JUST THREE MINUTES A DAY : THE BEHAVIOUR OF YOUNG RABBITS VIEWED IN THE CONTEXT OF LIMITED MATERNAL CARE

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In any mammalian species a proper understanding of the mother-young system is of major importance if productivity is to be optimised under conditions compatible with the animals' welfare. The European rabbit *(Oryctolagus cuniculus)* is particularly interesting in this regard given its unusual and generally little appreciated pattern of maternal care. In contrast to most mammalian mothers, doe rabbits have only limited contact with their young and visit them briefly just once a day to nurse. This makes it difficult in questions of management to extrapolate from other, better known mother-young systems, and underlines the importance of considering the rabbit in its own right.

In trying to meet this aim we have divided the following report into three parts: a brief description of rabbit maternal behaviour, an outline of several distinctive behavioural characteristics of the young making such limited care possible, and a brief consideration of the possible consequences of these observations for management and production practices. Although we focus primarily on the young, it is of course difficult to appreciate the significance of their behaviour without considering the role of the mother. In fact, the central theme running through this report is that the behaviour and development of the pups can be best understood in the context of this species' limited but highly efficient maternal care. As to our knowledge there is little difference between wild and domestic rabbits in the behaviours discussed here, no distinction will be made between them (reviewed in 4).

LIMITED MATERNAL CARE: THE DEVELOPMENTAL CONTEXT

Maternal behaviour in the rabbit represents a well organised series of events under tight hormonal and circadian control (11, 19, 30, 33, 34; reviewed in 26, 28). Broadly, it can be divided into three main phases: prepartum preparation for the arrival of the young together with parturition and associated perinatal events, nursing during the period of complete dependence of the young, and weaning culminating in their independence (Figure 1).

Parturition and perinatal events

Towards the end of the approximately 31-day pregnancy, the doe normally digs a short nursery burrow which she lines with dried grass and fur pulled from her chest and belly, and in which she may deposite hard faecal pellets (reviewed in 11, 18, 19, 26). Parturition usually occurs in the morning, that is at the start of the rest period (cf. 32). 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 (30, 33, 34; reviewed in 26; see below). Parturition is extremely rapid, usually not lasting more than 10 to 15 minutes for the birth of 10 or more pups (9, 19, 30). As the vagina of the rabbit is long and the umbilical cord often ruptures in the birth canal, it is important that the pups are rapidly expelled (9, 38).

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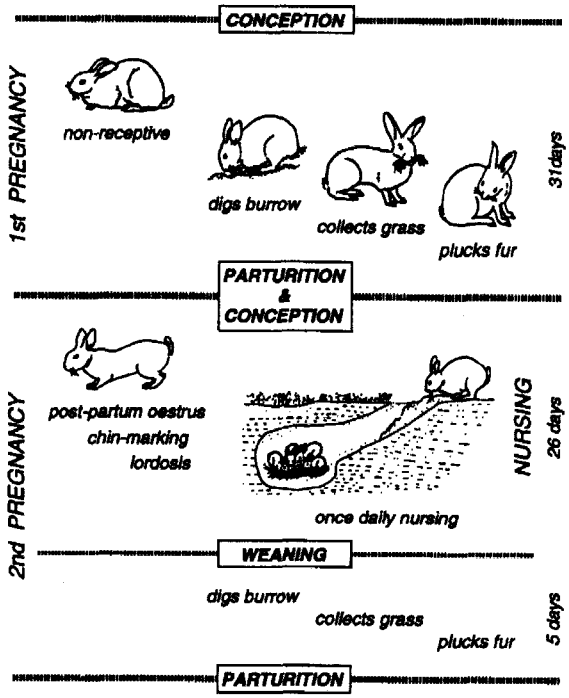
Immediately after giving birth the doe leaves the pups, closes the burrow entrance, and only returns to nurse briefly once each day (33, 34; reviewed in 19, 26). She does not brood the pups, cleans them little if at all, and does not even retrieve pups which stray from the nest (reviewed in 19, 26). At the height of the breeding season does typically show postpartum oestrus and may be mated again almost immediately after giving birth (6, 18, 30, 37). This means, at least in the wild, that they are often both pregnant and lactating, a situation which has marked consequences for the pattern of weaning of the litter currently being nursed (see below).

