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MATERNAL BEHAVIOUR IN PERIPARTUM INFLUENCES PREWEANING KIT MORTALITY IN CAGE-BRED WILD RABBITS

González-Redondo P.

Departamento de Ciencias Agroforestales, Escuela Universitaria de Ingeniería Técnica Agrícola. Universidad de Sevilla. Carretera de Utrera, km 1. 41013 Sevilla. Spain.

Abstract: This study describes and models maternal nest-building and parturition behaviour in cage-bred wild rabbits (*Oryctolagus cuniculus*), and its influence on the kits' pre-weaning mortality. In a total of 91 litters, perinatal mortality was 33%; mortality during the nursing period was 16.05%, and therefore the accumulated mortality up to weaning was 43.94%. These mortality rates, higher than those described in the literature among domestic breeds, were linked to failures in maternal behaviour. Such failures included the non-introduction of straw into the nest box (41.8% of births), a lack of hair lining in the nest (28.6%), births in which one or all of the kits were born outside the nest box (18.7%), and births in which one or all of the kits were cannibalised by the doe (13.2%). Maternal behaviour in relation to the kits' viability was modelled by performing multiple correspondence and cluster analyses with two dimensions and a 67.2% total inertia. The first dimension (inertia: 0.400) was represented by the presence of hair in the nest box; the place where the kits were born (inside or outside the nest box), and the doe's previous experience (primiparous or multiparous), while the total number of kits born represents the second dimension (inertia: 0.272). Three maternal behaviour types were identified: types 1 and 3 representing births in which the failure of maternal behaviour at kindling led to high kit mortality. Maternal behaviour type 1 corresponds to primiparous does of parity orders 1 and 2 with a high number of total kits born and of stillborn kits. Type 3 births were characterised by all of the kits died during peripartum, with a high incidence of cannibalism. Type 2 included births of experienced does showing successful development of maternal behaviour, as well as high kits' survival rates during the peripartum and nursing periods. Although wild rabbits are subject to the same modulating factors in the development of the maternal repertoire as domestic does, showed a lower preweaning viability due to the failure to display maternal behaviour during peripartum.

Key Words: wild rabbit, kit mortality, peripartum, preweaning period, maternal behaviour.

INTRODUCTION

The semi-intensive breeding of wild rabbits (*Oryctolagus cuniculus*) for game restocking is widespread in countries such as France, Portugal, and Spain (Arthur, 1989; González-Redondo, 2001). Breeding in cages, however, is both difficult and relatively unproductive (Parer *et al*., 1987; González-Redondo, 2003), mainly due to the low proportion of does giving birth (Adams, 1975; Ward, 1971; González-Redondo, 2003) and to the failure of maternal peripartum behaviour (González-Redondo, 2003). This in turn leads to a low number of nursing, and therefore weaned, kits per doe that gives birth (Parer *et al*., 1987; González-Redondo, 2003).

The development of the maternal repertoire among wild rabbit does during peripartum in the wild is well-known (Lloyd and McCowan, 1968; Gibb, 1993), as is that of the domestic breeds raised in captivity (Ross *et al*., 1956; Deutsch, 1957; Venge, 1963). This hormonally-controlled maternal repertoire

Correspondence: P. González-Redondo, pedro@us.es
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(González-Mariscal *et al*., 1996; González-Mariscal, 2001; Negatu and McNitt, 2002) comprises a set of components: i) digging a breeding burrow (Lloyd and McCowan, 1968) or digging into a substrate (González-Mariscal *et al*., 2009); ii) the introduction of nesting materials into either the breeding burrow (dried vegetable matter, Deutsch, 1957; Lloyd and McCowan, 1968; Gibb, 1993) or the nest box (straw or wood chips, Ross *et al*., 1956; González-Mariscal *et al*., 1994); iii) the loss of hair on the belly, used to line the nest (Ross *et al*., 1956; Deutsch, 1957; Sawing *et al*., 1960; Lloyd and McCowan, 1968); iv) giving birth inside the nest box or the breeding burrow (Deutsch, 1957; Lloyd and McCowan, 1968; Gibb, 1993); and v) the brief duration of the nursing bout (reviewed in González-Mariscal, 2007). Such nursing usually occurs once a day (Venge, 1963; Zarrow *et al*., 1965; Lloyd and McCowan, 1968) with circadian periodicity (Jilge, 1993 and 1995), although some does nurse more than once per day (Hoy *et al*., 2000; Selzer *et al*., 2004). A correct development of this maternal behaviour is also characterised by the absence or the low incidence of aberrant behaviours such as cannibalism of the newly-born kits or their being crushed by the mother (Delaveau, 1979; González-Redondo and Zamora-Lozano, 2008).

