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Do newborn domestic rabbits *Oryctolagus cuniculus* compete for thermally advantageous positions in the litter huddle?

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Abstract Competition among mammalian siblings for scarce resources can be severe. Whereas research to date has focused on competition for the mother's milk, the young of many (particularly altricial) species might also be expected to compete for thermally favorable positions within the nest, den, or litter huddle. We investigated this in newborn pups of the European rabbit *Oryctolagus cuniculus*, a species in which the altricial young are not brooded by the mother, and in which competition for milk is severe. In eight unculled litters (N=86 pups) of a domestic chinchilla strain, we calculated huddling indexes for individual pups on postnatal days 2–5 as a measure of the degree of insulation they received from littermates. Pups maintained almost constant physical contact with the litter huddle. They performed brief but frequent rooting and climbing behaviors, which usually improved their huddling index, interspersed with longer periods of quiescence during which their huddling index declined. As expected, we found a significant positive relation between pups' mean huddling index and body temperature. Unexpectedly, however, we did not find a relation between huddling index and pups' birth weight, survival, milk intake, or efficiency of converting milk to body mass. We conclude that rather than competing for thermally advantageous positions within the huddle newborn rabbits share out thermally advantageous positions as they move in a continual dynamic flow through it. Thus, in newborn rabbits, competition for the mother's milk exists alongside mutual "cooperative" benefits of littermate presence.

Keywords Sibling relations · Mammals · Competition · Cooperation · Individual differences

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Introduction

Interest in sibling relations and the influence of these on individual growth, survival, and in shaping behavioral phenotypes is growing among behavioral ecologists and developmental psychologists (Sulloway 1996, 2001; Mock and Parker 1997; Mock et al. 1998; Stockley and Parker 2002; Forbes 2005; Drummond 2006). Emphasis has been on competition among siblings for limited resources, particularly food, and has been most often studied in birds (Mock and Parker 1997; Drummond 2001, 2006; Forbes 2005; Hudson and Trillmich 2007). Although less is known about sibling relations in mammals, there is increasing evidence from a range of species that competition, particularly for the mother's milk, can be severe (Bautista et al. 2005; Drake et al. 2007; Hofer and East 2007; White 2007; Trillmich and Wolf 2007). Milk, however, is only one resource for which newborn mammals may compete.

Another, particularly among altricial young, is a thermally favorable position within the nest, den, or litter huddle.

Most altricial mammals cannot maintain homeostasis if kept alone, and depend on parental brooding or on the insulating presence of littermates for normal growth and survival (Rheingold 1963; Alberts 1978a, b; Harri et al. 1991; Schank and Alberts 1997; Rouvinen-Watt and Harri 2001; Sokoloff and Blumberg 2001; Bautista et al. 2003). Although mechanisms of behavioral thermoregulation have been studied in the altricial young of several mammalian species (Ogilvie and Stinson 1966; Leonard 1974, 1982; Satinoff et al. 1976; Alberts 1978a, b; Freeman and Rosenblatt 1978; Hull and Hull 1982; Schneider et al. 1995; Blumberg and Sokoloff 1998; Sokoloff and Blumberg 2001; Bautista et al. 2003; Pacheco-Cobos et al. 2003) there has been no study of differences among littermates in occupancy of thermally advantageous positions within the litter huddle, and possible effects on individual growth and survival are unknown.

Due to its unusual pattern of maternal care, the European rabbit *Oryctolagus cuniculus* provides a particularly good opportunity to investigate this. In the wild, rabbits give birth in an underground nest, leave the young almost immediately, and both in nature and the laboratory only return to nurse for 3 to 4 min once every 24 h (Deutsch 1957; Zarrow et al. 1965; Hudson and Distel 1982, 1989; Hudson et al. 1999; Jilge and Hudson 2001). Despite the altricial state of the young, this is the only maternal care they receive other than the provision of a specially constructed nest (reviewed in González-Mariscal and Rosenblatt 1996). This limited maternal presence makes it possible to observe and manipulate the pups without interfering with the mother–young relationship, and to separate the influence of the mother on pups' development from that of their siblings to an extent not possible in most other mammals (Denenberg et al. 1973; Hudson and Distel 1986; Drummond et al. 2000; Bautista et al. 2003, 2005). However, it also confronts the pups with a number of challenges, including maintenance of an adequate body temperature. Rabbits are born without fur and with a large surface area relative to body mass. To maintain an adequate body temperature, they depend on the insulating properties of the fur-lined nest and on the presence of littermates. If they are separated from these, growth is retarded, and the probability of survival markedly reduced (Ross et al. 1956; Zarrow et al. 1963; Bernard and Hull 1964; Canali et al. 1991; Bautista et al. 2003).

