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## Postnatal development and thermoregulation in the precocial European hare (*Lepus europaeus*)

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**Abstract** We investigated postnatal development of captive juvenile European hares (*Lepus europaeus*) with respect to growth, food intake and thermoregulation. Leverets increased their body weight on average 8.5-fold within 35 days, with a peak in relative growth rate on day 8. Although leverets started to take up solid food in the 2nd week of lactation, milk was the main energy source. Leverets of larger litters (two or three young) had less energy supply via milk than those of smaller litters (one young), and digested more energy in form of solid food. Weaning weight was positively correlated with body weight at birth and decreased with increasing litter size. Metabolic rates were largely determined by ambient temperature ( $T_a$ ) and the increasing body weights. Leverets were able to maintain normothermic body temperatures from the 1st day of life during cold exposure down to  $T_a - 8$  °C. In their 1st week of life leverets showed reduced rates of heat loss in the cold, possibly by using peripheral vasoconstriction. Our results suggest that the precocial development of leverets is characterised by high maintenance costs due to rapid growth and thermoregulation, which may lead to negative energy balances when food supply is inadequate and  $T_a$ s are low. We hypothesise that these physiological characteristics have played an important role in the recent decline of European hare populations.

**Keywords** Thermoregulation · Energy budget · Metabolic rate · *Lepus europaeus* · Precociality

**Abbreviations** *MR* metabolic rate · *RMR* resting metabolic rate ·  $T_a$ : ambient temperature ·  $T_b$  rectal temperature

### Introduction

With respect to their postnatal development, mammals can be divided into altricial and precocial species. Altricial young are typically born in a naked and helpless state and have a long postnatal period of parental dependency. Precocial young, on the other hand, are furred at birth, their eyes open soon after and they mature rapidly (Hill 1992). There are several advantages of a precocial development. For example, precocial young achieve parental independence relatively early and thus are typically quicker than altricial juveniles to become mature enough to survive the death of their parents. Furthermore, precocial young are more able than altricial young to evade predators (Pagel and Harvey 1988). On the other hand, postnatal development of precocial mammals is energetically costly. Altricial young need less energy for thermoregulation as they are usually warmed by their parents and live in insulated nests. Most studies contributing to the ongoing debate on the costs and benefits of precocial versus altricial life have focused on reproductive costs of mothers (e.g. Koteja et al. 1993; Künkele and Trillmich 1997; Lambin and Yoccoz 2001). Only a few studies in this context concentrated on the energy budgets of juveniles, (e.g. Webb and McClure 1989; Hill 1992).

In this study we investigated the consequences of precociality for juvenile European hares. Recently, we found that female hares have very high reproductive costs during lactation and reach physiological limits of energy turnover even at normal litter sizes of one-to-three young (Hackländer et al. 2002). This points to costly young with high-energy demands for maintenance and growth. Leverets (i.e. juvenile hares during lactation) are fully furred at birth with their eyes open. They

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are born above ground, lack insulated nests, and mothers visit their young only once a day for 2–3 min for suckling (Broekhuizen and Maaskamp 1980). In Europe, the breeding season of this species lasts from January to October (Flux and Angermann 1990). This relatively long period results in exposure of juveniles to extremely variable climatic conditions. In the region of Lower Austria, where hare abundance is rather high (Hackländer et al. 2001), air temperatures can fluctuate between  $-26\text{ }^{\circ}\text{C}$  and  $+38\text{ }^{\circ}\text{C}$  during the breeding season, and monthly precipitation ranges from 0 mm to 244 mm (Auer et al. 2001). Because leverets living above ground experience all climatic changes, they assumedly have to allocate a substantial part of their energy resources to thermoregulation. As thermoregulation in the very early stages of a mammal's life is a major part of total energy expenditure (Hull 1973), leverets under cold conditions may have to spend more energy for thermoregulation than for growth which could counteract the advantages of precociality. Although leverets are furred at birth, it is unclear whether this pelage has important insulation advantages or serves predominantly as camouflage.

There are several field studies showing that in years of cold and wet springs, recruitment in natural hare populations is impaired (e.g. Puppe 1966; Janovic et al. 1973; Eiberle et al. 1982) or that population density is negatively correlated with yearly precipitation (e.g. Hackländer et al. 2001). These results are indirect evidence that high precipitation and cold temperatures have negative effects on survival rates of leverets. However, to our knowledge, there is only one study (Rogowitz 1992) on metabolic responses of juveniles of another hare species (*Lepus townsendii*) to moderate cold ( $>0\text{ }^{\circ}\text{C}$ ). Therefore, we investigated postnatal development and survival of juvenile European hares in relation to litter size and food consumption, and measured metabolic rates of leverets exposed to  $T_a$ s between  $-13\text{ }^{\circ}\text{C}$  and  $+36\text{ }^{\circ}\text{C}$ . Based on these data, we computed energy budgets of European hares in the early stage of life.

## Material and methods

### Animals

We analysed data on postnatal development of 491 leverets out of 213 litters in our outbred colony at the Research Institute of Wildlife Ecology in Vienna (Austria). Data were collected from January to December over a period of 13 years. Generally, mothers and their leverets lived separated in outdoor cages with a wire-netting floor ( $0.5\text{ m}^2$ ). These individuals were exposed to natural photoperiod and natural temperatures. A subset of leverets ( $n=24$ ) and their mothers were kept in indoor cages to determine food intake and metabolic rates. Because the animal housing facilities of this subset were not fully air-conditioned, ambient temperature ( $T_a$ ) varied seasonally between  $10\text{ }^{\circ}\text{C}$  and  $20\text{ }^{\circ}\text{C}$ .

