

IMPACT OF REARING MANAGEMENT ON HEALTH IN DOMESTIC RABBITS: A REVIEW

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Abstract: High mortality in rearing of domestic rabbits is not only an economic problem but also an animal welfare issue. Among the reasons for this high mortality are some common rearing practices. In this review, we point out several commonly used management practices, which neither represent adequate housing conditions according to the animals' behavioural requirements nor correspond to their nutritional needs. Sometimes, the doe has to build the nursery nest on the cage floor or in a box with a permanently open entrance, often not protected from the light. This can lead to perinatal mortality due to disturbed behaviour of the mother such as failure to build a proper nest, depositing the kits outside the nest, or infanticide. Furthermore, continuous housing of the doe with the kits does not conform to this species' pattern of unusually limited maternal care. Possibly stimulated by olfactory and acoustic signals emanating from the nest, the doe can disturb the inactivity of the kits by her frequent entries to the nest or attempts to close the entrance. Cooling of the kits caused by maladaptive maternal behaviour under such conditions can also contribute to increased mortality and morbidity during the nursing period. In addition, when the doe is left to nurse the kits longer than four weeks, which does not conform to the reproductive biology of the rabbit, kit morbidity can be increased by the following factors. Although the doe's milk has a high protective role against main digestive disorders, prolonged mother-offspring contact might increase the risk of the kits becoming infected with pathogens such as coccidiosis, EPEC and pasteurellosis persisting in the doe. Pre-disposition of the kits to bacterial enteropathies can be encouraged by the delayed development of the enzymatic system, the delayed establishment of a stable gut flora, as well as by consumption of the doe's feed. The increased energy demands of lactation as well as mastitis incidence due to prolonged suckling by the kits could decrease the fertility and the lifespan of the doe. Feed with a high content of non-fibre carbohydrates (compared to green forage) can promote bacterial enteropathies when given before the development of the kits' digestive functions is completed. The risk of the outbreak of such diseases is enhanced by intestinal coccidiosis and unstable gut flora. Enteropathies are also exacerbated by the use of deep litter as opposed to housing rabbits on perforated floors.

Key Words: animal welfare, digestive disorders, maternal behaviour, early weaning, housing conditions, rabbit.

INTRODUCTION

Ever since first reports on domestic rabbit rearing became available (Seidel, 1936; Fangauf and Dreyer, 1940), it has been clear that early mortality in this animal is high, independently of the purpose of breeding. This cannot be explained solely by genetic factors as pre-weaning mortality varies by less than 10 up to 100% within populations with similar genetic status (Rashwan and Marai, 2000). Furthermore, post-weaning mortality of hybrid populations in commercial rabbitries has been found to be more than 4 times higher (Tetens, 2007) than the mortality of the same breeds under standardized conditions in random sample tests (Lange and Schlolaut, 1981; Lange, 1985; Lange, 1997) (see Table 1). This high variation clearly suggests that environmental factors, i.e. differences in rabbit rearing management, can have an impact on health and mortality.

Table 1: Variation of kit mortality in domestic rabbits under different housing conditions.

	Source (examples)	Perinatal period		Nursing period		After weaning	
		% Mortality	Age (postnatal days)	% Mortality	Age (postnatal weeks)	% Mortality	
Non-commercial and laboratory rabbitries	Fangauf and Dreyer (1940)		56	25.6	12	8.5	
	Lösing (1979)		28	16			
	Reiter (1995)				14	5 (2-6)	
	Selzer (2000)	8-17	28	8-10			
	Toplak <i>et al.</i> (2007)				12	19 (0-38)	
Commercial rabbitries	Fischer (1978) ^a	11	36	16		8	
	Renalap-Itavi (2002) ^c			18.6-24.3		11.5-14.9	
	Tetens (2007) ^a	8 (1-10)	35 (28-40)	7.4 (2-17)	14	20.5 (4-43)	
Random sample tests	Fangauf and Dreyer (1940)		56	25.6	12	8.5	
	Lange and Schlolaut (1981) ^b	4.6	25	11.3	12	3.8	
	Lange (1985) ^b	5 (4-6)	25	7.5 (6-9)	12	3.5 (2-5)	
	Lange (1997) ^b	5.3 (4-8)	27	5.6 (5-6)	12	4.8 (4-6)	

^a Information from commercial rabbit breeders. ^b Random-sample tests according to the guidelines of the German Agricultural Society (DLG, 1981) of hybrid populations, which are used in commercial rabbitries (Tetens, 2007). ^c Variation in average annual mortality rates from 1983 to 2000.