Previously, we showed that rabbit pups can orient adaptively on thermal gradients from birth (Pacheco-Cobos et al. 2003) and that sibling presence contributes to thermoregulatory efficiency, growth, and survival (Bautista et al. 2003). In this paper, we ask whether siblings compete for thermally advantageous positions within the litter huddle, that is, if there are individual differences in relative position within the huddle, if these are associated with differences in body mass and body temperature, suckling success, growth and survival, and with differences in displacement behavior within the huddle. We limited the study to postnatal days 1–5 as this is the period of highest pup mortality (Coureaud et al. 2000a, b; Drummond et al. 2000), and the period when pups are most dependent on the presence of littermates to meet their thermal needs (Bautista et al. 2003).

Based on previous findings that heavier pups have a competitive advantage during nursing, grow faster and are more likely to survive (Coureaud et al. 2000b; Drummond et al. 2000; Bautista et al. 2005), we expected that they would occupy better insulated positions in the litter huddle and that they would be more efficient in attaining these than their lighter sibs.

Materials and methods

Animals

We collected data between January 2004 and July 2005 from chinchilla-strain domestic rabbits bred and maintained at the Centro Tlaxcala de Biología de la Conducta, Tlaxcala, Mexico. Mothers weighed between 3.0 and 3.5 kg and had four pairs of nipples. We used eight unculled litters of 10–12 pups (N=86; mean litter size 10.8±0.7) from eight different multiparous females (one or two previous litters) mated with eight different males. Large litters, not unusual in this breed, were used to maximize differences in position within the huddle. The females were kept in individual stainless steel cages 90×60×40-cm high, under fluorescent lights and on a 16:8 h light/dark cycle to approximate conditions at the height of the summer breeding season for rabbits in Europe (Hudson and Distel 1990). Ambient temperature was maintained between 18 and 20°C, and water and food (Purina rabbit chow) were always available. For nest building, straw and an open-top wooden box 40×35×15-cm high and lined with wood shavings were placed in the females' cages 3 days before term.

Experimental procedure

On the day of birth (day 0) we left pups with their mother so they could be nursed at least once without human disturbance.

Day 1 At 0900 hours, we removed the nest box containing the young from the mother's cage and took it to a cold room with the temperature set at 25°C (Oregon Scientific electronic thermometer, EMR963HG). This temperature, below the approximately 35°C thermal neutral zone for newborn rabbits (Bernard and Hull 1964; Hull 1965; Sokal and Sinclair 1976; Pacheco-Cobos et al. 2003), induces them to huddle but without compromising pup survival (Bautista et al. 2003). In nature, ambient temperatures in the nest chamber can drop below pups' thermal neutral range and well below the temperatures maintained here (H. Rödel for burrows in Bayreuth, Germany, personal communication).

The pups (dark gray in color) were weighed individually using an electronic balance (Ohaus, Navigator), numbered on the ventrum, back and flanks with white correcting fluid (Nukote, Pelikan) for individual identification in video recordings, and placed in a cloth-lined box the same as the nest box but without nest material so as to allow behavioral observation (Fig. 1). To keep the pups in the center of the box and prevent them becoming trapped in the corners, we placed them inside a 28 cm-diameter wire mesh hoop, which we enlarged to diameter 30 cm on day 5 to accommodate pup growth. A video camera (Sony CR-TRV) was mounted above the box to record pups' behavior.

At 1000 hours, we filmed the litter for 5 min and then measured each pup's temperature at the throat and groin (representing high and low temperatures on the body surface, respectively; Bautista et al. 2003) with a quick-reading mercury thermometer (cloacal Schultheis type, Miller and Weber, T-600), and used the mean of these two measures for all further calculations. Although this cannot be considered an accurate measure of core temperature (reviewed in Blumberg and Sokoloff 1998) it gives consistent readings of relative differences in body temperature among pups (Bautista et al. 2003), which was the main interest in the present study. The litter was filmed again for 5 min every hour until 1800 h (a total of nine recordings), and body temperature measured again at 1130, 1430, 1630 and 1830 hours (a total of five recordings), determining the order in which pups were removed from the box using a random numbers table. Measuring temperature took about 2 min per pup, after which pups were returned to the box to minimize cooling of the other littermates.

