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# Role of mother–young interactions in the survival of offspring in domestic mammals

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The defining characteristic of mammals is that females nurse and care for their young; without this, the neonate has no chance to survive. Studies on wild and domestic species show that the neonatal period is the most critical step in the lifetime of a mammal. This review compares three well-studied species (the rabbit, pig and sheep) that differ in their parental strategies and in the problems that neonates have to overcome. As a general trend, mother–young interactions vary according to the maturity of the newborn, and the size of the litter. Neonatal survival relies to a great extent on an environment that is ecologically appropriate for the developmental stage of the neonate, and on optimum interactions with the mother. Adaptive maternal care supposes that the mother provides the basic needs of the neonate: warmth (in pigs and rabbits) or shelter, food, water and immunological protection (via colostrum) and, in some instances, protection from predators and other conspecifics. A major risk facing all neonates, other than the birth process itself, is inadequate colostrum intake owing to delayed suckling or competition with siblings, which leads to starvation, hypothermia or even crushing, as has been observed in pigs.

Behaviours associated with the birth and care of young are essential for the survival of mammals. For the mother, they represent a means of investing in her reproductive fitness; for the young, it is a question of individual survival, as the mother is the only source of food, at least in the early stages of development. The pattern of mother–young interactions varies according to the developmental status of the neonate and the litter size (Gubernick, 1981; Mendl, 1988). In altricial species (canids, felids, most rodents and lagomorphs), the female builds a nest or seeks a sheltered area in which she gives birth to a large litter of young that are not fully developed and have limited sensory and locomotor abilities. Mother–young interactions occur within the nest and do not in general imply mutual recognition. However, precocial species (most ungulates) are characterized by a small litter of fully developed young capable of following the mother shortly after birth. The rapid development of inter-individual recognition and exclusive care is a main feature of these animals. Between these two extremes there is an intermediate type of mammal: the sensory systems of their neonates are functional but thermoregulation is inefficient (suids) and locomotor capabilities are limited (primates). The mothers and neonates of these three types of mammal have to face both common and more specific problems during the perinatal period. In this review, this point is illustrated by considering several contrasting species that have been studied in detail: the rabbit, as an example of an altricial mammal, ruminants (mainly sheep, goats, and cattle) as precocial mammals, and the pig as an intermediate type. Comparisons with additional species will only be included to emphasize converging points or to provide information that is not available in the pre-cited species.

## Parental investment

The evolutionary–genetic consequence of reproduction is the direct transmission of the parents' alleles to the next generation. Individuals who produce a relatively large number of surviving, reproductively capable offspring thereby pass on more of their genetic material than do individuals with lower reproductive success. In mammals, effective reproduction entails considerably more than fertilization, gestation and birth. Neonates are entirely dependent upon the care and resources provided by their mother (as well as paternal care, in some species). Care of offspring is associated with substantial costs to the mother, including the expenditure of metabolic energy for milk production and thermal regulation, and the increased risk of predation resulting from the presence of conspicuous neonates and limited mobility (Clutton-Brock, 1991). Because the mother's resources and reproductive lifespan are limited, postnatal investment in developing young through weaning, and perhaps beyond, ultimately reduces her opportunity to produce additional offspring (Trivers, 1972). Therefore, it follows that natural selection should favour the evolution of mechanisms to ensure that the offspring of a caregiver are the beneficiaries of such parental investment. When a parent's own young are likely to intermingle with unrelated neonates, as commonly occurs in a variety of gregarious mammals, such as elephant seals, reindeer, wildebeests and sheep, mothers rapidly develop the ability to recognize their individual offspring. In this context, parents that respond indiscriminately to their own and alien young jeopardize their own reproductive success, since their offspring are deprived of necessary resources, which are 'wasted' on unrelated young. In contrast, when young are born in isolation from other


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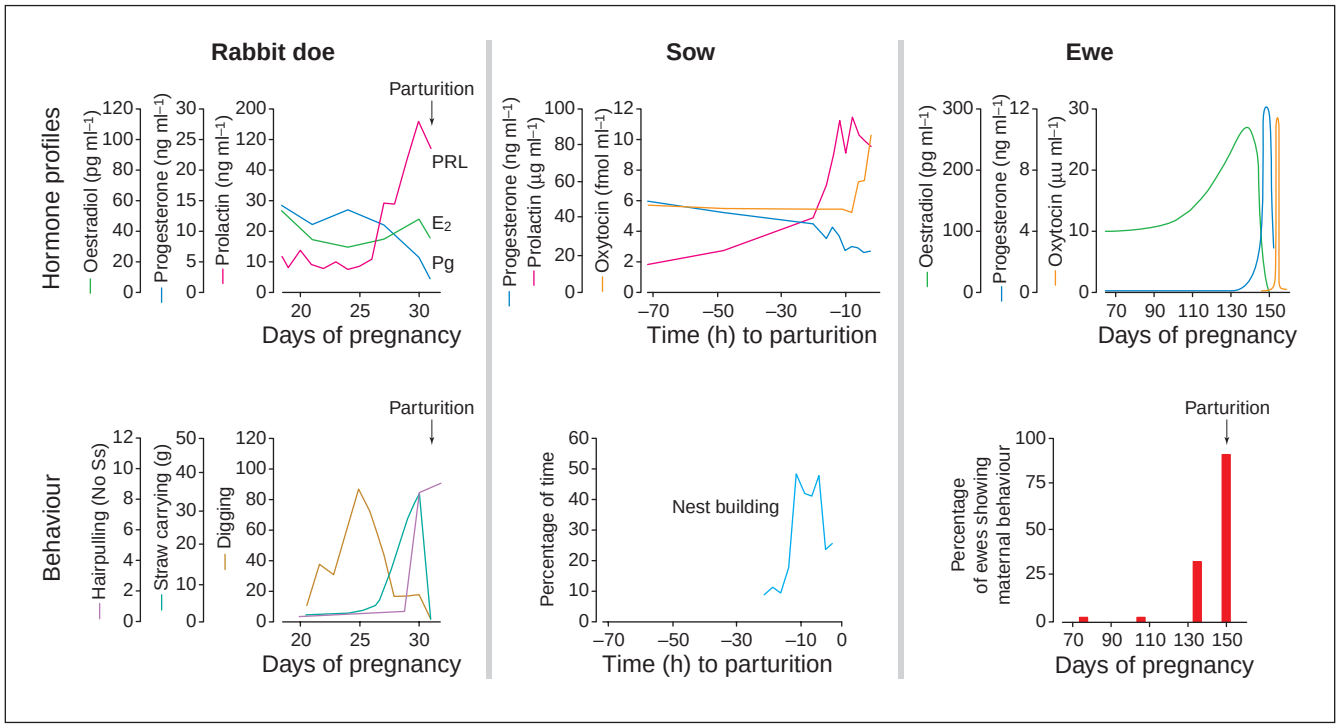



