Animal Behaviour 130 (2017) 233–240

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Conflict or consensus? Synchronous change in mother–young vocal communication across weaning in the cat

Oxána Bánszegi [a, *], Péter Szenczi [b], Andrea Urrutia [a], Robyn Hudson [a]

[a] Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
[b] Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala, Tlaxcala, Mexico

ARTICLE INFO

Article history:
Received 7 August 2016
Initial acceptance 26 October 2016
Final acceptance 15 May 2017

MS. number: A16-00699R3

Keywords:
domestic cat
Felis silvestris catus
mammal
motivation
parent–offspring conflict
separation call
vocal communication
weaning

Since parent–offspring conflict theory was first proposed, a number of studies in a range of mammalian species have questioned its importance, suggesting that coordination, rather than conflict, occurs during weaning. In this study we propose a set of behaviours for studying the development of the mother–offspring relationship: offspring separation calls and the corresponding maternal response, which can be used to describe the continually developing motivational changes in both parties accompanying weaning. We recorded and analysed separation calls of kittens of the domestic cat, *Felis silvestris catus*, during the first two postnatal months, and performed playback experiments to observe their mothers' behavioural response. Three different stimuli were played back: calls of the mothers' kittens at their correct age, calls of their kittens from an earlier age (1 week old) and a control sound. We found that kittens' separation calls changed in several respects across the 8 weeks of the study. After the first postnatal month, the number, intensity and fundamental frequency of calls declined markedly, while kittens' latency to call increased. In parallel, we found that during playback tests, mothers' willingness to return to the nest or reunite with their kittens decreased notably as the kittens approached weaning age. Since this decline was present even when mothers were played back the calls of their own kittens previously recorded at an earlier age, we conclude that the decline in responsiveness was not due to a change in the kittens' vocalizations, but rather to a change in the mothers' motivational state. Our findings support the view that weaning in the domestic cat is a well-synchronized process between mothers and offspring, at least under the favourable nutritional conditions of the present study.

There has been long-standing tension bordering on the philosophical, in the manner in which theoretical biologists, behavioural ecologists, ethologists and psychologists view the evolution of social (particularly reproductive) behaviour and the developmental processes that shape it. At one pole there are those taking what might be considered a Hobbesian view of life as essentially competitive and exploitative, while others emphasize the coevolution of well-synchronized behaviours to the mutual benefit of the parties involved (e.g. Feldman, 2016; Hinde, Johnstone, & Kilner, 2010). This tension is epitomized by the continuing debate surrounding one of the most influential ideas in behavioural biology of recent times, parent–offspring conflict theory (POC; see also the ambiguity surrounding the related issue of sibling competition; Hudson & Trillmich, 2008). As first formulated by Trivers (1974), this essentially states that the optimal amount of parental investment in offspring is unequal for the two parties, such that offspring can be expected to try to obtain a greater amount of resources than their parents are willing to provide.

Although theoretical support for this proposal has been provided (reviews in Kilner & Hinde, 2008, 2012), there continues to be a lack of unambiguous empirical evidence, leading to suggestions that the existence of such conflict might be exaggerated and overstated (Bateson, 1994; Bateson, Gluckman, & Hanson, 2014; Mock & Forbes, 1992). Some authors even point out that the relationship between mother and offspring is more one of cooperation than it is of conflict (Bateson, 1994; Bateson et al., 2014; Cassinello, 1997; Galef, 1981) and suggest to take into account equally the conflict and the coadaptation between parental investment and offspring demand (Hinde et al., 2010; Kölliker, Brodie, & Moore, 2005).

In mammals, POC has typically focused on weaning, commonly defined as the process of the offspring becoming nutritionally independent of the mother's milk (reviewed in Cameron, 1998; Galef, 1981; Martin, 1984). This is understandable, given the high

* Correspondence: O. Bánszegi, Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, AP 70228, Ciudad de México, CP 04510, Mexico.
E-mail addresses: oxana.banszegi@gmail.com (O. Bánszegi), peter.szenczi@gmail.com (P. Szenczi), andreaurrutia@outlook.com (A. Urrutia), rhudson@biomedicas.unam.mx (R. Hudson).

http://dx.doi.org/10.1016/j.anbehav.2017.06.025
0003-3472/

energetic costs of lactation to mammalian mothers (Gittleman & Thompson, 1988), and where it may be expected that the optimal duration of the lactation period is longer for the offspring than it is for the mother. However, measuring the nature of this possible conflict or of its physiological and motivational underpinnings has proved difficult due to the lack of reliable, objective measures of maternal costs or offspring benefits. The most common measure of putative conflict is the time the young spend suckling or trying to suckle, although by weaning age there may be little correlation between time spent on a nipple or teat and actual milk consumption (reviewed in Cameron, 1998).

Given the difficulty of evaluating conflict using suckling as a proxy for the provision of milk mentioned above (Cameron, 1998), we decided to use another, easily measured set of behaviours, mother–young vocal communication (as originally proposed by Trivers, 1974) to evaluate the mother–young relationship and its motivational underpinnings. Vocalizations seem a useful behavioural measure, as their tight integration with brain centres of emotional control means they closely reflect the emotional and motivational state of an individual (Briefer, 2012; Jürgens, 2009; Scheumann et al., 2012).