The development of the maternal repertoire among intensively-bred caged wild rabbits and the relationship between this complex and the kits' viability has never been investigated. The aim of this study was to describe and model maternal behaviour during peripartum in wild rabbits housed in cages and to relate the expression of the components of this behaviour to kits' preweaning mortality.

MATERIALS AND METHODS

Animals and housing

The study was performed on an experimental farm in the province of Córdoba (southern Iberian Peninsula; Spain), with geographical coordinates 37º 53' N and 4º 47' W at an altitude of 180 m above sea level and with a southern exposure. During the study period (January to June), average daily temperatures ranged from 9.2 to 23.5 ºC, and average relative humidity ranged from 77 to 52 %. Only natural light was used, with a photoperiod ranging from 9.5 to 14.5 h per d.

The 19 cage-born wild rabbit does (*Oryctolagus cuniculus algirus*) used in the study came from an initial stock of rabbits that were caught in breeding burrows when they were approximately 25 d old and were from the same region where the study was undertaken. The does were housed individually in metal mesh cages (38×51×35 cm; width, length, and height) located in the open air. Each cage was equipped with a chipboard nest box comprising a closed internal chamber measuring 17×23×20 cm (width, length, and height) with a 9×8 cm (width by height) access tunnel. A plastic container (16×22×11 cm; width, length, and depth) was placed inside the nest box's internal chamber for the does to build their nest, give birth to and suckle their kits in (González-Redondo, 2006). It was decided to give the does permanent access to the nest box so that they could also use it as a refuge in order to reduce their stress levels. This is because it is well known that if nest boxes are available, captive wild rabbits will spend most of the day time inside them (Selzer and Hoy, 2003).

The does were fed *ad libitum* with a pelleted commercial feed containing 16.5% of crude protein and 16.5% crude fibre. They also received water *ad libitum*.

Breeding management and variables measured

Mating took place in the buck's cage, where the does stayed for 7 d. After the 7 d period, the does were returned to their own cages. Twenty-eight days after mating, straw was placed upon the cage floor to enable the does to build their nests. Weaning of the kits took place 30 d post-partum. If they had raised a litter, the does were mated again on the same day as weaning. If the whole litter died in the peripartum,

they were mated the following day and if they had not given birth, they were mated again 35 d after the last mating. In order to avoid unnecessary stress, the does were not palpated to detect pregnancy. When checking the nest boxes on the day of birthing, live kits were weighed and dead kits were removed. During the nursing period, the nest boxes were checked every 10 d in order to remove the dead kits.

The following data were recorded from a total of 91 births occurring between February and June: the parity order; the doe's previous experience (primiparous or multiparous); the presence of straw in the nest box; the presence of hair in the nest box; the total number of kits born; the number of live-born kits; the number of kits dying during the peripartum (this period being set as the first 24 h post-partum); perinatal mortality (the percentage of kits dying during the peripartum compared with the total number of kits born); the number of kits cannibalised after birth; the place in which they were born (inside or outside the nest box); the number of weaned kits; mortality during the nursing period (the percentage of kits dying during the nursing period compared with the number of live-born kits); accumulated mortality up to weaning (the percentage of kits that die before weaning with respect to the total number of kits born) and finally, the age of the doe at the time of birth.

Statistical analysis

A multivariate analysis was performed to detect the factors that best characterise and typify the births. Each variable was divided into categories (as shown in Table 2), and multiple correspondence analysis (MCA) was performed on the set of variables in order to achieve dimension reduction. Using the two dimensions yielded by the MCA, 4 of the initial 14 variables were selected for discriminating maternal behaviour typologies. A hierarchical cluster analysis performed by Ward's method, using the squared Euclidean distance, classified maternal behaviour into 3 typologies (clusters). The analysis of the relationships among variables of the 3 maternal behaviour typologies was performed using contingency tables on which Pearson's chi-square tests were performed and the standardised residuals were calculated. Statistical analyses were performed using SPSS software (SPSS Inc., 2006).

RESULTS

Table 1 shows the main descriptive statistics of the variables related to the litters' viability and the development of maternal behaviour in the doe.

