Published in final edited form as:

Gen Comp Endocrinol. 2008 February 1; 155(3): 680–685. doi:10.1016/j.ygcen.2007.09.015.

The effects of early environmental conditions on the reproductive and somatic development of juvenile guinea pigs (*Cavia aperea f. porcellus*)

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Abstract

Little is known about the effects of the early environment on the development of non-seasonally reproducing species like the domestic guinea pig (*Cavia aperea f. porcellus*). Although guinea pigs reproduce throughout the year, there is evidence for environmental sensitivity of their reproductive physiology. To investigate the sensitivity of juvenile body weight and puberty to differences in the prenatal and early postnatal environment, subjects were exposed to either of two experimental conditions mimicking seasonal variation: a long photoperiod with 25 °C ambient temperature ("LD/25 °C"), or a short photoperiod with 15 °C ("SD/15 °C"). Mean body weight of F1-males from LD/25 °C-conditions was higher than that of SD/15 °C-males during the whole pubertal period, although the difference was significant only during the early growth phase. Testosterone concentrations also differed significantly between the two treatment groups, pointing to an earlier pubertal onset in LD/25 °C- than SD/15 °C-males. In F1-females, treatment effects on body weight or age at first estrus were absent. This indicates that the somatic and reproductive development is more sensitive to early photoperiod and temperature conditions in male than female guinea pigs, and that other environmental factors may also play a crucial role for reproductive maturation in this species.

Keywords

Guinea pigs (*Cavia aperea f. porcellus*); Photoperiod; Temperature; Puberty; Testosterone; Body weight

1. Introduction

In many species of the temperate zone, seasonally fluctuating environmental conditions can influence growth and age at puberty (e.g. Adam and Robinson, 1994; Horton, 2005). It has been hypothesized that these seasonal cues experienced during the pre- or early postnatal period prepare the offspring for the environment they will encounter in the future (Horton, 2005). In order to optimize energetically demanding activities like mating, gestation, and lactation, young born early and late in the breeding season, respectively, often express different growth and reproductive maturation strategies. Juvenile montane voles (*Microtus montanus*), for instance, seasonally reproducing, short-lived arvicoline rodents of the

northern temperate zone, grow rapidly and attain sexual maturity at an early age if born early in the season but grow slowly and mostly delay reproductive maturation until the next season if born late (Negus et al., 1986, 1992). Similar effects on growth and future reproduction can also be observed in the laboratory, if environmental conditions such as photoperiod (Heideman and Sylvester, 1997; Heideman et al., 2000) or ambient temperature (Barnett and Manly, 1956; Biggers et al., 1958; Kgwatalala and Nielsen, 2004; Benderlioglu et al., 2006) are manipulated. These laboratory data indicate that even in non-seasonally breeding species, an environment-sensitive system may exist.

The understanding of the sensitivity of non-seasonally reproducing animals to seasonally fluctuating environmental conditions during early development is particularly important in the context of the increasingly acknowledged phenomenon of the effects of early life conditions on later life events in humans: environmental conditions experienced during fetal and neonatal life are supposed to influence early developmental processes (McCance and Widdowson, 1974; Barker, 1994; Godfrey, 1998). Although such birth seasonality effects have been demonstrated for a variety of parameters such as, for instance, growth (e.g. Weber et al., 1998) and reproduction (e.g. Huber et al., 2004a,b), it still remains unclear which environmental forces may cause these effects. Experimental studies on animal models, where environmental conditions can be manipulated during early development, may help to elucidate such causative effects.

The domestic guinea pig (*Cavia aperea f. porcellus*) is a suitable model species for this kind of experiments because it reproduces throughout the year and, in contrast to rats and mice, gives birth to precocial young, i.e. most developmental processes occur prenatally. In addition, the guinea pig is a widely used rodent model for human physiology (see e.g. Keightley and Fuller, 1996). There is some evidence that at least in its wild form *Cavia aperea*, reproduction can be influenced by the season: it may almost cease during the southern midwinter in Argentina (Rood, 1972; Rood and Weir, 1970), though in captivity, Trillmich (2000) did not find any significant effect of either temperature or photoperiod on the reproductive performance of adult female wild guinea pigs. The domestic guinea pig also appears to retain sensitivity to environmental signals to a certain extent even though the responsiveness to environmental cues may have been weakened by the process of domestication: Rood (1972) and Rood and Weir (1970) reported that female domestic guinea pigs born in winter were able to delay their reproductive onset.