Leverets were fed with standard hare pellets (Raiffeisen, Salzburg, Austria) and had access to food and water in excess. As leverets are nursed only once a day in the wild (Broekhuizen and Maaskamp 1980), captive leverets were allowed to suckle only once a day. They were removed from their cage, weighed to the nearest

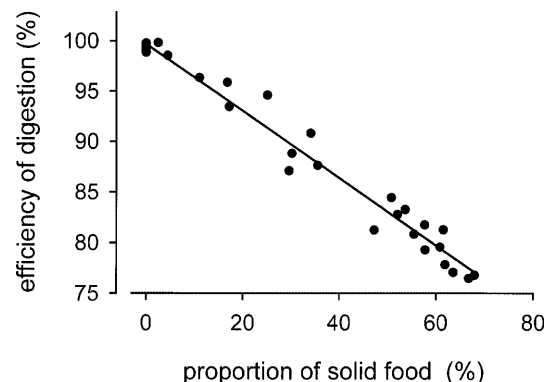
1 g, and placed into the cage of their mother at 8 a.m. At 9 a.m., leverets were removed from their mothers' cage, re-weighed to the nearest 1 g, and returned to their own cage. Weight gain during that hour was considered as milk intake. Since does intensively lick urine from the anogenital region of their leverets immediately after suckling, possible weight losses during the 1 h nursing periods due to urination could not be determined. Natural weaning age in European hares varies between 3–5 days and 67 days (reviews in Hediger 1948 and Zörner 1996), but we know from long-term experience that in captivity, does start to behave aggressively towards leverets after 5 weeks lactation. Thus, we stopped placing leverets to their mothers for suckling when they reached an age of 35 days.

Food was checked for spilled pellets daily and weighed once a week to determine food intake. In some cases the determination of food consumption was impossible due to spilled drinking water leading to an inseparable mixture of food and faeces, which resulted in different sample sizes for milk and food uptake. Pellets were dried at  $40\text{ }^{\circ}\text{C}$  for 24 h before weighing. The amount of consumed energy was calculated using the caloric value of diet ( $11.26\text{ kJ g}^{-1}$ ) and milk ( $10.46\text{ kJ g}^{-1}$ ), which does not change significantly over the lactation period (Hackländer et al. 2002). From 5 litters (12 leverets) we additionally collected 35 samples of faeces over 5 weeks of lactation and determined their caloric content by means of bomb calorimetry (C4000 A, IKA, Staufen, Germany). To minimise possible problems with gut passage time (i.e. faecal samples may cover a period different from food intake) we pooled daily samples on a weekly basis. The energy digested was computed from the difference between the caloric content of food consumed and caloric value of the faeces excreted. To compute the energetic efficiency of digestion, digested energy was divided by energy intake and multiplied by 100.

On the basis of these calorimetric data we calculated a linear model to determine the energetic efficiency of digestion and digested energy of all leverets from the assessment of the relation of energy intake via solid food and milk alone (Fig. 1) Intake of milk alone resulted in very high energetic efficiency of digestion (mean of direct measurements:  $99.35 \pm 0.09\%$ ,  $n=11$ ). Note that Fig. 1 gave no indication for a substantial nonlinearity in the relation between the efficiency of digestion and the proportion of energy intake via pellets, suggesting that the digestion efficiency of solid food did not change significantly over the lactation period. Given the high coefficient of determination (97.8%), this model allowed an excellent estimate of the energetic efficiency of digestion.

### Respirometry

Metabolic rates were measured in 24 leverets during daylight hours, the period of day in which hares are sedentary. During the experi-



**Fig. 1** Energetic efficiency of digestion as a function of the proportion of energy intake as solid food. Data from 12 leverets over 5 weeks of lactation. The linear regression is given by: energetic efficiency of digestion (%) =  $99.675 - 33.257 \times$  proportion of energy intake via solid food;  $r^2 = 0.978$ ,  $F_{1,32} = 1430$ ,  $P < 0.001$

ments (each lasted 90 min), animals were placed in polyethylene boxes (volume: 16 l) with a Plexiglas window to allow observation of the animals. Hares usually rested after a few minutes following the start of the experiments. Boxes were placed in a climate chamber that allowed us to vary ambient temperatures between  $-13^{\circ}\text{C}$  and  $+36^{\circ}\text{C}$  with an accuracy of  $\pm 2^{\circ}\text{C}$ . Ambient temperatures inside the boxes were measured with copper-constantan thermocouples to the nearest  $0.1^{\circ}\text{C}$ .

To determine oxygen consumption we used a multi-channel, open-flow respirometry system with an arrangement of components and airflow as outlined in Heldmaier and Ruf (1992). Air was pumped through the cages with a flow rate of about  $250\text{ l h}^{-1}$ . Flow rates of air were determined with mass flow meters (AWM 5000, Honeywell, Freeport Ill., USA) and oxygen concentration was measured every 5 min for each animal using a paramagnetic oxygen analyser (Oxox 610, Maihak, Hamburg, Germany). Computer-controlled solenoid valves allowed for a comparison of air from the boxes with reference air from the climate chamber at 5-min intervals. Measurements were converted to STPD conditions and metabolic rate (MR) was computed as  $\text{MR} (\text{l O}_2 \text{ h}^{-1}) = \text{dVol}\% \text{ O}_2 \text{ flow} (\text{l h}^{-1})$ . As animals were not fasting in our experiments we converted oxygen consumption to energy expenditure ( $\text{kJ day}^{-1}$ ) by using an energy equivalence of  $20.1\text{ kJ l O}_2^{-1}$  (Blaxter 1989). To determine resting metabolic rate (RMR) we discarded the 1st h of each experiment and calculated the mean of the three lowest values of oxygen consumption of the remaining data set.

