Absentee Mothering – Not So Absent? Responses of European Rabbit (Oryctolagus cuniculus) Mothers to Pup Distress Calls

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Abstract

Longer-range acoustic parent-offspring communication is widespread, but might be absent in species in which young are hidden in burrows during the mother’s absence. The European rabbit (Oryctolagus cuniculus) is such a species, with unusually limited maternal care largely restricted to a short daily nursing bout. Based, however, on evidence of frequent infanticide in this species, we hypothesize that rabbits possess a mechanism promoting a maternal response to pup distress calls. We conducted playback experiments with distress calls of pre-weaning pups played next to the breeding burrows of mothers in a field enclosure (i.e. next to the burrows where mothers give birth and raise their young). Calls were played shortly after pups were born (T1) when infanticide risk is maximal, and shortly before the pups start dispersing from the breeding burrow (T2). A high proportion of mothers (60.6%) responded to pup calls by rapidly returning to their breeding burrow and 40% of them investigated the area around the entrance. Return responses to the playback of pup calls did not differ between mothers during T1 and T2. Thus, our results confirm that rabbit mothers respond rapidly to pup distress calls and that this responsiveness may adaptively serve to repel potentially infanticidal females.

Introduction

Efficient parent–offspring communication is crucial for the development and survival of dependent young and can include various acoustic, olfactory, visual and tactile stimuli (reviews in: Numan & Insel 2003; Bradbury & Vehrencamp 2011; Lingle et al. 2012). Parents, and among mammals in particular mothers, emit various signals eliciting specific behavioural patterns in the young (Tinbergen 1960; Hudson & Distel 1983; Vaňková et al. 1997; Schaal et al. 2003), and offspring emit a variety of signals inducing appropriate parental care (Tinbergen 1960; Noirot 1972).

Most research on acoustic parent-offspring communication has focused on begging in birds, where dependent young use acoustic signals to beg for food (Budden & Wright 2001; Wright & Leonard 2002). Acoustic signals, however, are also used by mammalian young to alert the mother or other care givers to situations of need, for example by care or contact calls in ungulates (Richardson et al. 1983; Shillito Walser & Eurof Walters 1987) and in pinnipeds (Trillmich 1981; Phillips & Stirling 2000), or by separation calls in several rodents (Kober et al. 2007, 2008), often eliciting parental retrieval behaviour of altricial young (Sewell 1970; Hofer 1996). In various species, offspring calls (distress cries, fear screams) are emitted in situations of direct threat when young are injured or at risk of being killed. For example, domestic sow mothers (Sus scrofa) respond strongly to the playback of piglet distress calls by approaching to defend their young (Spinka et al. 2000; Held et al. 2006). Such defensive maternal behaviour in response to offspring vocalization has also been observed in white-tailed...
deer (*Odocoileus virginianus*) during capture sessions of neonates, where fawn distress calls induced mothers to attack the capture crew (Garner & Morrison 1980).

Maternal offspring defence driving off predators or infanticidal conspecifics is a common phenomenon in a variety of mammal and bird species (Montgomerie & Weatherhead 1988; Clutton-Brock 1991; Agrell et al. 1998), where the efficacy of this strategy can be facilitated by permanent contact between mother and young or, over larger distances, by mothers’ responses to offspring distress calls. Furthermore, a variety of mammals follow the strategy of hiding the offspring in the mother’s absence (Sibly & Brown 2009). Various studies have been conducted in ungulate hider species such as white-tailed deer and mule deer (*Odocoileus hemionus*), where fawns are left by the mother hidden in the vegetation during the first weeks of life and mothers only visit them for nursing (Lent 1974). Fawns emit loud distress calls when discovered by predators and are then defended by their mothers or even by other females (Lingle et al. 2005; Torriani et al. 2006).

Maternal behaviour of the European rabbit (*Oryctolagus cuniculus*) is usually considered to be an extreme example of such a hider strategy. Mothers leave their altricial young in a burrow and only visit them for a brief nursing bout of around 3 min once a day (Hudson et al. 1996; Rödel et al. 2012). For the rest of the day, the pups remain alone in the nursery burrow, which is closed by the mother after each visit with a plug of soil (Lloyd & McCowan 1968). At first sight, it seems unlikely that a species with such a strategy of hiding offspring in a burrow would possess a mechanism whereby pup alarm calls elicit appropriate maternal responses given that longer-range acoustic communication between mothers and young appears to be excluded by the pups’ confinement underground. Nevertheless, rabbit pups are capable of producing trains of rapidly repeated high-pitched vocalizations in situations of distress (Fig. 1). In the burrow and during contacts with the mother, rabbit pups do not display such vocalization, except some soft ‘wheeking’ shortly before and during nursing (Schuh et al. 2004), which might reflect their high level of arousal.