Days 2 to 5 At 1000 hours we followed the same procedure as on day 1 except that after measuring pups' temperature at 1130 hours, we induced them to urinate by lightly brushing their genital area with an index finger, weighed them, and returned them to the observation box. Urination was induced to enable accurate measurement of milk intake after nursing 30 min later. After filming at 1200 hours, we removed the mesh hoop without disturbing the huddle, and took the mother from her cage and placed her beside the box so that she could jump in for the approximately 3 min nursing (Hudson and Distel 1983; Bautista et al. 2005). We weighed the pups individually immediately after the mother jumped out of the box at the end of nursing, and took the difference between their pre- and postnursing weight as a measure of milk intake.

To ensure the continued thermal importance of the litter huddle despite pups' increase in body volume and growth of fur (Bautista et al. 2003; cf. Sokal and Sinclair 1976), the temperature of the cold room was decreased by 1°C at 1000 hours each day (cf. Alberts 1978b). Although information is lacking on the relationship between ambient temperature, pup size and body temperature, and the relationship between these variables is unlikely to be linear, here we were principally interested in relative differences among littermates rather than in changes in absolute values with age.

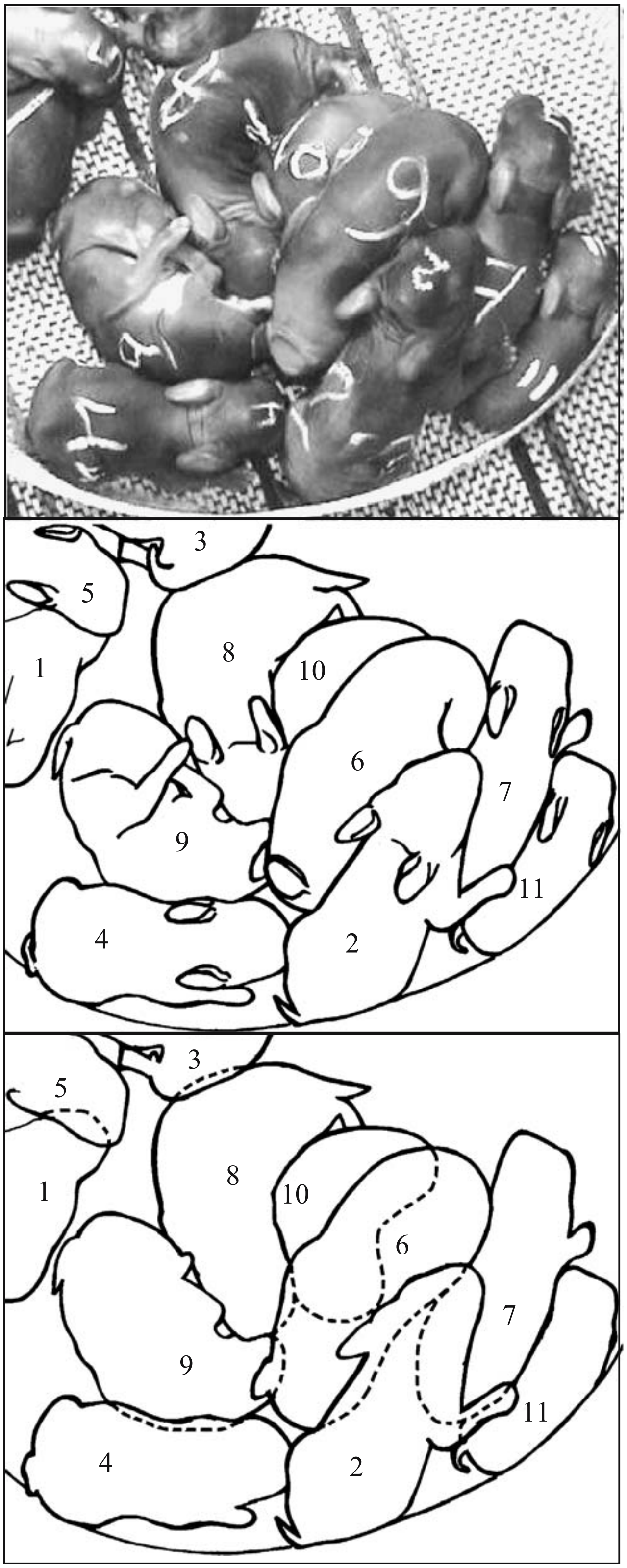
At the end of the study, we returned the litters to their mothers until weaning on postnatal day 25. Sex of pups, difficult to determine at birth, was established by genital inspection at weaning or by dissection if pups died earlier.