In the present study, we investigated whether the pre- and early postnatal environment affected body weight and reproductive maturation of female and, to our knowledge, for the first time also male juvenile domestic guinea pigs. We used two different environmental conditions mimicking seasonal variation: long day and warm ambient temperature (LD 16:8/25 °C) vs. short day and cool ambient temperature (LD 8:16/15 °C). Furthermore, we performed the experiment under controlled feeding conditions to rule out that potential treatment effects might be caused or masked by differences in food intake between the treatment groups. With this experimental design, we aimed to investigate whether differences in environmental conditions, typical for the seasonal variation experienced by modern humans in temperate zones, may exert any effect on the early somatic and reproductive development of the animals.

2. Methods

All husbandry and experimental procedures were conducted with the permission of the animal care committee of the Federal Ministry for Science and Research in Austria.

2.1. Housing conditions of F0-subjects

The guinea pigs used for breeding (F0-generation) were part of a heterogeneous, short-haired, and multicolored stock. Age ranged from 8 to 16 months at the beginning of the experiment. All animals (F0- and F1-generation) could be identified by natural markings. Body weight in males and females and the number of previous litters in females did not differ significantly between experimental groups (Wilcoxon–Mann–Whitney-*U* test, $P > 0.1$). The 12 female F0-subjects were neither pregnant nor lactating at the start of the experiment. Each F0-subject and their weaned F1-offspring received 20 g guinea pig pellets daily (Altromin 3013, Lage, Germany) supplemented with 40 g fresh fruit, vegetables, and hay: this quantity meets the recommended daily feeding requirements of adult guinea pigs (Hamel, 2002). Pregnant females in their last trimester as well as lactating mothers received additional 20 g pellets daily. Each juvenile received 10 g pellets/day during the lactation period. Water was available ad libitum.

We divided F0-subjects randomly into two experimental treatment groups, kept in ventilated, photoperiod- and temperature-controlled climatic chambers ($2.5 \times 2.5 \times 2$ m): Treatment group 1 (6 females, 3 males) was kept in L16:D8 and $25(\pm 3)^\circ\text{C}$ (“LD/25 °C”), treatment group 2 (6 females, 3 males) in L8:D16 and $15(\pm 3)^\circ\text{C}$ (“SD/15 °C”). Lighting was entirely artificial and provided by 22 65-W fluorescent tubes (Philips TL 65W 25 universal white, Osram L 65W/20 R cool white, distribution 1:1) in each chamber. Light intensity ranged from 1800 to 2000 lux at the bottom of the cages.

During a 2-week acclimatization phase, animals were housed in isosexual groups of two (cage size: $100 \times 50 \times 40$ cm). Then an F0-male was introduced into each F0-female group. In this way, we established three breeding groups in each of the two climatic chambers. The onset of pregnancies was measured by daily visual inspection of the vaginal membrane. In non-pregnant guinea pigs, the vagina is covered with a membrane that ruptures at the onset of physiological estrus and regenerates 1–6 days afterwards (Young, 1937; Weir, 1970). In pregnant females, on the other hand, the vaginal membrane stays intact until parturition. If a female’s vaginal membrane stayed intact for more than 30 days, we considered her to be pregnant. The first day of the last vaginal opening was designated day 1 of pregnancy. This method proved to be successful in all female subjects. Shortly before parturition, we transferred each F0-female into a separate littering cage to prevent further postpartum pregnancies.

