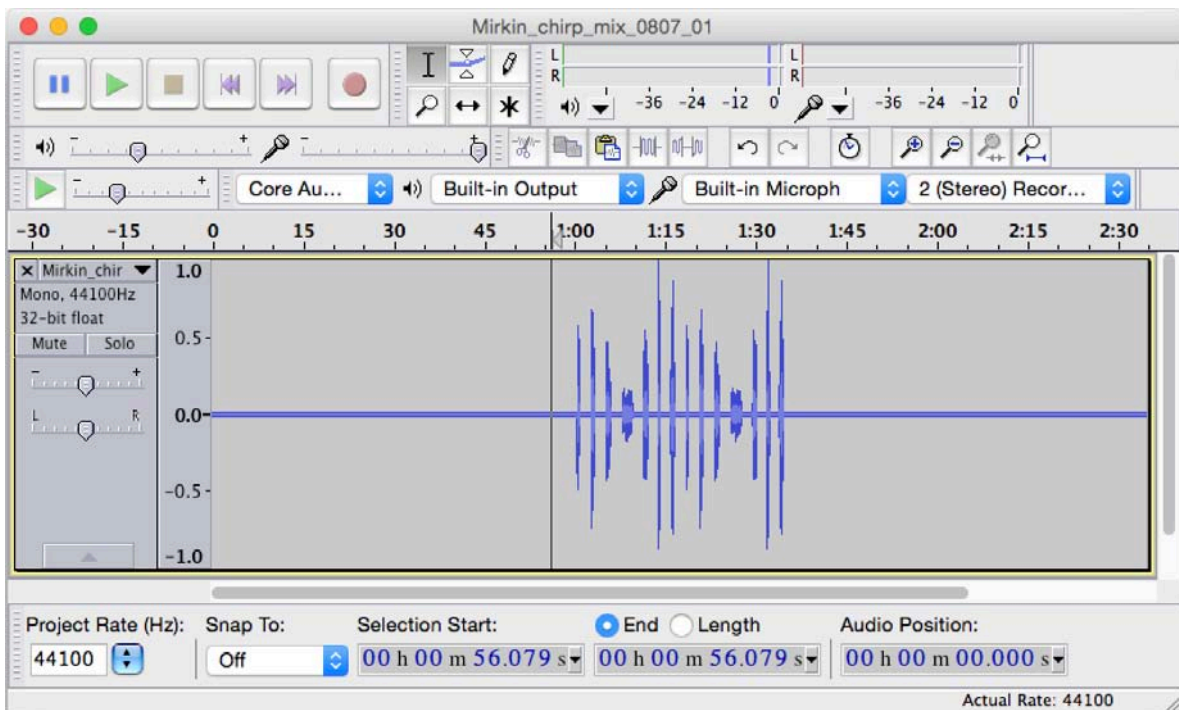


Figure 7. Example of a prepared stimulus. Prepared chirp stimulus in Audacity consisting of a train of 14 chirps belonging to one mother (7 different chirps, repeated once), each separated by 2s of silence, with one minute of silence at the beginning and the end.

Experimental procedure

Each litter was tested twice for each type of vocalization (represented by two different prepared stimuli). The tests took place from 10:00–12:00 and 15:00–17:00 h on four consecutive days, starting when the kittens were 32–33 days old. The testing schedule was balanced, such that test days were alternated between chirps (first and third days) and meows (second and fourth days); the order of the own mothers' and alien mothers' vocalizations were played in reversed sequence the second time (Table 1).

Day	Morning	Afternoon
1	Own mother chirp	Alien mother chirp
2	Own mother meow	Alien mother meow
3	Alien mother chirp	Own mother chirp
4	Alien mother meow	Own mother meow

Table 1. Test schedule. A balanced design was used to alternate between own and alien mothers' voices, and chirp and meow vocalizations.

A 40 × 50 cm screen made of white corrugated plastic was placed in the litters' room four days before the start of testing so that the kittens could adapt to its presence. The screen was placed between the nest and the future site of playback speaker, around 1.5 m from the nest (Fig. 8). Two hours before each experiment, the mother and the food were removed from the room. Playback of stimuli was presented by a wireless speaker (SoundLink® Mini, Bose Inc., Framingham MA, USA) connected to a 5th generation iPod® (Apple Inc. Cupertino CA, USA) placed behind the screen. Experimenters made sure the kittens were awake and in the nest, then left the room.