Behavioral measures

In addition to daily measures of pups' weight, body temperature, milk intake, and efficiency of converting milk to body mass (C_t=increase in prenursing body weight over $t+1$ days/weight of milk ingested over t days; Drummond et al. 2000; Bautista et al. 2003) we collected three sets of behavioral data.

Position within the huddle We used the first frame of each of the nine daily video recordings to calculate a huddling index (HI) for each pup representing the area of its body in physical contact with littermates (36 measures/pup; Fig. 1). Using the image analysis programs PhotoPaint 11 and SigmaScanPro 4.01 for Windows (Jandel Scientific), we applied the formula HI $=X+2Y+Z$, where X is the percent of a pup's dorsally viewed body outline in contact with another pup(s), Y is the percent of a pup's dorsally viewed body surface covered by another pup(s) multiplied by 2 because of the greater insulation gained from being covered rather than covering another pup, and Z is the percent of a pup's dorsally viewed body surface covering another pup(s; Fig. 1). We then used these 36 values to calculate a mean huddling index for each pup.

Displacement within the huddle We transferred the video recordings to a computer using the Microsoft program Movie Maker 2.1.4026.0 for Windows, and for days 2–5, we used four of the 5-min video recordings—at 1000 and 1200 hours (before nursing), and at 1600 and 1800 hours (after nursing)—to score the following behaviors shown by pups in relation to the litter huddle: the frequency and duration of *rooting*, defined as a pup pushing its head between or beneath other pups while vigorously scrabbling with its forelegs and thrusting with its hind legs (Fig. 1, pup 8); the frequency and duration of *climbing*, defined as a pup



◀**Fig. 1** *Upper panel*, huddle of pups in the observation box on postnatal day 1 recorded by video camera from above and used to determine pups' huddle indexes. Pups have been numbered with white correcting fluid for individual identification; part of the mesh hoop enclosing the litter can be seen across the bottom. *Middle panel*, outline of pups in the huddle above. *Bottom panel*, outline of pups overlaid with the computer-generated contours used to measure the percent of an individual's body surface in physical contact with other pups; *broken lines* indicate the estimated non-visible parts covered by neighboring pups. Note the large difference in size among pups (for example, light pups 11=26.9 g and 4=52.6 g compared to heavy pups 6=63.4 g and 8=70.1 g)

placing its forequarters over another pup(s) while thrusting with its hind legs whether or not this resulted in displacement across the top of the huddle (Fig. 1, pup 2); the frequency and duration of *staggering*, defined as a pup lurching from side to side when locomoting but without overbalancing; the frequency and duration of *overbalancing*, defined as a pup performing a half (180°) or a full (360°) body roll; and the duration of remaining *immobile* while in contact with the huddle, defined as absence of the behaviors described above (Fig. 1, pup 9). The frequency and duration of pups loosing physical contact with littermates was also recorded. Because of the time-consuming nature of this analysis (16 recordings, 80 min total/pup), only the behavior of the lightest and heaviest surviving pup in each litter, defined by mean body weight across the 5 days of the study, was scored (256 evaluations, 21.3 h total observation time).

Effectiveness of displacement behaviors We estimated this by comparing the huddling indexes of the lightest and heaviest pups as defined above at the start and finish of rooting and climbing episodes, considering the end of episodes as ≥1 s without further displacement or clearly attempted displacement. We also evaluated the consequence for the pups of remaining immobile within the huddle by comparing their indexes at the start and finish of bouts of immobility of ≥1 s.

Data analysis

Except for factors influencing early pup survival, analysis was based on data from animals surviving to the end of the study, and mainly on data from days 2–5 after pups had some time to adjust to the experimental situation. Statistical analyses were performed using SPSS 14.0 for Windows. We examined the influence of huddling on pup survival and growth using general linear model analysis (GLM), first by taking survival as the dependent variable, litter as a random factor, and mean huddling index, mean body temperature, birth weight, and total milk intake as covariates; second, by taking mean milk conversion as the dependent variable, litter as a random factor, and mean huddling index, mean body temperature, mean body weight, and total milk intake as covariates; and third by taking mean body temperature as the dependent variable, litter as a random factor, and mean huddling index, mean weight and total milk intake as covariates. Using partial correlations, we then examined first the relation between huddling index and body temperature with body weight and milk intake as the controlled variables; second, the relation between huddling index and milk intake with body temperature and body weight as controlled variables; and third, the relation between huddling index and birth weight, with body temperature, and milk intake as controlled variables. Descriptive statistics are given as means±SD, and as medians and ranges for frequencies of behavioral measures. An alpha value of 0.05 was taken as the level of significance throughout.

