MOTHER-YOUNG RELATIONS IN THE EUROPEAN RABBIT : PHYSIOLOGICAL AND BEHAVIORAL LOCKS AND KEYS

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ABSTRACT : Mother-young relations in the European rabbit : Physiological and behavioral locks and keys.
In any mammalian species a proper understanding of the natural, co-evolved mother-young system is of major importance if productivity is to be optimized under conditions compatible with the animals' welfare. The European rabbit (*Oryctolagus cuniculus*) is particularly interesting in this regard given its unusually limited and stereotyped pattern of maternal care and the equally stereotyped set of corresponding specializations in the young. For each of five key topics - the nest, parturition, nursing, suckling, and weaning - the behavior of the mother and then of the kits is described, followed by a consideration of the possible application of this information to improving husbandry.

RESUME - Les relations mère-jeunes chez le lapin européen : Serrures et clés physiologiques et comportementales. Chez toute espèce mammalienne la compréhension du système naturel d'interactions co-évoluées entre la mère et la progéniture est un préalable important pour l'optimisation de la productivité dans des conditions compatibles avec le bien-être des animaux. Le lapin (*Oryctolagus cuniculus*) est une espèce particulièrement intéressante à cet égard du fait de la structure inhabituellement brève et stéréotypée du comportement maternel et, réciproquement, du fait des réponses spécialisées complémentaires, tout aussi stéréotypées, des lapereaux. Nous décrivons un certain nombre de connaissances relatives au comportement de la lapine et des lapereaux dans cinq contextes fonctionnels : le nid, la parturition, l'allaitement, le comportement de succion et le sevrage. Ces données éthologiques sont envisagées dans un cadre d'applications potentielles visant à améliorer les pratiques d'élevage.

INTRODUCTION

The following report was originally presented at the 11th Conference on Rabbit Production, Kaposvár, and has been published in summarized form in Hungarian (HUDSON et al., 1999a). As ethologists, our principle interest is in natural behavior as it has evolved in the wild. Although most of our own work has been conducted in the laboratory with domestic breeds, wherever possible we try to relate findings to the natural situation and the still too scanty information available on wild populations. Most of our experience has been with Chinchilla-breed does, and wherever we have been able to compare the behavior of this breed with findings from the wild we have been impressed by the similarity, including in the competence of Chinchilla-breed mothers even with their very first litter. However, we are aware that there may be considerable differences between breeds and that not all features of the general pattern we present below will be represented equally strongly in all populations. Nevertheless, guided by the belief that a knowledge of natural, evolved behavior may be useful for the producer, we have based the following report on what we currently think to be the natural pattern of mother-young relations in the European rabbit.

Modern-day commercial rabbit production faces two major challenges ; the need to optimize productivity under pressure from an increasingly competitive international market, and to do so in a manner compatible with increasingly stringent welfare requirements. These two aims often conflict and in some quarters may even be regarded as mutually exclusive. However, it is the basic argument of this report that the better we understand the natural, evolved behavior of a species, the better able we should be to maintain and breed it in a manner compatible with commercial interests and modern welfare demands.

The commercial viability of the rabbit as a domestic species is due in large part to its unusually efficient pattern of maternal care, combined with an equally efficient set of corresponding behavioral specializations in the young. In fact, mother-kit relations in the rabbit have co-evolved to the point where they can be thought of as a well aligned system of behavioral and physiological "locks" and "keys". Since many aspects of this unusual relationship are not widely known even among experts, it is the purpose of this report to briefly describe several of them and to stimulate discussion regarding their possible application in optimizing production.

Mother-young relations in the rabbit are characterized by three notable features : i) the highly stereotyped nature of the behavior of both mothers and young, meaning that largely independent of breed, country and conditions of maintenance, the same basic patterns are reliably expressed ; ii) tight patterning of behavioral and physiological events across the 24-hour day, regulated in the cases where it has been investigated by endogenous circadian processes ; iii) closely connected to ii), precise timing and tight regulation of physiological events underlying and co-ordinating the finely tuned interactions between mothers and young. These three factors are recurrent themes in the description of key aspects of the mother-young relationship presented below.

1. The nest

Towards the end of the approximately 31-day pregnancy, the doe normally digs a short nursery burrow which she lines with dried grass or other plant material and fur pulled from her chest and belly. She may also defecate in the nest before and several days after parturition. Nest-building behavior and the loosening of fur enabling the doe to pluck it out, depend on the decline in the level of progesterone relative to estrogen which occurs several days before term and which is a necessary precondition for parturition. Thus, nest building and fur loosening and plucking can be elicited in estradiol- and progesterone-treated, ovariectomized females by withdrawing the progesterone treatment. Following parturition, nest building ceases and there are no reports of does adding to or modifying the nest after this time. The construction of this maternal nest is vital for the survival of the kits and nests are not constructed by rabbits at any other time (DEUTSCH, 1957 ; HUDSON et al., 1996a ; general reviews in ZARROW et al., 1962 ; GONZÁLEZ-MARISCAL and ROSENBLATT, 1996 ; HUDSON et al., 1996b).