**Fig. 1.** Changes in the plasma concentrations of various hormones during pregnancy in the rabbit doe, the sow, and the ewe (upper panels) and their concomitant maternal responsiveness (lower panels). The elements represented for each species are: (i) digging, straw carrying, hair pulling for the rabbit doe; (ii) nestbuilding (carrying and depositing straw) for the sow, (iii) acceptance of young for the ewe. In rabbits, digging is stimulated by oestradiol and progesterone, while straw carrying and hair pulling is under the control of steroids and prolactin. In sheep, maternal behaviour (low-pitched bleats, licking and nursing) is triggered by changes of plasma progesterone and oestradiol around parturition, and the release of oxytocin in the brain. No data about the endocrine regulation of maternal behaviour is available in pigs but the changes observed at the end of gestation are likely to play some role. (Adapted from Poindron and Le Neindre, 1980; Glatz *et al*., 1981; Castrén *et al*., 1993; Gonzàlez-Mariscal and Rosenblatt, 1996.)

neonates and remain in a den or nest during the period of dependence on maternal care (for example, rabbits, rats and mice), there is little need for the mother to recognize her offspring during that stage of development. Rather, by providing care to all neonates in the parental nest or den, the mother effectively restricts her investment to her own offspring alone. Functionally, this parental strategy is equivalent to one based on discrimination between the parents' own and alien young.

Although young mammals cannot survive without maternal resources, they are not simply passive recipients of parental care. Soon after birth, neonates participate actively in nipple localization and sucking and influence the caregiving behaviour of their mother by communicating their needs to her. Neonates may benefit further by responding discriminately to their own mother. For example, in species in which adults reject, react aggressively to, or even cannibalize strange offspring, it is clearly to the advantage of the neonates to recognize their own mother and avoid unfamiliar adults.

## Mother–young interactions

### *Onset of maternal care: physiological aspects*

Spontaneous maternal behaviour is very rarely observed in females that are not periparturient or lactating. Such females tend to be aggressive towards young or, more often, to avoid them. In fact, the onset of full maternal responsiveness is closely related to the birth process itself, and investigations of the physiological changes related to parturition have shown that they facilitate maternal responsiveness.

The first major physiological event that characterizes the parturient rabbit, sow and ewe is the rapid change in ovarian steroids: a decrease in the plasma concentration of progesterone is combined with an increase in oestradiol (Fig. 1). Oestradiol returns to basal concentrations a few hours after parturition. A parallel increase in prolactin is observed but high concentrations are maintained after parturition because of the sucking stimulation. The second important physiological event is the mechanical stimulation of the genital tract caused by the expulsion of the fetus, which is associated with a short but important release of oxytocin, which, like prolactin, is later maintained by sucking activity.

In rabbits, it is maternal nest building that has received particular attention. Hormone treatments have shown that oestradiol and progesterone stimulate specific motor patterns observed before parturition, such as digging. Straw carrying, which is initiated after digging, is observed after progesterone withdrawal and continuation of oestradiol treatment. Hairpulling is also observed after progesterone withdrawal but affects only 40% of treated does (Gonzàlez-Mariscal *et al*., 1996).

Aside from progesterone and oestradiol, other hormonal factors are involved. Straw carrying and hair pulling, but not digging, are abolished in bromocriptine-treated animals, indicating a role for prolactin (Gonzàlez-Mariscal and Rosenblatt, 1996; Fig. 1). Little is known of the endocrine basis of maternal behaviour in sows. Widowski *et al*. (1990) reported that it is the increase in prolactin rather than changes in steroid concentrations in periparturient females that is important for triggering nest building. However, Castrén *et al*. (1993) showed that nest building starts when prolactin concentrations increase and ends when oxytocin begins to increase, and suggested further that progesterone may influence the amount of time spent carrying and depositing nesting materials (Fig. 1). In sheep and goats, ovarian steroids do not seem to be directly responsible for the onset of maternal care. Although progesterone and oestradiol may induce maternal responsiveness in nonpregnant ewes, high doses are required and, even then, only a few characteristics of maternal behaviour are expressed (Lévy *et al*., 1996; Fig. 1). Rather, it appears that steroids may have a priming role, allowing the expulsion of the fetus to trigger this behaviour. Thus, 80% of ewes primed with ovarian steroids and experiencing 5 min of vagino–cervical stimulation developed complete maternal behaviour in response to the presentation of a newborn lamb. By contrast, only 20% of females did so in the absence of such mechanical stimulation (Lévy *et al*., 1996). So far, attempts to demonstrate that prolactin plays a role in the onset of maternal behaviour have failed. The neuroendocrine and neuroanatomical changes that occur in the brain of parturient domestic mammals have been investigated only in sheep (Lévy *et al*., 1996). A major neurotransmitter that increases markedly in the cerebrospinal fluid at parturition is oxytocin. Intracerebroventricular injections of oxytocin induce maternal responses in oestrogen-treated females. However, as for vagino–cervical stimulation, oxytocin is ineffective when given without oestrogen priming. Other neurotransmitters (for example, opiates and corticotrophin-releasing factor) can modulate the effect of central oxytocin. Among the numerous sites of oxytocin release during parturition, the paraventricular nucleus and the medial preoptic area appear to be responsible for triggering maternal behaviour. Infusions of oxytocin in the paraventricular nucleus induce full maternal responsiveness whereas, in the medial preoptic area, they reduce only rejection behaviour towards newborn lambs. Thus, oxytocin could act at different sites to exert its effects on different components of maternal behaviour.