Since in this and previous studies (Drummond et al. 2000; Bautista et al. 2003, 2005; Martínez-Gómez et al. 2004) no differences on any parameter were found between males and females, we have combined their scores.

Results

Growth and survival

Despite the experimental conditions under which litters were raised, total milk intake (40.74 g±13.94) and final mean body weight of surviving pups on day 5 (60.84 g±12.73) were within the normal range for this breed (Hudson et al. 1996; Martínez-Gómez et al. 2004; Bautista et al. 2005), and even considering that in contrast to the previous studies, these were relatively large, unculled litters.

Fourteen pups (16.3%) died in six of the eight litters apparently from starvation; they had no milk in their stomachs and weighed mean 29.2%±15.2 less than their respective littermates on the day of death (for example, pup 11 in Fig. 1). This mortality was also within the range for normally raised, unculled litters of this breed (Drummond et al. 2000) and so did not seem to be due to the particular experimental conditions of the study. Comparing the values for the 14 victims with values for 14 randomly chosen littermates at the time of death of their respective siblings showed that the victims had significantly lower mean birth weights (39.1 g±9.61 versus 48.59 g±9.51; paired *t* test: t_{13}=3.46, *P*=0.004), that they obtained on average significantly less milk (1.9 g±3.4 versus 9.5 g±3.5; t_{13}=7.65, *P*=0.002), had significantly lower mean body temperatures (33.8°C±1.34 versus 36.1°C±0.75; t_{13}=6.77, *P*<0.0001), and that they had significantly lower mean huddle indexes (77.7±25.3 versus 100.1±9.7; t_{13}=3.07, *P*=0.009).

Behavior within the huddle

Although the litters usually formed a single huddle, they sometime broke up into two physically separate subhuddles (Fig. 1). In either case, the pups remained in almost constant contact with littermates. The individuals became separated from a huddle on only 19 occasions, and then for

Table 1 Comparison of motor behavior of lightest and heaviest pups from postnatal days 2 to 5

	Lightest pups	Heaviest pups	*P* values
Median frequency (events/hour)			
Rooting	61.9 (8.3–158)	39.0 (6.8–73.5)	0.02
Staggering	48.8 (7.5–122)	20.6 (8–3–66.8)	0.02
Climbing	6.4 (0–21.8)	12.4 (0.8–46.5)	
Overbalancing	6.0 (0–18.0)	2.6 (0–6.0)	
Loosing contact	5.6 (0–21.0)	0 (0–11.3)	
Total	133 (34–310)	76 (25–189)	0.01
Median duration of events			
Rooting	3.9 s (2.8–4.5)	3.6 s (3.0–4.3)	
Staggering	1.3 s (1.2–1.5)	1.2 s (1.0–1.3)	
Climbing	3.1 s (2.0–6.8)	3.1 s (2.7–4.0)	
Overbalancing	1.2 s (1.0–1.7)	1.0 s (1.0–2.3)	
Loosing contact	3.4 s (2.0–9.7)	4.1 s (2.5–5.8)	
Median percent of observation time			
Rooting	5.0% (0.8–9.3)	3.2% (0.4–5.5)	
Staggering	1.4% (0.2–3.3)	0.5% (0.2–1.5)	
Climbing	0.6% (0–1.4)	0.9% (0.1–2.6)	
Overbalancing	0.2% (0–0.6)	0.1% (0–0.1)	
Loosing contact	0.4% (0–2.0)	0% (0–0.6)	
Median percent of observation time immobile			
	91.9% (85–98)	95.7% (91–99)	0.01

Minimum–maximum values are given in brackets. *P* values are given only for significant differences.

only 1–2 s comprising less than 0.5% of the total observation time. Of the motor behaviors recorded rooting was the most frequent (median 45 events/pup/h) followed by staggering (median 31 events/pup/h), climbing (9.4 events/pup/h), overbalancing (4.5 events/pup/h), and loosing contact (0.4 events/pup/h). All these behaviors were brief (median duration 1–4 s) and together constituted a median of only 5.8% of the total observation time, meaning that pups spent 94.2% of the time immobile. However, a notable feature of huddling behavior was the wide range in the scores of any individual pup. Thus, across the 36 recordings used to assess huddling during the study, for each pup high index scores (140–300) as well as low index scores (0–50) were recorded, although with different frequencies. Consequently, although the mean indexes of individual pups ranged from 55.7±40.3 to 132±50.7, with an overall mean score of 98.1±46.9, variance was very large.