We measured rectal temperature ( $T_b$ ) in resting leverets immediately before and after the 90-min RMR-measurements by inserting a veterinary thermocouple (Almemo 2190-2 incl. N856 FNA8561, Ahlborn, Holzkirchen, Germany) 1–1.5 cm into the rectum.

## Statistics

All data from energy intake and RMR records were examined with repeated measurement analysis, using linear mixed effects models (Pinheiro and Bates 2000; procedure "lme" in S-Plus 2000). Energy intake data were analysed controlling for random effects of the litter (for solid food), or the individual leveret (in the analysis of milk intake). For data on solid food intake, the unit of sampling and statistical analysis was the litter. To ease comparisons with data from milk intake, however, all data are presented per leveret. Two variables (digested energy content of milk and solid food) were significantly skewed to the right. Therefore, these variables were log-transformed to produce normal distributions (Kolmogorov-Smirnov tests:  $P > 0.3$  in both cases).

Weekly intervals (instead of daily measurements) as a time unit were used for two reasons: (i) there was a considerable day-to-day variation in all data and (ii) most variables changed non-linearly over the lactation period. Thus, we considered it more appropriate to replace the original data by weekly means, and to treat lactation week as a factor rather than a continuous variable. Therefore, our analyses represent ANCOVA models with the covariate week (five levels), and the covariate litter size (one-to-three). Differences in body weight at birth and at weaning, and differences in litter size during the course of the year were tested by one-way ANOVA. Comparisons of solid food intake of leverets were restricted to the time at which all leverets had started to feed on pellets (i.e. lactation weeks 3–5). Expectedly, RMRs showed a nonlinear relation to body weights. Using an iterative procedure, we found that an exponent of 0.50 minimised the residual sum of squares in linear regressions of RMR versus body weight. Hence,  $\text{body weight}^{0.5}$  was used in statistical analyses. The probability of death of juveniles during lactation as a function of litter size and season (coded as a factor with 3-monthly intervals) was modelled with a logistic regression.  $P$  values resulting from these statistical procedures were always computed from Type III sum of squares. Due to the fact that not all data could be measured in all individuals, error degrees of freedom varied and are given (next to treatment degrees of freedom) as subscripts for the  $F$  values. Data are given as means  $\pm$  SE.

## Results

### Litter size, body weight and survival rate

During the course of the year litter size at birth changed significantly ( $F_{10, 212} = 5.02$ ,  $P < 0.001$ , Fig. 2). Between November and March does gave birth to one or two leverets, whereas between April and October the average litter size was between two and three. This seasonal change of litter size was paralleled by changes in mean litter weight (Fig. 2). Litter size affected juvenile body weight at birth ( $F_{4, 174} = 8.56$ ,  $P < 0.001$ ), i.e. the body weight of each leveret decreased from 123 g for singletons to 95 g for quintuplets (Fig. 3a). In litters without losses leverets increased their body weight on average 8.5-fold from  $121 \pm 3$  g to  $1031 \pm 26$  g at weaning. The relative growth rate peaked on day 8 ( $9.17 \pm 0.46\% \text{ day}^{-1}$ ). Weaning weight was positively correlated with body weight at birth ( $r^2 = 0.26$ ,  $P < 0.01$ ,  $n = 99$ ) and decreased with increasing litter size ( $F_{3, 118} = 3.28$ ,  $P < 0.05$ , Fig. 3b).

About 20% (52 of 258) of the leverets were stillbirths or died during lactation, predominantly due to infectious diseases of the gastrointestinal tract. The probability of death increased with increasing litter size at birth (logistic regression:  $G = 15.32$ ,  $P < 0.001$ ) but was not affected by the season ( $G = 0.24$ , ns).

### Energy intake

As shown in Fig. 4, leverets increased the amount of digested energy during 5 weeks of lactation from 203 kJ in the 1st week to 609 kJ in the 5th week ( $F_{4, 63} = 34.25$ ,  $P < 0.0001$ ). Leverets of larger litters had less energy supply via milk than those of smaller litters ( $F_{2, 61} = 3.23$ ,  $P < 0.05$ , Fig. 5). Leverets started to take up small

