



Early development and the emergence of individual differences in behavior among littermates of wild rabbit pups



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HIGHLIGHTS

- We studied associations between body temperature, growth and behavior in rabbit pups.
- Pups with relatively higher body temperatures grew better than their siblings.
- Correlated handling and open field responses indicated personality differences.
- In these two tests, lighter siblings showed greater reactivity than heavier ones.
- Associated differences in growth and behavior emerged within litters, among siblings.

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ABSTRACT

The ontogeny of associated individual differences in behavior and physiology during early postnatal life, and in particular the emergence of such differences among litter siblings, has been hardly explored in mammals under natural conditions. We studied such within-litter differences in behavior in European rabbit pups *Oryctolagus cuniculus* prior to weaning, and whether and how these differences co-varied with other individual characteristics such as postnatal body temperature and early growth. The study was conducted under semi-natural conditions in a colony of rabbits of wild origin, where the young were born and developed in nursery burrows. We equipped two siblings per litter with interscapular skin temperature loggers on postnatal day 2 and recorded temperature profiles for 48 h. Individual body (skin) temperatures of pups within litters were repeatable across time, indicating the existence of consistent individual differences. Such differences within litters were associated with relative differences in pre-weaning growth, revealing that relatively warmer pups showed a greater increase in body mass during the nest period. Between postnatal days 12 and 17, after the pups had reached a developmental stage of greater mobility, we carried out different behavioral tests: a handling-restraint test, an open field test and a jump-down test from a platform. Individual responses in the former two tests were associated, as those pups showing a quicker struggling response to restraint during handling also exhibited greater exploratory activity in the open field. This correlation across contexts suggests the existence of personality types in wild rabbits at an early developmental stage. Furthermore, pups' behavioral responses were strongly associated with their relative within-litter body mass at testing. Animals with a lower body mass compared to their siblings showed a relatively quicker struggle response to handling restraint and covered a relatively larger distance in the open field, suggesting greater reactivity and responsiveness of relatively lighter pups in these tests. In contrast, relatively heavier pups jumped sooner from the platform, which may have been due to their greater physical maturation. In conclusion, our study shows that individual differences in behavior and associated differences in body temperature and growth are already present during early postnatal life, although such relationships can be easily overlooked, as they predominantly emerge as relative differences among littermates.

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1. Introduction

Increasing evidence suggests that animals show individual differences in behavior consistent over time and context, often termed animal personality or temperament [1–3]. The ontogeny of such individual differences, and in particular when and how these differences emerge during early life stages still needs attention, although there has been a growing body of studies on this subject during recent years [4–10]. However, the link between individual differences in behavior and an animal's physical characteristics including its resulting developmental trajectories very early in life, have been hardly explored so far.

For example, in altricial mammals, individuals born into larger litters typically show a comparatively lower birth mass and growth until weaning and beyond, mainly due to the lower share of maternal resources an individual will obtain when the number of littermates is high [11,12]. Generally, the slower growth and slower physical development in young animals (including humans) with a lower birth mass might affect their behavioral responses in challenging situations due to compromised motor skills [13–16]. Consistent with this, a study in laboratory rats (*Rattus norvegicus*) suggested that pups with a comparatively higher body mass, and stemming from smaller litters, were more successful at mastering challenging situations, and thus adopted a more active behavioral style, probably via positive feedback loops [17]. In addition, these findings are confirmed by long-term studies in European rabbits (*Oryctolagus cuniculus*), where animals with a higher body mass around weaning were more exploratory in a novel environment, and showed fewer anxiety-related behaviors when confronted with predator odor during adulthood [18]. Furthermore, male European rabbits with a higher body mass around weaning showed more offensive behavior during social play with same-aged young and initiated more competitive interactions with same-aged adult males during their first breeding season [19]. Further support for long-term associations between birth mass and aspects of personality comes from studies in humans. Non-impaired young adults born with very low birth mass have been found to be more cautious, risk averse and less sociable than subjects born within a normal birth mass range [20,21]. On the other hand, some studies in laboratory rats obtained partly contradictory results, reporting that individuals from larger litters, and thus individuals with a lower body mass and growth at least before weaning [11], showed comparatively higher activity in several test settings [22] and comparatively lower levels of anxiety-related behavior in the elevated plus maze than subjects from smaller litters [23]. Another study in laboratory mice (*Mus musculus*) points out that associations between litter size or body mass and behavior later in life are indeed rather complex. Lighter young stemming from larger litters showed more signs of anxiety in the open field test. However, such animals were more aggressive in initial encounters in a food competition test later on, although became more submissive over repeated tests compared to heavier individuals from smaller litters [24].