Figure 1 : Schematic representation of the cycle of maternal behaviour in the rabbit



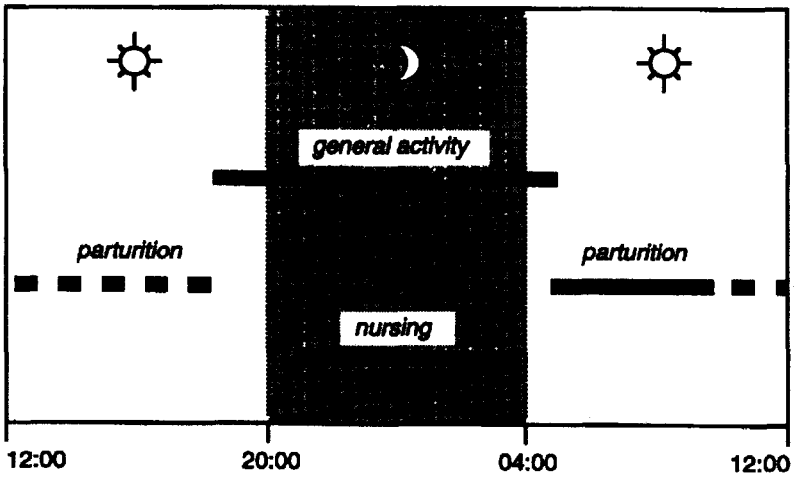
(HUDSON *et al.*)

Nursing

As mentioned above, nursing usually takes place at night with the early hours of the morning before dawn apparently being preferred, at least during the first two weeks when the pups are confined to the blocked nursery burrow (33; reviewed in 26). The nursing visit is extremely short, lasting only about 3 to 4 minutes (11, 18, 19, 20; reviewed in 26). On entering the nest, the doe simply positions herself over the litter, remaining almost motionless and not giving the pups any direct behavioural assistance to suckle. Towards the end of nursing she deposits a few hard faecal pellets in the nest but never urinates there. Nursing itself ends abruptly with the doe jumping out of the nest and leaving the pups alone until the following day (18, 19; reviewed in 26).

Although nursing normally occurs at night, in the laboratory 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 postpartum and forced to nurse during the daytime show disturbed nursing behaviour 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, at least in part, 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 (30; Figure 2).

Figure 2 : Time windows for nursing and parturition in relation to general activity and time of day (16).



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Such an extreme pattern of maternal care may be explained by the fact that rabbits are fugitive animals and heavily preyed upon. Their main protection is to flee into the communal warren, which, with its many entrances and exits, offers some chance of escaping even predators able to pursue them underground. In such a situation the newborn pups would be unable to escape, and it is probably for this reason that the doe constructs a separate nursery burrow, the single entrance of which she closes and effectively disguises after each visit. Presumably to reduce the risk of predators locating the nest and trapping her and the pups there, the time spent with the young is kept to a minimum (37, 49; reviewed in 22, 26).

Weaning

Despite this rigorous nursing regimen the young develop rapidly, and by weaning at about post-natal day 27 they may have increased their birth weight as much as twelve-fold (17, 18). Such rapid development is important given that the doe normally comes into oestrus again immediately after giving birth. While this enables her to raise several litters in a season, it also means that the pups must be weaned quickly. This normally begins at about day 20 with a decline in milk yield which 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 behaviour, the following day they refuse to enter and vigorously strike at, cuff away or even bite any pup trying to suckle. This contrasts with the behaviour of non-pregnant does which nurse their pups much longer and rarely seem to respond aggressively to them (17, 18, 37). The abrupt weaning is important not only so that does can prepare for the coming litter but also to prevent parturition being stimulated prematurely by the release of oxytocin in response to suckling (37; reviewed in 30).

SOME BEHAVIOURAL SOLUTIONS

For the pups, however, such limited care poses a range of problems, particularly as they are rather immature at birth. They are born naked, with eyes and outer ears sealed, and with poor motor co-ordination. By day 7 they are capable of limited orienting responses to auditory stimuli, and may also perceive light changes, although they only begin to open their eyes on day 9 or 10. They start to leave the nest when 13 to 18 days old, by which time they are able to maintain a stable body temperature and have much improved motor co-ordination (reviewed in 19, 22, 24, 26). Survival of such altricial young under conditions in which they receive no direct maternal care other than the brief, once daily provision of milk, is only possible because of several behavioural specialisations.

Circadian synchrony

The first of these is the ability of the pups to anticipate and prepare themselves for the regular daily arrival of their mother (19, 26, 33, 34, 42; Figure 2). While the pups spend most of the time between feeds lying quietly together under an insulating cover of nest material, one or two hours before nursing they become more active and gradually exposed from this. At this time they are particularly sensitive to tactile and vibrational stimuli and react to even slight disturbances with increased activity, rearing movements and vocalisation. They respond to the doe entering the nest by rearing their heads up and pushing their muzzles deep into her belly fur to start the search for nipples. Despite the heat loss presumably incurred by exposure from the nest material, the anticipatory uncovering appears important as it enables pups to reach the doe's belly unhindered. Experimentally covering over young pups with nest material just before the doe's arrival greatly reduces milk intake despite the doe spending longer in the nest attempting to nurse (19).