We therefore hypothesized that such pup distress calls may also elicit maternal defensive behaviour in European rabbits. Previous studies have shown that female conspecifics sometimes scratch out the whole nest including pups, presumably to take over the breeding burrow (i.e. the burrow where mothers will give birth and raise their young), for which rabbit females compete (Mykytowycz & Dudzinski 1972; Cowan 1987a; von Holst et al. 1999). During such incidents, pups are usually killed by bites or scratches inflicted by the infanticidal female (Cowan 1987a; Künkele 1992; Rödel et al. 2008). Infanticide is a major source of juvenile mortality in various species of mammals (Hausfater & Hrdy 1984; Ebensperger 1998) including the European rabbit, where around 2-5% of the litters of a population can be affected (Künkele 1992; Rödel et al. 2008, 2009). Rabbit pups will presumably emit distress calls during incidents of infanticide (as has been observed in a few cases; H. G. Rödel unpubl. data), in particular when attacked in and dragged from the breeding burrow. Intervention by the mother might then save at least part of the litter. Altricial young are particularly vulnerable to infanticide during the early post-natal period (Elwood & Ostermeier 1984). In European rabbits, in which the young stay in their breeding burrow until around post-natal day 19 or 20, it has been shown that infanticide usually occurs during the first 10 post-natal days (Rödel et al. 2008).

To investigate whether such a form of mother–young communication might have evolved in the European rabbit, we conducted playback experiments with animals of a field enclosure population to test whether pup distress vocalizations induce maternal behaviours indicative of offspring defence. Considering the above, we expected that rabbit mothers should respond to pup distress calls by rapidly returning to their breeding burrow in order to check for infanticidal intruders. Furthermore, we expected that mothers would respond more strongly during the early post-partum period when pups are most vulnerable given...
their limited locomotory ability and paucity of protective fur.

Methods

Study Animals and Study Site

The study was conducted in 2006 and 2007 in a colony of wild-type European rabbits (O. cuniculus cuniculus) living in a 2-ha enclosure on the campus of the University of Bayreuth, Germany (49°55′N, 11°36′E, elevation 359 m a.s.l.), since 1985. The animals (subspecies: O. c. cuniculus) were descendants of wild rabbits caught in southern Germany (around 80 km from the enclosure) in 1984, and the enclosure population which was established in 1986 (von Holst et al. 2002). Vegetation in the enclosure consisted mainly of the grasses Lolium perenne and Festuca rubra interspersed with groups of trees and with a pond in the middle. The vegetation in the enclosures was the only food source for the animals outside the winter season.

In addition to the burrows dug by the rabbits (around 40–50), the area contained 16 artificial concrete warrens with interconnected chambers and removable tops. These were used by the rabbits as the main warrens of their group territories and also for breeding. Similar to the natural burrow systems, the nests were built by the animals with artificial vertical openings to the nest chambers, which we covered with concrete flagstones. By checking the nests daily, we were able to record the birth of litters to within 24 h and we considered the day when we found the nest with the pups as post-natal day 1.

Identification of Mothers

The animals were trapped once a month from Feb. to Oct. For this, we used peanut-baited live traps made of wood (dimensions: 90 cm × 30 cm × 30 cm). The traps were set overnight and checked at dawn the next morning. They were then set again and left open until noon, during which time they were checked at 1–2-h intervals. Approximately 100 of these were permanently distributed around the enclosure and between trapping sessions they were left open. Captured animals were removed from the traps and placed singly in sunny sacks.

We dyed the abdominal fur of the adult females with different colours (silk colour; Marabu, Germany) and 1–2 h later we returned the animals to the enclosure. As female rabbits pluck out abdominal hair to build their nests (González-Mariscal & Rosenblatt 1996), we were able to determine the mother of each litter by the location of the nest in combination with the colour of the hair it contained; this was additionally confirmed by the analysis of females’ reproductive state during the regular trapping sessions and by behavioural observations (Rödel et al. 2008).