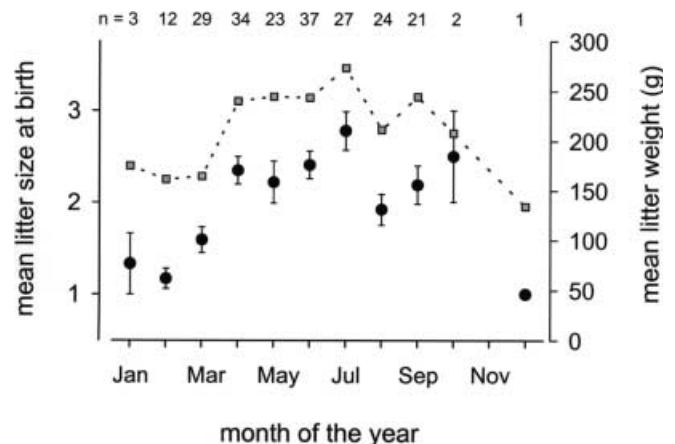
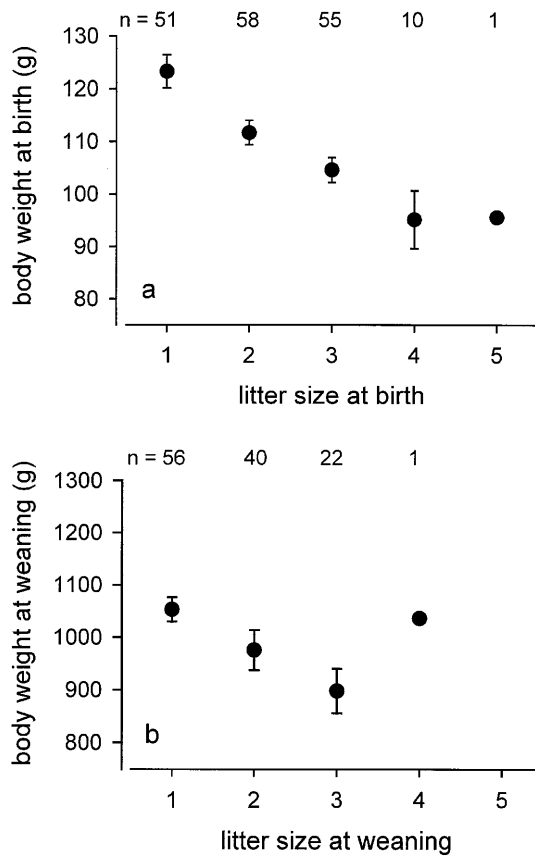


Fig. 2 Mean ( $\pm$  SE) litter size at birth (filled circles) and mean litter weight (grey squares, dotted line) per month of 67 females and 213 litters during the years 1989–2001. Animals were kept in outdoor cages and experienced natural photoperiod and ambient temperature. Numbers of litters ( $n$ ) are given at the top

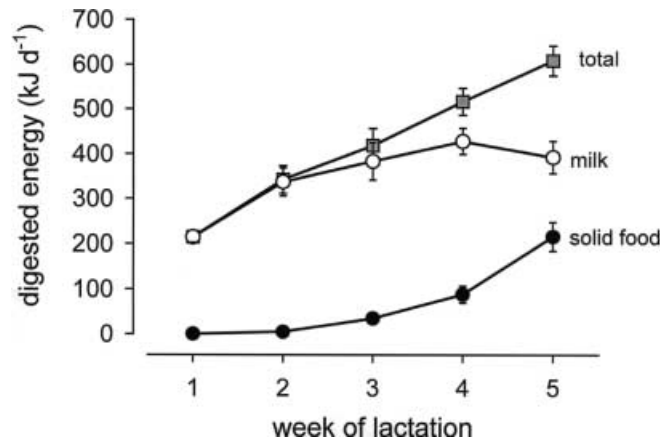


**Fig. 3** Mean ( $\pm$ SE) body weight of leverets at birth (a) and at weaning (b) as a function of litter size. Weaning weights were considered only when there were no losses of leverets during lactation. Numbers of litters are given at the top

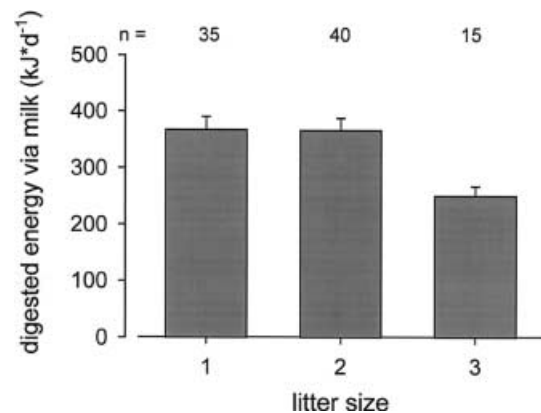
amounts of solid food in the 2nd week of lactation (digested energy:  $6 \text{ kJ day}^{-1}$ ) and increased solid food intake up to the 5th week ( $216 \text{ kJ day}^{-1}$ , Fig. 4). However, milk was the main energy source as its contribution to the entire amount of digested energy was on average five times larger than the contribution of digested energy via solid food. With increasing litter size leverets digested relatively more energy in form of pellets ( $F_{1,8} = 6.99$ ,  $P = 0.03$ , Fig. 5). For example, in week 3, leverets from litters of sizes one, two and three digested  $22.29 \pm 5.9 \text{ kJ day}^{-1}$ ,  $54.49 \pm 21.4 \text{ kJ day}^{-1}$  and  $92.01 \text{ kJ day}^{-1}$ , respectively.