When the doe jumps out of the nest at the end of nursing, the pups drop immediately from the nipples which prevents them being dragged from the nest. They then urinate simultaneously, become very wet, and vigorously burrow back under the nest material and disperse throughout the nest. This activity lasts about 10 to 15 minutes, during which time the pups become dry and the nest material fluffed up again. The pups then gradually reassemble in the warmest part of the nest (19; cf. 31) where they remain covered until the next nursing visit. Although this behaviour clearly serves the thermoregulatory needs of these altricial young which are neither groomed nor brooded by their mother, the pups also need to stay together because those away from the group are ignored by the doe and have little chance to suckle (19).

Contrary to what one might expect, the anticipatory arousal of the pups 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

behaviour on the first day of separation but when the doe does not arrive, they gradually become less active and covered again. The following day, approximately 47 hours after last being nursed, the pups again become aroused, uncover, and are able to suckle normally (19, 33, 34, 42). Thus the pups' anticipatory behaviour appears to represent a true endogenous circadian rhythm. When and in what way this cycle develops and becomes synchronised with that of the mother remains to be investigated although the observation that at least some litters anticipate the very first nursing suggests that this may occur prenatally (33; reviewed in 26; Figure 2).

The nipple-search pheromone

Having achieved contact with the doe's ventrum, the pups are then dependent on a second behavioural specialisation - the ability to locate nipples and drink up to 25% of their body weight in the short time available each day. Once the doe has settled to nurse, pups take only a few seconds to attach to the nipples (20, 37). Their search behaviour is highly stereotyped and is shown in response to any nursing doe at any time of day. While making rapid probing movements with the muzzle deep into the fur, pups move 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 they spend on nipples to an average of only about 110 seconds per nursing (8, 20).

By investigating the cues governing this effective orienting behaviour it could be shown that an odour on the doe's belly is essential for the release and maintenance of searching (20) and for nipple attachment (47). Neither shaving the doe's belly nor creating a negative thermal gradient by cooling the nipple area has a significant effect on the pups' behaviour. However, if the shaved belly is covered with adhesive tape but the nipples left bare, pups do not search and only attach to nipples when they chance to come near them. Further, covering the nipples or the surrounding area in various ways has shown that the short-ranging odour cues releasing and sustaining the search behaviour increase in strength towards nipples, and thus may help guide pups there. The pups are very sensitive to these cues which are not only present on the doe's ventrum but also in the milk (35, 39). By testing the reaction of pups 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 (35).

This dependence on olfactory cues explains why newborn rabbits are so difficult to raise by hand (2, 45) and why they are completely unable to suckle from the mother when made anosmic (7, 23, 46, 47). The unusually reliable and stereotyped nature of their response would seem to qualify this signal as a true releasing pheromone (cf. 3; 28), and particularly as it appears to be species-specific. Thus, rabbit pups fail to respond to lactating rats, cats, guinea pigs or even hares with nipple-search behaviour or nipple attachment (12, 39; unpublished observations).

As the reaction of mammals to pheromones or pheromone-like substances is usually at least partly dependent on experience (3), it is notable that rabbit pups are able to respond appropriately to their mother at the very first nursing. Even pups delivered by caesarean section one day before term respond with normal search behaviour to a lactating doe, and take no longer to attach to nipples than normally delivered one-day-old pups (12). However, this does not exclude the possibility that the response is dependent on prenatal experience of, for example, chemical characteristics of the uterine environment. In fact, this might even be considered likely given the steep rise in pheromone production in late pregnancy (21), and reports that rabbit pups are able to learn odour cues associated with their mother's diet prenatally, (5, 48; see below).