2.2. Procedures and housing conditions of F1-subjects

Nine out of the 12 F0-females became pregnant (LD/25 °C: 4 litters, SD/15 °C: 5 litters). F1-pups remained with their mothers in the littering cage until 21 days of age (“weaning”); afterwards mothers were removed from the cage. After separation from their mothers, litters were kept in the original experimental conditions (LD/25 °C or SD/15 °C, respectively) for additional 3 weeks (until 42 days of age). At 43 days, all F1-juveniles were transferred to intermediate conditions of L12:D12 photoperiod and $20(\pm 3)^\circ\text{C}$ to limit treatment conditions to the pre- and early postnatal period. At this age, each F1-female was paired with a non-littermate F1-male from the same treatment group. Since there were more F1-males than females, four SD/15 °C- and three LD/25 °C-males could not be paired with a female. In this way, an isosexual male group in addition to male–female pairs was established in both environmental treatment groups. It is known that housing conditions can influence testosterone concentrations of males (Harding, 1981; Sachser and Pröve, 1988; Trillmich et al., 2006). Consequently, we ensured that overall social conditions did not differ between environmental treatment groups.

We counted and sexed F1-offspring within 24 h after birth (day 1). Each F1-pup was weighed within 24 h after birth (birth weight) and afterwards on a weekly basis (± 1 day). In F1-males, we compared body weight and hormonal puberty, in F1-females, body weight and the age at first estrus between both treatment groups. The onset of puberty cannot be defined as a single event in males. We therefore focused on hormonal puberty of F1-males, which is characterized by a strong testosterone increase from the age of 16 to 50 days, relatively high and stable levels between 50 and 90 days, and a subsequent decrease after 90 days of age (Rigaudière et al., 1976). In F1-females, we defined the onset of puberty as the first vaginal opening (first estrus). As already mentioned above, we determined vaginal opening by daily visual inspection of the vaginal membrane, beginning at weaning in F1-females. As physiological estrus correlates with vaginal opening (Young, 1937), we defined estrus as the first day the vagina was fully opened (day 1 of the cycle).

2.3. Blood sampling and endocrine analysis

We took blood samples from each F1-male in 2-week intervals (± 2 days), beginning at 12 days of age, for the later analysis of testosterone concentrations. Each blood sample (100 μ l) was taken without anesthesia at 9 a.m. by punctuating the marginal ear vessels with a sterile lancet and collecting the blood with a heparinized capillary (Sachser and Pröve, 1984). After centrifugation, the plasma was stored at -20°C until further analysis. The whole procedure (catching the animal, taking the sample, and returning the animal to its cage) took maximally 3 min per subject.

After a diethylether-extraction (85% recovery rate), we measured testosterone levels using an enzyme immunoassay as described by Palme and Möstl (1994). The antiserum used in the assay showed cross-reactions with relevant steroids (Steraloids, Wilton, NH, USA) as follows: testosterone (100%), 5α -androstane- 17β -ol-3-one (23%) and 5β -androstane- 17β -ol-3-one (12%), 4-androstene- 3β , 17β -diol (8%), 5α -androstane- 3α , 17β -diol (6%), 5α -androstane- 3β , 17β -diol (1%), 5β -androstane- 3β , 17β -diol (1%). All other steroids tested cross-reacted $<1\%$. The intra- and interassay coefficients of variance were 9.2% and 17.5%.