#### Thermoregulation and energy budget

A multiple regression showed that changes in metabolic responses over the lactation period were largely explained by  $T_a$  ( $F_{1, 131} = 16.91$ ,  $P < 0.0001$ ) and the increasing body weights of leverets ( $F_{1, 131} = 258.9$ ,  $P < 0.0001$ ). The week of life (as an indication for possible other time-dependent processes, such as rapid changes in fur-insulation) had no additional effect. As shown in Fig. 6, the slopes of regressions of RMR versus  $T_a$  for each week of life decreased from  $0.54 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$



**Fig. 4** Mean ( $\pm$ SE) amount of digested energy via milk (open circles), solid food (filled circles), and total digested energy (grey squares) during lactation. Data from eleven leverets in which both milk and solid food intake was measured over 5 weeks

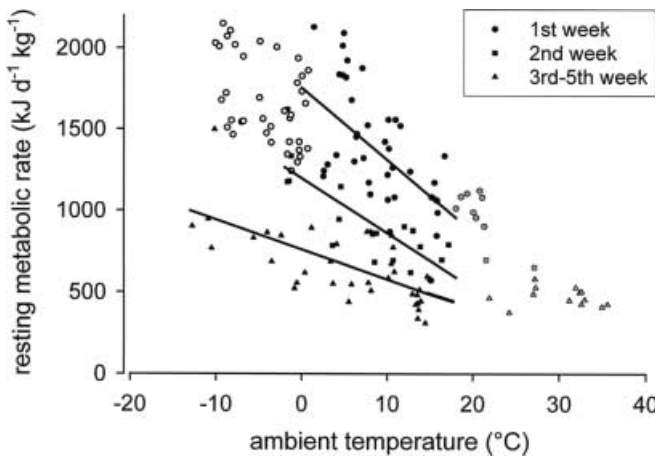


**Fig. 5** Mean ( $\pm$ SE) amount of digested energy via milk during lactation for 18 leverets of different litter sizes. Numbers of weekly measurements are given at the top

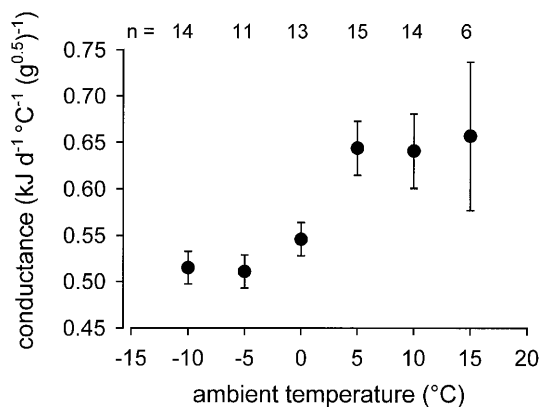
in week 1 to  $0.21 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$  in weeks 3–5. These regressions were restricted to  $T_a < 18 \text{ }^\circ\text{C}$  to avoid inclusion of possibly thermoneutral MRs. Also, for the 1st week of life, the regression was restricted to  $T_a > 0 \text{ }^\circ\text{C}$ , because leverets showed unexpectedly low RMRs at lower temperatures. This observation may partly be explained by a slight decrease of body temperature in 1st-week leverets from  $37.7 \pm 0.12 \text{ }^\circ\text{C}$  to  $36.7 \pm 0.19 \text{ }^\circ\text{C}$  during the measurements, with a magnitude that increased as  $T_a$  decreased ( $F_{1, 52} = 11.56$ ,  $P < 0.002$ ). However, even when these slight reductions of  $T_b$  are taken into account, there was also a marked decrease in thermal conductance at  $T_{as} < 5 \text{ }^\circ\text{C}$  (Fig. 7). Hence, the main reason for low RMRs in the cold among these leverets appeared to be reduced heat loss.

#### Discussion

One should expect that leverets are strongly selected to grow relatively fast to reduce the risk of mortality due to



**Fig. 6** Resting metabolic rates of leverets of week 1 (circles,  $n=20$  leverets), week 2 (squares,  $n=10$ ) and weeks 3–5 (triangles,  $n=23$ ). The regression line for week 1 was computed for  $T_{a,s}$  between 0 °C and 18 °C, for the other weeks for  $T_{a,s} < 18$  °C only. Data for  $T_{a,s} > 18$  °C are shown in grey, data of week 1 at  $T_{a,s} < 0$  °C in white. For further explanations, see text



**Fig. 7** Thermal conductance ( $C$ ) of 1st week leverets as a function of  $T_a$ , calculated from  $C = \text{RMR}/(T_b - T_a)$ , where  $T_a$  is ambient temperature,  $T_b$  is rectal temperature and RMR is resting metabolic rate. Means  $\pm$  SE. Thermal conductance significantly decreased with  $T_a$  ( $F_{1, 52} = 57.6$ ,  $P < 0.001$ ). Sample sizes are given at the top

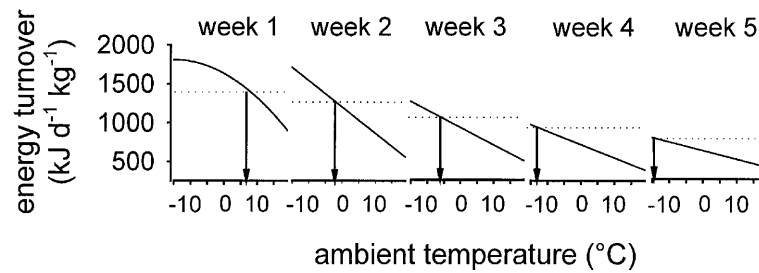
their exposition to adverse climatic conditions, predation and other causes of death. Leverets increased their body weight by a factor of 8.5 during 35 days with a maximum relative growth rate within the 1st week of life. It is difficult to answer the question whether this relative growth rate is faster than in typical altricial species because of a lack of homogeneity between the conditions under which studies have been conducted (naturally vs. hand reared; field conditions vs. captivity). Also, there is arguably an altricial-precocial continuum rather than two distinct types of ontogenesis (Kirkwood and Mace 1996). As a consequence, the “average” growth rates of altricial and precocial species are not clearly different, neither among mammals in general (Case 1978; Millar 1981), nor in the group of Lagomorphs (Flux 1981; Swihart 1984; Gaillard et al. 1997).