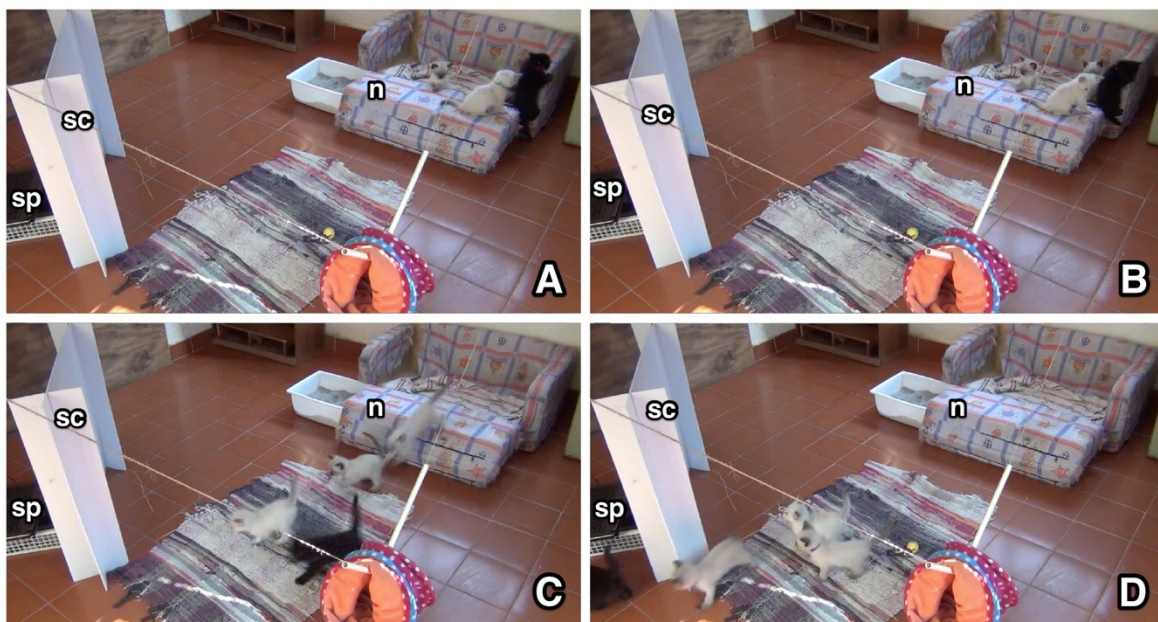


Figure 8. Experimental set-up. A) Kittens begin the test awake in the nest, B) the stimulus (a train of the kittens' own mother's chirps) begins to play, the kittens become alert, C) kittens leave the nest and run towards the speaker, D) Kittens stand next to the speaker. sp= speaker, sc= screen, n=nest.

Video recording and analysis

Trials were video recorded (Sony HDR-CX130) in the absence of the experimenter for posterior analysis. Using Solomon Coder software (Fig. 9) (Péter, 2011), the following behaviours were scored separately for each kitten from the video recordings:

Latency and duration of alertness (s): alertness was defined as a kitten stopping what it was doing, lifting its head, pricking up its ears, and/or orienting towards the stimulus.

Latency to approach the speaker (s): time taken by a kitten to approach and remain within a 15-cm radius of the speaker or the screen.

Time spent near the speaker (s): time a kitten spent within a 15-cm radius of the speaker or the screen.

In addition, we calculated *the percentage of the kittens* from each litter that *approached the speaker*: defined as a kitten within 15 cm of the speaker or screen.

The screenshot displays the Solomon Coder software interface. On the left, a video window shows several kittens in a room with a tiled floor, a rug, and a pet bed. On the right, a table titled 'f_1_red' records behavioral observations. The table has columns for Time, Alertness, Neutral, Move, and Vocal. The 'Alertness' column is highlighted in blue, and the 'Vocal' column is highlighted in green. To the right of the table, a diagram shows four colored boxes: a blue box for 'Alertness', a yellow box for 'Approach the speaker', a green box for 'Near the speaker', and a red box for 'Vocalization'.

Time	Alertness	Neutral	Move	Vocal
82.50	Alertness		Approac	
83.00	Alertness		Approac	
83.50	Alertness		Approac	
84.00	Alertness		Approac	
84.50	Alertness		Approac	
85.00	Alertness		Approac	
85.50	Alertness		Approac	
86.00	Alertness		Approac	
86.50	Alertness		Approac	
87.00	Alertness		Approac	
87.50	Alertness		Approac	
88.00	Alertness		Approac	Vocalizat
88.50	Alertness		Approac	
89.00	Alertness		Approac	
89.50	Alertness		Approac	
90.00	Alertness		Approac	
90.50	Alertness		Approac	
91.00				
91.50				
92.00				
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93.00				
93.50				
94.00				
94.50				
95.00				
95.50				
96.00				
96.50				
97.00				
97.50				

Figure 9. Video analysis on Solomon Coder. The buttons (right) are used to individually score each kitten's behaviour (displayed in the middle column) as the video is played.

Acoustic analysis of own mothers' versus alien mothers' vocalizations

Given the ability of kittens to distinguish between the chirps of their own and alien mothers (see Results), the acoustic properties of the chirps and meows of mothers contributing to the stimulus material were analysed. Sixty-one good quality recordings of chirps from 11 bouts (at least 5 calls per bout) and 89 meows from 11 bouts (at least 3 calls per bout) free of background noise were selected and were analysed using a custom made PRAAT script (Boersma & Weenink, 2015). The quantified parameters are listed in Annex 1.

Data treatment and statistical analysis

All behavioural data were normalized for analyses with the Box–Cox transformation; normality of distributions was checked with Shapiro-Wilk tests. For response variables lacking homogeneity of variance, non-parametric statistics were used. We used Linear Mixed Models (LMMs) for normally distributed and Kruskal-Wallis tests for non-normally distributed data. Litter identity was included as a random factor to control for repeated measures in the LMM models. In the case of significant results, Tukey multiple comparison post-hoc tests with Bonferroni adjustment were used to identify differences between groups.