Although pre-weaning mortality rates in wild European rabbits is also high, the causes of mortality are very different. Here, nest mortality is to a great extent due to flooding, cooling of the kits (with ambient temperatures of the soil surrounding the nest chamber as low as 5°C), predation, or to infanticide by other females (Myers, 1958; Mulder and Wallage Drees, 1979; Palomares, 2003; Rödel *et al.*, 2008a,b; Rödel *et al.*, 2009a). In contrast, disturbed or maladaptive behaviour of the domestic doe due to housing conditions that do not satisfy all her behavioural requirements, can contribute to kit mortality during the nursing period. In the wild, predation and diseases such as coccidiosis, myxomatosis and rabbit haemorrhagic disease are the main causes of mortality in European rabbits once the young leave the breeding burrow at around postnatal day 17-20. These factors account for around 50-70% mortality during the first few weeks after emergence (Richardson and Wood, 1982; Cowan, 1987a; Seltmann *et al.*, 2009). If these diseases are prevented in the domestic rabbit, juvenile mortality is to a large extent due to digestive disorders (Licois *et al.*, 2006). The effects of such pathologies can be reduced by the use of feeds appropriate for the developmental state of the kits' digestive functions.

In summary, a proportion of the mortality in domestic rabbit rearing can be accounted for by environmental factors such as management practices that do not conform to the behavioural requirements or to the nutritional needs of this species. The prevention of avoidable mortality is considered a primary goal of animal welfare regulations (Hoy and Verga, 2006), and thus it is our aim to point out causal relationships between some features of current rearing practices on mortality and health in the domestic rabbit.

DISEASES RELATED TO REARING PRACTICES

Before weaning

Housing

Wild rabbits give birth in the nest chamber of a subterranean breeding burrow, which is situated either in the main warren or dug by the mother as a separate breeding burrow (Mykytowycz, 1959). The nest chamber is lined by the mother with grass and/or leaves and with the mother's abdominal hair, which she plucks out prior to giving birth.

After parturition, the mother immediately leaves the young, closes the burrow entrance with soil and sometimes with additional grass and leaves, and only returns to nurse for a few minutes once approximately every 24 h (Broekhuizen *et al.*, 1986; see Table 2). During the first 10-12 postnatal days, the kits have only a limited capacity for independent thermoregulation (Poczopko, 1969; Hull, 1973 and typically huddle together and actively cover themselves with the nest material by crawling under it (Hudson and Distel, 1982; Bautista *et al.*, 2008). On about postnatal day 17-20, the kits emerge from their breeding burrow and start to explore the environment (Broekhuizen *et al.*, 1986). At this time, they also start to ingest larger amounts of solid food, in particular at dawn and dusk (Hudson and Altbäcker, 1994; Hudson *et al.*, 1996a,b, 1997; Coureaud *et al.*, 2008).

Domestic rabbit does kept under non-commercial, laboratory or commercial housing conditions sometimes have to build the nest either flat on the floor of their cage (not frequent) or in a nest box with a permanently open top or entrance, exposing the doe while building the nest as well as the kits after birth to (artificial) daylight (Table 2). In addition to other factors, we suggest that this might be one reason for behavioural disturbances in the doe leading to failures in nest building, to giving birth and placing the kits outside the nest, or to infanticide. About 19% of all parturitions in non-commercial rearing conditions are reportedly affected by such problems (Lösing, 1979). Using a nest box with a lid, accessible by the mother via a tubular entrance and thus mimicking natural breeding conditions by protecting the nest from light might help prevent negative effects of the doe's behaviour. This has been shown by lower perinatal mortality in domestic rabbits (Table 3) as well as in wild rabbits under laboratory housing conditions (González-Redondo, 2010). Furthermore, we suggest that providing hay outside the nest box (e.g. in a rack in order to prevent contamination with faeces) so as to allow the doe to show her natural behavioural repertoire of grass collection and nest building might also promote the quick birth of the young essential in the rabbit (Hudson *et al.*, 1999) and help to improve maternal behaviour.

Table 2: Comparison of the environmental conditions and the diet of wild rabbit and domestic rabbit kits during early development. [Zarrow *et al.* (1965); Hudson and Distel (1982); Broekhuizen *et al.* (1986); Gibb (1993); Hudson *et al.* (1996a); Rödel (unpubl.)].

	Wild rabbit	Domestic rabbit
Nest	Situated in breeding chamber of the breeding burrow Up to 40 m apart from the main warren Entrance closed and kits inside the burrow; only opened by the doe shortly before the daily nursing event	Usually situated on the floor of the cage of the doe or in an open nest box Inside or next to the cage of the doe Usually always open
Nest material	Grass and leaves in addition to the doe's abdominal hair	Litter from the floor of the cage, often contaminated with faeces and urine; usually wood shavings and/or straw
Contact of the doe with the kits	Less than 5 min/d	Permanently
Exploration of new environment	Leaving of the nest on day 12; leaving the breeding burrow (except for short nursing episodes) on day 17-20	Leaving of the nest on day 12 and activity in the mother's cage – potential access to mothers' food and germs persisting in it
Duration of nursing	Usually terminated by the mother on day 25-28, as wild rabbit mothers usually have postpartum pregnancies and so overlapping litters	Up to 8 weeks due to prolonged communal housing of kits and doe
Housing after weaning	Usually in the burrow during day time	Permanently exposed to light during the day or during the artificial light period
Diet after around day 17	Selected leaves and shoots; larger stems and shoots are usually avoided if the animals have the choice	Green forage and hay including stems and shoots (high content of lignocellulose), or foods containing nutrients which are only partly digestible (e.g. starch)

Table 3: Impact of the use of a nest box with a tubular entrance (approx. 40 cm) on early mortality. All litters were born to mothers, which previously had a complete breeding failure. Differences were significant (Fisher's Exact test: $P=0.001$; data of W. Schlolaut).