Even within the species *Lepus europaeus*, four studies on postnatal development (Hediger 1948; Pilarska 1969; Broekhuizen 1971; Pielowski 1971) produced five different growth curves that were obviously affected by energy supply (natural lactation vs. hand rearing) and climatic conditions (indoor vs. outdoor). Low growth rates in leverets exposed to outdoor conditions (Pielowski 1971) indicate that energy budgets of juveniles may be particularly affected by thermoregulatory costs.

In our study, leverets were able to thermoregulate immediately following birth, i.e. they maintained normothermic  $T_b$ s and increased their RMR with decreasing  $T_a$  even when 1 day old. Juveniles of the closely related altricial rabbit (*Oryctolagus cuniculus*) in their 1st week of life also showed an increased RMR at moderate cold exposure, but had already reached their cold limit at a  $T_a$  of 20 °C (Hull 1965), whereas 1-week-old, but already furred leverets in our study increased RMR down to – 8 °C (and may have been able to increase it further at lower  $T_a$ s, which was not tested here). Thus, our data show that similar to other precocial species, European hares mature rapidly with respect to their thermoregulatory abilities and respond to cold by increasing heat production very early in life (Waldschmidt and Müller 1988; Webb and McClure 1989).

This thermoregulatory capacity is clearly linked to the way leverets grow up: they are born on the ground, maternal care is restricted to a once-a-day nursing for a few minutes, no insulated nest is available, and huddling of siblings is restricted to the 1st few days (Broekhuizen and Maaskamp 1980). Thus, leverets clearly require metabolic rates sufficient to maintain a high  $T_b$  in the cold. Costs of thermoregulation are augmented by the fact that leverets are not exceptionally well insulated. In their 1st week, thermal conductance of leverets (at  $T_{a,s}$  0–18 °C) was 0.54  $\text{W kg}^{-1} \text{°C}^{-1}$ . The expected thermal conductance for a mammal with a body weight of 159 g (the average for 1st-week leverets) is 0.49  $\text{W kg}^{-1} \text{°C}^{-1}$ , i.e. about 10% lower (Bradley and Deavers 1980). In view of their relatively high thermal conductance, it is not surprising that, at least under severe cold load (at  $T_{a,s} < 0$  °C), 1-week-old leverets employed additional mechanisms to reduce heat loss. At  $T_{a,s}$  below 0 °C, leverets reduced the increase of RMR with decreasing  $T_a$ . We suppose that this temperature-dependent decrease of thermal conductance (Fig. 6) was caused by peripheral vasoconstriction. We did not measure skin temperatures, but leverets felt cool to the touch after cold exposure only in the 1st week of life, but had normothermic rectal temperatures above 36 °C. The benefits of lowered thermal conductance due to peripheral vasoconstriction should be two-fold: this thermoregulatory response will result in both a reduction of the cold limit (i.e. an extension of the range of  $T_{a,s}$  tolerated) and significant energy savings at all  $T_{a,s} < 0$  °C.

Additional costs for thermoregulation may limit the allocation of energy to growth. Based on our measurements of daily energy intake and RMRs we computed energy budgets. As illustrated in Fig. 8, cold exposure of



**Fig. 8** Energy budgets of leverets from week 1 to week 5. *Solid lines* are regression lines of resting metabolic rates at  $T_{a,s} < 18$  °C extended to the axes. As leverets during week 1 showed a non-linear response to decreasing  $T_a$ , we used a first order polynome. *Dotted line* is mean amount of digested energy per kilogram body weight

leverets must lead to negative daily energy balances, especially in the first weeks, even if they remained at rest all day. In week 1, leverets spent more energy than they received via milk when  $T_{a,s}$  fell below 8 °C. This threshold temperature was shifted to lower  $T_{a,s}$  with increasing age (body weight) and 5-week-old leverets digested more energy via milk than they needed for thermoregulation down to a  $T_a$  of -14 °C. European hares start to give birth to juveniles in January (Zörner 1996), and in Lower Austria, for instance,  $T_{a,s}$  can reach -26 °C in February and the average yearly temperature in this area is 9.5 °C (Auer et al. 2001). Thus, despite their early development of thermoregulatory capacity, leverets have insufficient energy intake to resist severe cold load and simultaneously allocate sufficient energy to additional demands, such as locomotion or immune responses. It has been argued that costs related to immunocompetence, for example, are comparable in magnitude to those for growth (Lochmiller and Deerenberg 2000). Not surprisingly then, unfavourable climatic conditions (extremely low temperatures or moderate cold combined with high precipitation) are often the cause for high mortality rates in leverets, especially during their first 2 weeks of life. It is well known that infectious diseases in hares are favoured by high precipitation and low temperatures (review in Zörner 1996).

In our study the probability of death in leverets increased with increasing litter size. This was due to two reasons: body weight at birth was negatively correlated with litter size, and energy supply per leveret via milk was lower in larger litters. Hence, leverets originating from large litters (more than two littermates) were not only light, they also had a relatively low energy supply. Thus, it may be more advantageous to produce smaller litters with heavier young during the coldest part of the breeding season. Beneficial effects of huddling in larger litters cannot be expected as leverets separate in their 1st week of life (Broekhuizen and Maaskamp 1980), apparently to reduce the risk of predation. Thus, free-ranging hares indeed show a seasonality in litter size with smallest litter sizes during the early, cold part of the reproductive season (Raczynski 1964; Flux 1967). In-

terestingly, our data from the captive breeding colony showed a similar seasonality in litter size even when food availability was unlimited. A likely proximate signal that may govern this rhythm in litter size is photoperiod, because it is known that other reproductive functions, such as the size and activity of gonads in European hares are primarily controlled by changes in day length (Martinet 1976; Meunier and Martinet 1986). The selective forces underlying this rhythm may, however, involve the nutritional physiology of females. We have data (Hackländer et al. 2002) indicating that milk production (and hence litter size) is limited by gut capacity of does that reach maximum rates of energy assimilation during lactation. However, our present results suggest that the seasonality of litter size is actually driven by the high thermoregulatory and hence total maintenance costs of leverets during the cold part of the season, which ultimately creates very high-energy requirements of lactating does.