For acoustic analysis of the vocalizations we applied Principal Component Analysis (PCA) with covariance matrix and Varimax rotation to simplify the set of acoustic

variables. In order to do this we standardized the variables by transforming them to Z scores and ran the PCA on these values. For chirps we formed 8 and for meows 9 factor scales (for detailed structure and Chronbach alpha values see Annex 2). We then performed conventional and permuted Discriminant Function Analysis (DFA and pDFA) to test the acoustic discriminability of the three mothers' vocalizations. During the conventional DFA we applied a forward stepwise method based on Wilk's lambda changes to find the subset of factors which best discriminated between the three individuals. For validation we used leave-one-out cross validation. Finally, as the calls were obtained from call bouts and so cannot be considered as independent data points, we performed pDFA following the suggestion of Mundry & Sommer (2007) to validate our findings. We used an R script (written and provided by Roger Mundry) with nested design, where our test factor was the individuals, while the ID of bouts from which the calls originated was used as a fixed factor. We fed the factor scores best discriminating the individuals based on the DFA results into the analysis. This pDFA picked 100 random selections from the bouts to balance the sample and to determine the baseline level of correct classification, and then it generated 1000 randomly permuted samples and reran the classification for each. The low number of random samples (ratio less than 0.05) with better discriminability than the balanced sample showed good validity of the discrimination. Again, a cross-validation was performed with the unused items in the balanced DFA.

Results

Behavioural response of kittens to mothers' vocalizations

Kittens showed similar latencies of alertness in response to all stimuli, independently of type (LMM: $F_{3,18} = 2.34$, $P = 0.11$), which suggests that they were able to hear all of them. However, further responses differed depending on the kind of stimulus. During and after playback of own mother's chirps, kittens remained alert longer (LMM: $F_{3, 18} = 6.03$, $P < 0.01$; Fig. 10) than with other types of playback. They also sometimes approached the speaker, predominantly when they heard their own mother's chirps. We found significance differences in their latency to approach the speaker (Kruskal-Wallis test: $H_3 = 19.8$, $P < 0.001$; Fig. 11), and in the time that they spent near it ($H_3 = 19.3$, $P < 0.001$; Fig. 12) across the different stimulus types. During and after playback of their own mother's chirps, kittens were quicker to approach the speaker and stayed near it for longer than for any other stimulus type. We also calculated the percentage of kittens from each litter that approached the speaker. A significantly higher proportion of kittens did so during and following the playback of their own mother's chirps than when other types of stimuli were used (Kruskal-Wallis test: $H_3 = 19.5$, $P < 0.001$; Fig. 13).

Since there was very likely a social effect, where some kittens imitated their siblings' responses, or their responses were socially facilitated, we also compared the data across stimuli of the first kitten of each litter to show alertness and to go to the speaker. We obtained results similar to those for the analyses of the whole litter: latencies of the first kittens to become alert during the playbacks did not differ for the different vocalizations (LMM: $F_{3,18} = 2.35$, $P = 0.10$), but they approached the speaker significantly sooner

during their own mother's chirps than during other types of playback (Kruskal-Wallis test: $H3 = 18.1, P < 0.001$; Fig. 14).