Study Design and Sample Size

In total, 25 different mothers were tested. Five mothers were primiparous when first tested and the other 20 were in their second, third or fourth breeding season. Nineteen tests were conducted when pups were 3–6 days old (early post-partum period) and 14 tests when pups were 12–16 days old (later post-partum period). Mothers were only tested once per year, but eight mothers were again tested during the following year, that is, during the early post-partum period in 1 yr and during the late post-partum period in another year or vice versa (min 10 mo between repeated individual tests). This resulted in a total sample size of 33 separate tests.

Acoustic Stimuli

All animals were part of long-term studies, and therefore, all pups were fitted with ear tags. This sometimes provoked vocalization by the pups, which we recorded digitally, using a microphone (Logitech International S.A.; frequency range: 100–10 000 Hz; sensitivity: 39 dBV/Pa) connected to a portable computer. These recordings were made during the year prior to the start of the playback experiments in smaller, adjacent enclosures with wild-type rabbits of the same origin. Thus, we never used calls from offspring.
of the mothers tested in the experiments. Calls from five pups were recorded on post-natal day 4, and calls from six pups were recorded on post-natal day 12. Individual pup calls were either recorded on day 4 or on day 12. On average, calls lasted 11.2 s (±2 SE) in 4-day-old pups and 11.1 s (±0.6 SE) in 12-day-old pups and consisted of trains of rapidly repeated high-pitched calls (Fig. 1). From these calls, we constructed in Audacity 1.2.6 (http://audacity.sourceforge.net/; sample frequency 44.1 kHz; sample format: 8-bit), 10-s playback stimuli consisting of five different combinations of two sequences of 5 s from two different pups (around 12 single calls per sequence). This was performed separately using calls from the 4-day-old pups and from 12-day-old pups. Always one of the five different sequences per age class was randomly chosen for playback, that is, we chose from the five sequences from 4-day-old pups when testing mothers during the early post-partum period, and we chose from the five sequences recorded from 12-day-old pups when testing mothers during the respective later post-partum period. Pup calls were played at 48 dB (A), corresponding to their natural volume. A 10-s pure tone of 400 Hz was used as a control stimulus (48 dB(A); all measurements at 1 m distance from the loudspeakers). We standardized the amplitude of the stimuli, using the ‘normalize’ function in Audacity.

Apparatus
Stimuli were played back from a portable cassette recorder (model 6727, 50 Watt; Elta GmbH, Roedermark, Germany) beside the breeding burrows. We cannot rule out that presentation of the stimuli did not cover all the natural frequencies of the distress calls, but the different responses between the two treatments clearly showed that the stimuli contained sufficient information to elicit a maternal response to the pup calls. The apparatus, equipped with a 20-cm antenna and a tele-control (Conrad Electronic, Germany) closing the circuit of the player’s battery power, was started and stopped by remote control from a distance of up to 70 m. The whole system was small enough, apart from the antenna, to fit inside one of the wooden traps.

Experimental Procedure
On post-natal day 1, we placed a wooden trap directly (around 1 m) next to the target breeding burrow to habituate mothers to the presence of the trap. Mothers appeared undisturbed by this, and none abandoned their young. On the day of testing, the playback apparatus was installed inside this trap in the morning between 08:00 and 10:00 h (CET) during the daily check walks. Tests were conducted during the early- and mid-breeding season (mid-April until early June) in the late afternoons/evenings between 17:00 and 19:00 h (CET), that is, at least 7 h after the installation of the apparatus and at a time of peak activity for rabbits (Wallage Drees 1989). During the tests, the experimenters remained in one of the two observation towers 4–5 m above ground and at least 15 m from the animals. To exclude any influence of the experimenters on the behaviour of the subjects, we used a remote control to start and stop the playback.