Looking for a mammal that provides the opportunity for close observation and experimental manipulation of mother–offspring relations under more naturalistic conditions than is usual in the laboratory, we considered the domestic cat, *Felis silvestris catus*. Even under seminatural free-ranging conditions, the cat is easy to keep and to manage in behavioural experiments, as mothers usually give birth in their customary human habitation and readily permit the handling and manipulation of newborn young by familiar caretakers (Hudson, Raihani, González, Bautista, & Distel, 2009; Raihani, González, Arteaga, & Hudson, 2009; Szenczi, Bánszegi, Urrutia, Faragó, & Hudson, 2016). Cat mothers normally raise their kittens alone, with no paternal or other assistance, meaning there are no other natural caregivers who might influence the weaning process or subsequent raising of the young (Bateson, 2014). Kittens are able to vocalize from birth and during the first month their calls increase the probability of the mother returning to the nest (Haskins, 1977, 1979). The weaning process begins when the kittens start to eat solid food, usually in the fourth postnatal week, and the full transition from milk to solid food is largely completed by the seventh postnatal week (Martin, 1986).

Since kitten separation calls have a strong effect on the mother's behaviour (typically she returns to the nest and/or retrieves strayed kittens, both of which are forms of parental investment), one aim of the present study was to investigate how mother–offspring vocal communication in the context of separation changes across the weaning process, and whether such changes might be interpreted as conflict (e.g. maternal 'resistance' to offspring calling for assistance), or rather as consensus (e.g. a synchronous decline both in kittens' production of such calls and the strength of mothers' response to them). Specifically, we looked at how some basic characteristics of the kittens' separation calls and the mothers' responses to them change from birth to independence from the mother's milk. Since we expected a decline in maternal responsiveness, we also investigated whether modifying a particular quality of the separation calls, specifically, the age of the kittens producing them, would maintain the maternal response, or rather, whether a decline in maternal response to kittens' calls is driven by a change in mothers' motivational state.

METHODS

Study Site and Animals

Mothers and kittens participating in the study belonged to an established breeding colony of cats. With the intention of studying animals in seminatural conditions, the cats were kept in a private house with a garden, which the adults 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 commercial litter pans were always available. There was sufficient space in the house for mothers to raise their kittens 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 the adult cats, even the pregnant females, were able to jump in or out, but kittens under 2.5–3 months of age were not. Mothers showed little interest in the litters of other females and communal nursing did not occur.

Mothers always gave birth in the house. The day after delivery, the litters with their mothers were moved to one of the rooms in a quiet, undisturbed part of the house. In each room a nest site was provided: a commercial foam cat bed (oval, 68 × 57 cm) inside a large cardboard box (60 × 80 × 70 cm), with a small floor-level opening (22 × 27 cm) cut out for the mother. The box was removed (but the bed left in place) when litters were 28 days old and began leaving it. Kittens were weighed at birth and daily thereafter to check for normal growth.

Recording Kittens' Separation Calls

We collected separation calls from 55 kittens of 12 litters (2–7 kittens per litter) from 12 different mothers (see Experimental Procedures below). In order not to disturb the mothers, the recordings were made at a time when they had spontaneously left their nest and the house (between 1000 and 1700 hours). The kittens were removed individually from the nest into a box lined with a flannel cloth and transferred to a separate room containing a cardboard recording box lined with acoustic foam (1 × 1 × 1 m). Until they were placed into the recording box, almost no kittens vocalized. Placing the kittens in the recording box resulted in the almost immediate production of separation calls, particularly at younger ages. After the first call, we continued recording each

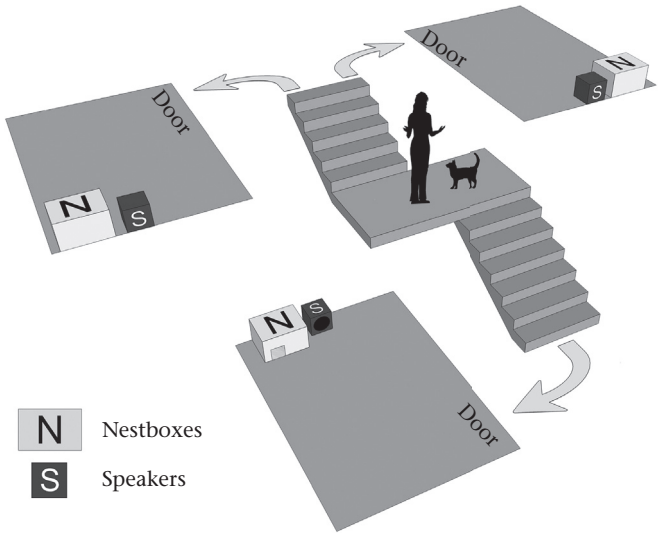

Figure 1. Schematic representation of the test situation. Test sessions started by using a food reward to lead the mother to be tested to the starting point on the landing of a staircase approximately midway between three rooms, one of which contained that particular mother's kittens in their nestbox (N). When the mother had eaten the food, playback of the recorded separation calls of her kittens or of the control stimulus (bleating goats) started from a speaker (S) positioned next to her nestbox. The distance from the landing to each of the nest sites was 10–12 m. Details of behavioural recording are given in the text.