The altricial young, which are not brooded by the mother, spend most of their time huddled quietly together under the nest material. However, approximately an hour before the regular, once-daily arrival of the doe to nurse, they become active and exposed from this insulating cover. Despite the heat loss presumably incurred by this, anticipatory uncovering appears important as it enables kits to reach the mother's belly unhindered. Experimentally covering over young kits with nest material just before the doe's arrival greatly reduces milk intake despite the doe spending longer in the nest attempting to nurse. As soon as the doe leaves the nest the kits urinate simultaneously and vigorously burrow back under the nest material, fluffing it up and becoming dry again as they do so. They then gradually reassemble in the warmest part of the nest where they remain covered until the next nursing visit. Although huddling behavior clearly serves

the kits' thermoregulatory needs, they also need to stay together because those away from the group at nursing time are ignored by the doe and have little chance to suckle (HUDSON and DISTEL, 1982 ; general review in HUDSON and DISTEL, 1989).

During the second postnatal week the kits start eating the fecal pallets deposited by the doe in the nest and also start nibbling at the nest material. At first they simply bite through the stalks, reducing the grass to a kind of rough chaff, but by the middle of the third week clearly measurable amounts are consumed. In addition to eating the fecal pellets, kits may use them as a source of olfactory information. Thus, by 10 days of age they can distinguish by smell between fecal pellets from their own mother and a strange doe, and the particular scent of the fecal pellets kits encounter in the nest, later influences their choice of solid food at weaning (MYKYTOWYCZ and WARD, 1971 ; BILKÓ et al., 1994 ; ALTBÄCKER et al., 1995 ; HUDSON et al., 1996a ; general reviews in HUDSON and ALTBÄCKER, 1994 ; HUDSON et al.,. 1996a ; HUDSON et al., 1999b).

1.1. Possible applications

The stereotyped nature of does' behavior in depositing plant material and fecal pellets in the nest and of kits' behavior in eating these suggest that ingesting such substances might have functional value. Since the amount of nest and fecal material eaten per day is rather small, the direct nutritional benefit to the kits is probably negligible. However, roughage provided by the nest material and possibly gut flora from the fecal pellets might help prepare kits for digesting plant foods at weaning. With this in mind, it would be interesting to compare gut flora and post-weaning growth and survival of kits raised with and without access to edible nest material and/or fecal pellets. Raising kits in nests corresponding in composition to natural rabbit nests may well improve growth and reduce mortality during the critical post-weaning period. In addition, some form of olfactory match between nest material and the standard food given at weaning might also facilitate the transition to solid food (cf. COUREAUD et al., 1997 ; general review in HUDSON et al., 1999b).

2. Parturition

Parturition usually occurs in the morning, that is, at the start of the rest period in this basically nocturnal animal. However, it may also occur at other times of day with the apparent exception of a period of several hours before dawn which seems to be reserved for nursing (see below). Parturition is extremely rapid, usually not lasting more than 10 to 15 minutes for the birth of 10 or more kits. Since the vagina of the rabbit is long and the umbilical cord often ruptures in the birth canal, it is important that the kits are rapidly expelled.

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An increase in the duration of parturition of even a few minutes is associated with an increase in still births and in lethargic, non-viable kits. The rapid expulsion of kits is ensured by a large release of oxytocin into the blood at this time, and probably also by the action of an unusually complex array of strong muscles associated with the doe's vaginal tract (HUDSON *et al.*, 1995 ; JILGE, 1995 ; MARTÍNEZ-GÓMEZ *et al.*, 1997 ; HUDSON *et al.*, 1999c ; general reviews in HUDSON, 1995 ; HUDSON *et al.*, 1996b).

The kits are usually born separated from the placenta and free from membranes. The are very active and vigorously start the search for nipples and attempt to suckle while birth is still in progress. Although does frequently lick the kits and avidly consume the placentas, the kits are able to cast off any remaining membranes, suckle and survive whether directly attended to by the mother or not (HUDSON *et al.*, 1999c).