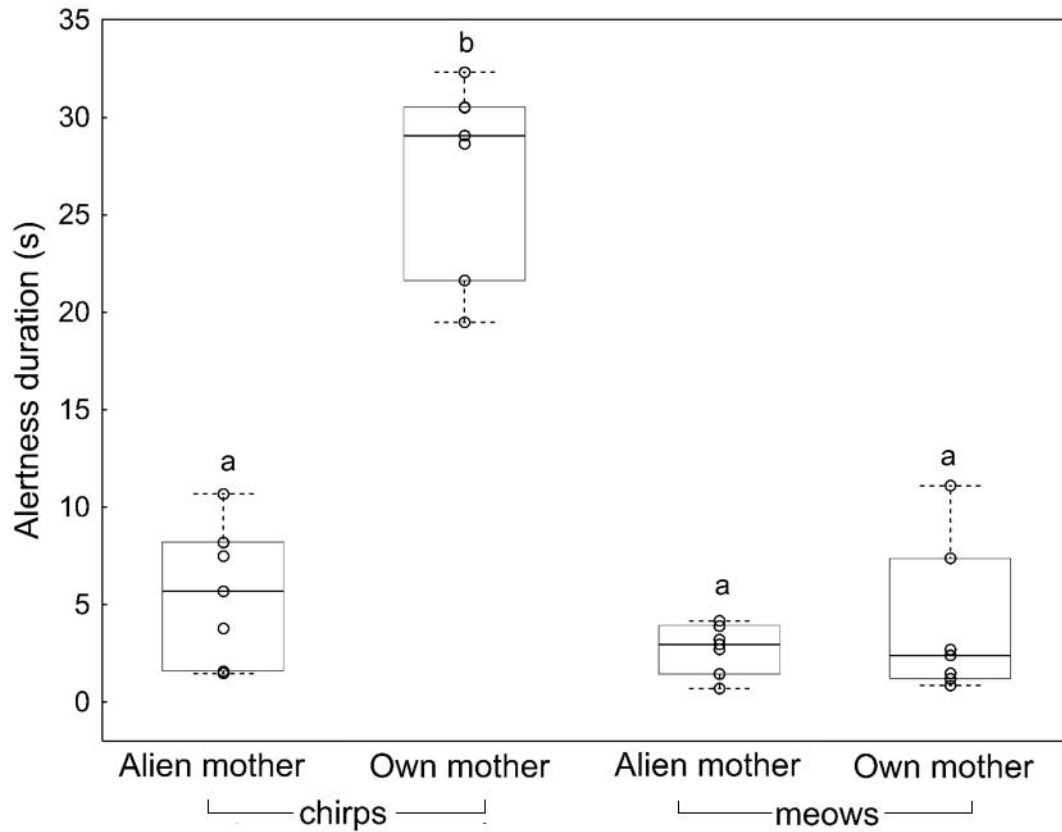


Figure 10. Kittens were alert for significantly longer during and after the playback of own mother's chirps than playback of other vocalizations. The data are presented as medians (bold horizontal lines), upper and lower quartiles (boxes), and minimum and maximum values (dotted lines). Each circle represents the average value for a litter. Letters indicate significant differences as reported by Tukey post-hoc multiple comparisons with Bonferroni adjustment following application of a Linear Mixed Model. Details of statistical tests are given in the text.

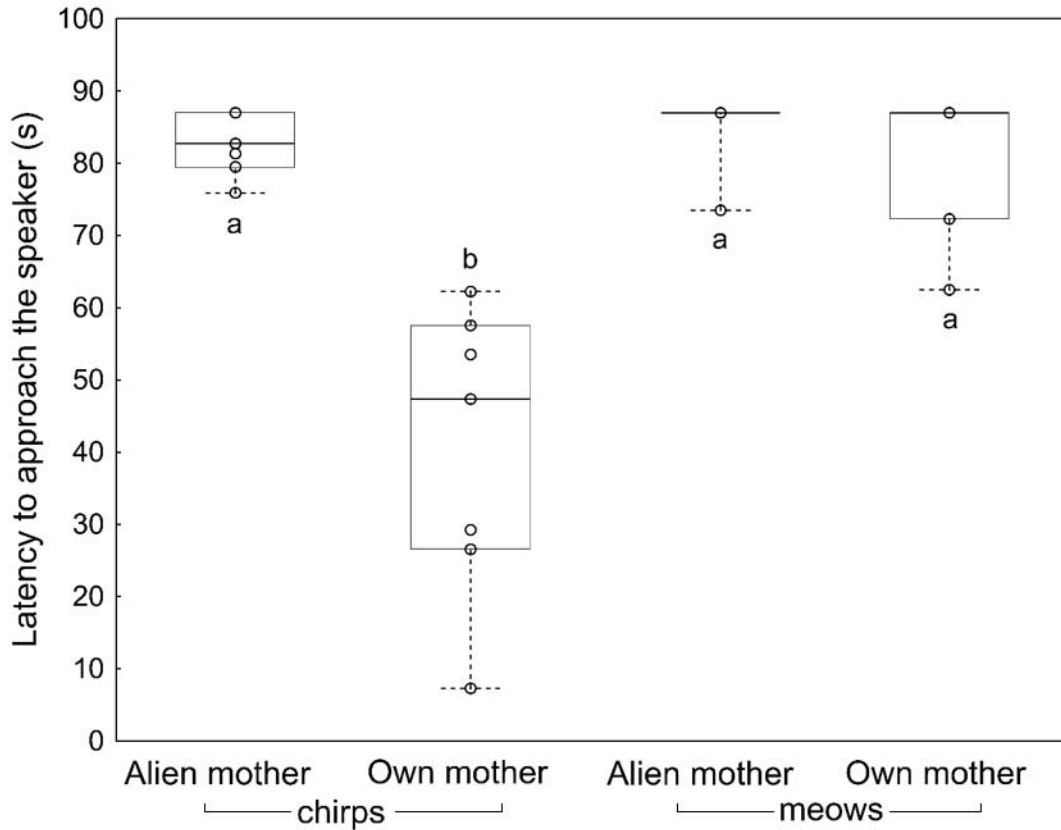


Figure 11. Kittens approached the speaker significantly sooner during and after playback of own mother’s chirps than other types of playback. The data are presented as medians (bold horizontal lines), upper and lower quartiles (boxes), and non-outlier minimum and non-outlier maximum values (vertical lines). Each circle represents the average value for a litter. Letters indicate significant differences reported by multiple Tukey post hoc multiple comparisons with Bonferroni adjustment, following application of a Kruskal-Wallis test. Details of statistical tests are given in the text.

