Z. Säugetierkunde **61** (1996) 39–48

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Nursing, weaning and the development of independent feeding in the rabbit (*Oryctolagus cuniculus*)

By Robyn Hudson, Ágnes Bilkó, and V. Altbäcker

Institut für Medizinische Psychologie, Ludwig-Maximilian-Universität, München, Deutschland and Department of Ethology, Eötvös Loránd University, Budapest, Hungary

Receipt of Ms. 28.09. 1995
Acceptance of Ms. 02. 11. 1995

Abstract

Maternal care in the European rabbit is limited to one brief nursing visit a day. To investigate the nature of this unusual mother-young relationship, four domestic does and their litters were kept separately except for the once-daily nursing, and the following parameters were recorded; from post-natal days 1 to 30, the duration of nursing bouts, daily milk yield, deposition of faecal pellets in the nest by does, daily weight gain of pups, eating of faecal pellets and nest material by pups, their water intake, and from post-weaning days 31 to 44, their weight gain. Does were mated immediately after giving birth, and the measures for the first litters raised when does were pregnant were compared with the results for the second litters raised when does were not pregnant. Four control does and their litters were treated in the same way but without separating mothers and young. Pups progressed from drinking milk alone, to nibbling faecal pellets, to ingesting nest material, drinking water and finally to eating lab food. However, growth rates and the pattern of weaning depended on does' reproductive state. The first litters, raised by pregnant does, were significantly lighter and were weaned earlier than the second litters raised by the same does when not pregnant. The rabbit thus provides a particularly good opportunity to investigate the processes underlying the transition to independent feeding in a mammalian species.

Introduction

Mammals are defined as a taxonomic class by the ability of the mother to feed the newborn young on milk from the mammary glands. This is a physiologically and behaviourally complex process for both parties. For the young, the transition from the suckling period during which this milk represents the sole or primary source of nourishment to adult patterns of ingestion is certainly one of the major challenges of early life (Galef 1981; Hall 1990). For the mother, on the other hand, the provision of milk represents a major investment, the costs of which presumably must be weighed against the consequences for her future reproductive fitness (Trivers 1974; Partridge et al. 1982; Clutton-Brock et al. 1989). This apparent conflict of interests raises many questions concerning the nature of the weaning process and the relative contribution of the mother and young to it (Galef 1981; Bateson 1994).

The European rabbit (*Oryctolagus cuniculus*) provides an unusually good opportunity to investigate the weaning process in a familiar laboratory species. Not only is the reproductive physiology and natural ecology of the rabbit relatively well understood (Thompson and King 1994) but its remarkably limited pattern of maternal care (Hudson and Distel 1982, 1989) and renowned reproductive efficiency make it particularly suitable for the study of mother-young interactions.

When given the opportunity both wild and domestic does dig a nursery burrow in which they build a nest of grass, and fur pulled from their chest and belly. After giving birth the doe leaves the pups, blocks the burrow entrance and only returns to reopen it and nurse approximately every 24 hours for about 3–4 minutes. On entering the nest the doe simply positions herself over the litter, remaining almost motionless during nursing and not giving the pups any direct behavioural assistance to suckle. Towards the end of nursing she deposits a few faecal pellets in the nest and then jumps abruptly away, leaving the pups alone until the following day (Deutsch 1957; Zarrow et al. 1965; Broekhuizen and Mulder 1983; Hudson and Distel 1982, 1989).

Despite such limited care the young develop rapidly, and by weaning at about postnatal day 27, have increased their birth weight approximately twelve-fold. Eyes and ears open around day nine, and during the third week both domestic and wild pups start to leave the nest (Zarrow et al. 1965; Mykytowycz and Dudzinski 1972; Kraft 1979; Hudson and Distel 1982). This rapid development is important as the doe normally comes into oestrus immediately after parturition and is particularly receptive at this time (Brambell 1944). While this enables her to raise several litters in a season, the rapid weaning of the young associated with preparation for the birth of the next litter means that pups have to make the transition to independent feeding largely alone (Hudson and Altbäcker 1994).

