DEVELOPMENT OF SOCIAL AND FEEDING BEHAVIOUR IN YOUNG RABBITS

Coureaud G.[1]*, Fortun-Lamothe L.[2], Rödel H.G.[3], Monclús R.[3,4], Schaal B.[1]

[1] Ethology and Sensory Psychobiology Group, Centre Européen des Sciences du Goût, UMR 5170 CNRS /Université de Bourgogne/INRA, 15 rue Picardet, 21000 Dijon, France
[2] Equipe Tissus animaux, nutrition, digestion, écosystème et métabolisme, UMR 1289 INRA/Université de Toulouse INP-ENSAT/ENVT, Chemin de Borde Rouge, 31326 Castanet Tolosan, France
[3] Department of Animal Physiology, University of Bayreuth, Germany
[4] Departamento de Biología, Universad Autónoma de Madrid, Spain
*Corresponding author: coureaud@cesg.cnrs.fr

ABSTRACT

European female rabbits (*Oryctolagus cuniculus*) have evolved parsimony in the relationship towards their offspring. Lactating females nurse their litter immediately after parturition, but then leave the nest and will interact with their young only once per day, for a 5-minute nursing episode. Newborns are initially blind and deaf, and totally dependent of milk to survive. In domestic conditions as in the wild, they exhibit a typical behavioural repertoire controlled by olfaction and perioral somesthesis to locate the maternal nipples. Thus, chemosensory means of communication with the mother, based on previously learned odour cues and predisposed odour signals, promote high success in obtaining milk at least over postnatal days 10 to 15. Then, audition and vision become functional and involved in social and feeding behaviour. The present paper aims to survey the behaviour of young rabbits between birth and weaning, and to offer indications on how it is controlled in the context of mother-offspring interactions by multiple sensory and environmental factors.

Key words: Mother-young relationships, Behavioural development, Learning, Feeding, Olfaction, Pheromone, Milk, Rabbit.

INTRODUCTION

A critical need of all mammalian newborns is to rapidly and efficiently interact with the mother to locate the source of milk. Later, depending on species-specific constraints, the young also need to progressively reach autonomy from the mother, in both social and alimentary terms.

The critical mother-infant exchanges are displayed following strategies of nursing and sucking, which more or less overlap between species. Typically, mammalian females invest the greatest part of their time and energy budget caring for their offspring, staying often close to them to provide frequent opportunities to suck over the day. This is the general rule in species bearing altricial young, which are relatively immature in sensory, motor and physiologic terms. Some species, such as the European rabbit (*Oryctolagus cuniculus*), are in sharp contrast with this typical pattern of maternal care. While in rabbits, mothering begins with the construction of a safe breeding burrow, lined with both plant materials and her own abdominal fur (Mykytowycz, 1968; Hudson and Distel, 1982; González-Mariscal *et al.*, 1994), the post-parturient female returns to the nest only once per day to nurse the litter for 3-5 minutes (Lloyd and Mc Cowan, 1968; Mykytowycz, 1968; Broekhuizen *et al.*, 1986; Hudson *et al.*, 1996a). After each nursing episode, the female leaves the nest and blocks its entrance before moving away (Tinbergen, 1970; Broekhuizen *et al.*, 1986).

This pattern of mother/nest-offspring relationship appears well conserved in domestic breeds of rabbits. In rabbitries, the females can express their propensity to dig, collect hay and pull their own hair, and deposit them in a nest box appended to their cage 2-3 days before parturition. The females deliver then in this artificial "burrow", and after each nursing episode, jumps out to spend the remainder of the day in the cage. Of course, they cannot close the access to the nest as in the wild, but their nest closing behaviour remains part of their behavioural repertoire: it re-appears when domestic females are returned to semi-wild conditions (Deutsch, 1957; Kraft, 1979). Moreover, a number of investigators have recorded the stable, apparently undisturbed, once per day periodicity of their nest visits. These studies usually report only one, exceptionally two, nursing visits/day, especially during the first postpartum week (e.g., in continuous nest-access conditions: Venge, 1963, Zarrow *et al.*, 1965; in closed nest conditions with two periods of possible access per day: Zarrow *et al.*, 1965; Hudson and Distel, 1982). Some recent studies suggest, however, that the nursing visits may happen more frequently (Schulte and Hoy, 1997; Hoy and Selzer, 2002). Nevertheless, a nursing visit remains in all cases extremely short (< 5 min) (Zarrow *et al.*, 1965; Lincoln, 1974; Hudson and Distel, 1982; González-Mariscal, 2007).

It is the aim of the present paper to offer a rapid survey of the individual development of young rabbits during the first postnatal weeks, focusing on the social and feeding challenges they have to face for both domestic and wild conditions. An emphasis will be made on sensory and behavioural adaptations rabbit females and pups have co-evolved to optimize survival and growth.

FEEDING BEHAVIOUR OF YOUNG RABBIT: FROM MILK TO SOLID FOOD

Rabbit females give birth after about 31 days of gestation. Then, young rabbits undergo a period of rapid development, ending in weaning in about one month. The pups are thus progressively shifting from an almost exclusive milk diet to a diet composed of solid food that they have to select and ingest by themselves.

Milk intake

The first episode of nursing occurs shortly after birth. The female has the complete initiative in the onset of suckling until the period when pups become motorically mature to leave the nest (cf. section 3). In the nest, the female stands motionless, with the back arched over the pups, providing no direct assistance to the pups rushing to the nipples (Hudson and Distel, 1982, 1983). Nipple location and milk intake depend then on individual pups' abilities to behave efficiently under the female. During the first days of life, they can ingest up to 25% of their live-weight in milk (5 to 10 g at birth). Their avidity for sucking is important as they can suck twice a day if they are experimentally exposed to two females that have not nursed, with several hours between the nursing bouts (McNitt and Moody, 1988; Gyarmati *et al.*, 2000). Although it may happen that one or two pups in a litter do not succeed in obtaining milk at one nursing (around 10-15% on day 1; Coureaud *et al.*, 2007), the first sucking bouts are crucial for pup survival. Starvation is indeed a key explanation of mortality that usually peaks within the first postnatal days, among other factors such as maternal inexperience (Verga *et al.*, 1978, 1986; Coureaud *et al.*, 2000a). In fact, missing the first 2-3 nursing opportunities almost inevitably ends in the loss of the pup (Coureaud *et al.*, 2000b).