Immediately after giving birth, does leave the kits, close the burrow entrance, and only return to nurse for 3 to 4 minutes once each day (see below). They typically enter post partum estrus and may be successfully mated again immediately after giving birth. Thus, at the height of the breeding season wild does are frequently both pregnant and lactating, a circumstance allowing them to raise several litters in a season (BRAMBELL, 1944 ; LINCOLN, 1974 ; HUDSON *et al.*, 1996a).

2.1. Possible applications

One aspect of this unusual parturitional behavior which might be of practical significance to the producer is the fact that it should occur rapidly. Since stress is known to inhibit the release of oxytocin and to delay or prolong parturition in many mammals, for the breeder it should be important to keep disturbance in the maternal area to a minimum. Given that parturition usually occurs during the light phase and thus during the period of greatest human activity in most production units, this would probably require some re-scheduling of daily routines.

On an even more speculative note, when does are given hay for nest building just before term they seem to become highly aroused as they gather it and a marked increase in their respiration rate suggestive of underlying physiological changes can be observed even hours later (R.H., unpublished observations). Thus, it is possible that allowing pregnant does to build maternal nests in the natural way may provide a form of environmental feedback stimulating physiological mechanisms which help ensure rapid, well orchestrated parturition.

3. Nursing

Under natural conditions nursing usually takes place at night, with the early morning hours before dawn apparently being preferred, at least during the first two weeks when the kits are confined to the blocked nursery burrow. This visit appears to have a strong circadian basis since even mothers kept under constant light conditions continue to nurse their kits approximately every 24 hours. What triggers this visit is not known although failure to disrupt it by emptying the mammary glands demonstrates that pressure from accumulated milk is not the signal. Although domestic does with free access to the nest box may enter the nest more than once a day, their kits do not obtain more milk or grow faster than the kits of does only allowed to nurse once a day (ZARROW *et al.*, 1965 ; FINDLAY and ROTH, 1970 ; LINCOLN, 1974 ; JILGE, 1993 ; 1995 ; COUREAUD *et al.*, 2000a;b : general reviews in HUDSON and DISTEL, 1989 ; HUDSON, 1998).

As mentioned above, the nursing visit is extremely short, lasting only about 3 to 4 minutes. On entering the nest the doe simply positions herself over the litter, remaining almost motionless and not giving the kits any direct behavioral assistance to suckle. In fact, does frequently tread on kits, and even when struggling and vocalizing kits are pinned beneath their hind legs, does will not necessarily adjust their position to free them. Towards the end of nursing, does deposit a few hard fecal pellets in the nest but never urinate there. Nursing itself ends abruptly with the doe jumping out of the nest, closing the burrow entrance and leaving the kits alone until the following day. Domestic does show the same pattern of behavior if able to dig a burrow, and even in confinement often perform scratching and digging movements at the nest box entrance as if trying to close it (DEUTSCH, 1957 ; HUDSON and DISTEL, 1982 ; 1983 ; HUDSON *et al.*, 1996a)

Although nursing normally occurs at night, it can be readily shifted to the light phase by only allowing does access to their young at this time. However, in contrast to non-pregnant females, does mated post partum and forced to nurse during the daytime show disturbed nursing behavior as early as the first week of pregnancy. Furthermore, gestation is typically prolonged and often terminates in still births. That these birth difficulties might be due to the out-of-phase release of oxytocin caused by daytime nursing is suggested by the fact that administration of oxytocin during the day to pregnant but non-nursing does results in similar birth problems. Thus, in the rabbit nursing and parturition appear to be timed in such a way as to prevent the physiological processes underlying each of these vital reproductive functions from interfering with the other (HUDSON *et al.*, 1995 ; general reviews in HUDSON, 1995 ; HUDSON *et al.*, 1996b).

If does are pregnant from immediate post partum mating they will wean their kits early. Weaning normally begins at about post partum day 20, with a decline in milk yield that is considerably steeper if does are pregnant. As early as day 25, pregnant mothers then

suddenly refuse to nurse. Whereas on the preceding day they visit the nest for the usual time and show apparently normal nursing behavior, the following day they refuse to enter it and vigorously strike at, cuff away or even bite kits trying to suckle. This contrasts with the behavior of non-pregnant does, which nurse their kits much longer and rarely seem to respond aggressively to them. Abrupt weaning by pregnant does is important not only so they can prepare for the coming litter but also to prevent parturition being stimulated prematurely by the release of oxytocin in response to suckling (LINCOLN, 1974 ; HUDSON et al., 1996a ; general reviews in HUDSON, 1995 ; HUDSON et al., 1996b).