All behavioural observations were carried out with the aid of binoculars (10 × 40; Zeiss, Germany). Prior to the experiments, the focal mothers (i.e. animals with 3- to 6-day-old or 12- to 16-day-old pups) were observed. Several conditions had to be fulfilled before the experiments commenced. Mothers had to be (a) at least 10 m from their breeding burrow, (b) mainly resting or feeding for at least 5 min, that is, moving <2 m, and (c) on their own, that is, no other conspecific closer than 5 m. Furthermore (d), we ensured that no other adult conspecific was close (10 m radius) to the breeding burrow of the focal female, which might have had the potential to provoke the mother to return to the breeding burrow and expel adult females (Rödel et al. 2008). If these conditions were met, the experimenters activated the 10-s control sound, while observing the animal and recording its behavioural responses (see below). Then, after a break of 30 min, the experimenter activated a 10-s sequence of pup distress calls. Again, the same conditions as described above had to be met before presenting the stimulus, and again, the behavioural responses of the mother were recorded. Furthermore, we verified that there were no major changes in weather conditions (e.g. sudden heavy rain) during these two parts of the experiment. We recorded whether the females showed vigilance behaviour in response to the stimulus, and we recorded their behaviour at the burrow (in cases of returns) for the next 10 min such as vigilance behaviour, exploring or entering the warren if the burrow was located in one of these. Animals were considered to be vigilant when they abruptly raised the head above shoulder height while maintaining the feeding posture, or adopted an upright posture, either quadrupedal or bipedal, lifted the ears, often looked around and stopped all current activities (Monclús & Rödel 2008). Exploration at the burrow was defined as sniffing with head down to the ground with frequent head movements to left and right, while the animal was moving slowly or stopped moving forward.
We always started with the playback of the control sound, which we realize does not represent a randomized design. However, we decided to follow such a protocol because control playback was simply intended to rule out the possibility that individuals respond to any sound. Furthermore, preliminary tests had shown that females were in a high state of alertness after responding to the playback of pup distress calls. Starting the experiments with the pup distress calls treatment would have prevented us from obtaining reliable control responses (Kunc et al. 2007; McLaughlin & Kunc 2012).

Prior to the start of the playback of the pup calls or the control sound, the position of the mother was recorded. This was possible with the aid of a grid system (consisting of coloured and numbered wooden sticks), where animal locations were determined with an accuracy of 2 m. This accuracy was further increased by using landmarks. After the experiment, we measured the distance between the position of the female and her breeding burrow with the aid of a long nylon rope.

Experiments comply with the current law of the country in which they were performed (Germany) and were approved by the animal welfare officer of the University of Bayreuth. Permission for biological studies on European rabbits in our enclosure population was granted by the government of Middle Franconia, Germany (211-3894a), and all procedures were conducted in accordance with the ASAB guidelines for the treatment of animals in behavioural research and teaching (Anonymous 2000).

**Data Analysis**

All analyses were conducted in R, version 2.15.2 (R Development Core Team 2013). We applied multivariate generalized linear mixed-effects models (GLMM) for data with a binomial error structure (logit-link) using the package lme4 (Bates et al. 2012). The occurrence of mothers returning to the nest or of vigilance responses were used as dichotomous dependent variables. The major focus was to compare the responses to playbacks of pup distress calls and a control sound (fixed factor with two levels), and between the responses during the early and later post-partum period (fixed factor with two levels). Alternatively, we also used the exact post-partum age in days as a covariate, but this did not change our results.

We included female identity as a random factor allowing for repeated measurements as some of the females were tested twice, although never within the same year. In addition, we used a fixed factor coding for the experience of the females (naive: yes/no), considering whether females were tested for the first or second time. In addition, we included the age class of the females (1 year old vs. older) as a factor with two levels. We did not include age as a covariate because we explicitly wanted to test whether there was a difference between rather inexperienced first-season breeders and older females. All animals were individually marked, and thus, their age was known.

We also included the number of the experiment (trial) as a random factor to adjust for the dependency between the control and experimental trial of each experiment (n = 33). The distance between the speakers and the focal animal (ranging from 10 to 55 m) was used as a covariate in our multivariate models. Some of the tests (39.4%) were carried out with females with offspring in natural burrows and some (60.6%) with females with offspring in artificial (concrete) warrens. Thus, we also included this factor in our multivariate models. p-Values were calculated by likelihood ratio tests based on changes in deviance when each term was dropped from the full model (Faraway 2006).

**Results**

**Mothers’ Responses to Pup Calls and to the Control Sound**

Immediately after the playback of the pup distress calls, 69.7% of mothers (23 of 33 cases) showed vigilance responses, mostly by adopting a quadrupedal, upright posture with rapidly lifted head and with both ears erect. Such a response was only observed in 24.3% of mothers (8 of 33 cases) after the playback of the control sound, and the difference was statistically significant between the two conditions (GLMM: $\chi^2_1 = 17.01, p < 0.001$; Fig. 2a).

Whereas 60.6% of mothers (20 of 33 cases) returned to the breeding burrow in response to pup distress calls, a significantly lower proportion of only 9.1% of mothers (3 of 33 cases) returned to the breeding burrow after the playback of the control sound ($\chi^2_1 = 17.02, p < 0.001$; Fig. 2b).