In contrast with other newborn mammals (e.g., piglets - *Sus scrofa domesticus* -, kittens - *Felis sylvestris catus* -; McBride, 1963; Mermet *et al.*, 2007), newborn rabbits do not select one or two preferential nipples, but frequently (every 20 seconds, approximately) change among nipples within a same nursing bout. This change occurs despite the high level of competition within the litter (in domestic breeds, there are often more pups in the litter than available nipples - generally 4 pairs; Drummond *et al.*, 2000; Bautista *et al.*, 2005). The pups' scrambling under the female makes possible for all valid pups to attach to one of the usually eight nipples, in which milk yields are similar during the first postnatal days. But by the end of the first postnatal week, more milk seems to be produced on the two middle pairs (Bautista *et al.*, 2005).

The individual milk intake increases from an average of 5-10 g/d after birth to reach a peak of 30 g/d at 20-25 days of age. All over this period, the milk intake is variable between pups due to individual sensory-motor capacities, success in competition among littermates and milk availability (Fortun-Lamothe and Gidenne, 2000; Rödel *et al.*, 2008a). After day 25, the milk yield decreases progressively until weaning. Rabbit females can be fertilised soon after parturition and are able to sustain a new pregnancy throughout lactation. In this case, the milk production ceases 2-3 days before the following parturition (Lebas, 1972; Fortun-Lamothe *et al.*, 1999).

In breeding conditions, weaning occurs between days 28 and 35. In wild conditions, if food resources are sufficient and if females are not pregnant, milk production can continue up to 4-6 postpartum weeks. If females are lactating and pregnant (which is frequently the case in spring), young rabbits can be weaned at 3 weeks of age (Broekhuizen *et al.*, 1986; Gidenne and Lebas, 2006).

Solid food intake

Young domestic rabbits begin to eat significant quantities of solid food around 16 to18 days when they are able to leave the nest-box and move to access pelleted feed and the drinker in the maternal cage. Nevertheless, the first contacts with non-milk elements occur from the first postnatal week when the pups nibble hard faeces that the female left in the nest while nursing her litter (cf. the section "Sensory development of young rabbits"; Kovacs *et al.*, 2004; Moncomble *et al.*, 2004).

At the beginning, pups eat very small quantities of solid food (<2 g/d before 20 days of age). The food intake radically increases from day 25 to reach 40-50 g/d at weaning, although variability can be high between litters (Gidenne and Fortun-Lamothe, 2002). Thus, the feeding behaviour of young rabbits undergoes a radical shift within a few days, switching from a single meal of milk to 25-30 episodes of solid and liquid (water) intake per 24 h. The mass of ingested solid food + water exceeds that of milk during the 4th postnatal week (Scapinello *et al.*, 1999; Gidenne and Lebas, 2006).

One may note that when pre-weanling rabbits begin to leave the nest, they prefer eating at their mother's feeder rather than at a feeder introduced for them into the cage (Fortun-Lamothe and Gidenne, 2003). Even if this point remains to be investigated, it suggests that young rabbits initiating solid food ingestion may model the female's choice of feeding place or of type of food.

Finally, as ingestion of soft faeces represents an important component of rabbit nutrition, at least in adults (e.g., Belenguer *et al.*, 2005), it is interesting to better understand how it develops. A recent study suggests that caecotrophy starts around days 21-25 when the intake of dry food is sufficiently significant to lead to caecum and colon filling (Gidenne *et al.*, 2002).

Development of nutritional needs

In parallel to modifications in feeding behaviour, the nutrients ingested by young rabbits greatly change between birth and weaning (Figure 1). While rabbit milk abounds in lipids (13%) and in proteins (12%), it contains only traces of lactose (Maertens *et al.*, 2006). In contrast, pelleted food contains glucids (80%; more or less digestible, for instance starch being better digested than fibres), proteins (15-18%) and only few lipids (2-5%) all of vegetal origin. Therefore, the pups' digestive capacities must rapidly accommodate with the change of nutrient profile (Gidenne and Fortun-Lamothe, 2002). At about 25 days, the level of vegetal proteins reaches the level of milk proteins in the diet, and then it exceeds it within a few days. Otherwise, lipids come mainly from milk until weaning. While the ingestion of carbon hydrates is almost null until 17 days of age (< 0.3 g/d), it becomes significant from day 21 in the form of fibres and starch. However, milk proteins and fats remain the major source of energy until weaning.