Given this unusual pattern of maternal care it was the aim of this study to provide a first description of the changes in ingestive behaviour of young rabbits from birth, through weaning, to fully independent feeding, and of corresponding changes in the nursing behaviour of the doe. The findings demonstrate that the development of ingestive behaviour constitutes a well-defined sequence of stages but that the timing of weaning depends on the reproductive condition of the doe, and in particular, whether she is pregnant with a second litter.

Material and methods

Animals

A total of eight domestic chinchilla-breed does (Chbb, Thomae, Biberach, Germany) and their litters was used. Does were kept singly in standard metal rabbit cages (75×45×35 cm) at 20° ± 2 °C and on a 16L/8D light-dark cycle (lights on at 06.00 hours), with lab chow (Altromin®) and water available continuously. Several days before parturition they were also provided with nest boxes (40×30×30 cm) and hay.

Test procedures

To approximate the natural breeding situation in which does are frequently both pregnant and lactating, the development of the first litters from the eight does was studied after the mothers had been mated post partum and so were pregnant during lactation, and this was compared with the development of the subsequent eight litters raised without remating the mothers. On the day of birth (day 0) the nest boxes were removed, the pups were weighed and individually colour-marked in the ears, and the litters reduced to six pups each. After weighing the nest material, counting the faecal pellets deposited by the doe in the nest, and placing a foam rubber mat in the box to absorb pups' urine, the nest material, pellets and pups were returned to the nest boxes. Does were mated within a few hours of giving birth, and all responded with immediate lordosis and gave birth to large litters 31–32 days later. These second litters were raised and tested using the same procedure as for the first litters.

After weighing and returning newborn pups to the nest boxes, does and their litters were randomly allocated to one of two experimental conditions for the duration of the study.

Condition I: Pups separated from mother

This condition was designed to allow accurate recording of nursing behaviour and changes in pups' ingestive behaviour without does eating the nest material or causing other disturbance. On the day of birth the nest boxes were removed to a separate room and each morning between 09.00–10.00 h the pups and nest material were separately weighed, faecal pellets were counted, and the pups were returned to their box without nest material and brought to the doe for nursing. After nursing, pups were again weighed, fresh faecal pellets were counted, and the pups and fresh pellets, together with the nest material and old pellets were returned to the box until the following day. On post-natal day 14 the pups, nest material and pellets were transferred to large acrylic rodent cages (60 cm × 38 cm × 20 cm). On day 16 the nest material was replaced with 100 g of fresh hay which was renewed each day, and on day 18 the cages were equipped with a calibrated water bottle. Pups were brought to the doe each day until she refused to nurse, or until day 30, at which time they were transferred in pairs to standard metal rabbit cages, provided with lab chow and water ad libitum, and weighed daily until day 44.

Condition II: Pups with mother

In this condition the nest boxes containing the pups were left permanently with the mothers, enabling does to nurse at any time. The pups were only removed for weighing at 09.00 and 18.00 h each day to monitor their growth and to determine the approximate time of nursing. On post-natal day 26, pups of the first litters were separated from their mother (second litters on day 30), and were transferred in pairs to standard metal rabbit cages and treated as for Condition I.

Data analysis

Data were subjected to analysis of variance (ANOVA) for repeated measures followed by the Duncan post hoc test in the case of significant F values. For this analysis the nursing period was defined as days 1–25, and the post-weaning period as days 31–44. The alpha level was set at 0.05.