2.4. Statistical analysis

We used R 2.2.0 (R Foundation for Statistical Computing, 2005, Vienna, Austria; <http://www.R-project.org>) for statistical analysis. We compared litter size between groups using a Wilcoxon–Mann–Whitney–*U*-test. As litter mates can not be assumed to represent independent replicates and additionally repeated measurements from each subject were performed, we analyzed all F1-data using linear mixed effects (LME) models correcting for mother and subject as random factors in a nested design. In preliminary models, litter size, and age had an effect on body weight of pups and were therefore included in the models as covariates in addition to treatment. For the model with testosterone as response variable, only age had an effect, and was therefore included as a covariate. The housing condition of males after day 42 (with a female or with other males) had no significant effect on male body weight or testosterone and was therefore not included in the LME models. For non-normally distributed variables we applied either the $\ln$ —(testosterone, male body weight, age at first estrus) or the square root—(female body weight) transformation. We used the male body weight data of day 1 (birth), day 21 (weaning), day 43 (transfer to LD12:12/20 $^{\circ}\text{C}$), day 64, day 85, day 106, and day 127 (final measurement) for analysis. For testosterone, all data points measured in 2-week (± 2 days) intervals were included in the analysis: days 12 (first measurement), 26, 42, 56, 70, 84, 98, 112, and 126 (final measurement). In F1-females, body weight data were only analyzed until day 64, respectively, as on day 66 the first female got pregnant and by day 84, all females were. Due to spatial limitations in our facility, three F1-males, which were randomly chosen, had to be given away before the end of the study leading to missing values in the male data set.

Further, some male and female F1-subjects could not be sampled at each time point (due to lack of personnel) which also caused missing values. However, LME-models are suitable for longitudinal data sets with missing values (assuming that data is missing at random), because, in contrast to repeated-measurement ANOVAs, the subject's entire data set is not omitted, but all available observations per subject are used in the analysis. Further, LME models allow the time points of measurements to vary for different subjects. In this way, we calculated the models using all available measurements per subject, and age as a covariate. Observed differences were considered significant if $P \leq 0.05$.

3. Results

3.1. Litter size and body weight of F1-offspring

Litter size did not differ between treatment groups (LD/25 °C: mean = 3.8, min = 3, max = 4, $n = 4$; SD/15 °C: mean = 3.2, min = 2, max = 4, $n = 5$; $W = 6$; $P = 0.3378$). Litters were male biased in both treatment groups (number of male vs. female pups: LD/25 °C: 9 vs. 6, SD/15 °C: 10 vs. 6).

Body weight was significantly higher in F1-males ($n = 17$) than F1-females ($n = 11$) from day 1 through day 64 (last sample point in females before the initiation of pregnancies): mean $\pm$ SEM in males vs. females: day 1, 93.47 ± 2.82 g vs. 86.83 ± 4.91 g; day 21, 241.78 ± 8.24 g vs. 224.00 ± 8.44 g; day 43, 408.11 ± 9.21 g vs. 362.18 ± 8.63 g; day 64, 528.71 ± 10.12 g vs. 460.64 ± 8.95 g (LME model entering litter size, age, treatment, and sex as fixed factors, as well as mother and subject as random factors; litter size: $df = 1/6$, $F = 27.442$, $P = 0.0019$; age: $df = 3/82$, $F = 3738.548$, $P < 0.0001$; treatment: $df = 1/6$, $F = 9.497$, $P = 0.0216$; sex: $df = 1/82$, $F = 20.992$, $P < 0.0001$). Consequently, we further analyzed both sexes separately.

3.2. Body weight and plasma testosterone concentrations of F1-males

Mean body weight was higher in F1-males from LD/25 °C- than SD/15 °C-conditions at almost every sample point from day 1 through day 127 (Fig. 1). When all sample points were included in the model, the difference in body weight of F1-males between treatment groups was not significant after correction for the effects of litter size and age (LME model entering litter size, age, and treatment as fixed factors, as well as mother and subject as random factors; litter size: $df = 1/6$, $F = 25.16$, $P = 0.0024$; age: $df = 6/94$, $F = 1387.35$, $P < 0.0001$; treatment: $df = 1/6$, $F = 2.10$, $P = 0.1972$). Limiting the analysis to the period of most intense growth, i.e. day 1 through day 64, however, the model yielded a significant difference between treatment groups (LME model entering litter size, age, and treatment as fixed factors, as well as mother and subject as random factors; litter size: $df = 1/6$, $F = 26.58$, $P = 0.0021$; age: $df = 3/50$, $F = 4027.23$, $P < 0.0001$; treatment: $df = 1/6$, $F = 6.91$, $P = 0.0391$).