### *Onset of maternal care: behavioural aspects*

Females approaching parturition show behaviour patterns that vary according to the species. A striking example is the nest building displayed by lagomorphs and suids. Female rabbits dig a burrow and collect straw and grass from the neighbouring area. Loosening of the ventral hair precedes the initiation of nest building by a short time, and the hair is then pulled and used to line the nest, a behavioural feature unique to mammals (Gonzàlez-Mariscal and Rosenblatt, 1996). Wild sows build a nest of grass and small branches in an undisturbed place away from other adults. Although domestic sows and does kept under intensive rearing husbandry do not have the opportunity to perform such activities in their farrowing pens or nest boxes, free-ranging females display prepartum behaviour similar to that of their wild counterparts (Deutsch, 1957; Jensen, 1986). The fact that nest building has been retained in spite of domestication indicates how robust this maternal behaviour is. The importance of a nest for lagomorphs and suids is evident when the developmental stage of the neonates is considered. Young of these polytocous species are small, lack fur and have reduced thermoregulatory abilities, depending to some extent on an external source of heat, or at least on a mechanism of heat conservation. A nest serves this function, as does the marked tendency of the young to huddle close together in a cluster. At parturition, the mother rabbit licks her young, ingests the placenta and engages in nursing (Hudson *et al*., 1999). However, sows are characterized by rudimentary maternal care and the piglets free themselves from their fetal membranes without assistance. The sow devours the placenta but does not lick her neonates, nor does she assist them in their teat-seeking activity. During farrowing, the sow usually stands, turns around (if untethered) and lays down again, a very critical stage for the neonates as there is a risk of being crushed. Placentophagia is extremely common in parturient mammals. In species giving birth in a nest, its main function may be to keep the nest site clean. Furthermore, the supplement of proteins and hormones provided by the placenta may facilitate expulsion of the next young and regulate lactation (Kristal, 1980).

In goats, sheep and cattle, most preparturient females show a strong tendency to isolate themselves from the flock (Allan *et al*., 1991; Lidfors *et al*., 1994), a behaviour that is more likely around parturition at subsequent pregnancies. Isolation is an important preliminary step in the formation of the mother–young bond as it protects the dyad from disturbances by congeners and predators, and facilitates early interactions. In some species, isolation is maintained by vigorous aggression towards other females. However, not all the ungulates seek isolation at the approach of parturition. African buffalos or wildebeest, for example, give birth within the herd, a behavioural adaptation that may have been shaped by the communal defence against predators observed in the former species, and the tendency of the latter to congregate in huge herds during their annual migration (Estes and Estes, 1979).

There is little knowledge of the precise environmental features that are attractive to parturient females. Mountain sheep are said to be attracted to the security of high cliffs (Geist, 1971) while Soay sheep and feral goats usually seek a sheltered site (Shillito and Hoyland, 1971; O'Brien, 1984). Peripartum behaviour in ruminants is characterized by a number of very typical components. Within a few minutes after parturition, the mother licks the neonate and the fetal fluids that are spilled on the ground. The birth membranes are also consumed during the cleaning process. It has been shown in ewes, and less clearly in cows, that the birth fluids are normally repulsive but become temporarily attractive at parturition (Poindron *et al*., 1993; Lévy *et al*., 1996). This attraction highlights the primary importance of olfaction for the establishment of maternal behaviour. In sheep, suppression of visual or auditory cues from the lamb, and licking or nursing is without consequences. By contrast, suppression of olfactory cues is detrimental for maternal acceptance (Poindron and Lévy, 1990). In primiparous ewes, the lack of fetal fluids on the newborn leads to an