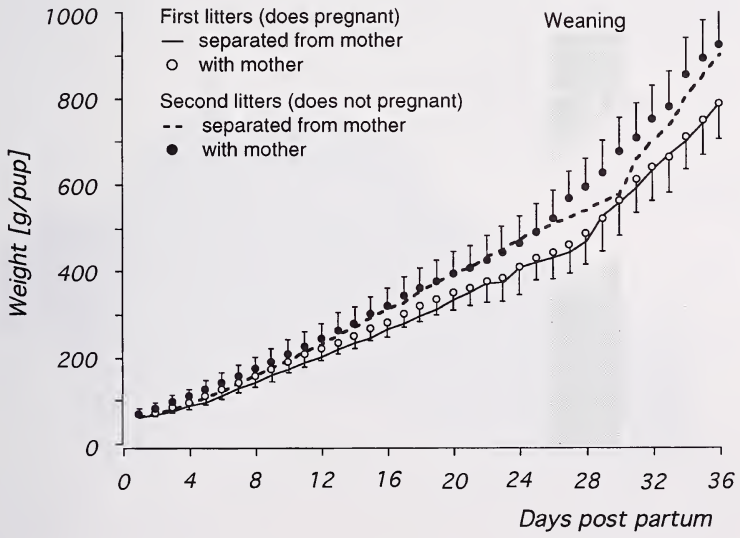

Fig. 1. Average daily cumulative weight gain of pups nursed by the eight does from Conditions I and II when pregnant ('first litters', N = 8 × 6 pups), and of pups nursed by the same does when not pregnant ('second litters', N = 8 × 6 pups). Means and SDs are given and the shaded zone represents the termination of nursing as determined by the pregnant does or by the experimenter on day 30.

Results

Two to three days before parturition all does built substantial nests of hay weighing between 98 and 155 g, which they lined with fur. In most cases some faecal pellets were also deposited in the nest at this time although does never urinated there. Using the measures described above for does and litters raised separately (Condition I), the period of maternal dependence was found to divide naturally into three main stages: the first week during which the pups' sole source of nourishment was the mother's milk; weeks 2-3 during which they started nibbling at the faecal pellets and hay and started drinking water; and week 4 during which they ate substantial amounts of solid food and at which time, if the mother was pregnant, nursing was abruptly terminated. Litters from Condition II, left permanently with their mother, only showed an increase in weight when weighed in the morning, suggesting that they also were only nursed once every 24 h and most probably during the night.

Week 1: Suckling

Figure 1 shows the average increase in the weight of pups from all eight first litters raised by pregnant does, and of the eight second litters raised by the same does when not pregnant. Using a 3-way ANOVA (state of pregnancy × condition × age) with repeated measures it was found that whereas the second litters from non-pregnant does showed a significantly greater weight gain by day 25 than the first litters from pregnant does [$F(1,86) = 21.5$, $p < 0.01$], there was no significant difference during the first week when most pups doubled their body weight. However, by day 25 the effect of age [$F(24,2064) = 3074.8$, $p < 0.01$] and condition [$F(1,86) = 9.74$, $p < 0.01$], as well as the interaction between state of pregnancy and age were significant [$F(24,2064) = 19.4$, $p < 0.01$], as was a threefold interaction among the factors [$F(24,2064) = 2.9$, $p < 0.01$].

The uniform growth of pups was reflected in the similar amounts of milk obtained by each of the separated litters during this period, which ranged from an average of 10 g/pup on day 1 to about 22 g/pup on day 7 (Fig. 2). As can be seen in figure 3, pups generally

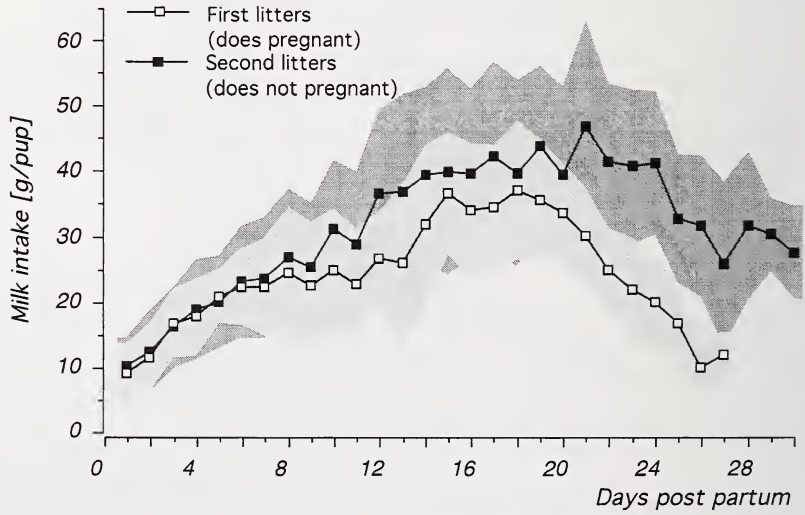

Fig. 2. Average daily milk intake of pups from Condition I nursed by does when pregnant ('first litters', N = 4×6 pups), and of pups nursed by the same does when not pregnant ('second litters', N = 4×6 pups). Data are from the same litters raised separately as in figure 1. Means and SDs are given.