Treatment	Total No. of litters	Litters with mortality of all kits (%)
Without nest box	22	36
With nest box ^a	27	0

^aIncluding a tubular entrance.

A further possible reason for maladaptive behaviour in breeding does is that they are usually constantly exposed to acoustic and olfactory cues emitted by the kits when a permanently open nest box is used. As a consequence, rabbit mothers not only check the nest by so-called "head contacts" up to 20 times a day, but also repeatedly jump into the nest without actually nursing the kits (Seitz, 1997; Wasserzier, 1997; Coureaud *et al.*, 2000a; Selzer, 2000). Such repeated interruptions of the kits, which usually show resting behaviour between the brief once-daily nursing events (Hudson and Distel, 1982; Jilge and Hudson, 2001), can be exacerbated by the mother's (ineffective) attempts to close the entrance of the nest box (Hudson and Distel, 1982; Gerold, 1993). These interruptions may also disrupt the anticipatory behaviour of the young necessary for efficient suckling and result in them obtaining less milk (Hudson and Distel, 1982; Coureaud *et al.*, 2000a). As a result of such disturbances, the young kits may keep emerging from their insulating cover of nest material and maternal fur, consequently becoming exposed to the ambient temperature of the animal facilities. This can lead to cooling, which in turn is known to increase mortality, or at least can reduce (by up to 50%) the early postnatal growth of the kits (cf. Hudson and Distel, 1982; Coureaud *et al.*, 2000b; Bautista *et al.*, 2003). Limiting access of the doe to the nest to the once-daily nursing visit considerably reduced nest mortality compared to nests where the mother had free access, from 18 to 8.1%, at least in primiparous does (Coureaud *et al.*, 2000a). In addition, this increases the pre-weaning growth of the kits (Verga and Luzi, 2006). Similar positive effects can be obtained by installing a swing door (Baumann *et al.*, 2003) or a tubular entrance to the nest box (Ruis, 2006; Table 3).

If the mother has to build the nest on the flat floor of the cage or the nest box, the young kits are at risk of becoming separated from the nest or litter huddle, and may not find their way back. This also can lead to cooling, which is reported to be one of the most common causes of death during the first 2 wk of the nursing period (Lölinger, 1982; Selzer, 2000). A shallow concave floor in the nest box, as in various forms is increasingly implemented in commercial rabbit farming, can help prevent newborn kits from becoming separated and ensure that they are grouped together for nursing.

Exposure to bright light and frequent disturbances by the mother (as described above) induces the kits to leave the nest at an earlier age. This can vary between postnatal day 12 and 20 (Bigler, 1986) and may have important implications for their health. It appears that the earlier the kits leave the nest and enter the doe's cage, the higher the risk of infections. Here, the kits are permanently in contact with pathogens of common diseases such as coccidiosis, acute dysentery (via infection with pathogenic *E. coli* (EPEC)), enzootic enteropathies (via infection with Clostridia) as well as pasteurellosis. During this time, the doe could be a source of such pathogens (Peeters, 1988; Matthes, 1993; Rossi, 2007). In addition, bacterial enteropathies may occur, partly as mixed infections together with intestinal coccidiosis (Lölinger *et al.*, 1969; Coudert *et al.*, 2000; Rosell, 2003) and also facilitated by the access of the kits to the mother's feed (Pascual and Mayo, 2001). This feed typically contains—in order to meet the increased nutritional needs of the mother during lactation—higher proportions of non-structural carbohydrates (to that recommended for the kits), which can overtax the digestive system of the kits (Pole *et al.*, 1980; Cheeke, 1994).

When the kits are kept together with the mother beyond the natural time of weaning at around postpartum days 25-28 (Hudson, 1995; Hudson *et al.*, 1996a), and particularly when they do not have sufficient access to water or green feed, they persistently try to gain access to the mother's teats. This has been observed to occur up to 20 times a day after postnatal day 25 (Wasserzier, 1997). Such approaches by post-weaning age kits (and even towards other lactating females of the social group) are also not unusual in nature and can be frequently observed in wild rabbits living in a natural social environment. However, under natural conditions the mother can readily escape or avoid these

approaches by moving away. Under the spatially restricted conditions of cage housing, does try to avoid the suckling approaches of the kits by escape behaviour or by lying down, which, however, is frequently not successful. Thus, it is likely that the behaviour of the potentially post-weaned kits constitutes a social stressor for the mother. Chronic exposure to such a stressor could have immunosuppressive effects (von Holst, 1998). Indeed, such a relationship between extended lactation and alterations in immune status has been shown in the domestic rabbit (Guerrero *et al.*, 2011). In addition, injury of the teats and related diseases are also common. Mastitis is a relevant disease in does, with a prevalence of 6% (Rosell, 2003; Rosell and de la Fuente, 2009; Sánchez *et al.*, 2012). This can be caused by injury of the teats, and also by the negative effects of stress (Fetherston, 1998). After pasteurellosis, mastitis is often considered one of the most common causes of culling in domestic rabbit does (Morisse, 1990; Tetens, 2007).