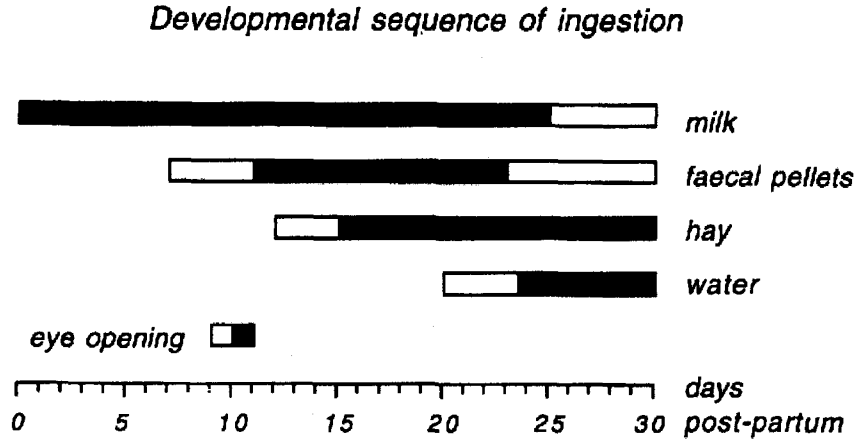
Using the response of newborn pups to regularly test for the presence of the pheromone has shown that emission is under hormonal control and that all mature does produce it in summer or under experimental long-day conditions (21, 27). However, pregnancy and lactation have the strongest influence on emission, overriding the effect of daylength. Pregnancy stimulates emission even in winter, so that by parturition and during early lactation the pups are able to reliably locate and attach to nipples within a few seconds. Strong evidence for the role of sex steroids in the production of the pheromone comes from the fact that emission is suppressed following ovariectomy but can be stimulated to reach long-day levels within a few days by the administration of estradiol, and further stimulated to the high levels characteristic of late pregnancy and lactation by the additional administration of progesterone and prolactin respectively (10, 21, 29; reviewed in 28).

Eating the nest

With the problem of suckling solved, a third set of behaviors soon comes into play which may help pups make the transition to independent feeding under conditions in which they receive little or no direct assistance from their mother.

During the first and for most of the second week of postnatal life the pups depend entirely on the mother's milk for their nutritional needs. However, during the second week they start eating the faecal pellets deposited by her in the nest and also start nibbling the nest material. At first they simply bite through the long stalks, reducing the hay to a kind of rough chaff but by the middle of the third week clearly measurable amounts are consumed. By the end of the third week the pups also start drinking water and eating other solid foods so that towards the end of the fourth week complete independence is possible (17, 18, 19). While this ingestive sequence is very similar across litters, the speed and manner in which weaning is achieved depends on whether or not the doe is pregnant. Furthermore, at least in the latter part of the suckling period, pups are able to adjust their ingestive behaviour according to the behaviour and physiological condition of their mother, eating more solid food and drinking more water if she starts to wean them early (17, 18; Figure 3).

Figure 3 : Developmental sequence in the ingestive behaviour of litters raised by pregnant or non-pregnant mothers until day 30. Open bars give the range of variation between litters. Litters from pregnant mothers are weaned four to five days before term; cf. Figure 1 (Data from 17).



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Although the stereotyped nature of does' behaviour in depositing plant material and faecal pellets in the nest and of pups' behaviour in eating these suggest that this ingestive behaviour might have some functional value, its actual significance remains to be investigated. As the amount of nest and faecal material eaten per day is rather small, the direct caloric benefit to the pups is probably negligible. However, roughage provided by the nest material, and possibly gut flora from the faecal pellets might help prepare pups for the digestion of plant food as weaning approaches. With this in mind, it would be interesting to test the effect of raising pups without access to edible nest material or faecal pellets, and to investigate according to what criteria, if any, does select plant material for the nest. In this regard it is interesting that findings from the Hungarian laboratory suggest that when given a choice of different grasses, pregnant does preferentially select the species from which their own natal nest was constructed (unpublished observations).

Early odour learning

The final characteristic to be considered here is the ability of even very young pups to learn odours associated with the mother or present in the nest, and to retain the memory of these for long periods. As the pups are born blind and are confined to the dark nursery burrow for a significant period of their early development, odours may have a particular saliency for them. Odour cues may not only help pups solve immediate problems of survival but may also influence their behaviour later, long after they have left the nest (Table 1).

Table 1 : Paradigms for early odour learning in the rabbit

	Odorant	Odour Experience Treatment	on Day	Odour Memory Behavioural Test	on Day	Refs. Nr.
Associative Learning		nursing by		nipple-searching		
one-trial	perfume citral camphor	perfumed mother	1	on cat	2 & 5	(12)
	citral	"	3 & 4	on ovariecto-mised rabbit	5	(23)
	perfume citral	"	1-4	"	5	(25)
	perfume mixture	"	1-6	on warm fur	2-7	(15)
sensitive period	perfume	"	1-5	"	6	(36)
				preference test		
	juniper	juniper-fed mother	1-28	choice of food	29	(5)
Incidental Learning		exposure to		preference test		
	hay perfume mixture	nest-material	1-5	side with odour	2-6	(15)
	juniper	ambient nest odour of juniper mother	1-28	choice of food	29	(1, 5)
Prenatal Learning		supplementary feeding of mother		preference test		
	juniper	raising by foster mother	foetal period	choice of food	29	(5)
	juniper	—	foetal	side with odour	1	(48)