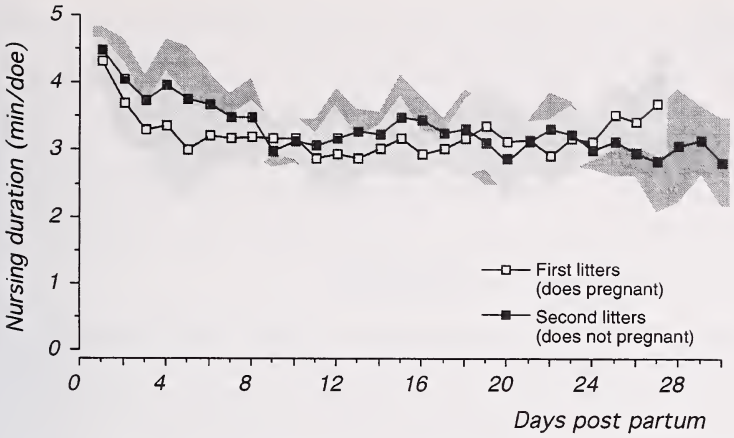

Fig. 3. Average time spent nursing each day by the four does from Condition I when pregnant ('first litters') and when not pregnant ('second litters'). These data correspond to the milk intake values in figure 2. Means and SDs are given.

had to obtain these amounts of milk in less than 4 min/day. While the four does from which these measures were taken showed small individual differences in the length of the nursing visits, the duration of these visits remained very stable and did not change markedly with the advance of lactation.

Weeks 2–3: Transition to solid food

During the second and third weeks milk intake increased steadily from about 25 g/pup on day 8 to about 40 g/pup on day 19 at the peak of lactation (Fig. 2). By this time pups weighed between 350–400 g although litters from non-pregnant does tended to be heavier (Fig. 1). Differences were also recorded in the average milk intake [$F(1,34) = 51.5$,

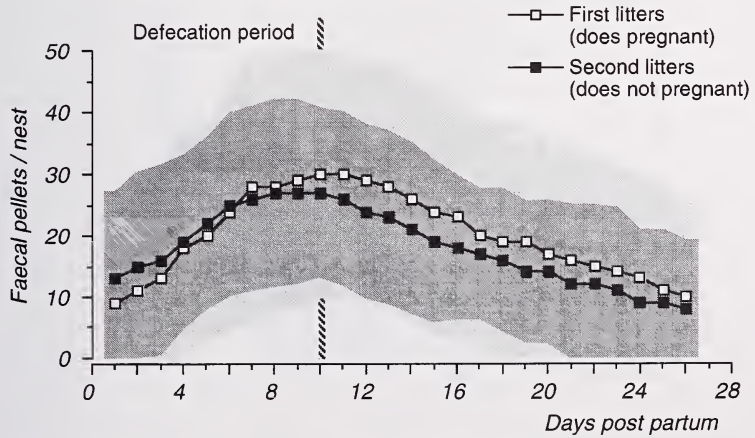

Fig. 4. Mean cumulative number of faecal pellets deposited in the nest by the four does from Condition I when pregnant ('first litters') and when not pregnant ('second litters') until the end of the defecation period (shaded bar), and the cumulative number disappearing from the nest, presumably eaten by the pups. Means and SDs are given.

$p < 0.01$], with litters from pregnant does obtaining significantly less milk by day 23 (Fig. 2) than the litters from non-pregnant does.

As shown in figure 4, early in lactation does usually deposited several faecal pellets in the nest at each nursing visit. Although there were considerable individual differences between does in the total number of pellets added to the nest, this behaviour was most consistent; pellets were deposited on almost every visit up to day 10, after which time this behaviour abruptly stopped. From about day 11 pellets showed clear signs of having been nibbled, and by the third week they started to disappear at the rate of about one a day. As pups were frequently seen chewing on fragments, the pellets appeared to have been actually eaten and not to have just disintegrated.

Towards the end of the second week pups also started nibbling the nest material. At first they appeared simply to bite through the long stalks, reducing the hay to a kind of rough chaff. Despite difficulties in accurately weighing the hay when it became damp from pups' urine, by about day 18 clearly measurable amounts were being eaten as deduced from the decrease in the net weight of the remaining material.