The MCA yielded two dimensions (Figures 1 and 2). Total variance explained by the solution was 67.2%: 40.0% by dimension 1 and 27.2% by dimension 2. The first dimension, corresponding to the abscissa, included three variables: the presence of hair in the nest box, the place in which the kits were born, and the doe's previous experience. The second dimension, corresponding to the ordinate, included one variable: the total number of kits born. Figure 1 shows the discrimination measures of the variables.

The classification of the births by the two dimensions above established three well-defined maternal behaviour types (clusters) (Figure 2). Table 2 shows the frequencies for each category of the variables showing differences among clusters and the statistical significances of the differences among the maternal behaviour types for the variables studied. The three differentiated maternal behaviour types are described as follows:

Type 1: "Primiparous does failing to nest-build" (n=18 births). Births in this group produced mainly: 3-4 total kits born, 0 live-born kits, 3-5 stillborn kits, and 0 weaned kits. This type scored high in all kits dying during peripartum and nursing periods and, therefore, accumulated deaths up to weaning. In most of these births, the nest boxes were not lined with hair or straw, and one or all of the kits were delivered outside the nest box by the does. A high proportion of births came from one-year-old primiparous does and of parity order 1 or 2.

Table 1: Main descriptive statistics of the variables related to the births (n=91) by caged wild does analysed.

	Mean±standar error	Minimum	Maximum
Doe's age (in years)	2.05±0.11	1	4
Parity order	3.67±0.25	1	10
Total kits born	3.23±0.13	1	6
Live-born kits	2.48±0.18	0	6
Kits born dead	0.75±0.13	0	5
Number of weaned kits	1.87±0.18	0	5
Perinatal mortality (%)	33.00±4.86	0	100
Mortality during the nursing period (%)[1]	16.05±3.78	0	100
Accumulated mortality until weaning (%)	43.94±4.78	0	100
Percentage of births			
Primiparous doe	20.9		
Doe lines the nest box with hair	71.4		
Doe lines the nest box with straw	58.2		
One or all of the kits born outside the nest box	18.7		
One or all of the kits cannibalised	13.2		

[1]Calculated taking into account only the litters with kits born alive (n=62).

Type 2: "Multiparous does successful in the peripartum" (n=61 births). Births in the second group produced mainly 3-4 live-born kits, 0 stillborn kits, and more than 1-2 weaned kits. This type scored high on 0 kits dying during peripartum and up to weaning. In most of these births, the nest boxes were lined with hair and straw and all of the kits were delivered in the nest box by the does. In most of the litters, no kits were cannibalised by the doe. A high proportion of births came from multiparous does aged two years old or more and of parity order 5 or 6.

Type 3: "Does failing in the peripartum" (n=12 births). Births in this group produced mainly 1-2 total kits born, 0 live-born kits, 1-2 stillborn kits, and 0 weaned kits. In all the litters, all of the kits died during the peripartum and, therefore, there were no nursing litters. In most of these births, the nest boxes were not lined with hair or straw, and one or all of the kits were delivered outside the nest box by the does, while one or all of the kits in half of these litters were cannibalised by the doe. A high proportion of births came from one-year-old does.

Table 3 shows the relationships between the variables related to maternal behaviour and kit mortality during the peripartum and accumulated up to weaning. Kit mortality during the nursing period did not reveal an influence ($P>0.05$) of any of the variables studied.

DISCUSSION

Model of maternal behaviour in peripartum

This study provides the first systematic description and modelling of maternal behaviour during peripartum in cage-bred wild rabbits and links the expression of their components to kits' preweaning mortality.

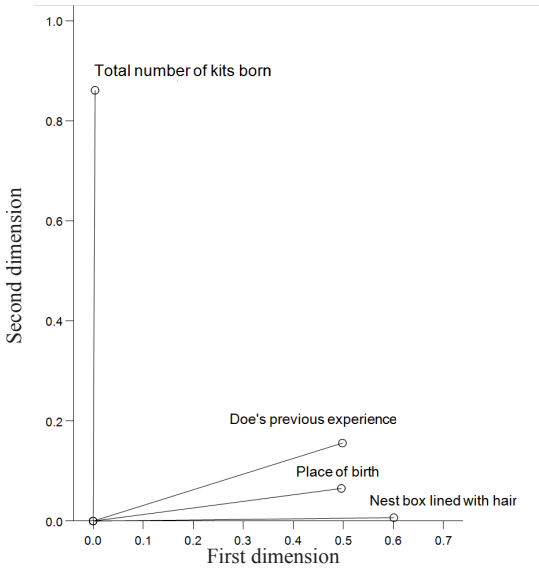

Figure 1: Discrimination measures of the variables according to the two dimensions obtained from the multivariate analysis.