As shown in the upper panel of Table 1, light pups were more active than their heavier sibs. We found significant differences between them and heavier pups in the total frequency of behavioral events (Wilcoxon signed ranks test: $T=35$, $N=8$, $P<0.01$), and particularly in the frequency of rooting ($T=34$, $N=8$, $P=0.02$) and staggering ($T=34$, $N=8$, $P=0.02$). Although we did not find a difference in the duration of behavioral events between light and heavy pups (Table 1, second panel), as a consequence of greater frequencies lighter pups spent significantly less time immobile than their heavier sibs (median times of 91.9 and 95.7%, respectively; $T=35$, $N=8$, $P<0.01$; Table 1, bottom panels).

Effectiveness of displacement behaviors Figure 2 shows the change in huddling indexes of lightest and heaviest pups after rooting and climbing (the two behaviors most obviously directed towards achieving a better insulated position in the huddle), and after remaining immobile. Although as reported above (Table 1) rooting and climbing episodes only lasted a few seconds, in most cases, they resulted in pups improving their huddling index, and as shown in Fig. 2, this was equally the case for lightest and heaviest pups. In contrast, when pups remained immobile their huddling scores declined markedly, but again, as shown in Fig. 2, to a similar extent for lightest and heaviest pups.

Influence of huddling on survival, growth and body temperature

We expected a positive relationship between huddling indexes and three main functional outcomes for the pups; greater probability of survival, enhanced growth as measured by efficiency of converting milk to body mass, and higher body temperature.

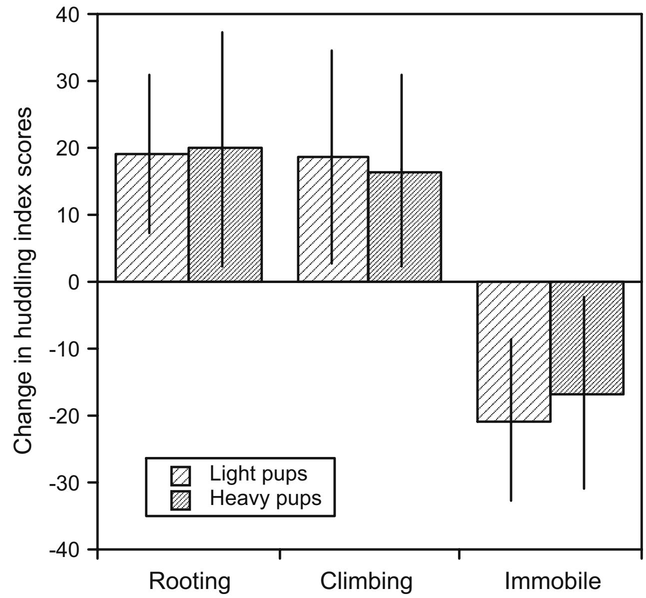


Fig. 2 Change in huddling index for the lightest and heaviest pup from each of eight litters following episodes of rooting, climbing, or remaining immobile. Means±SD are given ($N=8$ pups/group) calculated from a total of 16 sessions recorded on postnatal days 2–5. Whereas rooting and climbing resulted in improved huddling indexes, remaining immobile resulted in a decline, and to a similar degree for lightest and heaviest pups

Survival Taking into account all 86 pups born, GLM analysis reported a significant influence on pup survival of birth weight ($F_{1,74}=4.65$, $P=0.034$), of milk intake ($F_{1,74}=11.2$, $P<0.001$), and of body temperature ($F_{1,74}=6.36$, $P=0.014$) but not of huddling index ($F_{1,74}=1.56$, $P=0.22$) or litter ($F_{7,74}=2.01$, $P=0.07$; illustrated in Fig. 3).

Milk conversion For the 72 pups, surviving to the end of the study GLM analysis reported a significant influence on mean efficiency of converting milk to body mass for the three time points for which these data were collected (days 2–3, 3–4, 4–5) of milk intake ($F_{1,59}=13.1$, $P=0.001$) but not of huddling index ($F_{1,59}=2.3$, $P=0.14$), body temperature ($F_{1,59}=2.01$, $P=0.16$), birth weight ($F_{1,59}=3.9$, $P=0.053$) or litter ($F_{7,59}=1.4$, $P=0.22$).