Week 4: Termination of nursing

Weaning appeared to start between days 18–20 with a decline in milk yield which was considerably steeper when the does were pregnant (Fig. 2). At this time pups also started to drink from the bottle, with the litters from pregnant does drinking considerably more than litters from these same does when not pregnant (Fig. 5). Between days 26 and 28 the pregnant mothers completely refused to nurse. Whereas on the preceding day they remained in the nest box for the usual time (Fig. 3) and showed apparently normal nursing behaviour, the following day they refused to enter the box and vigorously struck at, bit and cuffed away any pup trying to suckle. In fact, the litters had to be quickly removed to prevent them coming to harm. This contrasted with the behaviour of the non-pregnant does which were never seen responding aggressively to their pups.

The transition to lab food resulted in an immediate acceleration in the growth rate of all litters (Fig. 1). This was particularly clear from the difference in weight gain between litters from non-pregnant does from Condition II left with the mother and thus with free

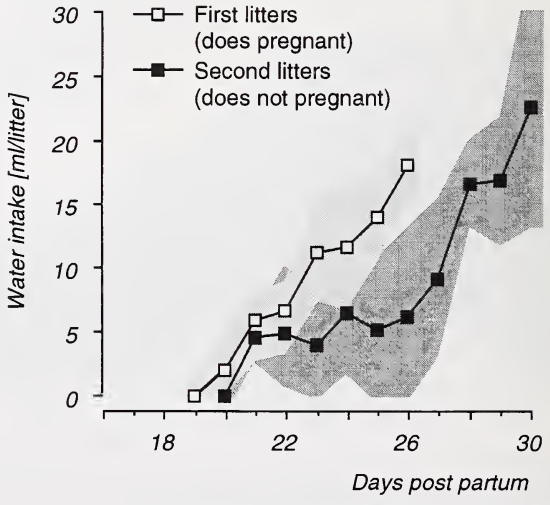

Fig. 5. Average daily water intake by litters from Condition I nursed by does when pregnant ('first litters', N = 4), and of litters nursed by the same does when not pregnant ('second litters', N = 4). Means and SDs are given.

access to lab chow during the period of declining milk intake, and litters from non-pregnant does from Condition I kept separately from the mother and so without access to lab food until they were fully weaned on day 30 (Fig. 1). Using a 3-way ANOVA (state of pregnancy × condition × age), it was found that during the post-weaning period from days 31–44, litters from pregnant does remained significantly lighter than litters from non-pregnant does [$F(1,85) = 21$, $p < 0.01$] although the difference between pups from Conditions I and II was no longer significant [$F(1,85) = 0.8$, ns].

Discussion

This study provides the first systematic description of the changes in ingestive behaviour of young rabbits from birth through to fully independent feeding, and of corresponding changes in the nursing behaviour of the doe. At first sight the pattern of behaviour of both mothers and young appears stereotyped and largely lacking in the flexibility we normally associate with mammalian mother-infant relationships. Thus, having no other contact with their mother than three to four minutes of suckling once a day, pups progressed from drinking milk alone, to nibbling faecal pellets, to ingesting nest material, drinking water and finally to eating lab food, and at very similar ages. Nursing behaviour was also stereotyped, with the duration of does' visits remaining very constant across litters and throughout lactation.

However, flexibility was clearly demonstrated by the marked differences in the pattern of weaning depending on does' reproductive state. In pregnant does, milk yield not only declined earlier and more steeply, but the willingness of does to continue nursing late in lactation ended more abruptly, with pups being rejected and even attacked from one day to the next. Furthermore, neither the limited care nor the change in does' nursing behaviour appeared to present difficulties for the pups, as evidenced by their steady growth during the period in the nest, clear acceleration in weight gain following the transition to solid food, and good survival rate.