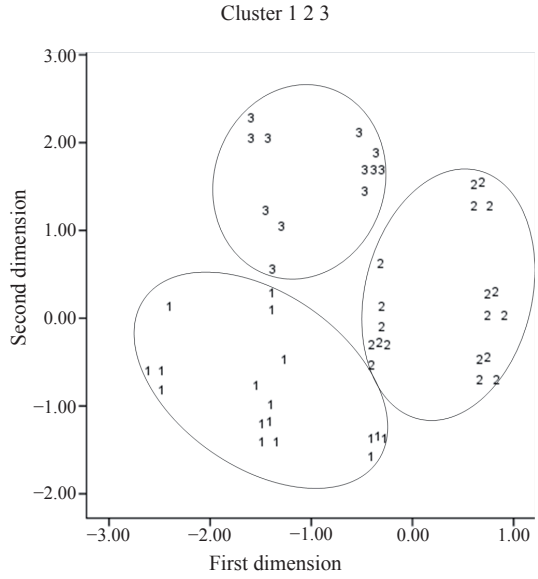

Figure 2: Spatial localisation of the births according to the two dimensions obtained from the multivariate analysis.

[1]First dimension (Eigenvalue: 1,599; inertia: 0.400): Higher values means birth from multiparous does, that line the nest with hair and that deliver all the kits inside the nest box.

[2]Second dimension (Eigenvalue: 1,089; inertia: 0.272): Higher values means births with fewer total number of kits born.

The model fit was satisfactory because the total inertia explained by the MCA solution was comparable with other studies using MCA and it is consistent and comprehensive due to the fact that it includes the same components involved in maternal behaviour and reproductive performance in domestic breeds. Dimension 1 was mainly influenced by the doe's breeding experience and its ability to prepare a nest in which to give birth and raise its offspring successfully; dimension 2 largely depends on total litter size at birth (Figures 1 and 2).

The cluster solution for maternal behaviour and reproductive performance is clear because the three clusters are well-defined and exclusive (Figure 2). Maternal behaviour type 2 includes the births from experienced does for which the development of the maternal behaviour and the kits' survival during the peripartum and nursing periods were successful (Table 2). Maternal behaviour types 1 and 3 represent the births in which the failure of the maternal behaviour at birthing led to a low kit survival rate (Table 2). The main difference between types 1 and 3 is that births from type 1 came from primiparous does of parity orders 1 and 2 with a higher number of total kits born and of stillborn kits, while births from type 3 are characterised by all the kits dying in the peripartum with a high incidence of cannibalism (Table 2).

Kit mortality

The kits' perinatal mortality (Table 1) was higher than that recorded among meat rabbits which, although potentially subject to great variations, usually ranges around 5-7% (Lebas *et al*., 1996). Mortality during the nursing period was also high, as the kits' survival rate up to weaning did not exceed 57% of the total number of kits born, a value close to that found by Parer *et al*. (1987) among wild rabbits bred under

Table 2: Frequencies (percentage of births) of the variables by maternal behaviour type as defined in Figure 2 (standardised residuals[1] in parentheses).