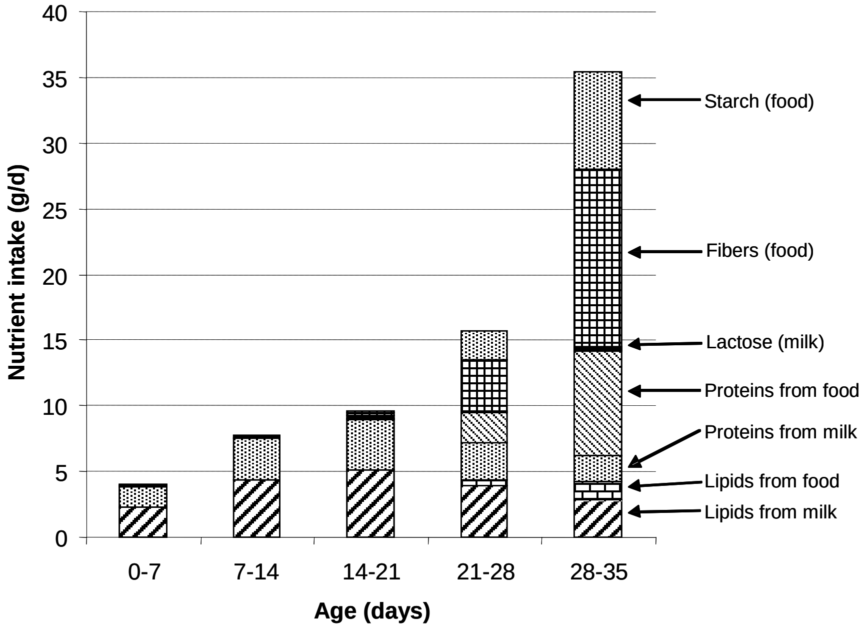

Figure 1: Evolution of the nutrient composition of food ingested by pre-weaning rabbits in breeding housing conditions

Regulation of feeding behaviour

The individual feeding pattern of pre-weaning rabbits and its regulation are not easily measured as they take place in interaction with the littermates and the mother. Nevertheless, it is known that the availability of milk is a key regulating factor of solid food ingestion before weaning. Thus, if the size of the litter is reduced from 10 to 4 pups or if milk production increases, the beginning of solid food ingestion can be delayed by 2-4 days (Fortun-Lamothe and Gidenne, 2000) and the intake of solid feed in the whole litter is lowered (Pascual *et al.*, 2001). Similarly, offering a second opportunity to suck each day (using a second lactating female) can delay the onset of dry feed intake by a few days (Gyarmati *et al.*, 2000). In contrast, early weaning (before 25 days of age) greatly accelerates dry feed intake (Gallois *et al.*, 2005; Xiccato *et al.*, 2005).

How the nutritional composition of food impacts pre-weaning feeding behaviour largely remains a mystery. Data from Pascual and co-workers (1998, 1999) suggest that suckling rabbits regulate their non-milk food consumption according to its digestible energy content, as in weaned rabbits. But Debray and co-workers (2002) showed a greater solid feed intake when suckling rabbits received a high-energy (11.3 MJ/kg) as compared to a moderate-energy diet (10.5 MJ/kg). Finally, the mode of food presentation, the size of the pellets and their quality (hardness, durability) can also affect the feeding behaviour of the young (Maertens and Villamide, 1998).

FACTORS INFLUENCING THE DEVELOPMENT OF YOUNG RABBITS IN NATURAL OR SEMI-NATURAL CONDITIONS

Due to the difficulty to observe behaviours of young rabbits under wild conditions, their feeding development remains partially unknown. However, studies based on direct observations or video-recording showed that rabbit females usually nurse their litter once per day in the burrow (Mykytowycz and Rowley, 1958; Broekhuizen *et al.*, 1983, 1986; but cf. Hoy and Selzer, 2002). Pups are active within their breeding chamber and start to leave the nest area and explore the burrow when their eyes open (shortly after day 10). At about days 15-16, they can approach the mother outside the breeding burrow, once she has opened it, but immediately return into the nest after nursing (Broekhuizen *et al.*, 1986; Rödel, unpublished observations). Young rabbits emerge from the burrow around days 20-22, when the female starts to leave the nest open (Broekhuizen *et al.*, 1986; Rödel, unpublished observations). Weaning generally occurs before day 28 (Mykytowycz and Rowley, 1958; Stodart and Myers, 1964; Lehmann, 1991).

In line with these studies in the wild, a recent series of investigations conducted on a European rabbit population living in a field enclosure, next to the campus of the University of Bayreuth, allowed researchers to confirm and expand some of the peculiarities of the development of wild-type pups born and living in a semi-natural environment.

Milk intake

As in domestic rabbits (cf. section 1), the milk intake per nursing event of individual pups (assessed by the body mass gain of pups) increases rapidly and considerably with age (Figure 2). For the data presented here (n = 172 pups, from 48 litters), the pups were taken out of the natural breeding burrows to be weighed early in the morning (around 06:00), shortly before the mothers visited the nests for nursing, and again around 10:00 after nursing. Even if the data may be somewhat lower as compared to those from domestic rabbits raised in domestic breeding conditions (collected immediately before and after the controlled nursing), the milk intake appears to increase from less than 5 g/pup on postnatal day 1 to more than 15 g/pup on day 17.

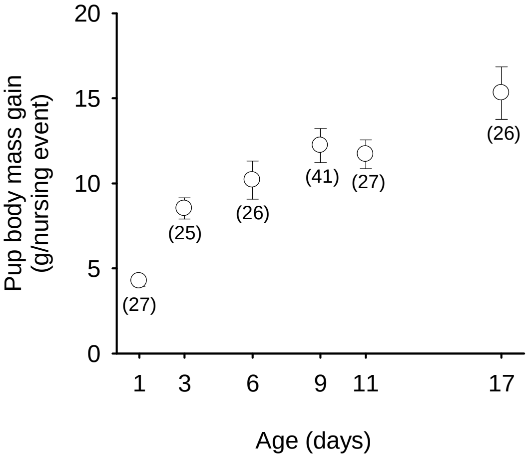

Figure 2: Body mass gain (means ± SE) per daily nursing of wild rabbit pups living in semi-natural conditions during different days of the nest period. Sample sizes are given in brackets; pups of different ages stemmed from different litters, in total 48 (Rödel, unpublished data)

Litter size

Litter size in rabbits varies considerably, usually ranging from 6 to 12 pups in domestic rabbits (depending on the breeds; Brien, 1986) and from 1 to 9 pups in wild rabbits (on average 3.5 to 6 pups, depending on the breeding cycle; von Holst *et al.*, 2002; Rödel *et al.*, 2004, 2005). Although the milk supply of mammalian mothers is reported to be partly adjusted to variation in litter size by the adaptive stimulation of pre-partum mammogenesis (Forsyth and Hayden, 1977; Jameson, 1998), there is evidence from a wide range of species that an increase in the number of siblings reduces the share of milk obtained by individuals. This results in a negative correlation between litter size and growth rates of the dependent young (Mendl, 1988; Mock and Parker, 1997; Hudson and Trillmich, 2007). Such an effect can also be found in the rabbit: there is a clear negative relationship between sibling number and pup growth rates or weaning weight in domestic breeds (Drummond *et al.*, 2000), as well as in European rabbits living under natural breeding conditions (Rödel *et al.*, 2008a) (Figure 3a).