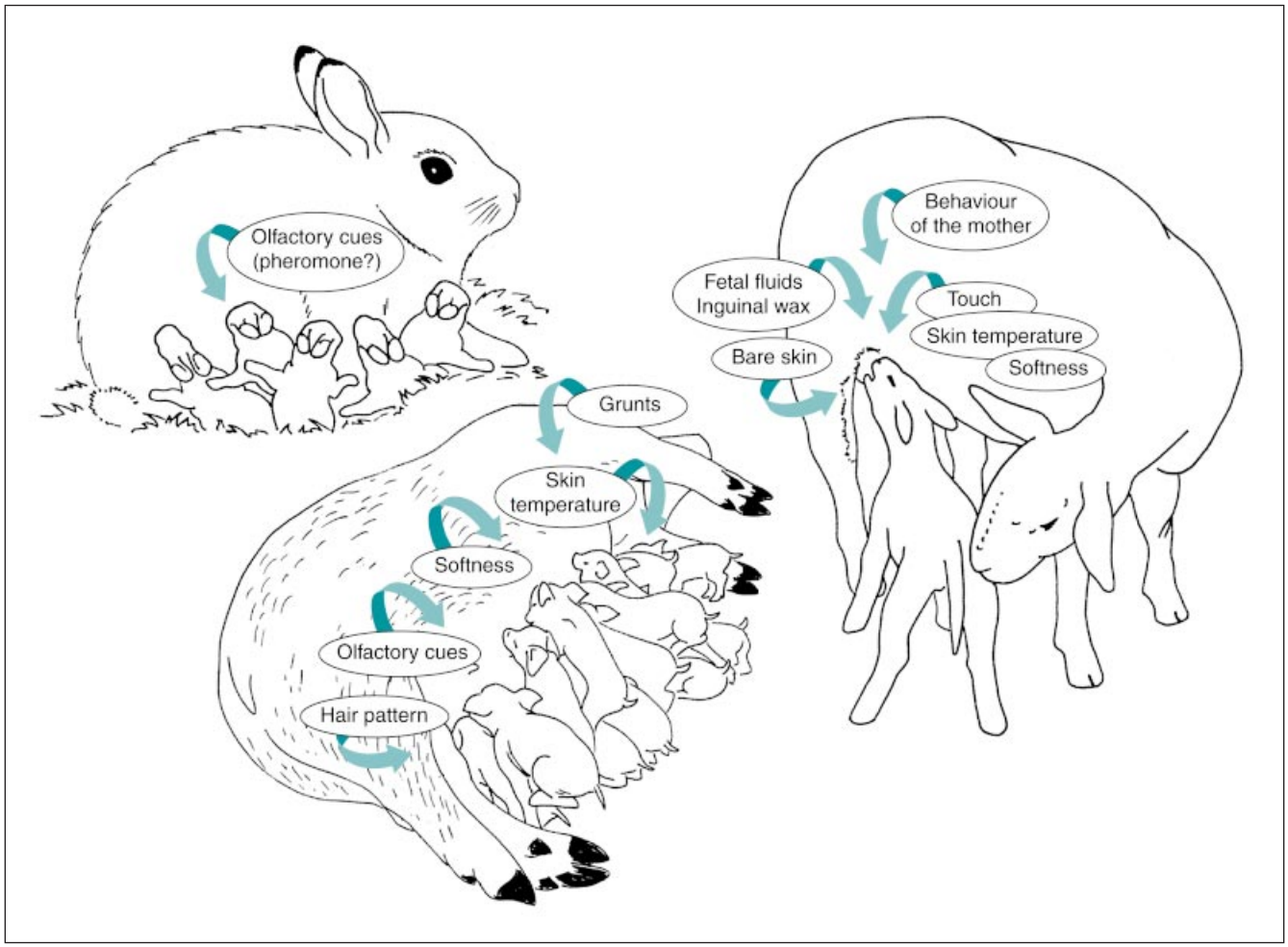



**Fig. 2.** Comparison between rabbit pups, piglets and lambs in the sensory cues used in their initial search for the teat (Drawings by R. Nowak).

absence of licking, refusal to nurse and aggressive behaviour. Several functions of grooming have been postulated, mostly with little or no experimental evidence. Grooming usually starts at the head, as failure to remove the fetal membranes from the face could lead to suffocation. Removal of the birth fluids may help dry the coat of the neonate and reduce heat loss. Licking may also stimulate the teat-seeking activity of the young. Moreover, it may contribute to early bonding, enabling the dam to learn the odour of her offspring. Placentophagia is sometimes seen in sheep but is particularly common in species that hide their young after parturition, such as Cervidae (Leuthold, 1977). This behaviour is believed to minimize the risk of predation by removing olfactory traces from the birth site. Additional direct effects on the physiology of the mother, such as improved milk production, have been reported in cattle (Kristal, 1980). Numerous vocalizations of low intensity are emitted at the time of parturition and are thought to orient the young towards the maternal body and to provide cues for later recognition of the mother. It has been further suggested that, in prey species, natural selection has favoured vocal communication of low intensity between mother and young as a strategy to avoid attracting predators, as these sounds can be perceived only at close contact.

### *Teat seeking and nursing behaviour*

Immediately after birth, the neonate is highly aroused as a consequence of the general stimulation of the birth process. This sustained arousal promotes exploratory movements of the mother's body and brings the neonate into contact with sensory cues that facilitate location of the udder (Fig. 2). In rabbits, the mother emits an odour signal from her ventrum that is perceived by the main olfactory system of the newborn pups. This olfactory signal triggers stereotyped nipple-searching behaviour, even in the absence of prior sucking experience (Hudson and Distel, 1983). Most surprisingly, mother–young interaction occurs only during nursing, which takes place once a day during a period of 3–5 min with an extraordinary circadian periodicity. During this short nursing episode, the young must locate the nipples and suck enough milk to sustain them for the next 24 h. In suids, the mother remains recumbent during parturition, which allows the young to follow the

surface of her body until they reach the ventrum, sometimes after making contact with the sow's snout, indicating an attractive role of her grunts. Several olfactory, tactile and thermal cues provided by the sow are used by the piglets to locate the udder (Rohde Parfet and Gonyou, 1990). The mother's hair pattern also assists the neonate as piglets consistently move with the direction of hair growth. Firstborn piglets spend less time searching for the udder than those born late, as there is considerable fighting over the selection of a teat with increasing litter size. Once a teat is grasped, the piglet obtains milk continuously and can suck from several teats as long as there is no competition. It is only at 12 h after the end of parturition that the release of milk becomes cyclic, and the sow develops a regular sequence of lactation. Piglets form a teat order after about 4 days, and then each piglet goes to its own teat (de Passillé *et al*., 1988). The stability of the teat order depends on the milk supply of the sow: it is maintained if the supply is adequate, but will be broken if it is inadequate, as the piglets will seek more milk. Sight, smell and recognition of neighbours are involved in the location of the teat and the maintenance of the teat order.