It has been suggested that the installation of an elevated platform might help reduce the stress on the mother caused by the presence of post-weaning kits. Generally, and independently of this purpose, such enrichment increases the area available to an animal, and helps to reduce other sources of stress and thus increases wellbeing (Stauffacher, 1992; Lang, 2010). However, a recent study has indicated that this is not usually successful in preventing suckling approaches by the young when they can also reach this platform (Szendrő, 2006). In addition, it should be noted that older kits as well as the mother frequently use such elevated platforms as latrines, i.e. by putting large amounts of faeces and urine on them (Ruis, 2006; but see Postollec *et al.*, 2008 for strategies to avoid such effects). When using a platform with a perforated floor, faeces will drop on the kits and can contaminate their fur, thereby increasing their risk of infection (Hoy and Verga, 2006; Trocino and Xiccato, 2006; Lang and Hoy, 2011). However, this problem no longer arises when the earlier separation of mother and kits is implemented according to the natural timing of weaning around postpartum days 25-28 (Hudson, 1995; Hudson *et al.*, 1996a).

The kind of nest material and also the structure and quality of the nest affects the early growth of the kits (Worden and Leahy, 1962). Wood shavings and straw are rather unsuitable as nest material, and it has been shown in choice tests that nest boxes containing wood shavings are avoided by primiparous does (Blumetto *et al.*, 2010). However, when the does were not given another choice, the number of weaned kits in nests with wood shavings was 21% lower than in nests with straw. Around 5% of does were reported to remove the straw from the nest boxes (regardless of whether these contained only straw or also wood shavings) and only used abdominal hair for nest building. If the nest material (such as wood shavings or straw) is unsuitable as first solid food for the kits (they start eating small amounts of nest material at around postnatal day 8: Hudson *et al.*, 1996a,b, 1997) in order to start the development of gut flora, then this developmental process will be retarded until the kits start to ingest solid food after leaving the nest (Piattoni and Maertens, 1999). Possibly for all these reasons we have obtained particularly good pre- and postweaning growth and survival when providing does (and their kits) with meadow hay rather than straw or wood shavings for nest building (Hudson, *unpubl.*).

Wild rabbits live in social groups of about 1-3 adult males and 1-6 adult females, characterized by a sex-specific social rank order established by sometimes highly aggressive interactions, particularly at the beginning of the breeding season (Southern, 1948; Myers and Poole, 1961; Cowan, 1987b; von Holst *et al.*, 1999, 2002). Relationships among females usually stabilize and aggression becomes ritualized once a rank order is established (Mykityowycz and Rowley, 1958; von Holst *et al.*, 2002), and bonding among female kin can help in stabilizing the social structure within a female group (Rödel *et al.*, 2008c). However, group territories in wild rabbits are large (in a field enclosure study, 0.05-0.7 ha; Rödel *et al.*, 2008b), and animals can avoid and escape aggressive encounters. This does not appear to accord with animal welfare recommendations (e.g. Stauffacher 1992, 1997) of keeping adult domestic rabbit females (and also uncastrated adult males) together in groups under the usually restricted spatial conditions of commercial and non-commercial breeding facilities. This recommendation appears particularly inappropriate given the injuries caused by fights for high rank positions, higher mortality of kits, and other negative effects on wellbeing and health, including infanticide by other females (Müller and Brummer, 1981; Maier, 1992; Hoy and Verga, 2006; Ruis, 2006; Szendrő, 2006; Szendrő *et al.*, 2013).

Diet

Wild as well as domestic rabbits nurse their young once a day approximately every 24 h (Zarrow *et al.*, 1965; Hudson and Distel, 1982; Broekhuizen *et al.*, 1986; Hudson, 1995; Hudson *et al.*, 1995, 1996a, 1997), although the variation in nursing intervals appears to be larger in wild rabbits (Hoy, 2006; Rödel *et al.*, 2012) than in domestic

breeds under standardized conditions. In the domestic rabbit, it has been shown that milk yield decreases steeply during the late nursing period (Lincoln, 1974; Hudson *et al.*, 1996a), and that increasing the number of potential nursing visits by does has no effect (Zarrow *et al.*, 1965; Szendrő *et al.*, 1993) or only a marginal impact (Seitz, 1997) on the pre-weaning growth and development of the kits.