Plasma testosterone concentrations differed significantly between F1-males from LD/25 °C- and SD/15 °C-conditions (LME model entering age and treatment as fixed factors, as well as mother and subject as random factors; age: $df = 8/106$, $F = 7.65$, $P < 0.0001$; treatment: $df = 1/7$, $F = 10.57$, $P = 0.0140$; Fig. 2). Testosterone levels increased from the first measurement at day 12 through days 70–84 and decreased thereafter in both treatment groups, with higher mean concentrations found in LD/25 °C-males than SD/15 °C-males between days 12 and 70 indicating a later pubertal peak in the SD/15 °C-group (Fig. 2).

3.3. Body weight and age at first estrus in F1-females

In F1-females, analyses were limited to the period prior to the onset of pregnancies at day 66. We did not find any significant differences between F1-females from LD/25 °C and SD/

15 °C conditions either in body weight (Fig. 3; LME model entering litter size, age, and treatment as fixed factors, as well as mother and subject as random factors; litter size: $df = 1/6$, $F = 10.43$, $P = 0.0179$; age: $df = 3/30$, $F = 1160.51$, $P < 0.0001$; treatment: $df = 1/6$, $F = 3.20$, $P = 0.1241$), or the age at first estrus (mean age $\pm$ SEM in LD/25 °C- vs. SD/15 °C-conditions: 43.17 ± 4.20 d vs. 40.17 ± 5.83 d; LME model entering treatment as a fixed factor as well as mother as a random factor; treatment: $df = 1/7$, $F = 0.38$, $P = 0.5568$).

4. Discussion

We found that differences in environmental conditions present during the pre- and early postnatal period, comparable to the seasonal variation typically experienced by modern humans in temperate zones, had an effect on the somatic and reproductive development of juvenile guinea pig males, albeit not females. Mean body weight of F1-males from LD/25 °C conditions was higher than that of SD/15 °C-males, particularly during the early growth phase. This finding is in agreement with comparable studies on laboratory rodents: young male Fisher 344 rats, for instance, showed inhibition of somatic and testicular growth if kept in LD 8:16 as compared to LD 16:8 (Heideman and Sylvester, 1997); also laboratory mice grew slower if gestated in 12 °C than 22 °C (Kgwatalala and Nielsen, 2004). The observed differences between treatment groups in body weight of pubertal F1-males apparently did not result from differences in food consumption of either the young or their mothers: both experimental groups received the same controlled amount of food that was always fully consumed. Though we did not control for individual food intake within a mother/litter group, neither body weight of F0- or F1-females nor weight loss of F0-females during lactation differed significantly between experimental conditions at any time which would be expected if individual food intake differed between treatment groups (Fig. 3; F0-data not shown).

The onset of the pubertal testosterone increase was earlier in F1-males from LD/25 °C- than SD/15 °C-conditions. In seasonally reproducing species, strong effects of photoperiod on testosterone titers have been reported. Juvenile deer mice, for instance, reared in a long photoperiod had significantly higher testosterone levels than subjects reared in a short photoperiod (Fail and Whitsett, 1988). Similar results were found in Djungarian hamsters (Yellon and Goldman, 1984), and bank voles (Tähkä et al., 1983). In each of these studies, differences in testosterone titers became even more pronounced with increasing age. However, this was not the case in our study where differences in testosterone levels were most pronounced during the early postnatal period (days 12 and 26) and leveled off thereafter, presumably because of the later pubertal testosterone increase in the SD/15 °C group.

In general, treatment effects on male body weight and testosterone levels were rather small in the present study compared to the effects found in the above mentioned studies (Tähkä et al., 1983; Yellon and Goldman, 1984; Fail and Whitsett, 1988; Heideman and Sylvester, 1997; Kgwatalala and Nielsen, 2004). On the one hand, domestication may have weakened the environmental sensitivity of guinea pigs. In addition, it has been shown that species giving birth to small litters of precocial young may respond less to environmental cues in their reproductive activity (Dieterlen, 1985a,b; Neal, 1986), presumably because the maximum energetic costs during lactation are lower than in rodents producing altricial young (Künkele and Trillmich, 1997). On the other hand, the weaker effects on somatic and reproductive development may have also resulted from different methodology: environmental treatments were applied from the perinatal period until the end of measurements in the aforementioned studies, whereas in the present study we limited treatment to the prenatal and early postnatal period.

