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Seasonally different reproductive investment in a medium-sized rodent (*Cavia aperea*)

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ABSTRACT

Pronounced seasonal variations in day length, temperature, and resource availability characterize the temperate regions and strongly influence the animals living in these environments. To survive and reproduce successfully, animals must allocate resources among competing physiological systems, and they usually adjust their time of breeding to the most adequate season. Here, we examined whether reproductive investment in the wild guinea pig (*Cavia aperea*) differs across seasons. We kept animals in combined indoor–outdoor enclosures under natural light and temperature year-round. We measured littering probability, litter size, and birth weight, as well as maternal weight loss during lactation. In addition, we measured ovulation rate as a parameter to adjust reproductive investment prenatally. Our data reveal strong seasonal variations in reproductive traits despite the fact that the animals reproduced year-round. The results show a reduced reproductive investment in winter, indicated by a lower litter size and birth weight of pups, whereas investment was highest in warm seasons (summer and autumn) with higher litter size and birth weight. Maternal weight loss in lactation was highest in cold seasons even if the litter size was lower. Furthermore, we found the regulation on the proximate level of the reproductive investment, the ovulation rate, to differ significantly between the seasons.

1. Introduction

Seasons strongly influence the energy balance of animals, particularly in small mammals [1]. In the temperate regions, small mammals usually adjust their timing of breeding to the most adequate season by using reliable cues such as photoperiodic variation [2]. In mammals spring and summer are the most adequate breeding season in which resources become more abundant, energy requirements for thermogenesis are low and weather conditions ameliorate [3]. Small mammals in the tropics and subtropics on the other hand often cue reproduction opportunistically on favorable environmental conditions. Species producing precocial young may be even more likely to reproduce aseasonally than species with altricial young [4]. This may be due to a different pattern of energy requirement during gestation and lactation in precocial animals. In general, mammals have the highest energy demand during lactation [5–7] with species-specific variations in timing and peak demands [8]. Künkele and Trillmich [9] showed that the overall energy demand for mothers of the highly precocial guinea pig was similar to that of altricial species of comparable size. However, they described the pattern of energy expenditure as prolonged, more constant, and with a lower energy peak during lactation compared to altricial rodents. Despite of the long pregnancy and enhanced energy demands during gestation, even pregnant females mated with less than 40 percent of adult body mass managed to grow at a comparable speed to nonreproductive females but deposited less

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than half fat reserves [10]. This balance between own body condition and reproductive costs as well as developed offspring allows a year-round reproduction [11].

Wild guinea pigs (*Cavia aperea*) are intermediate-sized rodents that produce highly precocial young [9]. *Cavia aperea* produces a mean litter size of 2.2 young after a pregnancy of on average 60 days [12,13]. The young are fully mobile only minutes after birth and even start nibbling solid food on their first day of life [12]. Information about seasonal differences in reproductive patterns is controversial. Young animals tune their reproductive decisions according to the seasons. Animals born in spring mature early, whereas animals born late in the year allocate their resources to growth and delay maturation [14–16]. Rood and Weir [11] reported wild guinea pigs in Argentina to reproduce continuously throughout the year, except for a short period in midwinter. They also reported a peak of births in spring (August in Argentina). When kept in pens or under laboratory conditions with food *ad libitum*, no seasonal pattern of breeding was observed [4,11]. Both studies [4,11], however, only investigated littering probability while neglecting other breeding characteristics such as litter size, birth weight, or postnatal maternal investment.

In the domesticated guinea pig *C aperea* f. *porcellus*, Künkele [17] showed that maternal performance depends on litter size during pregnancy. Larger litter sizes are associated with lower birth weights [13,18] and thus poorer body condition of the offspring.

We wanted to investigate whether seasonal variation in litter size and/or birth weight of pups occurs in the wild guinea pig. Therefore, a population of wild guinea pigs was bred year-round under natural photoperiodic and temperature regimes. We measured litter size and birth weight across the four meteorologic seasons. We hypothesized that increased physiological costs of mothers during unfavorable seasons such as autumn and winter would decrease either litter size or birth weight of pups. After birth, offspring are immediately exposed to environmental conditions because wild guinea pigs do not use burrows or holes but rather live aboveground. Following Künkele et al. [19], who observed an increase of energy expenditure for thermoregulation under low temperatures, we might expect an increase in maternal investment during lactation to sustain pups with enough energy reserves to maintain their thermoregulatory machinery in unfavorable seasons. As a predictor for maternal investment, we measured weight loss of the mother during the first 7 days of lactation. According to Künkele & Trillmich [9], the lactation peak occurs during the first 5 to 8 days after birth in the closely related domesticated guinea pig.

In a second experiment, we wanted to investigate how the expected seasonal variation is regulated on the proximate level. During pregnancy, mammalian females have various mechanisms to adjust their litter size. Especially rodents can influence the reproductive outcome by post-implantation abortion or absorption [18,20–22]. Before implantation, the availability of oocytes and the fertilization rate affect the number of fetuses and consequently litter size. To investigate a potential seasonal variation in ovulation rate, a second experimental group of females was bred across the four seasons. We determined the number of CL as indicator of oocyte availability.

In addition to the seasonal parameters, we observed how individual characteristics of mothers, here weight before pregnancy, influence reproductive output.

2. Materials and methods

All husbandry and experimental procedures were approved by the German committee of Animal Welfare in Research (permit no. V3-2347-35-2011).

2.1. Housing conditions

The animals were housed in combined indoor–outdoor enclosures (1.3 m^2) connected by a short tunnel with the possibility to change voluntarily at all times. Enclosures were equipped with woodchips for flooring, a feeding trough, a water bottle, and shelters for hiding. All animals were fed guinea pig pellets (Firma Altromin Spezialfutter GmbH & Co. KG, Lage, Germany). Water and hay were provided *ad libitum*, and apples, peppers, or carrots were given daily. Vitamin C was added to the drinking water once a week. The indoor enclosures were 0.75 × 0.75 × 1 m, and the outdoor enclosures were 0.75 × 1 × 1 m in size (length × width × height, respectively). The animals lived under natural temperatures and photoperiodic regimes. During periods of frost, a radiator prevented freezing of the drinking water indoors.

2.2. Animals

To assess the influence of different seasons on litter size, birth weight, and maternal investment, we investigated reproductive patterns across meteorologic seasons (see Fig. 1). The meteorologic seasons consist of three whole months each. The, on average, warmest months June, July, and August represent summer, whereas the coldest months December, January, and February represent winter (in Germany). Temperatures and photoperiod in Germany are highly comparable to those in the distribution area of cavies (30°–35°S) in South America, just displaced by 6 months.

Overall, 20 females were bred in groups of two per enclosure. Litters consisting only or partly of stillborn pups were excluded from the analyses. Females used for this breeding experiment differed in age and therefore also differed in weight and experience. To control for this variation, the weight of the female shortly before pregnancy (1 day before starting the breeding period) and the individual ID were included into the statistical analyses (see Section Statistical analyses).

One third of the females were nulliparous, and two third were multiparous at the time of mating. All females were bred in all four seasons. However, to control for potential differences in female performance arising from different levels of experience or age, females started breeding at different times of the year. About half of the females were first bred in spring or summer, whereas the other half of females started breeding in autumn and winter months.