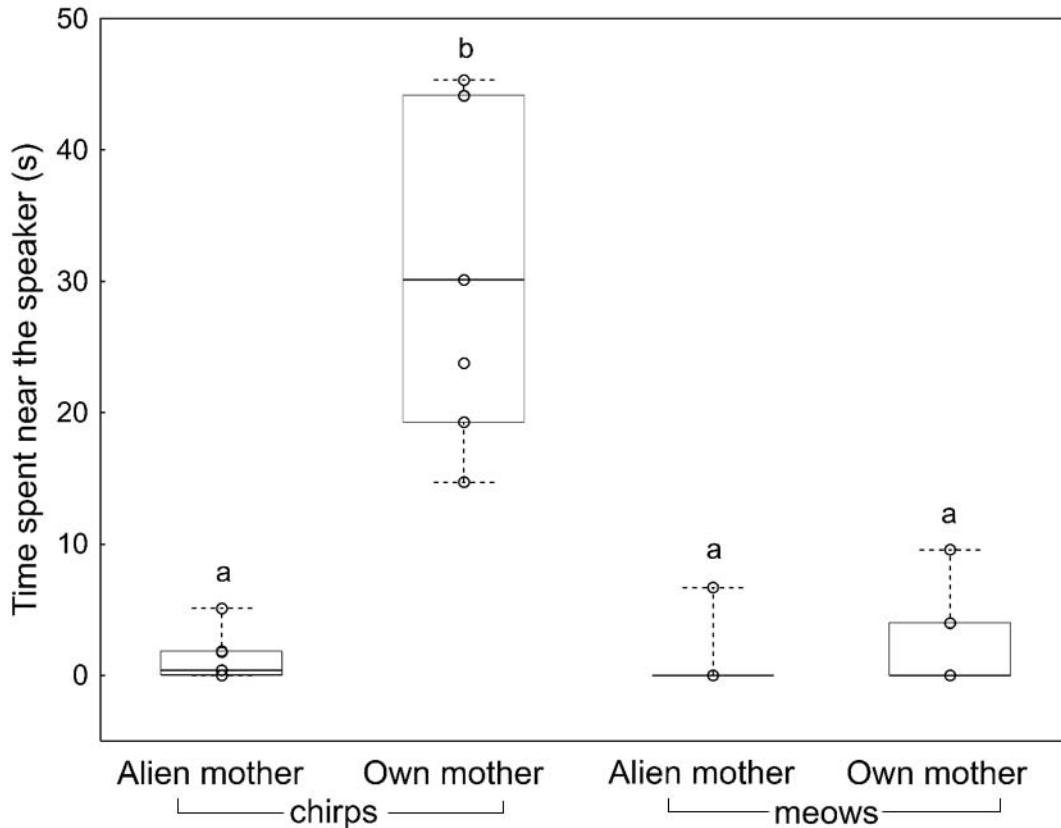


Figure 12. Kittens spent significantly longer near the speaker during and after the playback of own mother’s chirps than the other types of playback. The data are presented as medians (bold horizontal lines), upper and lower quartiles (boxes), and non-outlier minimum and non-outlier maximum values (dotted lines). Each circle represents the average value for a litter. Letters indicate significant differences reported by Tukey post hoc multiple comparisons with Bonferroni adjustment, following application of a Kruskal-Wallis test. Details of statistical tests are given in the text.

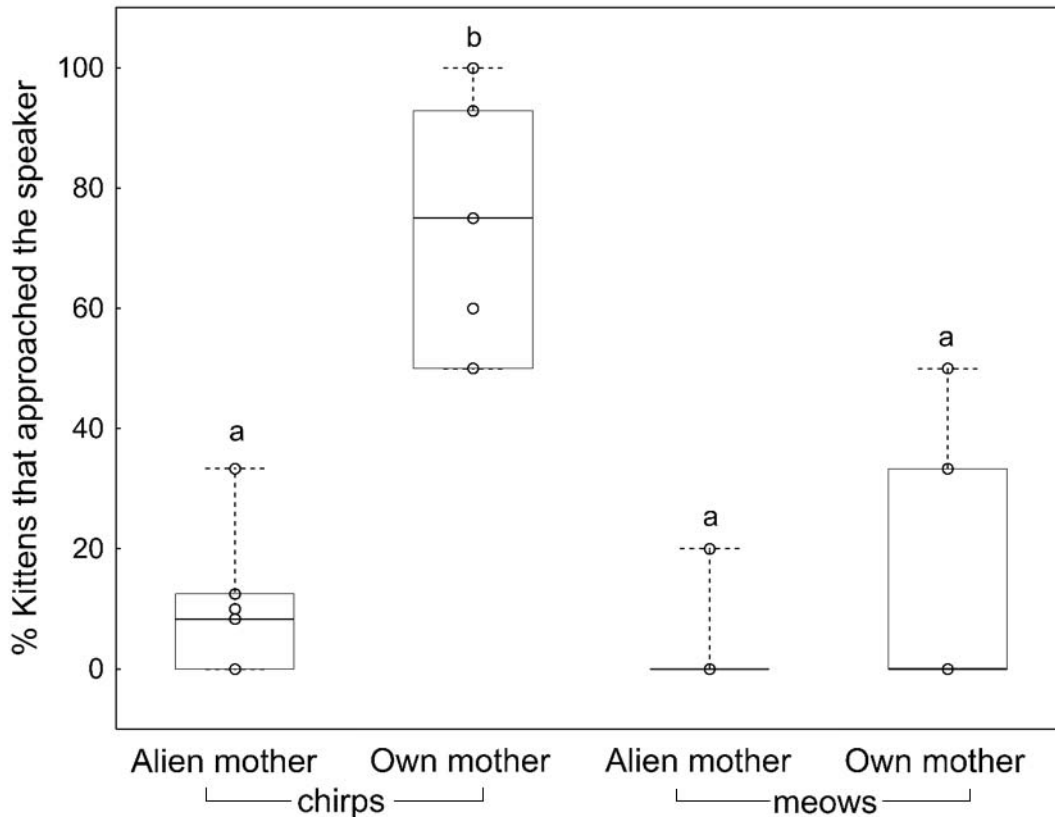


Figure 13. Significantly more kittens in each litter approached the speaker during and after the playback of own mother’s chirps than with playback of other types of stimuli.