The nipple-search pheromone described above - vital for the survival of the pups - is only one of a range of odours which they may encounter on the mother. Although the pups do not need to learn postnatally the odour cues governing nipple-search behaviour, they can nevertheless rapidly learn to associate novel odours present on the mother with suckling. Pups nursed by a doe whose ventrum has been scented with an artificial odorant quickly learn to respond to this scent as to the pheromone itself (12, 25, 36). After only one such three-minute pairing, pups show the full sequence of search behaviour, nipple attachment and vigorous sucking when placed on the belly of a non-pheromone producing doe or even a female cat scented with the specific odour they had experienced during suckling. In contrast, control pups with no experience of the scent respond to the test female by crawling around or resting, and cannot be induced to grasp nipples.

This rapid associative learning is dependent on specific reinforcing properties of the suckling situation (13). Merely exposing pups to the novel odour, even at the time of high arousal preceding the daily nursing, does not result in conditioning of the nipple-search response. Surprisingly, milk intake is not necessary as a reinforcer as pups allowed to search and attach to nipples for a standard five minutes on a non-lactating but pheromone-producing doe also show strong odour conditioning. However, the perioral stimulation associated with the consummatory act of suckling appears to be particularly important since pups allowed to search for but prevented from attaching to nipples show only weak odour conditioning.

That this learning might represent a form of olfactory imprinting is suggested by the finding that responsiveness to learned suckling odours is retained for some time without further experience (13; cf. 14). Just as pups raised without experience of the pheromone respond to it when tested on day 5, so pups conditioned on day 1 but then either bottle-fed or nursed by a non-scented doe still show vigorous nipple-search behaviour in response to the learned odour when tested on day 5. Furthermore, one-trial conditioning of the nipple-search response is restricted to a sensitive period and is only possible during the first three days of life. After this time repeated training is necessary and later may even be without effect. However, conditionability is maintained to at least

day 5 in pups deprived of normal suckling experience by bottle feeding, although not in hand-raised pups allowed to search on a doe for four minutes a day without drinking (36).

Given that the nipple-search pheromone does not need to be learned postnatally, what might be the significance of such odour learning? The ability of the pups to learn odours prenatally (see below) raises the possibility that the pheromone is also learned before birth and that odour learning during the early postpartum period represents an extension of this process, enabling pups to gain rapid confirmation of the pheromonal signal in the final context of suckling (cf. 43; 44). Longer term consequences of such experience are suggested by reports that in various species odour exposure early in development may affect filial attachment, mate preference, or food choice (reviewed in 15, 36). This is consistent with the report that rabbit pups learn the specific odour of their mother's anal glands, and that this information may help them recognise her territory when they leave the nursery burrow (40).

Possible longer term consequences are also suggested by the ability of pups to acquire information about the diet of their mother before leaving the nest, and to use this in selecting foods after weaning (1, 5; reviewed in 17). By supplementing does' lab food diet with juniper berries or thyme, it could be shown that contact with the faecal pellets deposited in the nest, with the mother during nursing, or even prenatal exposure in utero may all positively influence pups' later food choice. Moreover, these means of information transfer appear to be equally effective, and as ambient juniper odour also induces a preference, olfactory cues are adequate for this learning. Such redundancy may not only help insure that less aromatic substances or substances transmitted differentially by these various routes are learned, but also that pups can acquire a preference for a variety of foods eaten by their mother at different times (5).

Prenatal odour learning is of particular interest, not least with regard to the nature of early learning mechanisms (14, 44). As with the learning of ambient odours present in the nest, it is not yet clear what the nature of the reinforcer is supporting such learning - if indeed any is required. Related to this is the question whether the acquisition of responsiveness to ambient odours represents a form of incidental learning distinct from and supported by different mechanisms than the more familiar associative paradigms such as the conditioning to suckling odours described above (15; cf. 14). Whatever the case, it would seem to make biological sense that young animals are particularly receptive to stimuli present in utero or in the protected environment of the nest. Mothers are individuals that have succeeded in surviving to reproductive age and, having had time to learn the most nutritious and least poisonous plants in the local environment, represent a source of information which can be largely relied upon. Such a strategy would also help explain why pups from thyme-fed mothers develop a preference for thyme even under conditions in which it has toxic and teratogenic effects (1).