This unusually efficient pattern of maternal care cannot simply be attributed to the artificial conditions of this study in which young were raised separated from their mothers. The behaviour and development of the separated litters was very similar to that of the control pups left with their mothers, and is in good agreement with the previous report of similar growth rates for young whether left with the doe or raised separately (Zarrow et al. 1965). The present findings are also consistent with previous reports of constant nursing times (Lincoln 1974), peak milk yields at about day 20 (Cowie 1969; Lincoln 1974; McNitt and Moody 1990), the abrupt refusal of pregnant does to nurse four to five days before the birth of the next litter (Lincoln 1974), and with an acceleration in pups' weight gain following the transition to solid food (Venge 1963; McNitt and Moody 1990).

Such precise regulation of the mother-young relationship obviously raises important questions concerning the underlying mechanisms. With regard to the doe these concern the fine timing of the neural and endocrine processes motivating her to nurse at the same time and for a specific period each day (Hudson et al. 1995), and then if pregnant, to steeply reduce milk yield after day 20, and end nursing four to five days later. Almost without pause she must then repeat the cycle; build a new nest, and following parturition, produce milk with a composition appropriate for the newborn young (Cowie 1969) and resume the same tightly timed pattern of nursing.

With regard to the development of ingestive behaviour, the fact that pups started eating faecal pellets and hay at similar ages and at a time when milk intake was still increasing, suggests that the maturation of endogenous mechanisms associated with the hunger system probably play a significant role. This is consistent with the report of age-dependent changes in the motivation to attach to nipples and suckle in rat pups (Hall et al.

1977), and in rabbits by day 13 at about the time they start eating nest material (Distel and Hudson 1984). On the other hand, as all litters gained weight more rapidly after the transition to solid food, it also seems that pups might be pushed quite early to make this transition by the inability of the mother to provide enough milk to meet their increasing demands (Thiels and Alberts 1985), and by the steep decline in lactose, and therefore in the caloric content of milk after day 20 (Cowie 1969). Whether, as has been reported for the rat (Galef 1981), this transition is accompanied by a decline in lactase, the enzyme permitting the young to absorb and utilize lactose, has yet to be investigated.

A further question raised by this study concerns the significance of the faecal pellets deposited in the nest. As they only disappeared from the nest at the rate of about one/day, they can hardly have constituted a significant food source. However, they may provide pups with gut flora aiding in the digestion of plant food (Smith 1965; Hörnicke and Björnhang 1980), a possibility it would be simple to test by monitoring the weight gain and later survival of pups raised without pellets. In this respect it might be relevant that pellet eating was always observed to precede eating of hay by several days. Furthermore, previous findings suggest that does might transmit information concerning their diet via the faecal pellets, thus indirectly influencing pups' later food choice (Hudson and Altbäcker 1994; Bilkó et al. 1994; Altbäcker et al. 1995).

Similarly, it is not yet clear to what extent the provision of grass by the doe contributes to the development of ingestive behaviour. Again there are several possibilities; that the nest material is of direct nutritional value, that it is of little nutritional value but helps prepare pups for the digestion of plant food, that pups acquire information from the plants selected by the doe about what to eat at weaning, and possibly even from which plants to construct their own nests later. Whereas the first two possibilities could be readily investigated by raising pups in nests without plant material, the second two possibilities are currently being tested in the laboratory in Hungary, with first findings suggesting that when given a choice of grasses, pregnant does do indeed preferentially select those species from which their own natal nest was constructed.

In conclusion, the findings of this study demonstrate that the development of ingestive behaviour in the rabbit constitutes a well-defined sequence of stages but that the timing of weaning depends on the reproductive condition of the doe, and in particular, whether she is pregnant with a second litter. Given the costs to the mother of nursing one litter while pregnant with the next, as suggested by the slower growth rate of first litters in the present study, it should now be interesting to investigate under what nutritional or other conditions does invest in first or subsequent litters, and to what extent they vary litter size or sex ratio (Hammond 1965; Boyd 1985). Particularly interesting in this regard is the ability of rabbits to resorb foetuses and modify or reverse a reproductive decision as late as day 20 in the 31-day gestation (Brambell 1942, 1944). However, to assess the real costs and benefits of the different patterns rearing requires monitoring the later survival and subsequent reproductive performance of both mothers and young, and preferably under natural conditions (Clutton-Brock et al., 1989).

Acknowledgements

This work was supported by the Deutsche Forschungsgemeinschaft (Hu 426/1), by the Hungarian Academy of Sciences (F5 254/1 991), and by the MHB Foundation for Hungarian Science (No 90/92/III). We particularly thank Ádam Miklósi for assistance with the statistics.