The data are presented as medians (bold horizontal lines), upper and lower quartiles (boxes), and non-outlier minimum and non-outlier maximum values (dotted lines). Each circle represents the average value for a litter. Letters indicate significant differences reported by Tukey post hoc multiple comparisons with Bonferroni adjustment, following application of a Kruskal-Wallis test. Details of statistical tests are given in the text.



Figure 10: First kitten's response: latency to approach to speaker. The first kitten of each litter to approach the speaker did so significantly sooner during and after playback of own mother's chirps than other types of playback. The data are presented as medians (bold horizontal lines), upper and lower quartiles (boxes), and minimum and maximum values (dotted lines). Each data point represents the average value for a litter; outliers and extremes are marked with triangles and asterisks. Letters indicate significant differences as reported by Tukey post-hoc multiple comparisons with Bonferroni adjustment following application of a Linear Mixed Model. Details of statistical tests are given in the text.

Acoustic analysis of the mothers' vocalizations

Chirps: The conventional DFA showed that the chirps of the three mothers were acoustically distinct. For the best discrimination three factors were included (F2-Pitch, F3-Pitch change, F7-Pitch variability; $N = 3$, $n = 61$ calls, Wilk's $\lambda=0.085$, $P < 0.001$), and 93.4% of the cases were correctly classified (cross validated: 90.2%; Fig. 15, left panel). The pDFA including only the first two factors (due to the restriction that allows a lower number of variables than the lowest number of calls within one bout, in this case 3) showed poorer (51.79%) discriminability but significantly different from the permuted sample ($N = 3$; $n = 61$ calls, $P < 0.001$), supporting the validity of the conventional DFA.

Meows: In the case of meows the conventional DFA showed lower but still good discriminability (77.8%; 71.7% cross-validated, Fig. 15, right panel) by three factor scores (F1-Pitch; F3-Range of Intensity; F6-Call length; $N = 3$, $n = 99$ calls, Wilk's $\lambda=0.367$, $P < 0.001$). The pDFA was run with the first two factors again, resulting in lower (23.36%) but still significant discriminability ($N = 3$; $n = 85$ calls; $P < 0.05$).

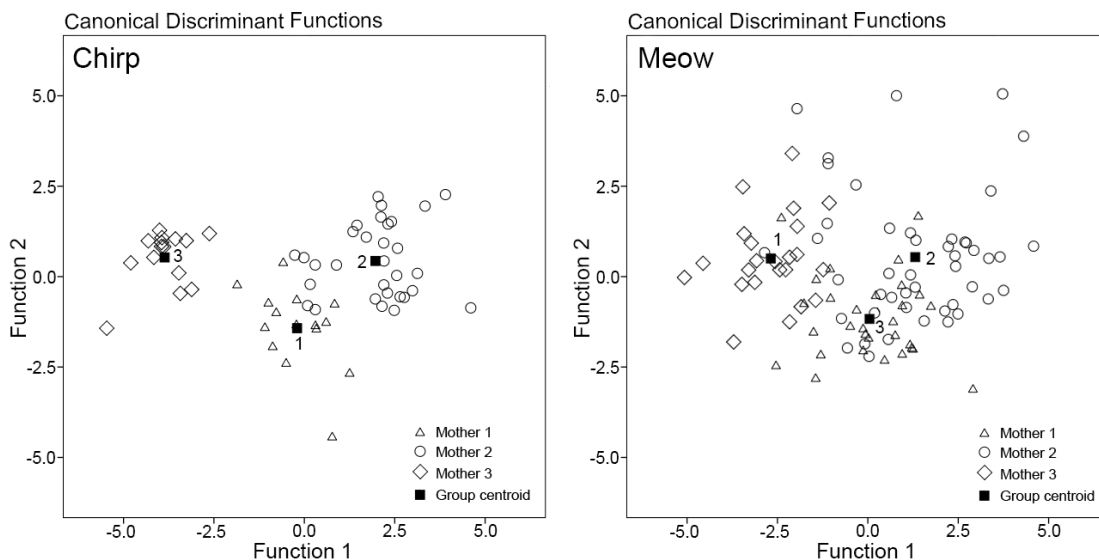


Figure 15: Vocal individuality in calls based on the first two canonical discriminant functions from the conventional DFAs. The data points represent individual calls of the three mothers. In the case of Chirps (left panel), Function 1 contained the Pitch factor with the highest loading (F2: 0.948), and was also moderately affected by the Pitch variability factor (F7: 0.547), while Function 2 was mainly affected by the Pitch change factor (F3: 0.855). The centroids (mean discriminant score of group) of Mothers 2 and 3 were close to each other, suggesting that their voices were more similar, but they were still distinguishable by the cross validation (87% of the two mothers' calls correctly assigned). In the case of Meows (right panel), Function 1 contained the Pitch and the Intensity range factors with the highest loading (F1: 0.842; F3: 0.739), while Function 2 was mainly affected by Call length (F6: 0,737). The centroids (mean discriminant score of group) of Mothers 1 and 2 were close to each other, suggesting that their voices were more similar, but that they were still distinguishable by the cross validation (72% of Mother 2's calls and 67% of Mother1's calls were correctly classified). Details of statistical analysis are given in the text.