As mentioned above, the kits anticipate and prepare themselves for the all-important and highly competitive nursing visit of their mother. In addition to becoming exposed from the nest material they are particularly responsive to tactile and vibrational stimuli at this time and react to even the slightest disturbance with increased activity, rearing movements and vocalization. Contrary to what one might expect, this anticipatory arousal is not due simply to the absence of food in the gut. Litters isolated from their mother and deprived of one nursing show the usual pattern of anticipatory behavior on the first day of separation, but when the doe does not arrive they gradually become less active and cover over again. The following day, approximately 47 hours after last being nursed, they again become aroused, uncover and are able to suckle normally. Thus, the kits' anticipatory behavior appears to represent a true, endogenous circadian rhythm. When and in what way this cycle develops and becomes synchronized with that of the mother is not known although the observation that at least some litters anticipate the very first nursing suggests that this may occur prenatally (HUDSON and DISTEL, 1982 ; JILGE, 1993 ; 1995 ; ALLINGHAM et al., 1998 ; ESCOBAR et al., 2000 ; DRUMMOND et al., 2000 ; general reviews in HUDSON and DISTEL, 1989 ; HUDSON, 1998).

3.1. Possible applications

Several consequences for nest box design and nursing regimens seem to follow from this unusual nursing pattern. Given the manner in which does jump in and out of the nest without apparent regard for the kits, nest boxes which allow does to enter through a hole and approach the kits from the side in a similar way to the natural burrow may result in less injury than when does jump into an open-topped box or jump in through a hole in the center. Furthermore, given that frequent visits to a permanently open box might also increase injury to kits or disturb their circadian pattern of thermoregulatory or other behavior, it would seem advisable to restrict does' access to the nest to just one regularly timed visit a day. Indeed, first evidence that survival, at least of young kits, is enhanced by such restriction is already available (COUREAUD et al., 2000a,b). However, the behavioral synchrony between does and kits in relation to the time of nursing suggests that if optimal milk transfer and growth are to be achieved and maternal stress minimized, does should be free to determine the daily nursing time or at least to have access to their young during the dark period.

4. Suckling

As mentioned above, does do not give their kits any direct behavioral assistance to locate nipples and suckle, and during nursing simply stand motionless over them. Despite this, kits can drink up to 25% of their weight in milk in one brief nursing session, and once the doe has settled to nurse, take only a few seconds to attach to nipples. Their search behavior is highly stereotyped and is shown in response to any lactating doe at any time of day. While making rapid probing movements with the muzzle deep into the fur, kits move rapidly across the doe's belly with a sewing machine-like action until a nipple is reached. Surprisingly, they do not remain on one nipple but change them frequently, repeating the whole search sequence several times even though this reduces the actual time spent on nipples to an average of only about 110 seconds per nursing (HUDSON and DISTEL, 1983 ; 1984 ; DISTEL and HUDSON, 1985).

By investigating the cues governing this effective orienting behavior it has been shown that an odor on the doe's belly, the so-called nipple-search pheromone, is essential for the release and maintenance of searching, for rapidly guiding kits to nipples and for nipple attachment. Production of the pheromone is under hormonal control, with the sequential administration of estradiol, progesterone and prolactin to non-pheromone producing, ovariectomized does stimulating emission within a few days. The kits are very sensitive to these cues, which are present not only on the doe's ventrum but also in the milk. Testing the reaction of kits to fresh milk presented on a glass rod, it was found that even milk diluted 10 000-fold elicits significantly more searching and grasping responses than cow's milk or other odorants. This dependence on specific maternal olfactory cues explains why newborn rabbits are so difficult to raise by hand and why they are completely unable to suckle and will starve if made anosmic (HUDSON and DISTEL, 1983 ; DISTEL and HUDSON, 1985 ; HUDSON et al., 1990 ; KEIL et al, 1990 ; GONZÁLEZ-MARISCAL et al., 1994 ; COUREAUD and SCHAAL, 2000 ; general reviews in HUDSON, 1995 ; HUDSON and DISTEL, 1995 ; HUDSON et al., 1996b).

The kits are able to respond appropriately to their mother at the very first nursing. Even kits delivered by cesarean section one day before term respond to a lactating doe with normal search and suckling behavior. However, this does not exclude the possibility that the response is dependent on prenatal experience of

chemical characteristics of the uterine environment. In fact, this might even be considered likely given the steep rise in pheromone emission in late pregnancy and reports that rabbit kits are able to learn prenatally odor cues associated with their mother's diet. However, they are also able to acquire information about their mother's diet in the context of suckling and to use this in selecting foods at weaning. By supplementing does' lab food diet with juniper berries or thyme, it could be shown that even the brief contact with the mother during nursing can positively influence kits' later decision to eat these substances in food-choice tests (HUDSON and DISTEL, 1984 ; HUDSON, 1985 ; BILKO *et al.*, 1994 ; SEMKE *et al.*, 1995 ; COUREAUD *et al.*, 1997 ; general reviews in HUDSON and ALTBÄCKER, 1994 ; HUDSON and DISTEL, 1995 ; HUDSON *et al.*, 1999b).