As leveret body weight was decisive for metabolic rates, females producing heavier leverets (i.e. smaller litters) in winter may have higher weaning success. However, the proportion of juveniles born early in the year is quite small in the autumn hunting bag, especially in areas of low habitat quality or in years of unfavourable climatic conditions (e.g. Möller 1977). The question then arises why females produce juveniles at all in January, despite their low survival chance. Juveniles may reach puberty by the age of 4 months (Caillol et al. 1992) and hence, leverets born early may actually participate in reproduction during the year of their birth. Thus, even though survival chances of early leverets are small, they may well have a high impact on the reproductive value of does.

Taken together, our data indicate that the reproductive strategy of European hares leads to very high energy demands of leverets, with little energetic reserve capacity to compensate for a worsening of environmental conditions. These physiological traits may explain why European hare populations have been decreasing during the last decades (Flux and Angermann 1990; Mitchell-Jones et al. 1999). There are several reasons why the energy budgets of leverets could be more negative than decades ago. Firstly, Europe's landscape has changed dramatically, resulting in a reduction of places of shelter (e.g. Schröpfer and Nyenhuis 1982; Panek and Kameniarz 1999). Secondly, there has been climate change resulting in an increase in precipitation in

several parts of Europe (Schönwiese and Rapp 1997; Rapp 2000). Thirdly, both food quantity and quality have decreased (e.g. Bunce et al. 1994; McCollin et al. 2000) which must lead to a reduced energy availability for does and leverets (Hackländer et al. 2002). We hypothesise that the combination of these three factors has been a major reason for the reduced population recruitment during the last decades and thus has played an important role in the Europe-wide phenomenon of decreasing numbers of European hares.