Arriving at the burrow, 85.0% of the returning females (17 of 20 cases) again showed vigilance behaviour, looking in different directions with both ears erect. During the next 10 min, 40.0% of the returning mothers (8 of 20 cases) examined the entrance of their burrow (i.e. showed exploration behaviour) or entered the warren (within 1–2 min after arrival) in cases where the nest chamber was located in one of these. Note that none of the few
females which returned in response to the control sound showed any exploration behaviour at the breeding burrow or entered the warren.

No Influence of Post-partum Period or Maternal Age on Behavioural Responses

The post-partum period (3–6 d post-partum vs. 12–16 d post-partum) did not have a significant effect on the occurrence of mothers’ vigilance responses ($\chi^2 = 0.17$, $p = 0.68$; Fig. 2c) or on the occurrence of return behaviour to the breeding burrow ($\chi^2 = 0.02$, $p = 0.90$; Fig. 2b). There were also no significant interactions between the post-partum period and the responses to the different treatments (control sound vs. pup distress call), either with respect to the display of vigilance ($\chi^2 = 0.01$, $p = 0.94$) or return behaviour ($\chi^2 = 0.93$, $p = 0.36$). The latter results indicate that the significant difference in mothers’ return behaviour was independent of the two post-partum periods.

There were also no significant differences in vigilance or return behaviour with respect to the mothers’ age class (1 year old vs. older mothers), or whether the mothers were naïve or not to the test situation ($p > 0.10$).

There was, however, a negative (logistic) correlation of the distance between mothers and the speakers with the occurrence of vigilance responses, indicating that the probability of vigilance behaviour in response to pup distress calls was lower when the distance was larger ($\chi^2 = 6.96$, $p = 0.008$). But most importantly, there was no significant 2-way interaction between the treatment (control sound vs. distress calls) and the mother’s distance to the burrow, either with respect to the display of vigilance ($\chi^2 = 0.08$, $p = 0.78$) or return behaviour ($\chi^2 = 0.20$, $p = 0.66$). This indicates that the differential response to distress calls or control sound was not modulated by the distance to the burrow and thus that our result was not biased by a differential probability of mothers perceiving either the control sound or distress calls at different distances from the speakers.

Mothers’ responses (vigilance as well as returning to the breeding burrow) were also not different for females with offspring in artificial or natural burrows ($p > 0.05$). There were no further significant interactions among the mentioned predictor variables ($p > 0.10$).

Discussion

Female rabbits with dependent offspring responded strongly to the playback of pup distress calls by returning to their breeding burrow and extensively monitoring the entrance and surrounding area. This behaviour occurred in a high proportion of mothers during the early as well as during the later post-partum period. To our knowledge, this is the first experi-
mental study reporting mothers’ responses to distress calls of the young in a species characterized by such an extreme strategy of absentee mothering, including the hiding of the young in a burrow or den.

Consistent with this, it has been reported that rabbit mothers remain in the vicinity of their breeding burrows (Mykytowycz & Dudzinski 1972), increasing their chance to perceive pup distress calls. Furthermore, rabbit mothers readily chase away potentially infanticidal females approaching close to their breeding burrow (Rödel et al. 2008). Infanticide by other females, most probably facilitating takeover of the breeding burrow as an important and often limiting breeding resource (Mykytowycz & Fullagar 1973; Cowan 1987a), can be considered a crucial factor affecting survival during the nest period in the European rabbit (Künkele 1992; Rödel et al. 2008, 2009) and also in other altricial small mammals (Agrell et al. 1998; Wolff & Petersen 1998). Thus, infanticide may exert selective pressure on the evolution of distress calls in offspring-hiding species. In addition, defence against predators is often discussed as a major evolutionary driving force, in particular in ungulate offspring-hiding species, where maternal defensive behaviour has been shown to reduce fawn mortality (Lingle et al. 2005). Predation also makes a major contribution to early juvenile mortality in the European rabbit, in particular during the first weeks after leaving the breeding burrow, when juvenile mortality rates of approx. 60–80% are usual (Richardson & Wood 1982; Cowan 1987b; Seltmann et al. 2009). During the nest period, the young are partly protected at least against attacks of smaller predators, and only medium sized or larger species (such as red fox Vulpes vulpes or badger Meles meles) are capable of opening the closed breeding burrows to access the nest with the pups (Mulder & Wallage Drees 1979). Thus, we propose that in the European rabbit, infanticide by conspecific females might be the most prominent driver of the evolution of pup distress calling and mothers’ responses to it, as rabbit mothers are probably not able to repel larger predators such as foxes or badgers.