Age and social rank of the mother

Maternal effects are also involved in shaping the postnatal growth of rabbit pups. Apart from litter size effects, the age of the mother indeed affects directly and strongly pre-weaning growth rates of the young. In the population of wild-type European rabbits from Bayreuth, Germany, offspring of middle-aged mothers showed the highest growth, while offspring growth rates of 1-year old mothers and of mothers older than 3 years were comparatively lower (Rödel *et al.*, 2008a (Figure 3b). One-year old rabbit females in natural environments usually have a comparatively lower body mass (Rödel *et al.*, 2004), and thus probably a lower food intake capacity, which might both restrict their lactational performance. In addition, young females usually occupy low social ranks and are frequently more stressed (von Holst, 1998), which might in turn reduce their milk release (Lau and Simpson, 2004). In older female rabbits, reproductive (see Rödel *et al.*, 2004) and lactational performance might be lowered due to reproductive senescence (Kirkwood and Austad, 2000; Tatar, 2001).

Maternal reproductive history

A third factor affecting pup growth in natural or semi-natural conditions is the mother's reproductive history. Due to the rabbit's post-partum oestrus, European rabbit females usually give birth to consecutive litters, starting every year in spring (between late February and late April in Bayreuth; Rödel *et al.*, 2008b). In the German population studied by Rödel and co-workers (2008a), pre-weaning offspring growth was significantly higher in the first litters of the breeding season compared to the following litters (Figure 3c), i.e. pup growth was lower in litters where the nursing females were also pregnant again.

Overall, in comparing these three effects (see the deviations of the residuals from zero; Figure 3a,b,c), it becomes obvious that litter size and maternal age show a comparatively stronger effect on pup growth rates, whereas the effects of the mother's reproductive history are rather small (Rödel *et al.*, 2008a).

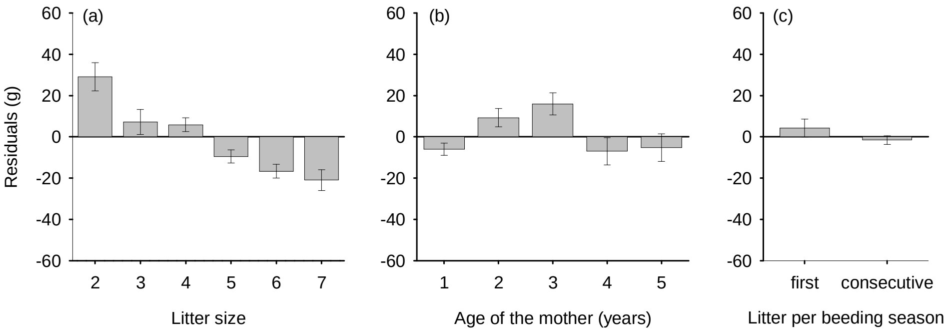

Figure 3: Comparison of residual growth rates (means ± SE) among European rabbit pups raised in natural breeding burrows (a) from litters of different sizes, (b) from mothers of different age and (c) from mothers' first or consecutive litters per breeding season. Data represent averaged growth rates from postnatal day 1 to 12 over all pups per litter (90 litters from 69 different mothers). Residuals in each graph represent the unexplained variation of the model including the other predictors, respectively. All three effects were statistically significant (Rödel *et al.*, 2008a)

Temperature

The thermal environment is another important factor affecting the growth rates of rabbit pups. While the temperature under laboratory conditions is usually kept stable (around 20°C), wild rabbit pups have to deal with a very wide temperature range in their natural breeding burrows. Studies on the population in Bayreuth, Germany, revealed that soil temperatures in 50 cm depth varied considerably across the breeding season, ranging from 3 to 21°C (Rödel *et al.*, 2008b). Such differences can strongly affect the metabolic rates in altricial young, which are involved in maintaining stable the body temperature, and can therefore affect the growth rate (Hull, 1973; Leon, 1986). For instance, the growth rates in medium-sized litters was found to be higher than in small litters under cold environmental conditions, despite the higher number of competitors for the mother's milk supply (Rödel *et al.*, 2008b). This shift in the optimal litter size for individual pup growth in response to the ambient temperature was most probably due to the thermal benefits of a greater number of littermates (Gilbert *et al.*, 2007).

SENSORY DEVELOPMENT OF YOUNG RABBITS BETWEEN BIRTH AND WEANING

Young rabbits develop very rapidly, despite the parsimonious pattern of maternal care. Thus, the birth weight may increase as much as 12-fold in less than 4 weeks (Hudson *et al.*, 1996a). Such rapid development ends in the weaning of the young, a mother-young separation that occurs relatively abruptly, especially when the female is pregnant again (Hudson *et al.*, 1996b; González-Mariscal and Rosenblatt, 1996). The sensory abilities of the pups, although initially limited, are highly specialised in newborns. Thereafter, sensory-motor performances are undergoing rapid changes that are causal and consequential to changes in social and feeding conditions.