The significance of early odour experience is reinforced by the finding that exposure in utero to odours associated with the mother's diet results in specific enhancement in the sensitivity of the olfactory receptors (48). Pups born to juniper-fed mothers demonstrate a preference for juniper in a side preference test on the first day of life, and electrophysiological recordings from the isolated olfactory epithelium indicate that this is accompanied by an increase in the sensitivity to juniper odour at the level of the primary receptor neurones. Early acquisition of odour preferences together with the enhancement of receptor sensitivity should not only help ensure sensory continuity between pre- and postnatal environments (43, 44), but may also help the young to detect biologically relevant odours in later life.

POTENTIAL CONSEQUENCES FOR MANAGEMENT AND WELFARE

Returning to the relevance of the mother-young system for questions of management and welfare, several points of potential interest follow from the unusual pattern of behaviour in the rabbit outlined above.

First, given the limited contact between mothers and pups, separating them for long periods - for example for experimental purposes - is much less of a problem than for most other mammalian species with altricial young (cf. 24). Nevertheless, the synchrony in behaviour of does and pups in relation to the time of nursing suggests that if optimal milk transfer and growth rates are to be achieved and maternal stress is to be minimised, does should be free to determine the daily nursing time or at least to have access to their young during the dark period.

Second, the fact that does start to wean at about day 20, and if they are pregnant again, 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 usually recommended (cited in 4) may be longer than necessary for the pups or appropriate for the mother. However, the ability of young rabbits to successfully make the transition to independent feeding by the end of the first month may depend on the quality of the nest in which they were raised. Given that pups eat the plant material and maternal faeces normally present in the nest, it would be interesting to systematically investigate the significance of such characteristics of the normal nest for the survival and weight gain of weanlings.

Third, brief contact between mother and young combined with a nursing time of only three minutes, provides potentially better conditions for artificially raising pups than in most other domestic species. Artificial feeding would have the significant advantages of freeing the doe for further breeding and of ensuring more even and faster growth of the young (39, 45). The single most important factor hindering this to date is the pups' dependence on the nipple-search pheromone - a substance which so far it has not been possible to isolate or to identify chemically (28). Nevertheless, until this is achieved, it may be possible to raise pups artificially by making use of their ability to rapidly associate novel odours with suckling. Thus, even very young pups might be induced to drink from an appropriately constructed milk delivery system perfumed with the same odour as their mother.

Fourth, isolation and chemical characterization of the nipple-search pheromone could help reduce the high mortality among very young pups from starvation. Applying artificial pheromone to the ventrum of parturient does should enhance the nipple-search response even of weaker pups and thus increase the rate of survival during the critical first few days.

Finally, the fact that newborn pups demonstrate a sensitive period for the learning of odour stimuli may relate to reports that even minimal handling reduces timidity (reviewed in 4, 41), particularly when performed during the first week of post natal life at around the time of nursing (BILKO *et al.*, this volume). Although little is known about the actual mechanisms underlying the effects of early handling, and whether the learning of olfactory cues is involved, it may be worth considering this as a routine practice to facilitate later handling and to reduce stress.

In conclusion, despite the rabbit's long history of domestication and its significance for industry, research, and as a household pet, we still know surprisingly little even about such basic aspects of its behaviour as the mother-young relationship. However, a more comprehensive understanding of this is surely important for the further development of management practices optimal both for the rabbit and user.