Discussion

The results clearly show that kittens of the domestic cat recognize and respond positively to the playback of the distinctive chirp vocalizations emitted by their mother as she approaches the nest and while she tends to them inside it. Furthermore, kittens distinguish the chirps of their own mother from those of other mothers at an equivalent lactational (maternal) phase, as well as from the meows of their own or from alien mothers: kittens were alert longer, approached the speaker sooner and spent more time next to it

when hearing the playback of their own mothers' chirps compared to the playback of any other vocalization. This suggests that the mother's chirp call may have evolved to have a specific communicatory function, on the one hand signalling to the young kittens her arrival at the nest, and as they grow older and start to be weaned, using it to call them to leave the nest and follow her (Moelk, 1944).

Acoustic analysis confirmed that the chirps of individual mothers are sufficiently distinctive and sufficiently stable on a range of physical characteristics to represent individual vocal "signatures" (see also annexes) so as to enable kittens to distinguish chirps of their own mother from those of other females. To more rigorously test this, and to avoid pseudoreplication (Kroodsma, 1989), each train of chirps used in the present study comprised seven different vocalizations cut from seven different chirp bouts recorded for each female, and the kittens were tested with two such trains of independently obtained and constructed material on two separate occasions. Thus, the kittens indeed seem to have perceived and to have used interindividual and not simply intervocalization differences when responding to their own versus another mother's chirps (cf. Sauv e, Beauplet, Hammill, & Charrier, 2015). In addition, the design of the experiments required that the kittens leave the nest to approach the speaker, rather than to return to their nest as in the study by Lushekin & Shuleikina (1989). This excluded them using olfactory, thermal or spatial cues as even much younger kittens have been shown to effectively use to return to their nest (Freeman & Rosenblatt, 1978a, 1978b).

A question arising from the present findings is: what prompts mothers to emit these distinctive calls on approaching or entering the nest? While we were recording at nests to obtain material to construct the playbacks, we consistently found, in agreement with previous reports (Lushekin & Shuleikina, 1989), that mothers emit only chirps and purrs at

the nest, and not, for example, meows. Somewhat unexpectedly (but noting that our sample size of mothers and litters was rather small), we also found that mothers did not start to emit chirps until the kittens were around two to three weeks of age (see also Martin, 1986). At present it is not clear what stimulated the mothers to start doing this: signals from the developing kittens such as an increase in motor activity or an increase in the squeaking vocalizations (which we often recorded from them in the nest) in response to their mother's arrival, or a change in the mothers' hormonal and motivational state across lactation, or both. Here cross-fostering studies might help provide an answer, for example, by investigating whether chirping is delayed in mothers given younger foster litters, or advanced in mothers given older litters.

The present findings also raise questions as to when and how the kittens learn to recognize and respond to their own mother's distinctive chirps. Apparently they do not do so prenatally (cf. Moon & Fifer, 2001) as they should then also have responded to the mother's apparently equally complex, distinctive and frequently emitted meows. Furthermore, they also would not be able to learn until around the second or third postnatal week, when as mentioned above, mothers first start to emit chirps. This is consistent with findings that the auditory canals are almost completely open and that kittens have good auditory function by this age, and virtually mature function by the age of one month when we started to test them (Ehret & Romand, 1981; Olmstead & Villablanca, 1980).

It is not difficult to understand how the kittens could be conditioned to respond positively to these calls. From previous studies it is already known that kittens are able to learn to identify their own nipple(s) in the litter's "teat order" within a few hours of birth, from which they will nurse almost exclusively (Hudson et al., 2009; Raihani et al., 2009). This is achieved through reinforcement either from the odour of the nipple, the milk

reward, or a combination of both. (Mermet, Coureaud, McGrane, & Schaal, 2007; Rosenblatt, 2010). Presumably, the same type of learning mechanism is in place when they learn the mother's chirp. The mothers emit chirps only when they approach the nest and during nursing and grooming; the kittens hear the mother's chirp and the learning is reinforced by nursing, as well as other tactile and olfactory stimuli which the mother provides (Rosenblatt, 2010). Nevertheless, the ability of kittens to learn such fine distinctions so early demonstrates their considerable cognitive abilities. It also raises the question whether they might in fact be pre-adapted to learning chirps, and/or whether these vocalizations have specific qualities (pitch etc.) particularly co-adapted to the kittens' developing auditory system. This could be addressed by presenting the kittens at the time of the mother's presence at the nest with chirps acoustically modified in specific ways, with other cat calls (for example meows), calls of other species, or even non-biological acoustic stimuli. Such experiments could also help decide how early kittens can learn such stimuli by presenting them before mothers start to emit chirps, thereby providing a means of investigating kittens' early cognitive abilities.