Postnatal week 1: Total reliance on olfaction and somesthesis

Rabbit pups are altricial: they are born glabrous, devoid of audition and vision, and with limited motor abilities. However, they are equipped with well-developed somesthesic and chemosensory systems, which are both functional from the end of the uterine life. Thus, rabbit newborns orient efficiently following gradients of thermo-tactile stimulations (Pacheco-Cobos *et al.*, 2003) and odours emanating from the maternal body (Schley, 1976, 1979; Hudson and Distel, 1983, 1986; Coureaud and Schaal, 2000; Coureaud *et al.*, 2001). In particular, odour cues and at least one well-characterized pheromone guide them to achieve the behavioural sequence necessary to obtain milk: contacting the female's abdomen, locating a nipple by searching movements, and orally seizing it to suck.

The sensory-motor capabilities of newborn pups also support the rhythm activity that they rapidly display in the nest after nursing. In the minutes after the female leaves the nest, the pups urinate and the litter disperses by digging into the nest materials. Once covered by these insulating materials, the pups reunite again for several hours in a quiet huddle in the depth of the nest, a collective behaviour allowing regulation of individual body temperature (Hudson and Distel, 1982; Gilbert *et al.*, 2007). Then, 1-2 hours before the next nursing episode, the pups become again restless, collectively emerging from the nest materials and remaining grouped at the surface. This vertical movement of the litter in the nest is considered to be anticipatory to the female's entry and preparatory to the immediate expression of searching and sucking behaviour (Hudson and Distel, 1982; Jilge, 1993, 1995; Bautista *et al.*, 2003).

During this period of development, the pups' masticatory abilities are poor. However, from days 3-4 peaking around days 7-8, they begin to nibble nest materials and the faecal pellets that the female drops in low quantity in the nest during nursing (Mykytowycz and Ward, 1971; Hudson *et al.*, 1996a, 1996b; Kovacs *et al.*, 2004; Moncomble *et al.*, 2004). Olfaction is involved in this attraction to the faecal pellets, which constitute their first contact with non-milk compounds (Moncomble *et al.*, 2004, 2006).

Postnatal week 2: emergence of audition, vision and mastication

From days 7-8 pups begin to hear (Gottlieb, 1971; Ripisardi et al., 1975). But they still remain in the nest to be nursed, under both domestic and wild conditions. Their eyes open between days 10-13, and it is approximately at the same period that the first oral manipulations of solid food and mastication can be seen (Langenbach *et al.*, 2001). In addition to the faecal pellets, pups may then bite through and ingest the nest materials, a presumable cause of decreasing amount of materials in the nest (females have also been observed eating nest materials; Hudson and Altbäcker, 1994; Coureaud, unpublished observations). By the end of the 2nd week, domestic pups begin to leave the nest and to ingest food pellets. The role of olfaction relative to vision in this initial orientation to the feeder remains to be investigated. In domestic conditions, rabbit pups also become able to solicit the mother for nursing, a solicitation that may occur independently from individual pups throughout the day, and lead to harassment of the female who finally tends to avoid the litter (Stauffacher, 1992; Mirabito *et al.*, 2004). In the wild, pups have sometimes been seen to start emerging from the nest and breeding chamber from days 12-13 (Broekhuizen *et al.*, 1986), but they rapidly returned into the burrow when the female closed it.

Postnatal week 3: sensory changes to localize, seize and ingest milk and solid food

At the end of the 3rd week, milk yield begins to rise to a maximum level, and so does milk consumption in young (in mass). In domestic conditions, pups leave the nest-box, easily locate the mother by vision, and almost systematically initiate sucking. They also progressively increase their consumption of solid food and water, supported by co-occurring sucking and fully functional chewing abilities (Langenbach *et al.*, 1992). However, milk intake remains higher than non-milk food intake until day 25 (Langenbach *et al.*, 1992; Scapinello *et al.*, 1999). In the wild, the young increasingly come up to the burrow entrance, where they are nursed. By observing this situation by video recordings in the field enclosure of a population of European rabbits from Bayreuth, Rödel (unpublished data) explained that when the pups reach an age of about 15-16 days, they approach the mother outside the breeding burrow once she has opened the soil sealing, are nursed in front of the entrance, and then immediately return into the burrow at the end of nursing before the mother closes the entrance again with soil. Similar observations are reported by Broekhuizen and Mulder (1983) and Lehmann (1991) in other wild populations.

Postnatal week 4: weaning

By now, the sensory equipment of the pups achieves excellent functional properties, which commensurate with the challenge of reaching social and feeding autonomy. In the wild, as well as in rabbitries, the females progressively cease to nurse, enforcing the young to ingest solid foods. This process is accelerated when the female is pregnant again. Then, she may even display agonistic behaviours towards her young (Mykytowycz and Ward, 1971). As previously stated, weaning usually occurs between days 28-35 in domestic conditions, and before day 28 in the wild.

CHEMOSENSORY COMMUNICATION BETWEEN MOTHER AND YOUNG

Several studies run during the last decades have highlighted the major role of female's odour cues in the rabbit newborns' searching and oral seizing responses directed to the nipples. These studies exploited different experimental tests, such as the inactivation of the pups' olfactory system (Schley 1981; Distel and Hudson, 1985; Hudson and Distel, 1986), the deodorization by washing or selective covering of the female's mammary areas (Müller, 1978; Hudson and Distel, 1983; Coureaud *et al.*, 2001), choice tests between odours from adult conspecifics contrasted in physiological state (Hudson and Distel, 1984; González-Mariscal *et al.*, 1994; Coureaud and Schaal, 2000), and the manipulation of the fetal and/or neonatal chemosensory experience (Semke *et al.*, 1995; Coureaud *et al.*, 2002). Here, we sum up some results of these experiments and present some recent ones, emphasizing the involvement of two kinds of maternal stimuli: odour cues that depend on pre- and postnatal learning and predisposed odour signals.