Lambs, and probably most ruminants, are attracted to their mother by sight and hearing (Vince, 1993) and the first contact is made with her chest or flank. Thereafter, the udder-seeking behaviour is under the guidance of thermotactile and olfactory cues (Vince, 1993). Touch on the face strongly activates oral exploration and orientation movements of the head, but the intensity of the response depends on the characteristics of the stimulus: lambs respond preferentially to warm, smooth, non-woolly, intermediate yielding surfaces. There is also evidence that the wax secreted by the inguinal glands, as well as the fetal fluids covering the udder, may act in combination with tactile stimuli to activate udder seeking behaviour (Vince and Ward, 1984; Schaal *et al*., 1995). In addition, when the lamb approaches the udder area, the ewe adopts a suckling posture (back arched, hind legs extended) which raises the teats and makes them more prominent. In their first days after birth, lambs are allowed to suck at any time and for as long as they wish (Ewbank, 1967). Afterwards, the ewes begin to restrict the frequency and duration of the suckling episode, generally by walking away from the lamb if it attempts to suck.

### *Hiders and followers*

Studies of ungulates have led to the generalization that the young may be roughly classified into two groups according to their type of spatial relationships with the mother: 'hiders' and 'followers' (Lent, 1974; Ralls *et al*., 1986). In 'hiders', mother and young are separated during most of the early postpartum period. The process of concealment appears to be initiated by the offspring, and regular changes in hiding places are observed. During the hiding phase, which lasts for several days or weeks, depending on the species, the young have limited daily contact with the mother only at nursing. Such behaviour has been observed in goats, cows, red deer, roe deer and pronghorn antelope. Hiding is thought to reduce the predation risk in closed habitats but may also protect the young from intraspecific aggression. In 'followers', the young stay close to their mother and join the flock very soon after birth. Suckling is very frequent and, when danger is sensed, the young show a strong flight response in imitation of the mother or other adults. Following has been viewed as a strategy for avoiding predators in open habitats and is often associated with migratory habits or defence of the young against predators. 'Followers' include mountain and domestic sheep, caribou, wildebeest, bontebok and bison. However, ungulates with intermediate behaviour have also been described. Thus, a third class labelled 'defenders' (Ralls *et al*, 1986) has been characterized by females that may leave the young alone while foraging but rest close to them and defend them against predators at other times (for example, moose and oryx).

### *Defence of the young*

The vulnerability of young to predators has shaped various behaviours considered to be anti-predator strategies in adults, some of which have been described in the previous sections. In some species, active defence of the young is displayed by the mother or other members of the group (Leuthold, 1977). Rabbits defend their litter against ravens and even brown hawks (Mykytowicz and Dudzinski, 1972). In suids, mothers are very reactive to the squeals of piglets. When danger is sensed, the young gather around the mother who may defend them with success. Several studies on African ungulates have reported physical attacks against predators by the mother or attempts to disrupt the chase (Leuthold, 1977). In African buffalo, an entire herd of adults may react to the distress call of a calf, and the musk ox is unique in its successful use of social defence against wolves. Domestic sheep have been observed to remain undisturbed in the presence of foxes but can repel ravens (Alexander *et al*., 1967), and Geist (1971) reported that mountain ewes were much less protective than larger mountain goats with their lethal horns.

## Recognition between mother and young

Indiscriminate care of young by adults is rare among animals. Preferential treatment of the biological offspring of an individual is often based on the ability of the parent to discriminate between its own and alien young. The same applies to the recognition of the mother by the young. An animal will use phenotypic traits, the 'kin signature', to distinguish between a relative and non-kin. However, in some species, true recognition of individuals is lacking. Rather, parental behaviour is based on spatial proximity and implies that there is a high probability that animals within a given location (such as the nest) will be genetically related to the parents. As a consequence, animals respond preferentially to all others found within the given location. This has been demonstrated in Belding's ground squirrels by Holmes (1990) and is likely to be the rule for most altricial mammals: parent–offspring recognition is not established as long as the young remain in the nest. It is only at weaning, when the juveniles emerge from the nest, that dam–young discrimination occurs. Rabbits are likely to follow this pattern, but data on mother–young recognition are scarce. Rabbit does leave the nest after each nursing bout, block the entrance with soil and deposit urine and faecal pellets. This marking guides them back to the burrow but also repels other females. As the young do not

leave the nest until 14–18 days, early recognition of the litter may be based initially on spatial proximity rather than phenotypic traits. However, some data indicate that does discriminate their young before their emergence from the nest (Mykytowicz and Dudzinski, 1972).

Sows are not able to recognize their litter in the days after parturition (Horrell and Hodgson, 1992a) but they do identify the nest site and, by caring for all piglets in the area, they care for their own young. Recognition of the litter is established by 7 days after birth, exclusively by smell, after the piglets start to leave the nest and explore the nearby area. Jensen (1986) observed that, under free-ranging conditions, abandonment of the nest by the sow and her piglets occurs suddenly and at a relatively consistent age of the young (9 days). In addition, the sow does not respond to the piglets that remain in the nest and makes no attempt to fetch them. This implies that the sow recognizes general characteristics of the litter (a family odour?) but does not develop bonds with each individual piglet. Unlike the sow, piglets are able to discriminate their home environment very reliably 12–24 h after birth. They can also distinguish maternal odours from alien ones and respond preferentially to their mother's grunts by 36 h of age (Horrell and Hodgson, 1992b).

Ruminant mothers acquire the ability to recognize their own young rapidly and reject any alien that attempts to suck. In sheep and goats, this discrimination is established within 2–4 h after birth (Poindron *et al*., 1993). While selective nursing relies on olfactory recognition of the young, mothers can also identify their young from a distance using vision and audition (Poindron and Le Neindre, 1980). Although the general view has been that distal recognition takes days to develop, recent studies indicate that ewes can recognize their lamb on the basis of cues other than olfaction as early as 8 h after birth (Terrazas *et al*., 1999). There is also evidence of early discriminative abilities in young ruminants. Lambs between 12 and 24 h of age can identify their mothers (Poindron *et al*., 1993), and kids within 48 h (Lickliter and Heron, 1984). Furthermore, the manner in which such discrimination occurs changes rapidly over time: on the day of birth, lambs discriminate their mother at close quarters, and at 3 days, from a distance of several metres. Olfaction does not seem to be the major cue used in the identification of the mother, even at close quarters. Although newborn lambs react to maternal olfactory cues (Vince and Ward, 1984), they rely on visual, vocal, and probably behavioural characteristics to locate their own dam at 24 h of age.