Almost certainly, first pups attacked and dragged out of the burrow by an infanticidal conspecific (or possibly by a predator) and which emit distress calls will not survive. However, by attracting the mother, they may contribute to the survival of at least some of their siblings, thereby benefitting via kin selection (Hamilton 1964). Indeed, previous studies reported partial survival of attacked litters in approx. 30% of cases of infanticide in the European rabbit (Künkele 1992; Rödel et al. 2008), suggesting that mothers might have successfully intervened.

The pattern of the reported rabbit pup vocalizations appears to be highly adapted to such purported infanticidal events: once triggered, the pups emit enduring distress calls for around 11 s. Such continuous vocalizations have been described as a typical feature of distress calls also in other mammalian young, for example in white-tailed deer fawns (Richardson et al. 1983). Furthermore, European rabbit pup distress calls show the typical pattern of a continuous frequency-modulated sound with a rich harmonic structure (Fig. 1) as has been described in other infant mammals (Esser & Schmidt 1989; Lingle et al. 2012).

Presumably, rabbit mothers have no chance to learn to distinguish the distress calls of their own particular offspring. Calling offspring dragged out of the burrow during an attack might be usually killed before the mother manages to intervene. In contrast, ungulate offspring-hiding species such as mule deer and white-tailed deer frequently manage to successfully intervene (Lingle et al. 2005), and mother–offspring communication is more frequent. However, even here, mothers are not always capable of successful and reliable discrimination of their own offspring based only on acoustic cues (Lingle et al. 2007; but see: Shillito Walser et al. 1981).

Our results also indicate that the motivation of the mother was not only to approach the source of the pup distress calls but also to monitor the entrance of her breeding burrow and the area close to it, possibly to detect potential damage and to check for the presence of infanticidal intruders or predators. This seemed clear from the display of vigilance behaviour once the mothers arrived at their burrows and by them exploring the burrow entrance. Additional, although anecdotal evidence comes from a case observed during our study, where a neighbouring female with dependent offspring responded to the pup distress calls played from a distance of approx. 20 m from her breeding burrow. This mother made several attempts to run either to her offspring or to the source of pup distress calls coming from the other direction, obviously motivated by conflicting stimuli. Finally, she ran to her own burrow and explored the entrance area.

The return of females to the breeding burrow or towards the source of pup distress calls occurred in primiparous as well as in multiparous mothers and thus appeared to be independent of prior reproductive experience. We also observed few cases, in which adult males moved towards a breeding burrow after

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the playback of pup distress calls. However, these cases were never independent of the responses of the mothers, that is, the males presumably followed the responding focal female on her way to the breeding burrow.

Not all mothers responded to the playback of pup calls, most probably due to unfavourable environmental conditions, such as opposing wind, long distance (up to 50 m in our study) and intervening obstacles (high pasture, bushes, small hills), which might have hampered the perception of the acoustic stimulus (Dusenbery 1992). Furthermore, we could not control for the direction of the loudspeakers (which were installed several hours before the start of the experiments to minimize disturbances) with respect to the position of the focal female. The negative correlation between mothers’ distance from the loudspeakers and their probability of showing a vigilance response implies that at least the distance was of some relevance here, although the other factors mentioned above were not quantified. Nevertheless, it has been reported that females often stay close to the breeding burrow (Mykytowycz & Dudzinski 1972; Rödel et al. 2008). This is consistent with data from other studies reporting relatively smaller home range sizes for rabbit females compared with males (Cowan 1987a; Gibb 1993; but see: Lombardi et al. 2007). Such a pattern of space use would make it possible for mothers to detect and respond to pup distress calls with a high probability.

Contrary to our expectation, we did not find any differences in mothers’ responses to pup distress calls during the first few days after parturition and in mothers with older dependent offspring, given our sample size of 19 vs. 14 tested females during the two different periods. Thus, it appears that this maternal behaviour leading to a potential defence of the young against potential threat is rather conservative and might be efficiently released during the complete nest period of the offspring.

The findings of the present study draw attention to the possibility that longer-range distress calls (i.e. apart from situations of direct mother–offspring contacts) from the young that elicit defensive behaviour in mothers might be widespread also among altricial mammals which follow a strategy of absentee mothering and hide their young in burrows or dens. The lack of information on this in altricial hiders is presumably due to the difficulty of observing such rare events under natural conditions, and without the aid of playback methods such as used here.

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