Odour cues acquired before birth

As in other mammals (Schaal *et al.*, 2001; Schaal, 2005), fetal rabbits acquire odour cues *in utero*, and such stimuli are generally attractive in the postnatal environment.When simultaneously exposed to the odour of placentae and to a (non-specific) control stimulus, rabbit pups preferentially orient to the former, indicating that they prefer familiar cues from the prenatal environment. Moreover, pups born from females that had eaten cumin during pregnancy orient preferentially to placentae from cumin-eating females as compared to placentae from females eating standard food (Coureaud *et al.*, 2002). Thus, rabbit pups are born with the memory of a dominant odour encountered *in utero*, and orient to it postnatally.

Similar results were obtained with other aromas introduced in pregnant females' diet, suggesting a general phenomenon (Semke *et al.*, 1995; Coureaud *et al.*, 2002). Further, pups born from females eating cumin-enriched food during pregnancy respond preferentially to the milk from such females as compared to the milk from females eating control food (Coureaud *et al.*, 2002). Thus, there is chemical overlap between pre- and postnatal environments, and newborns are sensitive to this transnatal continuity that may canalize their orientation to the mother and her milk. When this continuity is experimentally broken by cross-fostering pups born to a cumin-eating female to a lactating female that does not ingest cumin, they present difficulties to suck during the first nursing episodes, as compared to pups that are fostered to a lactating female whose feeding regimen is similar with that of the biological mother (Coureaud *et al.*, 2002). Thus, odours cues may gain significance in the postnatal environment by their mere presence in the prenatal environment.

The odour of rabbit milk

Rabbit newborns do not respond to the whole odour of rabbit milk just because they detect odour cues prenatally learned. Indeed, they also display strong appetitive responses to the milk of their species (i.e., the milk of any rabbit female), regardless of the fact that it carries a dominant odour encountered prenatally (Coureaud *et al.*, 2002). Thus, pups are sensitive to different odour cues in rabbit milk: those related to the individual mother (odours that reflect her diet or stress level) and those that are common to all lactating *Oryctolagus* females.

After exposing pups to the outlet of a chromatograph where they could sniff all the compounds from the effluvium of fresh rabbit milk, a monomolecular volatile compound, 2-methylbut-2-enal (2MB2), has been isolated and identified as a species-specific odorant (Figure 4a) (Coureaud, 2001; Schaal *et al.*, 2003). This compound is extremely efficient in releasing the typical searching-oral grasping behaviour in 2-3-day old pups (> 90% of the tested pups respond to it in a given range of concentration; Coureaud *et al.*, 2004). It has been screened for its possible pheromonal properties, according to a stringent definition of mammalian pheromones based on 5 criteria (Beauchamp *et al.*, 1976; Johnston, 2000).

A series of experiments confirmed that: (a) the behavioural activity of 2MB2 was similar to that of the whole effluvium of fresh milk, a mixture of more than 150 volatile compounds: this *chemically-simple signal* could thus by itself explain the activity of the original, entire mixture; (b) 2MB2 triggers relatively *invariant behavioural responses* (attraction, searching-oral grasping movements) *having a critical function for pups*, in that they are essential in the interaction with the female and in the achievement of milk intake; (c) the behavioural effect of 2MB2 is highly *selective* (and is not explainable in terms of a novelty effect or of a general attraction); (d) the behavioural effect of 2MB2 is *species-specific*, meaning that only pups from *O. cuniculus* respond to it without regard to their genetic origin or local feeding ecology (reciprocally milk from rats, ewes, cows, mare and women do not trigger any response in rabbit pups); (e) rabbit pups *do not learn* to respond to 2MB2 by previous exposure (*in utero* or right after birth), meaning that its activity is predisposed.
In sum, as 2MB2 satisfied these 5 criteria, it qualified as a mammalian pheromone. Moreover, as it appeared to be produced or liberated in the mammary tract (Moncomble *et al.*, 2005), 2MB2 was named "mammary pheromone" (Coureaud, 2001; Coureaud *et al.*, 2002, 2003; Schaal *et al.*, 2003).

A signal immediately active at birth and progressively controlled during the development

The behavioural activity of the mammary pheromone (MP) is extremely strong in newborn rabbits, even in normal term pups tested before any contact with the mother and milk, or in preterm pups born by caesarean delivery (Coureaud, 2001; Schaal *et al.*, 2003). As the MP releases responses that newborn pups display to locate the nipples and ingest milk, it may be suggested that its main function is to favour the success of sucking. This hypothesis has been tested in a sample of domestic rabbits housed in a rabbitry (n=293 pups from 30 litters). On day 1 (day of birth = day 0), before the daily nursing, all newborns were individually weighed and then tested for their response to the MP; these pups were weighed again after nursing to assess whether those who did not respond to the MP had difficulties in gaining milk. Moreover, mortality was checked between days 0 and 21. Results on day 1 showed that the rate of pups who did not respond to the MP was weak (8.7%). But interestingly, these non-responders ingested less milk than the responders, especially among the lightest pups (< 48g). Moreover, mortality was higher between days 1-21 among the non-responders than among the responders, and occurred mainly during the first postnatal week (Figure 4b) (Coureaud *et al.*, 2007). Thus, in this study, to respond or not respond to the MP makes a difference for pups in terms of early success in milk intake and subsequent viability (as do the birthweight and the weight gain during the first nursing bouts). This result illustrates the functional impact of the MP. The management implications may lead to the selection from among the lightest pups, which are those that cannot efficiently compete under the mother, and to reunite them to optimize their welfare and survival.