Milk production by the doe when again pregnant due to postpartum mating, reaches a maximum on postpartum day 17-18 (Hudson *et al.*, 1996a; Maertens *et al.*, 2006), and in non-pregnant mothers between postpartum day 20-22 (Schlolaüt and Lange, 1971; Hudson *et al.*, 1996a). After this age, the amount of milk provided by the mother soon no longer meets the kits' requirements for drinking water (Schlolaüt, 2003). Prior to this time the daily milk production of middle-sized breeds is as much as 300 g (Maertens *et al.*, 2006). Another study showed that maximum milk production is less than 150 g when does are fed predominantly with hay and fodder beets as is common in non-commercial breeding (Schlolaüt, 2003). In mothers left with their young, milk production then decreases by postpartum day 35 to 60-80 g/d, independently of the mother's maximum production (Schlolaüt, 2003).

In pregnant domestic does (and most probably also in wild rabbits), milk production terminates around postpartum day 25 due to hormonal mechanisms (Lincoln, 1974; Hudson, 1995; Hudson *et al.*, 1995, 1996a). This rather short nursing period corresponds to the natural situation in wild rabbits, where females usually give birth in the course of several successive breeding events in the same reproductive season as a result of postpartum oestrus (Brambell, 1944). Consistent with this, in the domestic rabbit it has been found that differences in the timing of weaning between postnatal days 21 and 42 had no effect on the body mass of the young at the age of 10 or 12 wk when they had been fed with pelleted all-mash feed *ad libitum* (Schlolaüt and Lange, 1971; Klausdeinken, 1992).

If the doe is not mated postpartum and the young remain in the same cage after postnatal day 25-28 (i.e. when they are usually weaned under natural conditions), then the constant stimulation by the kits prolongs lactation by the mother. The species-appropriate and natural duration of nursing is frequently –but misleadingly– referred to as “early weaning”. Although studies in wild rabbits have shown that occasional contact or even proximity of the kits to the mother may be beneficial by reducing their level of stress and thus increasing their health status (Starkloff *et al.*, 2009), such effects can hardly be mimicked under captive breeding conditions. Thus, any such benefits of communal housing of mother and potential post-weaning kits are almost certainly outweighed by the negative consequences of such housing under typically space-limited conditions. As mentioned above, diseases in the kits related to the prolonged nursing period can arise due to them being exposed longer to the infection pressure of pathogens persisting in the doe. In addition, ingestion of the mother's food may make them more vulnerable to digestive disorders (Pascual, 2001) if the food does not conform to the developmental stage of their digestive functions. In particular, it appears that such effects are caused by prolonged nursing delaying this development.

It has been reported that prolonging the nursing period from 25 to 34 d more than doubles kit mortality after postnatal day 34 (7.4 vs. 17.6%) due to enteropathies (Cesari *et al.*, 2009). We suppose that the reasons for this age-dependent difference are: first, that the kits' risk of being infected with pathogens carried by the mother is lower when they are around 25 d old compared to older kits (Garrido *et al.*, 2006), and second, that the pH in the gut is decreased because of the faster development of the gut flora (Piattoni and Maertens, 1999).

However, the situation might be more complicated, as suggested by reports of positive effects of continued access to milk in reducing kit mortality due to bacterial enteropathies (e.g., Licois *et al.*, 1992; Romero *et al.*, 2009). On the one hand, this might be due to the protective effects of milk against infections with *E. coli*, as it has been shown experimentally by Gallois *et al.* (2007). On the other hand, it might be also considered that prolonged nursing could reduce the ingestion of some kinds of feed. For example, it has been shown that kits with continued access to milk ingest less pelleted all-mash feed compared to weaned kits; about 55% less during the 4th postnatal wk and about 27% less during the 6th wk (Schlolaüt and Lange, 1971). This fact could have contradictory consequences by not promoting the digestive system but allowing less sudden weaning.

In addition to low milk production and low kit birth mass, mortality due to malnutrition can occur when the number of kits per litter exceeds the number of available nipples (Fleischhauer *et al.*, 1984), a situation which almost never occurs in the wild. Wild rabbits usually have 8 or 10, and in rare cases 9 nipples (Rödel, *unpubl.*), and their litter size rarely exceeds 7 or 8 (Rödel *et al.*, 2009b). In domestic rabbits, this problem can be readily solved by transferring

surplus kits to the nests of foster mothers with smaller litters of approximately the same age. By this method it is possible to reduce mortality of surplus kits by almost 50% (Lange *et al.*, 1979).

From around postnatal day 8, the kits start to ingest the meadow hay or other vegetation that the wild rabbit doe typically uses for building the nest. Around this time, the kits (as it has been shown in domestic rabbits) also start to nibble at the (few) faeces that the doe usually defecates in the nest (Hudson and Distel, 1982; Hudson and Altbäcker, 1994; Hudson *et al.*, 1996a; in wild rabbits, Rödel, *unpubl.*). It has been suggested that this may help the kits to establish a stable gut flora (Hudson *et al.*, 1996a,b, 1997), although if the doe is a chronic carrier of EPEC, the kits will be already infected at an age of 3-12 d (Peeters, 1988). Up to 24% of does are reported to be chronic carriers of colibacillosis without showing obvious symptoms. However, coccidiosis does not appear to be a problem during this age because the kits are protected by maternal immune factors (Coudert *et al.*, 1991). Nevertheless, this suggests that the presence of faecal pellets in the nest should not be considered a failure of hygiene but rather as an aspect of maternal behaviour of possible adaptive significance (Hudson *et al.*, 1996a).