	P-value	Type1 (n=18)	Type 2 (n=61)	Type 3 (n=12)	Total (n=91)
Litter size					
Liveborn kits	<0.001				
None		33.3 (1.6)	4.9 (−5.1)	75.0 (5.2)	19.8
1-2		22.2 (−0.3)	26.2 (0.3)	25.0 (0.0)	25.3
3-4		38.9 (−0.7)	57.4 (3.1)	0.0 (−3.4)	46.2
5-6		5.6 (−0.5)	11.5 (1.3)	0.0 (−1.2)	8.8
Kits born dead	<0.001				
None		38.9 (−2.8)	86.0 (5.7)	8.3 (−4.6)	67.0
1-2		22.2 (0.2)	8.2 (−4.2)	83.3 (5.7)	20.9
3-5		38.9 (3.9)	4.9 (−3.0)	8.3 (−0.4)	12.1
Total kits born	<0.001				
1-2		0.0 (−2.8)	21.3 (−1.6)	91.7 (5.5)	26.4
3-4		88.9 (2.7)	65.6 (1.1)	0.0 (−4.7)	61.5
5-6		11.9 (−0.1)	13.1 (0.6)	8.3 (−0.4)	12.1
Weaned kits	<0.001				
None		72.2 (3.4)	14.8 (−6.4)	100.0 (4.8)	37.4
1-2		11.1 (−0.9)	24.6 (2.1)	0.0 (−1.8)	18.7
3-5		16.7 (−2.6)	60.7 (4.6)	0.0 (−3.3)	44.0
Mortality of kits					
Perinatal mortality	<0.001				
No kits dead		27.8 (−3.5)	86.9 (6.5)	0.0 (−4.9)	63.7
Some kits dead		11.1 (1.6)	3.3 (−0.7)	0.0 (−0.8)	4.4
All kits dead		61.1 (3.0)	9.8 (−6.4)	100.0 (5.4)	31.9
Mortality during nursing[2]	<0.001				
No kits dead		57.1 (−0.7)	70.9 (0.7)	-	69.3
Some kits dead		14.3 (−0.6)	23.6 (0.6)	-	22.6
All kits dead		28.6 (2.1)	5.5 (−2.1)	-	8.1
Accumulated mortality until weaning	<0.001				
No kits dead		11.1 (−3.0)	60.7 (4.9)	0.0 (−3.2)	42.9
Some kits dead		16.7 (−0.4)	24.6 (1.6)	0.0 (−1.8)	19.8
All kits dead		72.2 (3.4)	14.8 (−6.4)	100.0 (4.8)	37.4
Nesting and perinatal behaviour					
Doe lines the nest box with hair	<0.001				
No		66.7 (4.0)	8.2 (−6.1)	75.0 (3.8)	28.6
Yes		33.3 (−4.0)	91.8 (6.1)	25.0 (−3.8)	71.4

(Continued Table 2)

	P-value	Type 1 (n=18)	Type 2 (n=61)	Type 3 (n=12)	Total (n=91)
Nesting and perinatal behaviour					
Doe lines the nest box with straw	<0.001				
No		72.2 (2.9)	23.0 (−5.2)	91.7 (3.8)	41.8
Yes		27.8 (−2.9)	77.0 (5.2)	8.3 (−3.8)	58.2
Place of birth	<0.001				
One or all of the kits born outside the nest box		44.4 (3.1)	3.3 (−5.4)	58.3 (3.8)	18.7
All of the kits born in the nest box		55.6 (−3.1)	96.7 (5.4)	41.7 (−3.8)	81.3
Cannibalism of kits by the doe	<0.001				
One or all of the kits cannibalised		16.7 (0.5)	4.9 (−3.3)	50.0 (4.0)	13.2
No kits cannibalised		83.3 (−0.5)	95.1 (3.3)	50.0 (−4.0)	86.6
Doe's age and experience					
Doe's age (years)	<0.001				
1		88.9 (5.3)	16.4 (−5.3)	50.0 (1.2)	35.2
2		11.1 (−2.5)	45.9 (2.7)	25.0 (−0.9)	36.3
3		0.0 (−2.1)	19.7 (1.2)	25.0 (0.9)	16.4
4		0.0 (−1.8)	18.0 (2.5)	0.0 (−1.4)	12.1
Doe's previous experience	<0.001				
Primiparous		88.9 (7.9)	1.6 (−6.4)	16.7 (−0.4)	20.9
Multiparous		11.1 (−7.9)	98.4 (6.4)	83.3 (0.4)	79.1
Parity order	<0.001				
1-2		94.4 (5.2)	24.6 (−4.5)	41.7 (0.1)	40.7
3-4		0.0 (−2.8)	31.1 (1.5)	41.7 (1.3)	26.4
5-6		0.0 (−2.3)	24.6 (2.1)	16.7 (−0.2)	18.7
7-8		5.6 (−0.7)	13.1 (1.5)	0.0 (−1.2)	9.9
9-10		0.0 (−1.0)	6.6 (1.4)	0.0 (−0.8)	4.4

[1] Standardised residuals strongly differentiating a cluster are in bold.
[2] Calculated taking into account only the births with kits born alive (n=62).

similar conditions (61.1%). This pre-weaning mortality was markedly higher than that of the meat rabbit, whose average values are around 20% (Lebas *et al*., 1996; Rashwan and Marai, 2000).

Influence of age and previous experience of the doe

With does of up to four years old, the kits' mortalities decreased (Table 3), coinciding with the trend described among domestic breeds in which preweaning mortality is higher among younger (Delaveau, 1979; Rashwan and Marai, 2000) and older does when compared to does of an intermediate age (Rashwan and Marai, 2000). In particular, kit mortality was markedly higher among kits born to first-year wild does (Table 3); in fact, maternal behaviour types 1 and 3, which exhibited higher kit mortality rates, included a high proportion of births in first-year does (Table 2).