## Inadequacies in parent–young interactions

Offspring mortality is invariably highest in the first few days after birth (Fig. 3), reflecting the problems of transition from the totally protected intrauterine life to an unpredictable extrauterine existence. In addition to the danger from various environmental hazards, the access of the neonate to food will be limited by the presence of the mother and competition with littermates. The first critical stage will be the birth process itself, and dystocia represents one of the major causes of mortality. After birth, survival of the newborn will depend largely upon the quality of the interactions with the mother. Behaviour patterns prejudicial to survival of the young have been documented in various species (Estes and Estes, 1979; Alexander, 1988; Fraser, 1990; Nowak, 1996) and the data available in rabbits, pigs and sheep are summarized (Fig. 4).

### *'Stealing' of young*

Pre-partum ewes, cows and mares often approach, sniff and remain close to the newborn of other females. This behaviour reflects the physiological changes that occur at the end of gestation and should be considered as normal. The interest displayed by ewes in lambs (Welsh and Kilgour, 1970) and cows in calves (Edwards, 1983) can be followed by acceptance of young that are nursed and 'stolen' from their biological mother. This 'stealing' is not necessarily detrimental to the young as long as lactogenesis in the foster mother is sufficiently advanced. However, once she has given birth, the chances of her own lamb surviving will be reduced, as there will no longer be enough colostrum to sustain its needs.

### *Abnormal maternal behaviour*

The maternal behaviour of inexperienced mothers has been identified as a possible cause of mortality in the young. In rabbits kept under breeding conditions, there is an improvement in the quality of nests with successive parturitions and this influences pup survival (Canali *et al*., 1991; Hafez *et al*., 1966). In addition to a nest of poorer quality, primiparous mothers may visit their litter repeatedly (instead of once per day like their wild counterparts), which results in higher mortality of pups due to wounding and soiling of the nest (Coureaud *et al*., 2000a).

Various forms of neonatal rejection can occur in primiparous mothers. Inexperienced ewes tend to show temporary delays in the expression of maternal care, or behavioural disturbances that can delay the access of a neonate to the udder (Poindron *et al*., 1993), thus reducing its chance of survival, especially under adverse climatic conditions. Primiparous sows may show aggressive behaviour at parturition against their own litter, resulting in the wounding or death of piglets (van der Steen *et al*., 1988). Cannibalism has been reported in pigs (van der Steen *et al*., 1988) and rabbits (Hafez *et al*., 1966). The causes of cannibalism are not fully understood, but there is evidence that primipara are less responsive to the physiological determinants of maternal behaviour and more prone to neophobic reactions in response to the presence of neonates.

Environmental factors such as nutrition can also shape the expression of maternal behaviour. Undernutrition during gestation depresses maternal behaviour and increases neonatal mortality, while supplementary feeding has the opposite effects (Langeneau and Lerg, 1976; Putu *et al*., 1988), which may be considered as an adaptive behaviour. According to parental investment theory, nursing young when resources are depleted would inflict such a large cost on the mother's future reproductive success that it is more beneficial for the long term to neglect the present offspring.

Research on the maternal behaviour of ungulates, other than Suidae, producing litters of more than one offspring has revealed limitations in the care of multiples. Although twin-bearing ewes express higher licking and nursing activities than single-bearing ewes, they do not provide twice as much care. Individual twins therefore receive less stimulation than