The decrease in pH in the gut at the beginning of solid food intake, which is related to the increasing development of the gut flora (Piattoni and Maertens, 1999), serves to protect the kits from the oral introduction and proliferation of pathogens (Hermann, 1989). In addition, the natural gut flora facilitates the microbiological production of amylase, which in turn supports endogenous enzyme production (Carabaño *et al.*, 2006).

After weaning

Housing

In the wild rabbit, the kits start to leave the breeding burrow at around postnatal day 17-20 (= first emergence above ground) including for the brief daily nursing episodes, which also occur outside the breeding burrow starting at about postnatal day 14 (Broekhuizen *et al.*, 1986). If they are born in a breeding burrow (i.e. a short nursery burrow of around 40-60 cm length separate from the main warren, cf. Mulder and Wallage Drees, 1979; Gibb, 1993), the kits usually move to a close-by larger burrow or to the main group warren, as the doe is frequently preparing the nest in the same breeding burrow for the next, successive litter (Rödel, *unpubl.*). During the day, they usually rest within a burrow or other refuge, where they huddle together with their siblings, usually in the absence of the mother. The main (feeding) activity in the wild rabbit is during dusk and dawn (Mykytowycz, 1958; Wallage Drees, 1989), although activity bouts also depend on the prevailing weather conditions and the presence of predators.

Kits of the domestic rabbit are constantly exposed to daylight or to artificial light for up to 16 h/d. Such a regime of 16 h light has been shown to double the activity of the kits as compared to individuals housed under a regime of only 8 h light (Bigler and Oester, 1997). These conditions, together with the shorter feeding time necessary to ingest sufficient amounts of nutrients when fed pelleted all-mash feed (in comparison to green forage or hay) may possibly be involved in prompting abnormal behaviour in the kits, such as trichophagy, i.e. fur chewing (Brunner, 1975).

Another hotly debated issue in animal welfare relating to the ideal environment for rabbit rearing is the question whether litter or perforated floors should be used. Straw litter is often used in non-commercial rearing facilities to keep the floor dry and for manure production. In addition, it has been suggested to meet animal welfare requirements (Stauffacher, 1997; Bigler and Oester, 2000). Nevertheless, several choice tests found that a significant majority of animals (including kits between 5-10 wk of age) spent more time on wire net or plastic slat floors than on deep litter (Morisse *et al.*, 1999; Bessei *et al.*, 2001; Orova *et al.*, 2004) at thermo-neutral temperatures. In addition, it has been shown that plastic slat floors are preferred to wire mesh floors (Princz *et al.*, 2008). We suggest that the risk of infection has to be considered here as a significant factor when rabbits are reared on deep litter. For example, it has been shown that around 92-94% of does excrete coccidial oocytes when kept on deep litter (Seidel, 1936; Kühn, 2003). In addition, it has been reported that coccidiosis-infected kits stop excreting oocytes when reared on wire mesh after about one month but will continue excreting oocytes when kept on deep litter (Ruis, 2006). Further studies found that kit mortality due to enteropathies was increased by 34 up to 100% (Dal Bosco *et al.*, 2002; Lange, *unpubl.*) when animals were reared on deep litter compared to housing in cages with wire mesh floors. Furthermore, the occurrence of pododermatitis (i.e., bacterial infections of the feet) is typically increased when

animals are kept on wet litter (Lölinger, 2003), and easily solved by the use of plastic mats in cages with wire mesh floors (Rommers and de Jong, 2011).

Diet

Natural weaning in the rabbit corresponds closely to the peak of lactation (Hudson *et al.*, 1996a). At this time, rabbits start with caecotrophy, but only when the development of a stable gut flora was possible due to the ingestion of appropriate nest material (hay, grass or leaves, and possibly of faecal pellets deposited by the mother in the nest (Hudson and Distel, 1982; Hudson *et al.*, 1996a; wild rabbits: Rödel, *unpubl.*). However, the development of the kits' gut enzymatic system is not completed before the kits reach an age of about 8 wk (Pascual, 2001). In particular, this applies to the production of amylase (Blas, 1986). On postnatal day 21, the concentration of this enzyme is only 12% of that produced by kits at 32 d of age (Lebas *et al.*, 1986). Amylase concentrations naturally produced in the body are supplemented by the microbial amylase production of the gut flora (Pascual, 2001; Carabaño *et al.*, 2006).

In most mammalian species, the increasing adaptation of offspring food intake to the development of digestive functions is governed by the decreasing lactation curve (milk provision) of the mother. In rabbits, the process of weaning appears to be rather abrupt, shortly after the maximum peak of the lactation curve. Wild rabbit kits may adapt their food intake to the developmental stage of their digestive system by gradually increasing their activity range around the breeding burrow and by increasing their feeding time (Boback, 1979).