Zusammenfassung

Säugen, Entwöhnung und die Entwicklung unabhängigen Freßverhaltens beim Kaninchen (Oryctolagus cuniculus).

Bei Kaninchen beschränkt sich die Jungenfürsorge auf einen einzigen kurzen Säugebesuch pro Tag. Um diese bei Säugetieren ungewöhnliche Mutter-Kind Beziehung näher zu untersuchen, wurden vier Würfe von ihren Müttern getrennt und für das tägliche Säugen zu ihnen gegeben. Folgende Meßdaten wurden erhoben: von Tag 1 bis Tag 30 die Dauer des Säugens, die Milchaufnahme und die Gewichtszunahme der Jungen, das tägliche Absetzen von Kot von der Mutter in das Nest, der Beginn des Fressens von Kotkugeln und Nistmaterial durch die Jungen, der Beginn und die Menge der selbständigen Wasseraufnahme, und nach dem Absetzen, von Tag 31 bis Tag 44 die Gewichtszunahme der Jungen durch selbständiges Fressen von Laborfutter. Die Mütter wurden unmittelbar nach der Geburt erneut gedeckt, und die Werte ihrer ersten Würfe – aufgezogen während sie trächtig waren – mit den Werten ihrer zweiten Würfe – aufgezogen während sie nicht trächtig waren – verglichen. Entsprechende Meßwerte wurden bei vier Kontrollhäsinnen erhoben, jedoch hatten diese Mütter jederzeit Zugang zu ihren Jungen. Das Freßverhalten der Jungen entwickelt sich von Milchaufnahme alleine hin zu zusätzlichem Knabbern der Kotkugeln, weiterhin zum Fressen von Nistmaterial, und schließlich zum selbständigen Fressen von festem Laborfutter. Gewichtszunahme und Zeitpunkt des Absetzens hängt jedoch vom Fortpflanzungszustand der Mütter ab. Diejenigen Würfe, die von gleichzeitig trächtigen Häsinnen aufgezogen wurden, waren signifikant leichter und wurden früher abgesetzt als diejenigen Würfe, die von nicht trächtigen Häsinnen aufgezogen wurden. Aufgrund dieser Untersuchungen scheint das Kaninchen für Untersuchungen über Entwöhnung und Entwicklung von Freßverhalten bei Säugetieren besonders geeignet zu sein.

References

Altbäcker, V.; Hudson, R.; Bilkó, A. (1995): Rabbit mothers' diet influences pups' later food choice. Ethology **99**, 107–116.

Bateson, P. (1994): The dynamics of parent-offspring relationships in mammals. Trends Ecol. Evol. **9**, 399–402.

Bilkó, A.; Altbäcker, V.; Hudson, R. (1994): Transmission of food preference from mother to young in the rabbit: the means of information transfer. Physiol. Behav. **56**, 907–912.

Boyd, I. L. (1985): Investment in growth by pregnant wild rabbits in relation to litter size and sex of the offspring. J. Anim. Ecol. **54**, 137–147.

Brambell, F. W. R. (1942): Intra-uterine mortality of the wild rabbit, *Oryctolagus cuniculus* (L.). Proc. Roy. Soc. London B **130**, 462–479.

– (1944): The reproduction of the wild rabbit Oryctolagus cuniculus (L.). Proc. Zool. Soc. London **114**, 1–45

Broekuizen, S.; Mulder, J. L. (1983): Differences and similarities in nursing behavior of hares and rabbits. Acta Zool. Fennica **174**, 61–63.

Clutton-Brock, T. H.; Albon, S. D.; Guinness, F. E. (1989): Fitness costs of gestation and lactation in wild mammals. Nature **337**, 260–262.

Cowie, A. T. (1969): Variation in the yield and composition of the milk during lactation in the rabbit and the galactopoietic effect of prolactin. J. Endocrinol. **44**, 437–450.

Deutsch, J. A. (1957): Nest building behaviour of domestic rabbits under seminatural conditions. Brit. J. Anim. Behav. **5**, 53–54.