From studies of mother-offspring vocal recognition performed in other species (see Introduction) there is evidence to suggest that the directionality of this recognition is at least in part related to the ecological context of a species. Mammalian species in which the young follow their mother or join her social group soon after birth show mutual vocal recognition (e.g. reindeer, sheep, goats: see previous references), whereas species in which the young are hidden at the beginning of their postnatal development show unidirectional recognition of the mother by the offspring (e.g. fallow deer, red deer, raccoon: see previous references). The results of the present study show that mother-offspring vocal recognition in the cat is consistent with this last pattern of recognition, insofar as this is a species where

offspring remain hidden and in which the young recognize their mother's voice. However, it is yet unknown whether acoustic recognition in the cat is bidirectional; that is, if cat mothers also learn to distinguish the vocalizations of their own from those of alien kittens?

While most studies of mother-young acoustic communication have been performed in herd- and colony-living species, the present study provides convincing evidence that the young of species as solitary in the wild state as the cat *Felis silvestris catus* may also learn to recognize a distinctive call of their mother and to distinguish it from equivalent vocalizations by other mothers. Whether this has a functional significance for cats later in life; for example when kittens leave the nest to follow their mother on hunting forays, remains to be investigated.

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Annexes

Annex 1

The quantified parameters in the acoustic analysis of the mothers' vocalizations.

Abbreviation	Variable
call_length	length of the call in sec from onset to offset
f0mean	mean frequency of the vibration of the vocal folds in the call
f0max	maximum value of the fundamental frequency
f0maxpoz	latency of the maximum fundamental frequency
f0mxpozr	Relative position of the maximum fundamental frequency within the call (f0maxpoz/call_length)
f0min	minimum value of the fundamental frequency
f0minpoz	latency of the minimum fundamental frequency
f0mnpozr	relative position of the minimum fundamental frequency within the call (f0minpoz/call_length)
f0st	fundamental frequency at onset
f0end	fundamental frequency at offset
f0sd	standard deviation of the fundamental frequency within the call
f0range	range of the fundamental frequency (f0max-f0min)

Abbreviation	Variable
f0chnng	change of the fundamental frequency ($f0_{end}-f0_{st}$)
intmean	average intensity of the call
intmax	maximum value of intensity within the call
intmaxpoz	latency of the maximum intensity
intmaxpozr	relative position of the maximum intensity within the call ($intmaxpoz/call_length$)
intmin	minimum value of intensity within the call
intminpoz	latency of the minimum intensity
intminpozr	relative position of the minimum intensity within the call ($intminpoz/call_length$)
intst	intensity at onset
intend	intensity at offset
intsd	standard deviation of the intensity within the call
inrange	range of intensity ($intmax-intmin$)
harmmean	tonality (harmonic to noise ratio - lower numbers mean more noisy, harsh sound)
harmmax	maximum value of the tonality
harmdev	standard deviation of the tonality within call

Abbreviation	Variable
ppp	number of voice cycles (opening and closing of the vocal folds) within the call
ppm	average length of the voice cycles
ppj	jitter (instability of the fundamental frequency)
energy	amplitude of the call (spectral energy)
power	change of energy over time within the sound (energy/call_length)
bandenergy	spectral energy between 2000 and 4000Hz
centgrav	centre of gravity of the spectral energy
devfreq	standard deviation of the frequency spectrum
skewness	skewness of the frequency spectrum
kurtosis	kurtosis of the frequency spectrum
cmom	central momentum (non-normalized skewness of the power spectrum)
endiff	spectral energy difference between 0-2000 and 2000-6000Hz frequency bands

Annex 2

Structure of factor scales and Cronbach alpha values. Asterisk indicates variables participating with negative loading. Scales highlighted with bold font discriminate the individuals best. See Annex 1 for full variable names.

Chirp									
Factors	F1	F2	F3	F4	F5	F6	F7	F8	F9
Acoustic variables	intmean	ppm*	f0maxpoz	skewness	intsd	intminpoz	f0sd	call_length	
	intmax	f0mean	f0mxpozr	kurtosis	intrange	intminpozr	f0range	ppp	
	power	f0end	f0minpoz*	centgrav*	harmmean	intmaxpozr*	ppj	intmaxpoz	
	cmom*	f0max	f0mnpozr*	endiff*					
	devfreq*	f0min	f0chnng						
	energy	f0st							
	intmin								
	intst								
	intend								
	bandenergy								
Cronbach alpha	0.95	0.94	0.85	0.81	0.76	0.79	0.82	0.78	NA

Meow									
Factors	F1	F2	F3	F4	F5	F6	F7	F8	F9
Acoustic variables	f0mean	intrange	cmom*	intmean	f0minpozr *	call_length	endiff*	intminpoz	f0sd
	ppm*	harmmean	intmin	power	f0chnng	ppp	defreq*	intminpozr	f0range
	f0min	harmdev	intmax	energy	f0mxpozr	intmaxpoz	skewness	intst	ppj
	f0max	intsd	intend	bandenergy	f0maxpoz	f0minpoz	kurtosis		
	f0st	centgrav harmmax			f0end				
Cronbach alpha	0.92	0.87	0.83	0.92	0.84	0.84	0.77	0.69	0.68