The wild rabbit, as a folivore (i.e. a leaf eater), optimizes the digestibility and protein content of the green forage by selecting leaves and shoots of ground vegetation (see a report on winter feeding behaviour in wild rabbits: Rödel, 2005). Larger (older) shoots and stems with a higher content of low-digested fibre (lignocellulose) are usually avoided if the animals have a choice. As a consequence, the content of protein and digestible nutrients in the ingested food is greater than the average content of the general vegetation. It has been shown that the protein content of the selected forage (which is highest in spring with about 19-20% protein) is about 3 times greater than the total protein content of harvested food plants (Rogers *et al.*, 1994). Such selective feeding, e.g. on herbs with many leaves, reduces the diversity of plant species in areas where wild rabbits are abundant (Worden and Leahy, 1962). Bark, twigs and grass roots are only browsed during periods when other food is scarce (Rogers *et al.*, 1994; Rödel, 2005).

The domestic rabbit also prefers plant material with a high proportion of leaves and with higher protein content (Somers *et al.*, 2008). For example, it has been shown that rabbits ingest about double the amount (dry mass) of red clover (*Trifolium pratense*) compared to the vegetation forming mixed pasture when both kinds of food are provided *ad libitum* (Schlolut *et al.*, 1981a). However, fresh green feed or roughage is usually not sufficient to meet the nutritional requirements for the growth of kits from domestic stock which typically reach a greater adult body mass than wild rabbits. This is mainly due to the fact that the relative capacity of the gastro-intestinal tract decreases with increasing body mass in domestic stock, thus leading to a lower relative digestive efficiency in larger breeds (Wolf *et al.*, 1997, 2005). Furthermore, the domestic rabbit usually has only limited possibilities to efficiently select plant parts with high digestibility and protein content when provided with freshly mown green feed. Kits of medium-sized stock only show about 50% of the growth even when fed *ad libitum* with usually preferred food plants (*Trifolium*) compared to animals fed with pelleted all-mash feed (Schlolut *et al.*, 1984). The daily dry matter intake of around 35 g pelleted all-mash feed on postnatal day 25 is equivalent to a quantity of green forage corresponding to about 60% of the live weight of the kits –when considering animals of middle-sized stock (Schlolut, 2003). A pelleted diet with 74% alfalfa meal (*Medicago sativa*) results in growth rates comparable to those achieved with pelleted all-mash feed, and such a diet is well suited for kits around weaning as it does not promote bacterial enteropathies (Pole *et al.*, 1980).

In order to meet the food requirements of growing rabbits, and independent of the season, it is necessary to use feeds with a comparatively high concentration of nutrients as well as high digestibility, at least in breeds with a greater adult body mass than the wild rabbit. In young animals the digestion of such feeds is initially limited by the development of the enzymatic system, in particular when the content of non-structural carbohydrates exceeds that of fresh or conserved green feed. In particular, the development of the endogenous production of amylase is not completed before 8 wk of age (Pascual, 2001). Thus, there is a danger that in younger kits non-absorbed and undigested nutrients may promote the proliferation of bacteria causing enteropathies. This can be exacerbated, for

example, when the still insufficient endogenous production of amylase is not supplemented by that of the gut flora (Fortun-Lamothe and Gidenne, 2006).

Diet also has the potential to influence the incidence of bacterial enteropathies. Since the mid 20th century, bacterial enteropathies have been considered one of the main causes of mortality in domestic rabbit kits from postnatal week 4-10, both in commercial and non-commercial rearing conditions (Ostler, 1961; Greenham, 1962; Peeters, 1988; Licois *et al.*, 2006; Fortun-Lamothe *et al.*, 2009). Large quantities of antibiotics have been used in order to prevent or to treat diseases such as bacterial enteropathies or pasteurellosis in the domestic rabbit (Fortun-Lamothe *et al.*, 2009). However, the success of such treatments is increasingly questionable due to the growing number and abundance of multi-resistant serotypes of EPEC (Peeters, 1988; Gracia *et al.*, 2004). In addition, the risk of the outbreak of bacterial enteropathies is further enhanced by the following additional factors:

(a) Infestation with intestinal coccidiosis (Sinkovics *et al.*, 1980; Coudert *et al.*, 2000; Kühn, 2003). Morbidity and mortality due to intestinal coccidiosis increase when animals are fed exclusively with fresh or conserved green forage due to body mass loss and low growth rates as a consequence of malabsorption of digested nutrients. Furthermore, coccidiosis causes a temporary increase in caecal pH (Peeters, 1988), increasing the likelihood of bacterial enteropathies. To prevent such bacterial enteropathies it is therefore essential to complement the usual alimentary prophylaxis with a coccidiosis prophylaxis.

(b) Mixed feeds contain mineral additives that bind acids, thus increasing the pH value of the stomach chymus (Hermann, 1989) and in the gut. This potentially facilitates bacterial enteropathies, in particular when the start of solid food intake is delayed (Piattoni and Maertens, 1999).