Body temperature For the 72 surviving pups, GLM analysis reported a significant influence on body temperature of huddling index ($F_{1,59}=18.0$, $P<0.001$), birth weight ($F_{1,59}=4.51$, $P=0.038$), milk intake ($F_{1,59}=14.3$, $P<0.001$), and litter ($F_{7,59}=14.4$, $P<0.001$).

The partial correlation examining the relation between huddling index and body temperature with birth weight and milk intake as controlled variables reported this to be significant ($F=68$, $r=0.27$, $N=72$, $P=0.024$; Fig. 3a). The partial correlation examining the relation between huddling index and milk intake with birth weight and body temperature as controlled variables reported nonsignificance ($F=68$, $r=0.01$, $N=72$, $P=0.92$; Fig. 3b). And the

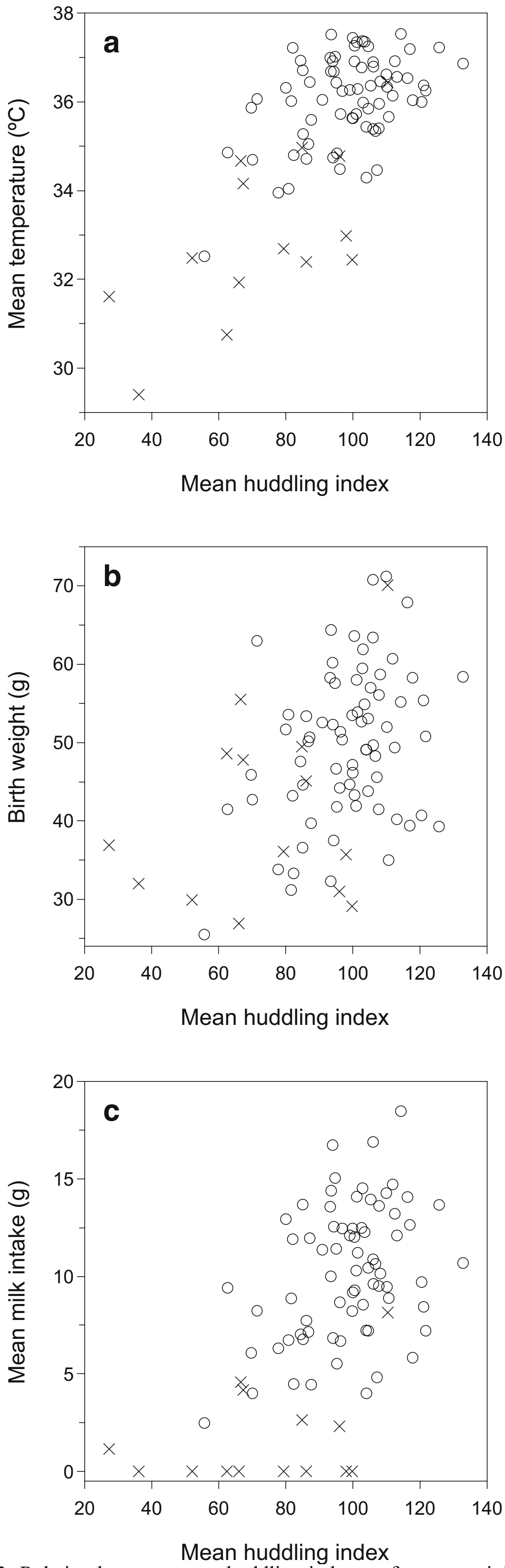


Fig. 3 Relation between mean huddling indexes of pups surviving to the end of the study on postnatal day 5 (*circles*, N=72) and of pups that died before (crosses, N=14) and **a** mean body temperature, **b** birth weight, and **c** mean milk intake

partial correlation examining the relation between huddling index and birth weight with body temperature and milk intake as controlled variables also reported nonsignificance (F=68, r=0.10, N=72, P=0.41; Fig. 3c).

Discussion

Survival and growth of pups in the present study corresponded to previous reports for this breed raised in more natural (laboratory) nests (Hudson et al. 1996; Drummond et al. 2000; Martínez-Gómez et al. 2004; Bautista et al. 2005). Thus, the present findings on the behavior of pups in relation to the litter huddle should be generally valid, at least for domestic rabbits raised under similar conditions. The situation in the wild, however, remains to be investigated.