4.1. Possible applications

Brief, once-daily contact with the mother, combined with the kits' ability to drink large quantities of milk in just a few minutes provides potentially better conditions for artificially raising rabbits than in most other domestic mammals. Artificial feeding would have the significant advantages of freeing does for further breeding and of ensuring more even and faster growth of the young. The single most important factor hindering this to date is the kits' complete dependence on the nipple-search pheromone, a substance which it has so far not been possible to isolate or identify chemically. However, given the availability of a robust bioassay for detecting its presence and detailed information on the hormonal basis of its emission, success on this front can be expected in the near future (HARDMAN *et al.*, 1970 ; KEIL *et al.*, 1990 ; general review in HUDSON and DISTEL, 1995).

Artificial nipple-search pheromone could also help reduce the high mortality from starvation among very young kits. Applying artificial pheromone to the ventrum of parturient does should enhance the nipple-search response even of weaker kits and thus increase survival rates during the critical first few days.

Finally, as with the learning of odors of fecal pellets described above, the fact that during suckling kits learn and develop a preference for the odor of foods associated with their mother's diet might be usefully used to increase sensory continuity between the pre- and the challenging post-weaning situation.

5. Weaning

Despite such a rigorous nursing regimen, young rabbits grow rapidly, and by weaning at about postnatal day 27 may have increased their birth weight as much as twelve-fold. During the first and for most of the second week of postnatal life they depend entirely on the mother's milk for their nutritional needs. However, as mentioned above, during the second week they start nibbling the fecal pellets deposited by the doe in the

nest, and by the third week are eating appreciable amounts of nest material and other solid foods and starting to drink water, so that by the end of the forth week complete independence is possible. While the development of this ingestive sequence is very similar across litters, as mentioned above, the speed and manner in which weaning is achieved depends on whether or not the doe is pregnant. Furthermore, at least in the later part of the suckling period, kits are able to adjust their ingestive behavior according to the behavior and physiological condition of their mother, eating more solid food and drinking more water if she starts to wean early (LINCOLN, 1974 ; HUDSON *et al.*, 1996a ; general reviews in HUDSON and ALTBÄCKER, 1994 ; HUDSON *et al.*, 1996b).

5.1. Possible applications

The main potential consequence of the pattern of mother-young relations described above is what it suggest regarding optimal weaning age. The fact that does start to wean at about day 20, and if they are pregnant, refuse to nurse and even act aggressively towards their young by the end of the fourth week, suggests that the weaning age of six to eight weeks often recommended may be longer than necessary for the kits or appropriate for the mother. However, returning to a point raised earlier, the ability of young rabbits to successfully make the transition to independent feeding by the end of the first month might depend on the quality of the nest in which they were raised and in particular, on the availability of fecal pellets and plant material.

CONCLUSIONS

In conclusion, three general points might be drawn from the description of mother-young relations in the rabbit given above.

First, as stated in the introduction, knowledge of natural, evolved patterns of behavior and their underlying mechanisms should provide insights relevant to increasing productivity and the animals' well-being. This does not imply slavish attempts to replicate the natural situation, but rather using such knowledge to guide the development and design of appropriate new procedures. Hand-raising kits with the help of commercially available nipple-search pheromone would be one such example.

Second, although it is possible to separate out and discuss behavioral patterns as above, these obviously do not occur in isolation and synergistic, cumulative advantages might accrue only when the broader pattern is considered. An example is the possible importance of combining early weaning with the provision of appropriate nest material. The one or other procedure applied separately might bring little, but in combination,

as in the natural situation, might result in an economically meaningful advantage.

Third, the unusual pattern of mother-young relations outlined above makes clear the importance of precise, first-hand knowledge of the behavior and requirements of any particular species. Lacking this, it is all too easy to be guided by preconceptions formed from experience with seemingly similar species but having very different biologies. An example is the limited time rabbit does spend with their young. Against this background, providing permanent access to the nest with the idea that the more contact between mother and young the better, may not only be superfluous but even detrimental.

Finally, although the rabbit is one of the best studied mammals both in the wild and captivity, important gaps in our knowledge remain. Filling these is not the exclusive province of laboratory-based research. Producers, in daily contact with large stocks of animals and - in the constant effort to improve production - engaging in often unacknowledged experiments, have much to contribute.

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