Apart from coccidiosis prophylaxis and the other above-mentioned measures, it has been shown that bacterial enteropathies can be reduced by a feeding regimen adjusted to the developmental state of the enzyme system of the gut during postnatal weeks 4-8 (Maertens and Peeters, 1988). This can be accomplished either using feed with low nutrient density or feed with a high structural carbohydrate content (Rodríguez-Romero *et al.*, 2011; Martínez-Vallespín *et al.*, 2011, 2013), by limiting the intake of pelleted all-mash feed until postnatal week 8 (Schlolaut *et al.*, 1978; Schlolaut and Lange, 1979; Gidenne *et al.*, 2003, 2009), or by actively restricting the feeding time (Schlolaut and Lange, 1990; Romero *et al.*, 2010). If despite the premature developmental state of the digestive system high growth rates are to be achieved by feeding pelleted all-mash feed *ad libitum* starting at postnatal day 17, or if the young have access to the mother's food, it is necessary to reduce the proliferation of pathogens by adding bacteriostatic or bactericidal food supplements. Apart from antibiotics (Licois *et al.*, 2006; Boulier and Milon, 2006), these are tannins (Zimmermann and Bessei, 2001), phytogetic extracts (Krieg *et al.*, 2005) or pro- and prebiotics (Marzo, 2001; Volek and Marounek, 2011).

INFLUENCE OF REARING MANAGEMENT ON MORTALITY AND FERTILITY OF BREEDING DOES

Reproduction clearly imposes costs, and a female's reproductive effort can affect future reproduction, survival and health (Stearns, 1992). An example is provided by wild rabbits, where the does' first litters of the season were characterized by higher pre-weaning kit growth rates than subsequent postpartum litters, presumably because of mothers' reduced lactational performance (Rödel *et al.*, 2008d).

Postpartum conceptions are a prominent feature of the wild rabbits' reproductive strategy (Brambell, 1944) and surely one of the reasons for its high potential population growth. Usually, females can have 2-3, or in rare cases 4, subsequent postpartum reproductive events before they will enter into a reproductive pause, presumably due to the accumulated costs of reproduction (Rödel, *unpubl.*). A long-term study quantifying wild rabbit reproduction in central Europe showed that females give birth on average to 2.5 litters (i.e. around 12 kits) per season, with a maximum of 6 and in rare cases 7 litters per individual female per season (von Holst *et al.*, 2002; Rödel *et al.*, 2009b). However, higher values are reported for other populations (e.g., up to around 45 kits per female and season in New Zealand; Gibb and Williams, 1994), indicating that wild rabbit females under suitable environmental conditions may produce a larger number of litters.

Approaches to optimize the timing of the reproductive regime in the domestic rabbit with respect to considerations of animal welfare and productivity have been the subject of various studies, suggesting different re-mating intervals

with delays of several days up to several weeks (reviewed in: Oguike and Okocha, 2008). Due to their reproductive biology, domestic does can be successfully re-bred even 24 h after kindling (Schlolaüt *et al.*, 1981b; Cheeke 1993; Mc Nitt *et al.*, 1996), as is frequently the case in wild rabbits under natural conditions. However, the usefulness of short re-mating intervals has been frequently questioned, as such a breeding management may not allow the doe to adequately compensate for the costs of prior reproduction (Bertazzoli and Rivaroli, 2008). Nevertheless, we draw attention to the results of 2 studies, where repeated postpartum inseminations indicate no appreciable reduction in the duration of usage of does, at least when they are fed with pelleted all-mash feed *ad libitum*. Domestic rabbit does with a reproductive effort of 7.5 litters within 11 mo revealed an average mortality rate of 12% (0-20%) (Lange, 1997). A further study, which monitored does giving birth to on average 15 litters over 2 yr revealed even lower mortality rates of 5% during the first and 2% during the second year (with kits being weaned at day 25). 23% of the does initially assigned to this study were discarded after 3 successive inseminations were not successful (Schlolaüt *et al.*, 1981b).

We conclude that current rearing practices that do not conform to the natural biology of the rabbit can have welfare consequences not only for the kits but also for the does. Commercial breeders use breeding does for about 230 to 300 d (Renalap-Itavi, 2002), with annual mortality varying between 27 and 46% (Fachin *et al.*, 1987; Iruetagona, 1991). In addition, culling rates of does of up to 50% due to infertility and disease have been reported (Fachin *et al.*, 1987), and monthly culling rates of 8 to 12% are not uncommon (Lebas *et al.*, 1986; Rosell and de la Fuente, 2009). In non-commercial rabbitries, mortality rates of does of around 46% per year have been reported in a study by Hoffmann (1990). We suggest that apart from the well-known contributors to female morbidity or the necessity for culling, such as diseases, consequences of cage design (e.g., sore hocks) and hygiene problems (Morisse, 1990; Rosell, 2003; Tetens, 2007; Bertazzoli and Rivaroli, 2008; Rosell and de la Fuente, 2009), the practice of prolonged nursing –given its negative consequences– should also be taken into account in rabbit production.

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