A first result, consistent with previous findings in the rabbit and other newborn altricial mammals (Bernard and Hull 1964; Alberts 1978a, b; Schneider et al. 1995; Schank and Alberts 1997; Harri et al. 1991; Rouvinen-Watt and Harri 2001; Sokoloff and Blumberg 2001; Bautista et al. 2003) was the evident importance of the huddle. Pups remained in almost constant physical contact with litter-mates, and the few occasions on which they became separated only lasted a few seconds (Table 1). Pups also worked repeatedly and effectively to obtain a better insulated position within the huddle as measured by their index scores. Most pups performed presumably energetically costly rooting and climbing behaviors many times an hour, and although each of these events only lasted a few seconds, they usually resulted in an improvement in pups' huddling indexes. In contrast, remaining immobile and failing to perform such behaviors resulted in a marked decline in huddling indexes (Table 1; Fig. 2). As predicted, GLM and partial correlation analyses reported a significant positive relation between huddling index and body temperature (Fig. 3a). Thus, we may conclude, in accord with other studies of newborn altricial mammals cited above, that the litter huddle and a well-insulated position within it represents an important resource for newborn rabbits.

Nevertheless, we failed to find support for the predictions that pups with higher birth weights would have higher huddling indexes or that pups with higher huddling indexes would be more likely to survive, would obtain more milk, and would be more efficient in converting milk to body mass. Thus, although pups worked to obtain better insulated positions within the huddle (rooting and climbing behaviors resulted in higher huddling indexes and huddling indexes were positively correlated with body temperature), we found no support for the prediction that pups compete for such positions with the advantage going to the heaviest members of the litter as is the case during nursing (Drummond et al. 2000; Bautista et al. 2005; but see Fey and Trillmich 2007). Rather, the findings suggest that the huddle is of mutual benefit and provides thermoregulatory advantages to all.

With regard to pup survival (remembering that more than 16% of pups died)—as in previous reports (Coureaud et al. 2000a, b; Drummond et al. 2000)—most deaths occurred early, and victims usually had the lowest birth weights and obtained little or no milk during the highly competitive once-daily nursing events. Thus, although the huddling indexes of victims and surviving pups overlapped to a considerable degree (Fig. 3), any thermoregulatory benefits conferred were not sufficient to offset the inability of lighter pups to gain sufficient milk or the presumably high energetic costs of achieving and maintaining well-insulated positions within the huddle (cf. Table 1 and Fig. 3). As in other species (Drake et al. 2007), the importance of birth weight as a predictor of postnatal survival and growth suggests that prenatal factors such as uterine position need to be considered in future studies of individual developmental trajectories in the rabbit. Relevant here is the finding by Roshan and Greene (1936) based on the examination of the uterine horns in a large sample of 71 pregnant rabbits close to term of a significant decrease in fetal and placental weights from the ovarian to the vaginal extremities.

Considering surviving pups, an unexpected finding was again the large overlap in huddling indexes (Fig. 3). In fact, during the study, for most individuals, we recorded huddling indexes across the whole or most of the possible range, albeit to different degrees. This might be understood as follows. Individuals occupying at any moment better insulated positions in the huddle were warm enough, possibly even too warm (we sometimes recorded body temperatures of 38°C or more; cf. Alberts 1978b) not to need to take behavioral action to maintain their position and so "drifted" to less well-insulated positions as a result of the behavior of more peripheral, cooler, and thus more active littermates. These, in turn, gained better insulated positions in the huddle, thereby becoming warmer and less active until they too drifted or were pushed out to more poorly insulated positions. The picture here is of a continual circulation of pups through the huddle in which all benefit to a somewhat similar degree from the presence of their littermates. This corresponds well with reports of huddle dynamics in rat pups (Alberts 1978b; Schank and Alberts 1997; Sokoloff and Blumberg 2001) and suggests the need for a more complex view of sibling relations in the rabbit. On the one hand, competition for milk is often severe (Drummond et al. 2000; Bautista et al. 2005), while on the other, the presence of littermates is important, at times vital, for thermoregulation (Bernard and Hull 1964; Bautista et al. 2003), and via the continual circulation of individuals through the huddle represents the sharing of a communally produced resource rather than competition (see Sokoloff and Blumberg 2001 for rats). To better understand this process, we now need a finer analysis of the conditions such as ambient temperature and age at which pups are motivated to try to penetrate the huddle or rather to remain quiescent.

In conclusion, the present findings draw attention to the fact that while newborn rabbits compete vigorously for resources such as the mother's milk, they also benefit from one another's presence in a mutual, and at least under the relatively mild ambient temperatures imposed here, seemingly nonconflictive way. Thus, a consideration of the possible benefits as well as costs for altricial mammals of having siblings, in what number and under what environmental circumstances is an exciting area for future research (Hudson and Trillmich 2007).

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