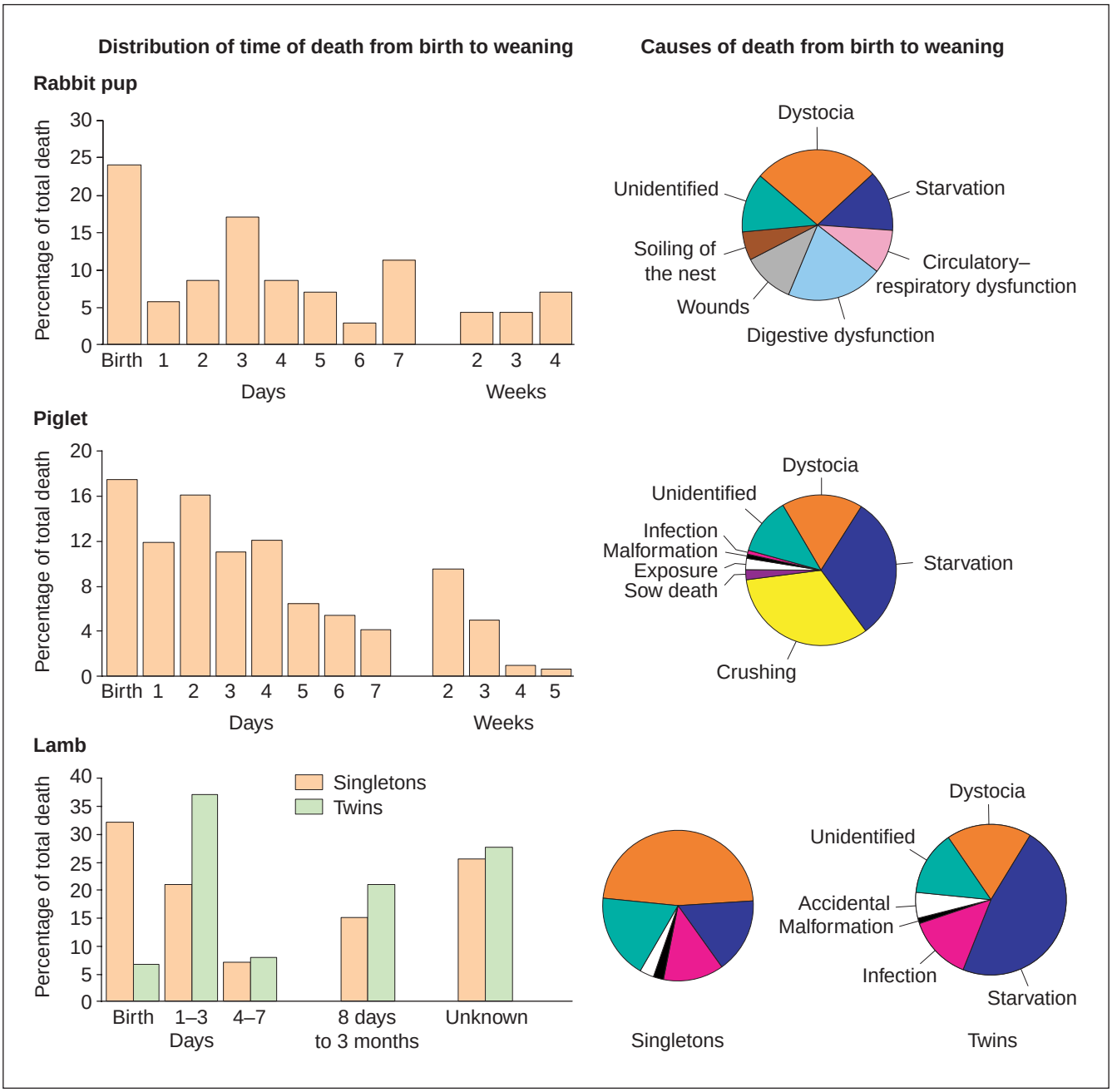
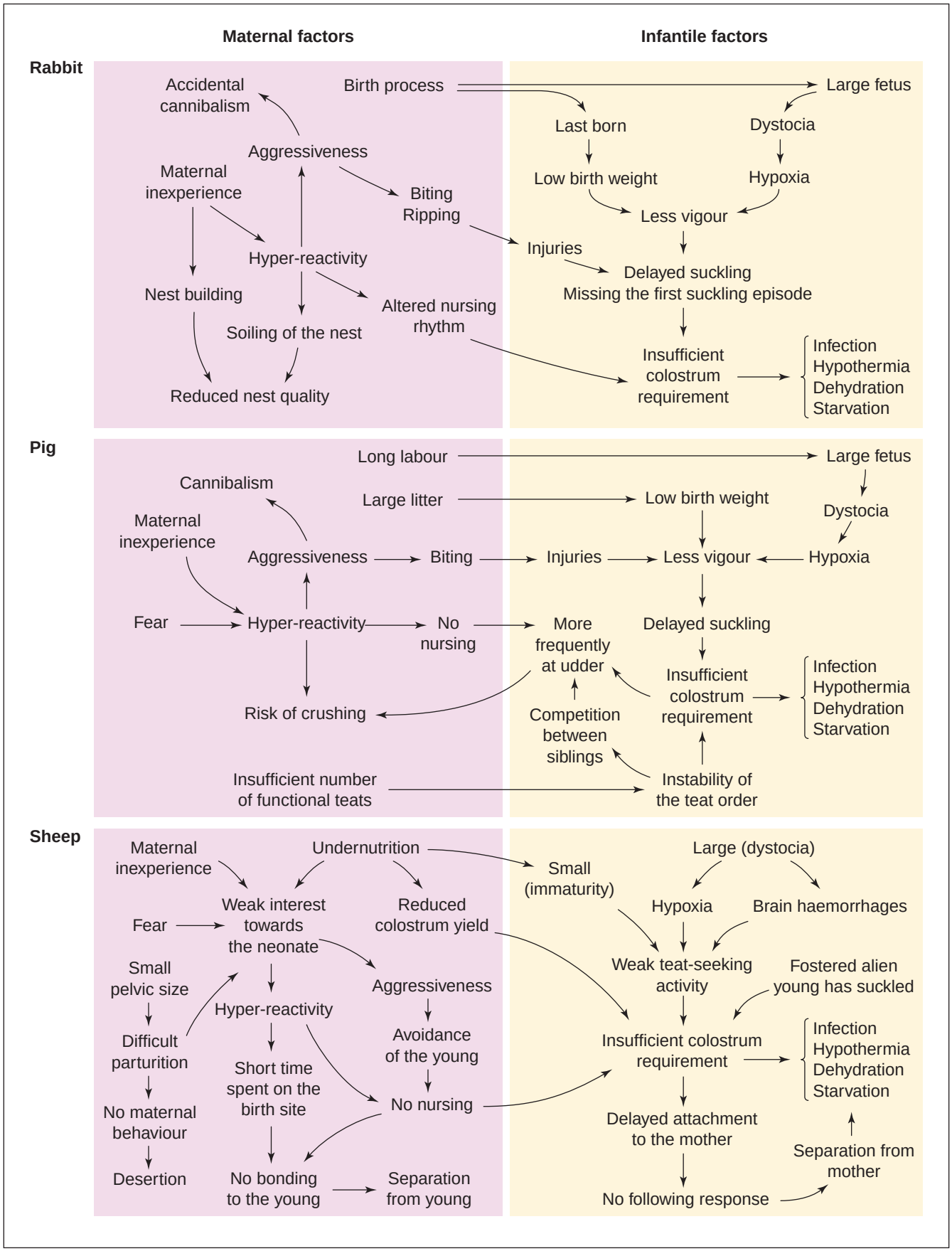