However, if the pup responsiveness to the MP is generally very high at birth, it is progressively coming under the control of at least two factors. First, the responsiveness changes as a function of the pup prandial state. During the first 3 postnatal days, rabbit pups respond to the MP at any period during the day without marked influence of their gastric filling with colostrum or milk. By day 5, the pattern slightly changes: when independent groups of pups are exposed to the MP at various periods in the 24-h cycle, their responsiveness remains high before milk intake, but it drops significantly after, with some recuperation 3h later. On day 10, the responsiveness to the MP remains high before nursing, but it decreases again, without recuperation during 12h (Montigny *et al.*, 2006). Summing up, it appears that the responsiveness of young rabbits to the MP develops in two steps during the first week. From birth to day 2 (at least), it is highly predictable and free from any feedback by post-ingestive events. Then, between days 5 and 10, the responsiveness to the MP comes under prandial regulation, remaining high only when the energetic need is high (before nursing). This fits well with the hypothesis that the MP is a signal that has its highest releasing power when pups require the milk starter to engage in survival, and when they need to refill their energy stores (as mentioned above, missing the 2-3 first nursing bouts jeopardizes survival; Coureaud *et al.*, 2000b).

Secondly, the responsiveness of young rabbits to the MP decreases with approaching weaning, even before the daily nursing. The developmental analysis of orocephalic responses (searching-oral grasping) of pups to the MP between birth and weaning reveals that responsiveness: (1) is maximal over the first 10 postnatal days; (2) begins to decrease after the eyes open; (3) continues to decrease when pups leave the nest and ingest solid food; and finally, (4) vanishes around weaning (Coureaud *et al.*, 2008; Figure 4c). Similarly, wild-type pups (from the population studied under natural seasonal variations by the Bayreuth group) show high levels of responsiveness to the MP during the first postnatal week. But their response rate drops as soon as day 10, and becomes almost null on day 22 (Figure 4c). In other words, rabbit pups of any genotype respond maximally to the MP during the first days of life, a point that further reinforces the notion of a signal acting as a message optimizing the newborns’ sucking success and fitness. Around weaning, the need for milk weakens, and a lesser dependence to the MP may favour detachment from the mother and acquisition of autonomy. Interestingly, the weakening of the releasing power of the MP goes hand in hand with its decreasing emission in milk in late lactation (Figure 4d; Coureaud *et al.*, 2006a). It is also remarkable that the responsiveness of wild-type pups to the MP vanishes earlier than in domestic pups. It may be suggested that this disparity is a consequence of domestication, domestic breeds having been selected for milk yield, body mass, and offspring growth. Their lactational period is thus longer than that of wild-type females (peaking on days 20-25, at an age when dispersion may have begun in the wild; Lebas, 1971; Broekhuizen *et al.*, 1983, 1986; Scapinello *et al.*, 1999; Coureaud *et al.*, 2008). Thus, domestic pups may remain responsive to the MP for a longer period since they are dependent on milk for approximately one week more than wild pups. Regardless, domestic pups also finally lose their sucking-related reactivity to the MP close to weaning.

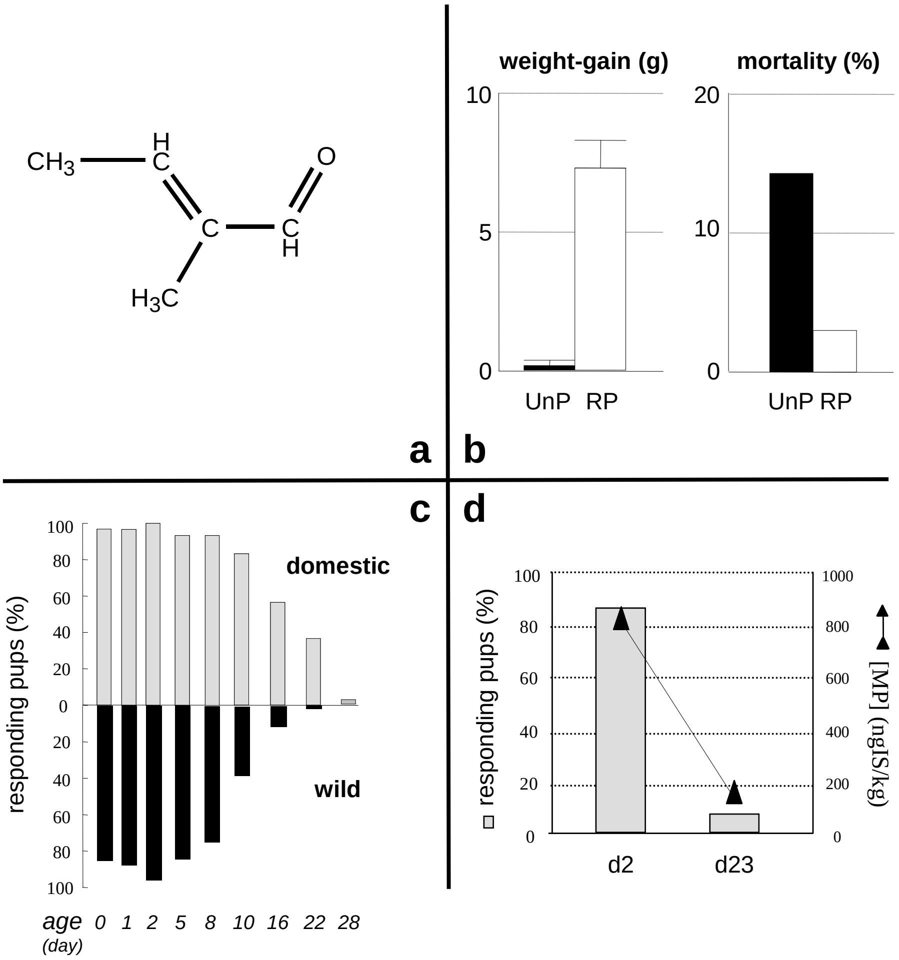

Figure 4: The mammary pheromone of the rabbit: (a) Formula of the 2MB2; (b) Weight gain during the day 1-nursing episode and mortality between day 1 and day 7 of pups unresponsive (UnP) or responsive (RP) to the MP on day 1; (c) Responsiveness of domestic (grey bars) or wild-type pups (black bars) to the MP between day 0 (birth) and day 28; (d) Proportion of pups responding to the milk from females in their 2nd or 23rd day of lactation, and mean concentration of MP in the milk of these females *(data in panels b, c, d are adapted from Coureaud et al., 2007, 2008 and 2006a, respectively)*