Distel, H.; Hudson, R. (1984): Nipple-search performance by rabbit pups: changes with age and time of day. Anim. Behav. **32**, 501–507.

Galef, D. G. Jr. (1981): The ecology of weaning. In: Parental care in mammals. Ed. by D. J. Gubernick and P. H. Klopfer. New York: Plenum Press. Pp. 211–241.

Hall, W. G. (1990): The ontogeny of ingestive behavior. In: Handbook of behavioral neurobiology. Vol.10: Neurobiology of food and fluid intake. Ed. by E. M. Stricker. New York: Plenum Press. Pp. 77–123.

–; Crammer, C. P.; Blass, E. M. (1977): Ontogeny of suckling in rats: transitions toward adult ingestion. J. Comp. Physiol. Psychol. **91**, 1141–1155.

Hammond, J. Jr. (1965): The effects of high and low planes of nutrition on reproduction in rabbits. New Zeal. J. Agric. Res. **8**, 708–717.

Hörnicke, H.; Björnhag, J. G. (1980): Coprophagy and related strategies for digesta utilization. In: Digestive physiology and metabolism in ruminants. Ed. by Y. Ruckebusch and P. Thivend. Lancaster: MTP Press. Pp. 707–730.

Hudson, R.; Altbäcker, V. (1994): Development of feeding and food preference in the European rabbit: environmental and maturational determinants. In: Behavioral aspects of feeding. Ed. by B. G. Galef, Jr.; M. Mainardi and P. Valsecchi. Chur: Harwood Academic Publishers. Pp. 125–145.

–; Distel, H. (1982): The pattern of behaviour of rabbit pups in the nest. Behaviour **79**, 255–271.

–; – (1989): Temporal pattern of suckling in rabbit pups: a model of circadian synchrony between mother and young. In: Development of circadian rhythmicity and photoperiodism in mammals. Ed. by S. M. Reppert. New York: Perinatology Press. Pp. 83–102.

–; Müller, A.; Kennedy, G. (1995): Parturition in the rabbit is compromised by daytime nursing: The role of oxytocin. Biol. Reprod. **53**, 519–524.

Kraft, R. (1979): Vergleichende Verhaltensstudien an Wild- und Hauskaninchen. I. Das Verhaltensinventar von Wild- und Hauskaninchen. Z. Tierzücht. Züchtungsbiol. **95**, 140–162.

Lincoln, D. W. (1974): Suckling: a time-constant in the nursing behaviour of the rabbit. Physiol. Behav. **13**, 711–714.

McNitt, J. I.; Moody, G. L. Jr. (1990): Daily milk intake by rabbit kits. J. Appl. Rabbit Res. **13**, 176–178.

Mykytowycz, R.; Dudzinski, M. L. (1972): Aggressive and protective behaviour of adult rabbits *Oryctolagus cuniculus* (L.) towards juveniles. Behaviour **43**, 97–120.

Partridge, G. G.; Fuller, M. F.; Pullar, J. D. (1982): Studies on the protein and energy requirements of the lactating rabbit. Anim. Prod. **34**, 384.

Smith, H. W. (1965): The development of the flora of the alimentary tract in young animals. J. Path. Bact. **90**, 495–513.

Thiels, E.; Alberts, J. R. (1985): Milk availability modulates weaning in the Norway rat (*Rattus norvegicus*). J. Comp. Psychol. **99**, 447–456.

Thompson, H. V.; King, C. M. (Eds), (1994): The European rabbit: the history of a successful colonizer. Oxford: Oxford Univ. Press.

Trivers, R. L. (1974): Parent-offspring conflict. Amer. Zool. **14**, 249–264.

Venge, O. (1963): The influence of nursing behaviour and milk production on early growth in rabbits. Anim. Behav. **11**, 500–506.

Zarrow, M. X.; Denenberg, V. H.; Anderson, C. O. (1965): Rabbit: frequency of suckling in the pup. Science **150**, 1835–1836.

Authors' addresses: Dr. Robyn Hudson, Institut für Medizinische Psychology, Ludwig-Maximilian Universität, Goethestr. 31, D-80336, München, Germany; A. Bilkó and V. Altbäcker, Department of Ethology, Eötvös Loránd University, H-2131 Göd, Jávorka S. u. 14, Hungary.