**Fig. 3.** Distribution of deaths from birth to weaning in rabbit pups ($n$ = 71), piglets ($n$ = 535) and lambs ($n$ = 713 singletons and 501 twins) expressed as a percentage of the total mortality (left panels). Causes of death between birth and weaning (right panels). (Data adapted from Coureaud *et al*., 2000a; Dyck and Swiestra, 1987; Hight and Jury, 1970.) Unlike in the original papers, antepartum deaths are not included in the present figure. In pigs, exposure is defined by 'piglets found dead away from the sow or the heated creep area' (Dyck and Swiestra, 1987). In sheep, accidental is defined by 'lambs dying from drowning, choking, physical injury due to castration, blowfly strike, intestinal obstruction' (Hight and Jury, 1970). Note that, in the three species, most postnatal death occurs in the first week after birth but, in sheep, the pattern of mortality differs between singletons and twins. Dystocia is an important cause of mortality and affects mainly mothers having large fetuses or a small pelvic size. Ewes giving birth to single rather than twin lambs are more prone to dystocia as their lambs are bigger. A major cause of neonatal mortality due to behavioural factors is starvation: rabbit pups missing the first suckling episode; piglets fighting over teats and missing the milk let down; inexperienced mothers refusing to nurse; twin lambs being abandoned by their dam. In rabbits, primipara can display inadequate maternal care by visiting the nest more than once a day, soiling the nest or wounding pups. Undernourished neonatal pigs are often crushed by their mother as they spend more time close to her trying to get milk.



singletons and this may delay bonding to the mother. The high mortality rate in lambs as a result of accidental separation of one twin from its mother on the day of birth (Stevens *et al*., 1982) reflects the problems of maintaining contact with all the members of a litter in a field situation. Littermates being born several metres apart, interference by other females, or physical characteristics of the birth site such as vegetation, can lead to uneven maternal bonding and later separation. Separation frequently occurs when ewes move away from the birth site to graze. Many ewes appear satisfied if accompanied by one lamb only, especially if this occurs within 4 h of birth. Under such circumstances, abandoned lambs have little chance of surviving unless they are adopted by periparturient ewes. It appears that the strength of bonding, or the awareness of the ewe of the size of her litter, depends on the time spent on the birth site and improves with maternal experience rather than with age (Alexander *et al*., 1983, 1984). Mother–young separation is also observed in pigs in field situations. Some piglets fail to follow their mother when they leave the nest (Jensen 1986) and sows do not appear aware that their litter is incomplete.

### *Behaviour of the neonate*

Newborn mammals have very limited energy reserves. A major factor affecting survival is the difficulty in maintaining homeothermy, especially in altricial species. Furthermore, as well as being a source of energy, colostrum provides immunoglobulins, especially in ungulates, which ensures passive systemic immunity. Therefore, an essential priority for survival of the neonate is early access to the udder or nipple (Hartsock and Graves, 1976; Sawyer *et al*., 1977; Coureaud *et al*, 2000b). Primiparous mothers frequently display reluctance to nurse their young but this is usually temporary and not detrimental for their young but, under adverse condition, it can put the survival of the newborn at risk as its thermostability is impaired. Furthermore, in lambs, a delay in suckling prevents the normal development of a relationship with the mother (Nowak *et al*., 1997). Early ingestion of colostrum triggers mechanisms that facilitate the establishment of this bond (Goursaud and Nowak, 1999). Delayed access to the udder, especially in twins, may account, at least in part, for the high incidence of loss of mother–young contact and subsequent death in such lambs. Additional support for this hypothesis is provided by the fact that twin lambs that are able to recognize their dam by 12 h are more likely to survive (Nowak and Lindsay, 1992). Thus, the establishment of early recognition of the mother may be vital for lambs. In pigs, competition among littermates is recognized as contributing significantly to neonatal mortality. This competition starts at birth and vigorous sibling disputes are observed until the establishment of a stable teat order. Once lactation is established, milk becomes a non-defendable resource because it can be obtained only during the brief periods of milk ejection that occurs at all teats simultaneously. Fraser (1990) has suggested that once the teat order is established, piglets compete indirectly by attempting to maximize their consumption of milk. Indeed, growth rate is not constant amongst littermates and some piglets appear to be more efficient at stimulating their own teats and, therefore, gain more milk. The advantage thus obtained by one piglet occurs at the expense of siblings sucking other teats. In extreme cases, piglets have been observed to die of starvation while maintaining fidelity to an involuted teat (de Passillé *et al*., 1988). Furthermore, malnourished piglets are often crushed as they spend more time massaging and sucking their teat. Being less vigorous, they are less able to escape from dangerous movements of the sow.

**Fig. 4.** Summary of maternal and infantile factors in rabbits, pigs and sheep, leading to inadequate mother–young interactions during the neonatal period and subsequent death of the neonate.

## Conclusions

There is no species of mammal in which the young can survive in the absence of maternal care. The primary immediate function of the mother–young relationship is to provide the offspring with an assured source of nutrition, protection against predators, and guidance. Mammals have developed an extreme diversity in the expression of maternal care to achieve this goal. Some species (for example, lagomorphs) minimize postpartum parental investment per individual neonate for the sake of producing litters containing many offspring while, in others (for example, ruminants), the investment is maximized in one young per reproductive cycle. The reproductive success of sheep and rabbits demonstrates that raising a single young each year, with months of caring, is as good a strategy as having several litters that receive minimal maternal care. The present review has focused on the neonatal period because it is a time of high vulnerability for the young. Problems of adjustment to extrauterine life represent the major cause of juvenile mortality. However, the behaviour of the young and its chances of survival will be shaped by its mother throughout lactation, and even beyond. Behaviour patterns acquired early through imitation of the mother, for example, the development of food preferences and predator avoidance, have advantages over inborn behaviour or learning by trial and error. Modelling the behaviour of the mother ensures a rapid adjustment to a changing environment, while it conserves all the behavioural responses that have been successful to the survival of the parent.

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