Interestingly, only male but not female offspring body weight and reproductive onset were affected by the early environmental conditions applied in our study. These sex differences might partially be caused by the higher male than female F1-sample size. However, some studies in humans found that male prenatal growth was more affected than that of females by maternal undernutrition or prenatal stress (e.g. Haas, 1976; Frisancho et al., 1977; Haas et al., 1980). Consequently, it was hypothesized that males might react more sensitively than females to adverse conditions during early development (reviewed in Stinson, 1985). This hypothesis is based on the assumption that female reproduction should be more buffered against environmental conditions in order to support pregnancy and lactation (Stini, 1975, 1982). In addition, in mammals, fetal development of males is more complex on the endocrine level than that of females: fetal androgens are needed for sexual differentiation processes in males whereas the fetal ovaries of females remain hormonally quiescent (Hadley, 2000).

In addition to climatic conditions, other seasonally fluctuating environmental cues such as food availability or food quality may also play an important role for somatic and reproductive development of guinea pigs. For example, many small mammals of the neotropic zone use food availability as a main cue for reproduction (e.g. Bergallo and Magnusson, 1999). Also seasonally varying levels of nutritional components like protein may have a crucial effect during perinatal development. Further experiments are needed to answer these open questions.

Acknowledgments

We thank Eva Millesi for providing the climatic chambers, Anna Schöbitz for her assistance performing the hormone assay, and Thomas Ruf for his help with the statistical analyses. This work was supported by the Austrian Science Fund (P18089-B03), the Austrian Academy of Sciences (APART), and the University of Veterinary Medicine in Vienna.

References

- Adam CL, Robinson JJ. The role of nutrition and photoperiod in the timing of puberty. *Proc. Nutr. Soc.* 1994; 53:89–102. [PubMed: 7913222]
- Barker, DJ. Mothers, babies, and disease in later life. BMJ Publishing Group; London: 1994.
- Barnett SA, Manly BM. Reproduction and growth of mice of three strains, after transfer to -3°C . *J. Exp. Biol.* 1956; 33:325–329.
- Benderlioglu Z, Eish J, Weil ZM, Nelson RJ. Low temperatures during early development influence subsequent maternal and reproductive function in adult female mice. *Physiol. Behav.* 2006; 87:416–423. [PubMed: 16343561]
- Bergallo HG, Magnusson WE. Effects of climate and food availability on four rodent species in southeastern Brazil. *J. Mammal.* 1999; 80:472–486.
- Biggers JD, Ashoub MR, McLaren A, Michie D. The growth and development of mice in three climatic environments. *J. Exp. Biol.* 1958; 35:144–155.
- Dieterlen F. Daten zur Fortpflanzung und Populationsstruktur der myomorphen Nager eines afrikanischen Tieflandregenwaldes (Ost-Zaire). *Z. Säugetierkd.* 1985a; 50:68–88.
- Dieterlen F. Beziehungen zwischen Umweltfaktoren und Fortpflanzungsperiodik myomorpher Nager eines afrikanischen Tieflandregenwaldes (Ost-Zaire). *Z. Säugetierkd.* 1985b; 50:152–166.
- Fail PA, Whitsett JM. Influence of photoperiod, ambient temperature and melatonin on testosterone synthesis and release during reproductive maturation in male deer mice. *J. Androl.* 1988; 9:21–30. [PubMed: 3346178]
- Frisancho AR, Klayman JE, Matos J. Influence of maternal nutritional status on prenatal growth in a Peruvian urban population. *Am. J. Phys. Anthropol.* 1977; 46:265–274. [PubMed: 848566]
- Godfrey KM. Maternal regulation of fetal development and health in adult life. *Eur. J. Obstet. Gynecol. Reprod. Biol.* 1998; 78:141–150. [PubMed: 9622311]