Notable individual differences in body mass and growth during early development are not only apparent between litters, but also among littermates [25–27]. However, only few studies have systematically considered associations between such differences in body mass or growth and differences in behavior within litters, i.e. individual differences relative to litter siblings. For example, our studies in domestic rabbits and laboratory rats revealed consistent within-litter differences in the occurrence of directed behaviors to reach thermally more advantageous central positions in the litter huddle [25,28,29]. In brief, pups with relatively lower birth mass typically occupied more peripheral positions in the huddle, although they showed comparatively more attempts to reach the center. Initially heavier pups, being more central in the litter huddle, typically maintained a higher body temperature and showed higher postnatal growth [25,30]. Furthermore, such early differences in directed behaviors to reach a central position have been suggested to translate

into differences in behavioral types during later life [31]. Such within-litter dynamics could be particularly relevant in species with comparatively low maternal care, and thus where interactions among siblings are largely shaping the early developmental environment of the young. The European rabbit is such an example, where the young develop in nests located in nursery burrows, predominantly in the absence of their mother [32,33], and in a litter huddle of 2–9, on average around 4–5 siblings [34]. Mothers only visit their offspring to nurse them once per day, for a period of around 3–4 min [35–38].

The main aim of the present study was to explore how individual differences in behavior of pre-weaning wild rabbit pups co-varies with differences in the animals' early body mass, as a proxy for their developmental state at a given age. In doing so, a particular focus of our study was on individual differences within litters, as we expected that relative differences with respect to litter siblings should be highly informative and biologically relevant during an altricial animal's early ontogeny, notably adding to the general analysis of overall differences among individuals from different litters [6,39,40].

In a first attempt we studied (i) associations between pups' body mass gain and their peripheral body temperature. Based on our studies in domestic rabbit pups [25,30,41–43], we expected that also in wild rabbits under semi-natural conditions, pups that are relatively warmer than their siblings would show a relatively greater gain in body mass. Furthermore, also based on our previous observations in domestic rabbits [30], we expected that such differences in body temperature profiles with respect to litter siblings would be rather stable at the individual level. In addition, we (ii) checked for consistencies in individuals' responses across different behavioral tests reflecting different contexts, a condition that is frequently used to test for the existence of animal personality [4,44]. To this end, we quantified different behavioral responses of pre-weaning rabbit pups, during an age before these had actively started to explore the closer environment around their nursery burrow. We quantified (a) the pups' latency to struggle in response to handling restraint, which might reflect their readiness to escape an infanticidal female during early life [45], (b) their locomotor activity in an open field, usually interpreted as an animals' exploratory tendency [46], and (c) their latency to jump down from a platform, which might reflect individual differences in the tendency to take a risk. Finally, we (iii) tested for associations between the animals' body mass, as an important feature of their early development within litters, and within-litter differences in individual responses in the behavioral tests.

2. Methods

2.1. Animals and study site

The study was conducted on animals from a European rabbit colony living in a 2.0 ha enclosure on the campus of the University of Bayreuth (Franconia, Germany). Animals were descendants of wild rabbits caught in 1984, and the population in the field enclosure was established in 1986 (further details in [34]). The enclosure consisted of grassland interspersed with groups of trees and had a pond in the middle. The number of adult animals at the onset of the breeding season of 2010 when the study was conducted was about 22 per hectare, with around 300 pups born during the season. According to field data, the density in the enclosure was high but within the range of wild rabbit population densities [47,48]. In addition to the burrows and short breeding stops dug by the rabbits (around 40 to 50), the area contained 16 artificial concrete warrens with interconnected chambers and removable tops. These were used by the rabbits as main warrens of their group territories and also for breeding. The whole study site could be observed from two towers. Entry of mammalian predators was restricted by several electric wires installed at the top of the enclosure fence. However, birds of prey had free access to the enclosure.

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