REFERENCES

1. ALTBÄCKER V., HUDSON R., BILKO A., 1995. Rabbit mothers' diet influences pups' later food choice. *Ethology* **99**, 107-116.
2. APPEL K., BUSSE H., SCHULZ K., WILK W., 1971. Beitrag zur Handaufzucht von gnotobiotischen und SPF-Kaninchen. *Z. Versuchtierkd.* **13**, 282-309.
3. BEAUCHAMP G.K., DOTY R.L., MOULTON D.G., MUGFORD R.A., 1976. The pheromone concept in mammalian chemical communication: A critique. In: R.L. Doty (eds) Mammalian Olfaction Reproductive Processes and Behavior. *Academic Press, New York*, pp 143-160.
4. BELL D.J., 1984. The behaviour of rabbits: implications for their laboratory management. (ed) Standards in Laboratory Animal Management. U.F.A.W., Potters Bar, England, pp 151-162.
5. BILKO A., ALTBÄCKER V., HUDSON R., 1994. Transmission of food preference in the rabbit: The means of information transfer. *Physiol. Behav.* **56**, 907-912.
6. BRAMBELL F.W.R., 1944. The reproduction of the wild rabbit *Oryctolagus cuniculus* (L.). *Poc. Zool. Soc. Lond.* 114-145, 1-45.
7. DISTEL H., HUDSON R., 1985. The contribution of the olfactory and tactile modalities to the performance of nipple-search behaviour in newborn rabbits. *J. Comp. Physiol.* **A 157**, 599-605.
8. DREWETT R.F., KENDRICK K.M., SANDERS D.J., TREW A.M., 1982. A quantitative analysis of the feeding behavior of suckling rabbits. *Dev. Psychobiol.* **15**, 25-32.
9. FUCHS A.R., DAWOOD Y., 1980. Oxytocin release and uterine activation during parturition in rabbits. *Endocrinol.* **107**, 1117-1126.
10. GONZALEZ-MARISCAL G., CHIRINO R., HUDSON R., 1994. Prolactin stimulates emission of nipple pheromone in ovariectomized New Zealand white rabbits. *Biol. Reprod.* 373-376.
11. GONZALEZ-MARISCAL G., DIAZ-SANCHEZ V., MELO A.I., BEYER C., ROSENBLATT J.S., 1994. Maternal behavior in New Zealand white rabbits: Quantification of somatic events, motor patterns, and stereoid levels. *Physiol. Behav.* **55**, 1081-1089.
12. HUDSON R., 1985. Do newborn rabbits learn the odor stimuli releasing nipple-search behavior? *Dev. Psychobiol.* **18**, 575-585.
13. HUDSON R., 1988. Das Kaninchen (*Oryctolagus cuniculus*) als Verhaltensmodell zur Untersuchung olfaktorischer Funktionen während der Ontogenese. Univ. München, Habilitationsschrift.