A signal that boosts the acquisition of new odour cues

Similar to other newborn mammals, newborn rabbits have to rapidly acquire novel information from their immediate environment. Learning is indeed a requisite to adapt one's behaviour to the unavoidable fluctuations of the environment (Gottlieb, 1976; Alberts, 1987). As mentioned above, rabbit pups start to learn in the womb, becoming familiar with odorants brought in by the maternal diet (Bilkó *et al.*, 1994; Semke *et al.*, 1995; Coureaud *et al.*, 2002). At birth, the learning abilities of pups are also strongly in demand. For instance, pups exposed to an initially neutral odour added into the nest (in absence of the mother) rapidly acquire the odour and later respond to it by preferential orientation (Hudson, 1993). Postnatal odour learning may thus guide the young to orient to safe spots in its immediate environment. Finally, the direct contact with the female during nursing may be the strongest means to learn odours associated with her. This has been shown repeatedly (Ivanitskii, 1962; Hudson, 1985; Kindermann *et al.*, 1991; Allingham *et al.*, 1999; Coureaud *et al.*, 2006b). In these conditions, it has been revealed that newborn rabbits can learn very rapidly (in only one exposure) an artificial odour painted on the mother's abdomen just before nursing: When this odorant is re-presented 24h later on the experimenter's hand, on a tanned rabbit fur, on an anaesthetized female or on a glass-rod, it releases the typical searching movement and, with the glass-rod, the complete searching-oral grasping sequence. Thus, some events during nursing act as reinforcers, transforming an initially neutral odorant into a meaningful odour cue. The candidate reinforcers are numerous in the nursing situation: they can involve tactile or thermal properties of the mother's pelt, the taste of milk, gastric filling or post-absorptive events, or even the pups' expression of searching or sucking motions. In an attempt to identify the nature of these reinforcers, Hudson *et al*. (2002) suggested that the intra-oral stimulation produced by the sucking of a nipple plays the key-role in early odour conditioning.

However, when they contact the maternal abdomen to suck, rabbit pups are also exposed to the MP carried in milk. One might therefore wonder about the capacity of the MP to influence their odour learning. When newborn rabbits are exposed for 5 min to a mixture of MP and an initially neutral artificial odorant (in absence of the mother), they exhibit a strong searching-grasping response when re-exposed to the odour alone 24 h later (Coureaud *et al.*, 2006b). In other words, they then respond to the initially neutral odour as to the MP. Thus, the MP directly contributes to an effective mechanism that facilitates the very rapid acquisition of novel odour cues, in particular odours carried on the mother's ventrum.

The adaptive consequences of such MP-induced odour learning may be numerous and some are still under investigation. For example, (1) it may expand the range of odorants that predict milk reward to pups, and hence may facilitate their orientation to the mother and improve their skill to localize the nipples (Müller, 1978; Drewett *et al.*, 1982; Hudson and Distel, 1983); (2) in a species in which newborns do not appear to olfactorily discriminate their mother from unfamiliar lactating females (at least in domestic conditions and during the first postnatal week; Patris *et al.*, in press; Val-Laillet and Nowak, in press), the MP-induced odour learning may affect early social recognition. Recent results indeed suggest that 2-3-day old rabbits having learned an odour paired with the MP orient preferentially to their mother, or to an unfamiliar female scented with that odour (Patris *et al.*, in press); (3) finally, it may also be suggested that the MP promotes the early acquisition of odour cues that will be used later, in particular when the young have to select safe foods and optimal mates. MP-induced odour learning may thus influence feeding preferences and mate choice after weaning, as other forms of perinatal odour learning were shown to do (Bilkó *et al.*, 1994; Altbäcker *et al.*, 1995).

CONCLUSIONS

To face the multiple constraints of reproduction, mother and young European rabbits have co-evolved a set of physiological, sensory, cognitive and behavioural adaptations. These adaptations allow efficient mother-young exchanges immediately following birth, despite the brevity of their daily contacts. These exchanges are first centred on the efficient transfer and intake of milk, and on the effective transformation of this energy into pups' body mass. These mother-young exchanges are highly dynamic to optimise survival of the present litter and maximise the chances to bear the next one. One point in these dynamic exchanges is to bring the pups to weaning somatically fit and endowed with predictive information about their environment.

In the present paper, we have surveyed the important changes in feeding and social interaction that occur between birth and weaning in domestic as well as in wild rabbit pups. At first, olfaction plays a crucial role in supporting the neonates in its orientation and oral treatment of the lactating female. During this high-risk life stage, the rabbit female communicates with the young through diverse olfactory means: she promotes odour acquisition in foetuses or in pups, but also sends out unlearned odour signals. Among the latter, the mammary pheromone has an extraordinarily strong potency to release neonatal behaviour and to enforce learning. This pheromonal factor has its highest functional activity in the first postnatal days. After that early period, it becomes progressively under the control of general mechanisms that remain to be explored.

Future studies investigating how and for how long young rabbits detect, process and respond to odours acquired in the maternal environment may contribute to develop breeding procedures aiming to improve pup survival, optimal growth and deferred adaptability when they have to become autonomous. Moreover, *Oryctolagus* constitutes an excellent animal model to address interrogations shared with other mammalian species, including our own, about chemosensory processes functioning during early life transitions (birth, weaning, sexual maturity). In particular, the rabbit offers remarkable conditions to investigate the odour-based mechanisms involved in the development of mother-offspring relationships, and the consequences of early olfactory exposure on the brain and behaviour.

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