Table 3: Relationship between the variables related to maternal behaviour and kit mortalities (Mean±standard error) in caged wild rabbits (n=91 births).

	n (%)	Perinatal mortality (%)	Accumulated mortality until weaning (%)
Doe's age (years)[1]		$P<0.05$	$P<0.01$
1	32 (35.2)	54.17±8.82 [b]	66.15±7.79 [b]
2	33 (36.3)	23.33±7.13 [a]	33.28±7.12 [a]
3	15 (16.4)	26.67±11.82 [ab]	41.67±12.83 [ab]
4	11 (12.1)	9.09±9.09 [a]	14.39±9.27 [a]
Previous experience		$P<0.001$	$P<0.001$
Primiparous	19 (20.9)	64.91±10.96	78.95±8.91
Multiparous	72 (79.1)	24.58±5.01	34.70±5.05
Parity order		$P<0.1$	$P<0.1$
1-2	37 (40.6)	49.55±8.23	60.23±7.55
3-4	24 (26.4)	26.87±8.90	33.82±8.46
5-6	17 (18.7)	23.53±10.60	39.71±11.56
7-8	9 (9.9)	13.89±11.11	25.00±14.43
9-10	4 (4.4)	0.00±0.00	14.58±8.59
Total kits born		$P>0.05$	$P>0.05$
1-2	24 (26.4)	45.83±10.39	56.25±10.12
3-4	56 (61.5)	30.06±6.02	37.95±5.84
5-6	11 (12.1)	20.00±12.06	47.58±13.32
Place of birth		$P<0.001$	$P<0.001$
All of the kits born inside the nest box	74 (81.3)	19.53±4.57	32.97±4.91
One or all of the kits born outside the nest box	17 (18.7)	91.67±5.72	91.67±5.72
Presence of straw in the nest box		$P<0.001$	$P<0.001$
Straw	53 (58.2)	2.89±2.00	15.69±4.04
No straw	38 (41.8)	75.00±6.93	83.33±5.39
Presence of hair in the nest box		$P<0.001$	$P<0.001$
Hair	65 (71.4)	10.05±3.63	23.82±4.51
No hair	26 (28.6)	90.38±5.38	94.23±4.00
Cannibalism of kits by the doe		$P<0.001$	$P<0.001$
One or all of the kits cannibalised	12 (13.2)	87.08±8.71	87.08±8.71
No kits cannibalised	79 (86.8)	24.79±4.82	37.38±4.95

[1]Values in the same column accompanied by a different letter are different ($P<0.05$).

Preweaning kit mortalities were significantly higher in primiparous than in multiparous does (Table 3). Maternal behaviour type 1, with many births in which all the kits died during the peripartum and nursing periods, included a high proportion of births from primiparous does and of parity orders 1 and 2 (Table 2). As in primiparous domestic does, mother-kit contact at birth is a crucial factor in establishing the

maternal response and the experience does gained from raising a previous litter therefore enables them to retain their maternal response (González-Mariscal *et al*., 1998b). This improves kit survival rates in successive litters, as is the case among the wild does considered in this study. Such is the influence of the does' previous experience upon the litters' viability in domestic breeds that not only is there a tendency for primiparous does to abandon litters, but also that such does are responsible for half the cases of cannibalism (Delaveau, 1979). In fact, in the wild rabbits used in this study, the incidence of cannibalism was higher than that found in meat rabbits, with no difference to be found between primiparous and multiparous does. This is probably due to stress affecting both groups equally (González-Redondo and Zamora-Lozano, 2008), something supported by the fact that maternal behaviour type 3 showed the highest proportion of births with all of the kits cannibalised, despite that the fact that it included few births from primiparous does (Table 2).

Litter size

In meat breeds, the kit mortality during the nursing period rises as the litter size increases. This is due to the fact that kits of a low weight are born in excessively large litters and have to compete for milk (Delaveau, 1979; Szendrö *et al*., 1996; Rashwan and Marai, 2000). We found that litter size (total kits born) did not influence kit mortality (Table 3), probably due to the fact that litter sizes were within the range of typical values for wild rabbits of the same subspecies (Soriguer, 1981). Moreover, in meat breeds the mother must receive a sufficiently large stimulus from the kits in order to continue lactating (González-Mariscal, 2001) and the presence of several siblings in the nest increases their chances of survival because the improved thermal efficiency contributes to keeping the nest temperature sufficiently high (Bautista *et al*., 2003). This could partly explain why in maternal behaviour type 3 the high proportion of births with only 1 and 2 kits born led to all of the kits dying during the peripartum period (Table 2).