- Haas, JD. Infant growth and development. In: Baker, PT.; Little, MA., editors. *Man in the Andes. A Multidisciplinary Study of High-Altitude Quechua*. Dowden, Hutchinson and Ross; Stroudsburg: 1976. p. 161-179.
- Haas JD, Frongillo EA, Stepick CD, Beard JL, Hurtado GL. Altitude, ethnic and sex difference in birth weight and length in Bolivia. *Hum. Biol.* 1980; 52:459–477. [PubMed: 7450728]
- Hadley, ME. *Endocrinology*. Fifth ed. Prentice Hall, Inc.; New Jersey, USA: 2000. p. 397-411.
- Hamel, I. *Das Meerschweinchen als Patient*. Second ed. Enke; Stuttgart, Germany: 2002. p. 14-25.
- Harding CF. Social modulation of circulating hormone levels in the male. *Am. Zool.* 1981; 21:223–231.
- Heideman PD, Bierl CK, Galvez ME. Inhibition of reproductive maturation and somatic growth of Fisher 344 rats by photoperiods shorter than L14:D10 and by gradually decreasing photoperiod. *Biol. Reprod.* 2000; 63:1525–1530. [PubMed: 11058561]
- Heideman PD, Sylvester CJ. Reproductive photoresponsiveness in unmanipulated male Fisher 344 laboratory rats. *Biol. Reprod.* 1997; 57:134–138. [PubMed: 9209091]
- Horton TH. Fetal origins of developmental plasticity: Animal models of induced life history variation. *Am. J. Hum. Biol.* 2005; 17:34–43. [PubMed: 15611963]
- Huber S, Fieder M, Wallner B, Iber K, Moser G. Effects of season of birth on reproduction in contemporary humans: Brief communication. *Hum. Reprod.* 2004a; 19:445–447. [PubMed: 14747195]
- Huber S, Fieder M, Wallner B, Moser G, Arnold W. Brief communication: birth month influences reproductive performance in contemporary women. *Hum. Reprod.* 2004b; 19:1081–1082. [PubMed: 15121731]
- Keightley MC, Fuller PJ. Anomalies in the endocrine axes of the guinea pig: relevance to human physiology and disease. *Endocr. Rev.* 1996; 17:30–44. [PubMed: 8641221]
- Kgwatalala PM, Nielsen MK. Performance of mouse lines divergently selected for heat loss when exposed to different environmental temperatures. II. Feed intake, growth, fatness, and body organs. *J. Anim. Sci.* 2004; 82:2884–2891. [PubMed: 15484938]
- Künkele J, Trillmich F. Are precocial young cheaper? Lactation energetics in the guinea pig. *Physiol. Zool.* 1997; 70:589–596. [PubMed: 9279926]
- McCance RA, Widdowson EM. The determinants of growth and form. *Proc. R. Soc. Lond. B.* 1974; 185:1–17. [PubMed: 4149051]
- Neal BR. Reproductive characteristics of African small mammals. *Cimbebasia.* 1986; 8:113–127.
- Negus NC, Berger PJ, Brown BW. Microtine population dynamics in a predictable environment. *Can. J. Zool.* 1986; 64:785–792.
- Negus NC, Berger PJ, Pinter AJ. Phenotypic plasticity of the montane vole (*Microtus montanus*) in unpredictable environments. *Can. J. Zool.* 1992; 70:2121–2131.
- Palme, R.; Möstl, E. Biotin-streptavidin enzyme immunoassay for the determination of oestrogens and androgens in boar faeces. In: Görög, S., editor. *Advances of Steroid Analysis*, 1993. Akadémiai Kiadó; Budapest: 1994. p. 111-117.
- Rigaudière N, Pelardy G, Robert A, Delost P. Changes in the concentrations of testosterone and androstenedione in the plasma and testis of the guinea-pig from birth to death. *J. Reprod. Fert.* 1976; 48:291–300.
- Rood JP. Ecological and behavioural comparison of the three genera of Argentine caviars. *Anim. Behav. Monogr.* 1972; 5:1–83.
- Rood JP, Weir BJ. Reproduction in female wild guinea pigs. *J. Reprod. Fert.* 1970; 23:393–409.
- Sachser N, Pröve E. Short term effects of residence on testosterone responses to fighting in alpha male guinea pigs. *Aggressive Behav.* 1984; 10:285–292.
- Sachser N, Pröve E. Plasma-testosterone development in colony and individually housed male guinea pigs. *Ethology.* 1988; 79:62–70.
- Stini, WA. Adaptive strategies of human populations under nutritional stress. In: Watts, ES.; Johnston, FE.; Lasker, GW., editors. *Biosocial interrelations in population adaptation*. The Hague; Mouton: 1975. p. 19-41.

