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Features of the early juvenile development predict competitive performance in male European rabbits

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ABSTRACT

The outcome of an intra-specific aggressive encounter between two competitors is frequently influenced by differences in individual characteristics. Apart from differences in adult body condition, aspects of the early juvenile development, which are commonly found to influence traits during later life, may be of particular importance. In an observational study on individually marked European rabbit males (*Oryctolagus cuniculus* L.) from a field enclosure, we investigated short-term and long-term consequences of different features of the early development on measures of competitive performance during later life. Males from smaller litters, which consequently had a higher nestling body mass, showed more escalated offensive behavior (chasing) against other juveniles during juvenile life. Furthermore, such males were more offensive and successful fighters in intra-sexual conflicts during their first breeding season. Interestingly, when comparing the effects of different measures of body mass during different life stages, the nestling mass was the best predictor for male competitive performance after maturity. The body mass measured during the late juvenile stage in autumn was also significantly, but more weakly correlated with the males' offensive behavior after maturity, whereas the adult body mass did not show significant effects. In conclusion our study points out, that parameters of the early development are involved in shaping the competitive performance during later life via other mechanisms than just by promoting a high adult body mass.

1. Introduction

The conditions that an animal experiences during early life can have profound influences on fitness-related characteristics [44,47,53]. Such delayed or long-term consequences have been found with respect to age at maturity, lifespan, senescence, reproductive performance, breeding success and health during adulthood, and these effects are often thought to be mediated via short-term effects on early growth and development [1,15,23,30,61,76,77,83,89]. In addition, the fitness of an animal can be influenced by the way it interacts with conspecifics. For example, the outcome of aggressive encounters with a competitor often regulates the access to fitness-relevant resources [27].

It is well known that an animal's social behavior during adulthood is also related to its early ontogeny. Many studies on social mammals point out that an animal's social skills, or the way how it copes with challenging situations during later life are shaped by social experience during its youth [12,80,81]. However, little attention has been given to the question whether an animal's competitive performance during adulthood can be influenced by different characteristics of its early environment or development shortly after birth.

Generally, the probability of winning an encounter with a competitor can be explained by differential trade-off decisions between the costs of fighting in relation to the benefits of winning, but may also depend to a considerable extent on asymmetries in individual characteristics of the opponents such as experience and body condition [32,49; examples in: 38,41,45,54,85]. Above all, an animal's competitive performance or resource holding potential is often related to age, since individuals which have just reached maturity typically have less experience than older animals, and do often show a lower body mass [29,68]. When considering opponents of the same age class, differences in adult body condition or body mass might be of particular importance. In turn, the adult body mass can be related to characteristics of an individual's early development. For example, the growth rate or the adult body mass has been frequently shown to be positively correlated with the body mass during the juvenile stage in several ungulate species [11,18,29].

Growth and development of young mammals can strongly depend on the conditions they experience shortly after birth. For example, litter size is a prominent feature of the early environment, which frequently influences the postnatal development [39,55] and can even have long-term consequences on an individual's lifetime reproductive success [77]. Particularly in altricial species, offspring from larger litters (i.e. with a higher number of siblings) receive a lower share of milk leading to reduced postnatal growth, or more generally to a slower physiological development [25,33,37,42,73,78].

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In addition, maternal characteristics, especially those which are directly linked to the mother's milk supply, are decisive. For example, offspring from young, first-time breeders or from mothers with low body mass or social rank often show lower growth and survival rates [14,22,58,73,76,77,93].

Exploring the link between parameters of the early postnatal development and the competitive performance during adulthood was the main goal of this study, which we conducted with individually marked male European rabbits (*Oryctolagus cuniculus* L.) from a field enclosure population. European rabbits are organized in social groups with linear intra-sexual rank hierarchies and have a polygynous mating system. The number of adult individuals per group usually varies from 1 to 3 adult males and from 1 to 6 adult females [20]. During the breeding season, the males compete for the access to mating partners by intensive agonistic interactions [57,92]. These interactions are not only restricted to territorial residents, but do also occur among subordinate, mostly one-year-old males, which frequently do not settle in a particular group territory during their first breeding season (unpubl. data). European rabbits grow up in litters of variable size (wild rabbits: 1 to 9 pups) with a clear negative relationship between litter size and postnatal growth or body mass around weaning [26,73]. Maternal effects have been shown to be relevant for the early postnatal development in this species. In particular the mother's age, which is collinear with her body mass and social rank, appears to be relevant with offspring from one-year-old mothers having lower growth rates than pups born to older mothers [68,73]. Moreover, the timing of birth may potentially affect the adult body mass, since offspring born early in the breeding season benefit from a longer vegetation period and consequently reach a higher body mass before winter [69].