14. HUDSON R., 1993. Olfactory imprinting. *Current Opinion Neurobiol.* **3**, 548-552.
15. HUDSON R., 1993. Rapid odor learning in newborn rabbits: Connecting sensory input to motor output. *German J. Psychol.* **17**, 267-255.
16. HUDSON R., 1995. Chronoendocrinology of reproductive behavior in the female rabbit *(Oryctolagus cuniculus)*. In: S. Matthes (ed) Bericht 9. Arbeitstagung über Haltung und Krankheiten der Kaninchen, Pelztiere und Heimtiere. Deutsch. Veterinärmedizin. Gesellsch. DVG, Celle, pp 1-11.
17. HUDSON R., ALTBÄCKER V., 1994. Development of feeding and food preference in the European rabbit: Environmental and maturational determinants. In: B.G. Galef, M. Mainardi, P. Valsecchi (eds) Behavioral Aspects of Feeding: Basic and Applied Research in Mammals. Harwood Academic Publishers, Chur, pp 125-145.
18. HUDSON R., BILKO A., ALTBÄCKER V., 1996. Nursing, weaning and the development of independent feeding in the rabbit. *Z. Säugetierkunde* **61**, 39-48.
19. HUDSON R., DISTEL H., 1982. The pattern of behaviour of rabbit pups in the nest. *Behaviour*, **79**, 255-271.
20. HUDSON R., DISTEL H., 1983. Nipple location by newborn rabbits: Behavioural evidence for pheromonal guidance. *Behaviour* **85**, 260-75.
21. HUDSON R., DISTEL H., 1984. Nipple-search pheromone in rabbits: Dependence on season and reproductive state. *J. Comp. Physiol.* **A 155**, 13-17.
22. HUDSON R., DISTEL H., 1986. Olfactory guidance of nipple-search behaviour in newborn rabbits. In: W. Breipohl (ed) Ontogeny of Olfaction. Springer, New York, pp 243-254.
23. HUDSON R., DISTEL H., 1986. Pheromonal release of suckling in rabbits does not depend on the vomeronasal organ. Physiol. *Behav.* **37**, 123-129.
24. HUDSON R., DISTEL H., 1986. The potential of the newborn rabbit for behavioral teratological research. Neurobehav. Teratol. *Toxicol.* **8**, 209-212.
25. HUDSON R., DISTEL H., 1987. Regional autonomy in the peripheral processing of odor signals in newborn rabbits. *Brain Res.* **421**, 85-94.
26. HUDSON R., DISTEL H., 1989. The temporal pattern of suckling in rabbit pups: a model of circadian synchrony between mother and young. In: S.M. Reppert (ed) Development of Circadian Rhythmicity and Photoperiodism in Mammals. Perinatology Press, Boston, pp 83-102.
27. HUDSON R., DISTEL H., 1990. Sensitivity of female rabbits to changes in photoperiod as measured by pheromone emission. *J. Comp. Physiol.* **A 167**, 225-230.
28. HUDSON R., DISTEL H., 1995. On the nature and action of the rabbit nipple-search pheromone: A review. In: R. Apfelbach, D. Müller-Schwarze, K. Reuter, E. Weiler (eds) Chemical Signals in Vertebrates VII. Advances in the Biosciences. Elsevier Science Ltd, Oxford, pp 223-232.
29. HUDSON R., GONZALEZ-MARISCAL G., BEYER C., 1990. Chin marking behavior, sexual receptivity and pheromone emission in steroid treated, ovariectomized rabbits. Horm. *Behav.* **24**, 1-13.
30. HUDSON R., MÜLLER A., KENNEDY G., 1995. Parturition in the rabbit is compromised by daytime nursing: The role of oxytocin. *Biol. Reprod.* **53**, 519-524.
31. HULL J., HULL D., 1982. Behavioral thermoregulation in newborn rabbits. *J. Comp. Physiol. Psychol.* **96**, 143-147.
32. JILGE B., 1991. The rabbit: a diurnal or a nocturnal animal. *J Exp Anim Sci* **34**, 170-183.
33. JILGE B., 1993. The ontogeny of circadian rhythms in the rabbit. *J. Biol. Rhythms* **8**, 247-260.
34. JILGE B., 1995. The ontogeny of the rabbit's circadian rhythms without an external zeitgeber. *Physiol. Behav.* **58**, 131-140.
35. KEIL W., STRALENDORFF F.V., HUDSON, R., 1990. A behavioral bioassay for analysis of rabbit nipple-search pheromone. *Physiol. Behav.* **47**, 525-529.
36. KINDERMANN U., HUDSON R., DISTEL H., 1994. Learning of suckling odors by newborn rabbits declines with age and suckling experience. *Dev. Psychol.* **27**, 111-122.
37. LINCOLN D.W., 1974. Suckling: A time-constant in the nursing behavior of the rabbit. *Physiol. Behav.* **13**, 711-714.
38. MARTINEZ-GOMEZ M., CARRO M., LUCIO R., PACHECO P., HUDSON R. (submitted) Striated muscles and scent glands associated with the vaginal tract of the rabbit. Anat. Record.
39. MÜLLER K., 1978. Zum Saugverhalten von Kaninchen unter besonderer Berücksichtigung des Geruchsvermögens. Univ. Giessen, Dissertation.
40. MYKYTOWYCZ R., WARD M.M., 1971. Some reactions of nestlings of the wild rabbit, *Oryctolagus cunniculus* (L.), when exposed to natural rabbit odours. *Forma et Functio* **4**, 137-148.
41. PODBERSCEK A.L., BLACKSHAW J.K., BEATTIE A.W., 1991. The effects of repeated handling by familiar and unfamiliar people on rabbits in individuals cages and group pens. *Appl. Anim. Behav. Sci.* **28**, 365-373.
42. SALDERN C.V., HUDSON R., DISTEL H., 1993. Coupled expression of *c-Fos* in diencephalic nuclei of the newborn rabbit in anticipation of and following suckling. In: N. Elsner, M. Heisenberg (eds) Gene-Brain-Behaviour Proc. 21st Göttingen Neurobiol. Conf. Thieme Verlag, Stuttgart, p 515.
43. SCHAAL B., 1988. Discontinuité natale et continuité chimiosensorielle: Modèles animaux et hypothèses pour l'homme. *Ann. Biol.* **27**, 1-41.
44. Schaal B., ORGEUR P., 1992. Olfaction in utero: Can the rodent model be generalized? Quart. *J. Exp. Psychol.* **44**, 245-278.
45. SCHLEY P., 1976. Untersuchungen zur künstlichen Aufzucht von Hauskaninchen. Univ.Giessen, Habilitationschrift.
46. SCHLEY P., 1977. Die Ausschaltung des Geruchsvermögens und sein Einfluß auf das Saugverhalten von Jungkaninchen. *Berl. Münch. Tierärztl. Wschr.* **90**, 382-385.
47. SCHLEY P., 1981. Geruchssinn und Saugverhalten bei Jungkaninchen. *Kleintier Praxis* **26**, 261-263.
48. SEMKE E., DISTEL H., HUDSON R., 1995. Specific enhancement of olfactory receptor sensitivity associated with foetal learning of food odors in the rabbit. *Naturwiss.* **82**, 148-149.
49. ZARROW M.X., DENENBERG V.M., ANDERSON C.O., 1965. Rabbit: Frequency of suckling in the pup. *Science* **150**: 1835-1836.