Nest-building and kit delivery

In domestic breeds, the causes of doe-attributed kit death are frequently due to a badly-made nest (Delaveau, 1979). Therefore, good nest-building behaviour is essential since both the naked kits' survival and their welfare depend directly upon the quality of nest-building (Szendrö *et al*., 1988; Negatu and McNitt, 2002). Nest-building behaviour is highly predictable and stereotyped but in some does the development of this behaviour can fail; the doe either gives birth without preparing the nesting material or gives birth outside the nest box. As discussed below, does failing to prepare the nesting material before giving birth are not successful in rearing their kits (Negatu and McNitt, 2002). This study found the same to be true for caged wild rabbits in which both the perinatal mortality and accumulated mortality up to weaning were linked to bad nest-building (Tables 2 and 3).

Place for delivery of the kits

In captivity, the natural burrow is substituted by a nest box that strongly determines the kits' survival during peripartum and nursing periods since the doe's ability to express her maternal behaviour more or less correctly depends upon their design. Parer *et al*. (1987) find a significantly lower survival among weaned kits born of cage-bred wild does in the conventional nest boxes used in rabbit meat farming and a greater survival in smaller nest boxes that have a refuge for the doe or in nest boxes provided with an entrance tunnel. The nest box used in our study was of small volume, completely enclosed and with a narrow entrance tunnel, thus imitating natural breeding burrows. It was therefore a suitable design in terms of satisfying the principal ethological demands arising from breeding of wild rabbits in cages (González-Redondo, 2006). Furthermore, once the perinatal period was over, we never once found kits outside the nest box when the doe left the box after nursing. As a result of the entrance tunnel's narrowness, does did not leave the box with kits hanging from her nipples –a frequent occurrence among meat rabbits

(Hudson *et al*., 1996b). Therefore, in our case the high incidence of kits on the cage floor after birth in maternal behaviour types 1 and 3 was due to the does giving birth outside the nest box, evidence of the failure in maternal behaviour (Tables 1 and 2) that increased the kit perinatal mortality rate (Table 3). The stress suffered by the does during the handling that usually took place in the peripartum might have provoked births outside the nest box and caused several does to abandon their litters. Similarly, domestic does disturbed during birth also give birth on the cage floor (Rashwan and Marai, 2000). Furthermore, handling the breeding burrow in the wild frequently results in the abandonment of the burrow (Lloyd and McCowan, 1968; Gibb, 1993). Moreover, when a failure in the development of maternal behaviour during peripartum causes births outside the nest box, the does are unable to take the kits into the nest box when the stress-inducing episode has ceased because this species does not display kit recovery behaviour (Deutsch, 1957). The incidence of such maternal behaviour alteration among the wild does in our experiment was much higher than that which occurs in domestic breeds. In fact, experiments have been undertaken with domestic breeds in which all of the does have given birth inside the nest box, even though some have not prepared the nest (Verga *et al*., 1984). Therefore, the high incidence of births in which kits were born outside the nest box observed in this study (Table 2) may be considered as a differentiating factor between the maternal behaviour of caged domestic and wild does.

Loss of hair

In domestic breeds, there is sometimes a failure in hair loss for nest-building (Sawing *et al*., 1960; Verga *et al*., 1984), with differences between does (Sawing *et al*., 1960) that are not due to previous experience but which may be related to specific stimuli such as endocrinal changes (Canali *et al*., 1991); environmental factors, including seasonal ones (Sawing *et al*., 1960; Szendrö *et al*., 1988); genetic factors including the breed (Ross *et al*., 1956; Sawing *et al*., 1960; Szendrö *et al*., 1988) and the type of material provided to make the nest's bedding (Verga *et al*., 1984). There are genetic differences with respect to nest quality with the result that the proportion of domestic does that do not place hair in the nest varies between 2.3 and 9% (Szendrö *et al*., 1988). In this study however, the number of wild does that did not place hair in the nest was much higher (28.6%; Table 1), something that seems to be related to the more stress-prone and reactive nature of wild rabbits when kept in strict captivity. The great importance of the layer of hair in the nest with regard to the kits' growth and survival up to weaning has been recognised in domestic breeds (Canali *et al*., 1991) since there are fewer deaths among nursing kits in nests with a better covering of hair (Szendrö *et al*., 1988; Canali *et al*., 1991), as found with regard to births in maternal behaviour type 2 (Table 2). When domestic does do not line their nests with hair, the kits are in an extremely prejudicial situation (Verga *et al*., 1984), with mortality among the kits in nests with no hair as high as 30% (Szendrö *et al*., 1988). In the wild rabbits used in this study, mortality up to weaning among kits in nests with no hair lining, corresponding to maternal behaviour types 1 and 3 (Table 2), was well above 90% (Table 3), confirming that the kits' chances of survival are minimum.