We predicted that the behavior or performance of one-year-old European rabbit males in competitive agonistic encounters depends on the adult body mass, and that different parameters of the individual early development, which potentially influence the adult body mass are related to male competitive performance. Therefore, we (i) evaluated the relationships between litter size, maternal age, date of birth and the male body mass during different life stages. We (ii) tested for effects of these early life parameters, including the nestling body mass, on male social behavior by considering the frequency of offensive agonistic interactions which male rabbits displayed during juvenile life. Finally, we (iii) investigated the long-term consequences of early life parameters or male body masses measured during different life stages on the frequency of offensive agonistic interactions displayed against other males, as well as on the proportion of fights won during adulthood.

2. Materials and methods

2.1. Study animals

The study was conducted on animals from a fenced population of European rabbits living in a field enclosure of 20,000 m^2 on the campus of the University of Bayreuth, Franconia, Germany. Vegetation consisted of grassland interspersed with groups of trees and bushes, which represents an adequate habitat structure for the European rabbit [19]. In addition to the burrows and 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 the main warrens of their group territories and also for breeding. The whole study site could be observed from two towers and all animals could be identified by their individual ear-tags.

The population consisted of descendents of animals that had been caught in the wild (Upper Palatinate, Germany) in 1983. During the study period (2001; 2004 to 2007) the number of animals at the start of the breeding season ranged from 18 to 35/ha (on average 16 animals/ha). The sex ratio (males/females) varied between 0.4 and 0.6. According to field data, the density in our enclosure was high but within the range of wild rabbit population densities [16,63,86,95]. During our long-term study, we found no signs of inbreeding such as changes in body mass, juvenile survival, or reduced fecundity of females. Further details on this population can be found in [93].

2.2. Determination of body masses by trapping

From early March until mid November we trapped the (adult) rabbits once a month using peanut-baited live traps. The traps were made of wood and so animals in the traps were not directly exposed to wind and rain. The traps were set overnight and checked at dawn the next morning. They were then set again and left open until noon, during which time they were checked every half hour. Between trapping sessions the traps were left open and were frequently used by the rabbits as resting sites. Animals were removed from the traps and placed singly in gunny sacks (60×110 cm) where they became calm immediately. The sacks containing the rabbits were taken to a quiet room and were permanently monitored by us until the animals were weighed with an accuracy of 1 g.

During the breeding season, we usually trapped around 70% of the adult population (about 20 to 50 animals). Trapping success of juveniles was lower, because they were often too small to activate the system of the traps. In mid November, we used especially prepared traps with a greater sensitivity for smaller (juvenile) animals in order to obtain a sufficiently high number of values for analysis.

2.3. Data collection during the nest period

The breeding season in our study population usually started in mid March (first parturitions were in mid or late April minus the gestation period of 30 days) until the end of September [71]. Every morning during the breeding seasons we checked for new born litters. To do this, we prepared all warrens and breeding stops dug by the animals with vertical openings to the nest chambers, which we covered with concrete flagstones. By checking the nests daily, we could record the birth of all litters to within 24 h and considered this postnatal day 1. We weighed the pups individually (to an accuracy of 1 g) on day 12, just before the age at which they start to eat the nest material [40]. Furthermore, we determined the litter size and sex of all pups per litter and marked them individually. Note that the litter size was determined on postnatal day 1 and day 12. Litter mortality usually affected the complete litter [76], and reductions in litter size during the nest period did not occur in animals which were later used as focal animals for behavioral observations. Mothers appeared undisturbed by these procedures and none abandoned their young.

2.4. Identification of mothers

During the monthly trapping sessions, we dyed the abdominal fur of the adult females with different colors (silk colour, Marabu, Germany). As female rabbits pluck out abdominal hair to build their nests [21,34], we were able to determine the mother of each litter by the location of the nest in combination with the color of the hair found in it. Identity of the mothers was additionally confirmed by the analysis of females' reproductive status during the regular trapping sessions (detection of pregnancies by abdominal palpation) and by behavioral observations (females entering particular breeding burrows; copulation as a sign of postpartum estrus; nest defense against other females, [74]).

2.5. Study animals and sample sizes

Juvenile European rabbits usually leave their breeding burrow on around postnatal day 20 and are weaned about one week later [40]. In