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## References

- Auer I, Böhm R, Schönwiese W (2001) Austria long-term climates: Multiple instrumental climate time series in Central Europe (1767–2000). *Oesterr Beitr Meteorol Geophys* 25:1–160
- Blaxter K (1989) Energy metabolism in animals and man. Cambridge University Press, Cambridge
- Bradley SR, Deavers DR (1980) A re-examination of the relationship between thermal conductance and body weight in mammals. *Comp Biochem Physiol A* 65:465–476
- Broekhuizen S (1971) Age determination and age composition of hare populations. *Trans IUGB* 10:477–489
- Broekhuizen S, Maaskamp F (1980) Behaviour of does and leverets of the European hare (*Lepus europaeus*) whilst nursing. *J Zool (Lond)* 191:487–501
- Bunce RGH, Howard DC, Barr CJ, Cummins RC, French D (1994) Botanical diversity in British hedgerows. In: Boatman N (ed) *Field margins: integrating agriculture and conservation*. BCPC Monograph 58. The British Crop Protection Council, Farnham, pp 43–52
- Caillol M, Mondain-Monval M, Meunier M, Rossano B (1992) Influence of season of birth on onset of gonadotrophic and ovarian functions in young doe hares (*Lepus europaeus*). *J Reprod Fertil* 96:747–753
- Case TJ (1978) On the evolution and adaptive significance of post-natal growth rates in the terrestrial vertebrates. *Quart Rev Biol* 53:243–282
- Eiberle K, Matter JF, Nizon V (1982) Über die Abhängigkeit der Hasenstrecken vom Witterungsverlauf während der Fortpflanzungsperiode. *Forstwiss Centralbl* 101:1–12
- Flux JEC (1967) Reproduction and body weights of the hare *Lepus europaeus* Pallas, in New Zealand. *NZ J Sci* 10:357–401
- Flux JEC (1981) Reproductive strategies in the genus *Lepus*. In: Myers K, MacInnes CD (eds) *Proceedings of the world lagomorph conference, Guelph, Ontario, August 1979*. University of Guelph, Guelph, pp 155–174
- Flux JEC, Angermann R (1990) The Hares and Jackrabbits. In: Chapman JA, Flux JEC (eds) *Rabbits, hares and pikas*. IUCN, Gland (CH), pp 61–94
- Gaillard J-M, Pontier D, Allainé D, Loison A, Herve J-C, Heizmann A (1997) Variation in growth form and precocity at birth in eutherian mammals. *Proc R Soc Lond B* 264:859–868
- Hackländer K, Frisch C, Klansek E, Steineck T, Ruf T (2001) Die Fruchtbarkeit weiblicher Feldhasen (*Lepus europaeus*) aus Revieren mit unterschiedlicher Populationsdichte. *Z Jagdwiss* 47:100–110
- Hackländer K, Tataruch F, Ruf T (2002) The effect of dietary fat content on lactation energetics in the European hare (*Lepus europaeus*). *Physiol Biochem Zool* 75: (In press)
- Hediger H (1948) Die Zucht des Feldhasen (*Lepus europaeus* Pallas) in Gefangenschaft. *Physiol Comp Oecol* 1:46–62
- Heldmaier G, Ruf T (1992) Body temperature and metabolic rate during natural hypothermia in endotherms. *J Comp Physiol B* 162:696–706
- Hill RW (1992) The altricial/precocial contrast in the thermal relations and energetics of small mammals. In: Tomasi TE, Horton TH (eds) *Mammalian energetics. Interdisciplinary views of metabolism and reproduction*. Comstock, London, pp 122–159
- Hull D (1965) Oxygen consumption and body temperature of newborn rabbits and kittens exposed to cold. *J Physiol* 177:192–202
- Hull D (1973) Thermoregulation in young mammals. In: Whittow GC (ed) *Comparative physiology of thermoregulation*, vol. 3. Academic Press, New York, pp 167–200
- Janovic V, Aleksic D, Katic P (1973) Zur Erforschung des Einflusses von meteorologischen Elementen auf den realen Jahreszuwachs der Feldhasen in der Vojwodina. *Beitr Jagd Wildforsch* 8:187–196
- Kirkwood JK, Mace GM (1996) Patterns of growth in mammals. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S (eds) *Wild mammals in captivity: principles and techniques*. The University of Chicago Press, Chicago, pp 513–527
- Koteja P, Krol E, Stalinski J, Weiner J (1993) Energetic cost of reproduction in altricial and precocial rodents. *Mésogée* 53:7–12
- Künkele J, Trillmich F (1997) Are precocial young cheaper? Lactation energetics in the guinea pig. *Physiol Zool* 70:589–596
- Lambin X, Yoccoz NG (2001) Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. *J Anim Ecol* 70:191–200
- Lochmiller RL, Deerenberg C (2000) Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* 88:87–98
- Martinet L (1976) Seasonal reproduction cycle in the European hare, *Lepus europaeus*, raised in captivity. Role of photoperiodicity. In: Pielowski Z, Pucek Z (eds.) *Ecology and management of European hare populations*. Polish Hunting Association, Warszawa, pp 55–57
- McCollin D, Moore L, Sparks T (2000) The flora of a cultural landscape: environmental determinations of change revealed using archival sources. *Biol Conserv* 92:249–263
- Meunier M, Martinet L (1986) Role of different photoperiodic treatments on the growth of the testis in juvenile and adult brown hares (*Lepus europaeus* P.). In: Assenmacher I, Boissin J (eds) *Endocrine regulation as adaptive mechanisms to the environment*. Centre National de la Recherche Scientifique, Paris, pp 155–159
- Millar JS (1981) Pre-partum reproductive characteristics of eutherian mammals. *Evolution* 35:1149–1163
- Mitchell-Jones AJ, Amori G, Bogdanowicz W, Krystufek B, Reijnders PJH, Spitzenberger F, Stubbe M, Thissen JBM, Vohralik V, Zima J (1999) *Atlas of European mammals*. Academic Press, London
- Möller D (1977) Zur postnatalen Mortalität des Feldhasen in der Deutschen Demokratischen Republik. *Beitr Jagd Wildforsch* 10:247–254
- Pagel MD, Harvey PH (1988) How mammals produce large-brained offspring. *Evolution* 42:948–957
- Panek M, Kamiński R (1999) Relationships between density of brown hare *Lepus europaeus* and landscape structure in Poland in the years 1981–1995. *Acta Theriol* 44:67–75
- Pielowski Z (1971) Studies on the European hare. XXV. The individual growth curve of the hare. *Acta Theriol* 16:79–88
- Pilarska J (1969) Individual growth curve and food consumption by European hare (*Lepus europaeus* Pallas 1778) in laboratory conditions. *Bull Acad Pol Sci Ser Sci Biol* 17:299–305

- Pinheiro JC, Bates DM (2000) Mixed effects models in S and S-plus. Springer, Berlin Heidelberg New York
- Puppe K (1966) Untersuchungen über die Variationsbreite des nutzbaren Zuwachses des Hasen in Abhängigkeit von regionalen Klimaunterschieden. Beitr Jagd Wildforsch 5:109–117
- Raczynski J (1964) Studies on the European hare. V. Reproduction. Acta Theriol 9:305–352
- Rapp J (2000) Konzeption, Problematik und Ergebnisse klimatologischer Trendanalysen für Europa und Deutschland. Ber Dtsch Wetterdienstes 212:1–145
- Rogowitz GL (1992) Postnatal variation in metabolism and body temperature in a precocial lagomorph. Funct Ecol 6:666–671
- Schönwiese Ch-D, Rapp J (1997) Climate trend atlas of Europe – based on observations 1891–1990. Kluwer Academic, Dordrecht
- Schröpfer R, Nyenhuis H (1982) Die Bedeutung der Landschaftsstruktur für die Populationsdichte des Feldhasen (*Lepus europaeus*, PALLAS 1778). Z Jagdwiss 28:213–231
- Swihart RK (1984) Body size, breeding season length, and life history tactics of lagomorphs. Oikos 43:282–290
- Waldschmidt A, Müller EF (1988) A comparison of postnatal thermal physiology and energetics in an altricial (*Gerbillus perpallidus*) and a precocial (*Acomys cahirinus*) rodent species. Comp Biochem Physiol A 90:169–181
- Webb DR, McClure PA (1989) Development of heat production in altricial and precocial rodents: implications for the energy allocation hypothesis. Physiol Zool 62:1293–1315
- Zörner H (1996) Der Feldhase. Westarp Wissenschaften, Magdeburg