- Stini, WA. Sexual dimorphism and nutrient reserves. In: Hall, RL., editor. Sexual Dimorphism in Homo Sapiens. Praeger; New York: 1982. p. 391-419.
- Stinson S. Sex differences in environmental sensitivity during growth and development. Yearb. Phys. Anthropol. 1985; 28:123–147.
- Tähkä KM, Ruokonen A, Wallgren H, Teräväinen T. Temporal changes in testicular histology and steroidogenesis in juvenile bank voles (*Clethrionomys glareolus*) subjected to different photoperiods. Endocrinology. 1983; 112:1420–1426. [PubMed: 6339204]
- Trillmich F. Effects of low temperature and photoperiod on reproduction in the female wild guinea pig (*Cavia aperea*). J. Mammal. 2000; 81:586–594.
- Trillmich F, Laurien-Kehnen C, Adrian A, Linke S. Age at maturity in cavies and guinea-pigs (*Cavia aperea* and *Cavia aperea f. porcellus*): influence of social factors. J. Zool. 2006; 268:285–294.
- Weber GW, Prossinger H, Seidler H. Height depends on month of birth. Nature. 1998; 391:754–755. [PubMed: 9486642]
- Weir BJ. The management and breeding of some more hystricomorph rodents. Lab. Anim. 1970; 4:83–97. [PubMed: 5535887]
- Yellon SM, Goldman BD. Photoperiod control of reproductive development in the male Djungarian hamster (*Phodopus sungorus*). Endocrinology. 1984; 114:664–670. [PubMed: 6418534]
- Young WC. The vaginal smear picture, sexual receptivity and the time of ovulation in the guinea pig. Anat. Rec. 1937; 67:305–325.

Fig. 1. Body weight (means $\pm$ SEM) of F1-males born and weaned in LD/25 °C (open circles) vs. SD/15 °C (full circles) from day 1 (birth) to day 127 (final measurement). Sample sizes: LD/25 °C, 9/9/9/9/9/7; SD/15 °C, 10/9/9/8/8/6. The black arrow indicates the time of weaning at day 21, the white arrow the switch to LD 12:12/20 °C at day 43.

Fig. 2.

Plasma testosterone concentrations (means $\pm$ SEM) of F1-males born and weaned in LD/25 °C (open circles) vs. SD/15 °C (full circles) from day 12 (first measurement) to day 126 (final measurement). Sample sizes: LD/25 °C, 7/9/9/9/8/7/9/5/9; SD/15 °C, 7/10/8/9/8/8/7/3/7. The black arrow indicates the time of weaning at day 21, the white arrow the switch to LD 12:12/20 °C at day 43.

Fig. 3.

Body weight (mean $\pm$ SEM) of F1-females born and weaned in LD/25 °C (open circles) vs. SD/15 °C (full circles) from day 1 to day 64 (final measurement due to the initiation of pregnancies at days 66–84). Sample sizes: LD/25 °C, 6/6/6/6, SD/15 °C, 6/5/5/5. The black arrow indicates the time of weaning at day 21, the white arrow the switch to LD 12:12/20 °C at day 43.