Building a layer of straw

The doe's placing of straw or similar materials as a thermal component in the nest (González-Mariscal *et al*., 1998a) is another element of maternal behaviour (Szendrö *et al*., 1988). This is a more plastic behaviour pattern than the lining of the nest with hair and improves over time with parity order and as a function of experience, not as the result of external stimuli (Canali *et al*., 1991). Since in this study the straw was supplied on the cage floor rather than in the nest, and given that the wild does only placed straw in the nest box when they developed correct nest-building behaviour, a high rate of maternal failure was revealed. In fact, in more than 40% of the births, the does failed to line the nest with straw. Most of the above does corresponded to maternal behaviour types 1 and 3 (Table 2), resulting in an increase in kit perinatal and preweaning mortality (Table 3).

Potential role of genetics and stress in maternal behaviour failure

There are different preweaning death rates among domestic breeds and genetic selection has led to a reduction in mortality rates (Rashwan and Marai, 2000). Therefore, the differences between domestic and wild rabbits will be even greater, given that the wild subspecies used in the study (O. *cuniculus algirus*) was different to the subspecies to which the domesticated breeds (O. *cuniculus cuniculus*) belong (Branco *et al*., 2000). In fact, sometimes, wild rabbits of the same subspecies as those in this study did not reproduce in captivity due to stress (Ben Saad and Baylé, 1984). Stress levels among the wild does in this study were not measured, although it is possible that, being more stress-prone than domestic breeds, they showed a greater vulnerability provoked by the housing and handling inherent to strict captivity. This might have triggered the high levels of maternal failure recorded, resulting in nest-building failures and in low kit survival rates. In fact, there is a multiplicity of hormones and cerebral structures involved in the maternal behaviour of does, particularly nest-building (González-Mariscal, 2001). Stress acts upon neuro-hormonal centres leading to alterations that affect hormone release. Moreover, the behaviour patterns of both the mother and her kits during the peripartum and lactation are stereotyped and lack the flexibility that is characteristic of most mammals (Hudson *et al*., 1996a). Once the doe has given birth, she does not complete or improve the nest, and the kits follow an endogenous circadian rhythm which prepares them for a single daily, synchronised visit by the mother to suckle them (Hudson *et al*., 1996b). Nursing, however, depends on the state of the mother and not on the demands of the kits (Zarrow *et al*., 1965). This suggests that any alteration of the environment in which birth and nursing take place, e.g. stressful episodes, could lead to a failure in the kits' ability to survive because they depend upon both the nesting material and the mother's lactation synchronicity. In addition, we can deduce that the wild does in this study were responsible for the low kit survival rates because they were inside the nest boxes in conditions that were practically identical to those found in a natural burrow (González-Redondo, 2006). Therefore, understanding how genetic differences, stress, handling, and cage and nest box enrichment can influence the maternal repertoire and preweaning kit survival in cage-bred wild rabbits is still a challenge for future studies.

CONCLUSION

The maternal behaviour in cage-bred wild rabbits recorded in the present study is consistent with that reported in the wild (Mykytowycz, 1968) and in domestic rabbits kept either in cages (Ross *et al*., 1956; Venge, 1963) or under semi-natural conditions (Deutsch, 1957). Caged wild does are subject to the same modulating factors in maternal repertoire development and their litters' viability as domestic does. This confirms that there are few differences between the maternal behaviour of both types of rabbits (Hudson *et al*., 1996b) and that, in essence, this behaviour has been unaffected by domestication (Kraft 1979a,b). However, when reared in strict captivity, the wild rabbit's more reactive and stress-prone behaviour leads to a lower preweaning litter viability, mainly caused by the does' failure to display maternal behaviour during the peripartum period. This failure is measured in terms of a high proportion of does that did not build a nest, does that gave birth to kits outside the nest box and does that cannibalise their offspring. This reveals a relative lack of adaptation of the wild rabbits to being both housed and handled in cages.

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