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The influence of food restriction and photoperiod on reproduction in male spiny mice (*Acomys spinosissimus*): evidence for terminal investment?

Ruan de Bruin^{1#}, André Ganswindt^{1,2}, Nigel C. Bennett¹, Katarina Medger^{1*}

¹*Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, RSA*

²*Endocrine Research Laboratory, Department of Anatomy and Physiology, Faculty of Veterinary Science, University of Pretoria, Onderstepoort 0110, RSA*

* *Corresponding author:*

Katarina Medger, Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa, kmedger@zoology.up.ac.za, Tel.: +27 (0) 12 420 4872

Current address:

Mammalian Cognition Research Group, Department of Zoology and Entomology, University of the Free State, Qwaqwa campus, Phuthaditjhaba, South Africa

Abstract

Photoperiod and food availability often interact in the regulation of reproductive activity in seasonal environments. We tested the effects of a 10% food restriction and short- (SD) and long-day (LD) photoperiods on reproductive preparedness of male spiny mice (*Acomys spinosissimus*) from South Africa. Males were either fed *ad libitum* or a 10% restricted diet and on both food regimes, they were exposed to either a 14h light:10h dark (LD) or 10h light:14h dark (SD). Testes size, seminiferous tubule diameter and faecal androgen metabolite concentrations were significantly larger in food restricted males subjected to LD than in any of the other groups. SD photoperiods did not suppress reproductive activity, despite earlier findings, which may be explained by “spontaneous” recrudescence due to prolonged exposure to SD. The high reproductive activity observed in food restricted LD males may indicate a terminal investment strategy in male spiny mice with males investing more into reproduction in the face of reduced future survival.

Key words: Faecal androgen metabolites, Food availability, Seasonal breeding, Seminiferous tubules, Terminal investment strategy, Testes

Reproduction is energetically costly (Hayward and Gillooly, 2011) and as a consequence most small mammals time reproduction in such a way that enough energy is available to maximize reproductive success (Tinney et al., 2001). As such, many rodents and other small mammals breed seasonally during times of maximum energy availability, usually during the spring and summer months, or the rainy seasons in the tropics and sub-tropics (Bronson, 1985; Bronson and Perrigo, 1987; Field, 1975).

Changes in photoperiod are consistent between years and therefore photoperiod is an ideal environmental cue to time reproductive activity in many mammals (Bradshaw and Holzapfel, 2007). In most temperate rodents, short-day photoperiods (SD) induce the regression of the reproductive organs and inhibit reproduction, whereas long-day photoperiods (LD) cause reproductive recrudescence (Hegstrom and Breedlove, 1999; Prendergast et al., 2009; Trainor et al., 2006). In the tropics and sub-tropics where photoperiodic changes are much less pronounced, both reproductively photoperiodic and non-photoperiodic mammals have been identified. In southern Africa, pouched mice (*Saccostomus campestris*) are reproductively non-photoresponsive (Bernard and Hall, 1995), whereas Namaqua rock mice (*Micaelamys namaquensis*) and Tete veld rats (*Aethomys ineptus*) decrease reproductive development under SD conditions (Muteka et al., 2006).

Reproduction is also often controlled by many other factors such as temperature, rainfall and food availability, with interactions between these factors influencing reproductive output (Bronson and Perrigo, 1987). Reduced food quality and/or quantity in conjunction with SD photoperiods suppresses reproductive function and reduces reproductive organ mass (Bazhan et al., 1996; Steinman et al., 2012; Young et al., 2000). Tinney et al. (2001) showed that both reduced food quantity and quality results in a decrease in body mass and body fat content and a reduction in

the mass of accessory glands as well as the epididymis in non-photoresponsive pouched mice (Bernard and Hall, 1995). Conversely, supplementing food to wild populations of the four-striped field mouse (*Rhabdomys pumilio*) in winter resulted in larger testes and epididymis in males and thicker uterine walls, endometria and myometria in females, although it did not override the winter inhibition of reproduction of this species (Jackson and Bernard, 2005). For spiny mice (*Acomys spinosissimus*), Medger et al. (2010) suggested that an increase in food availability and possibly quality with the onset of the rainy season are the main driving factors for seasonal reproduction. In a previous study, photoperiod was found to be important for the timing of reproduction in spiny mice (Medger et al., 2012a); however, it remains unclear if food quantity plays a role in the seasonal reproductive development of this species.

Spiny mice are small terrestrial rodents found from Tanzania to the north-eastern parts of South Africa (Skinner and Chimimba, 2005), although it has been suggested that the population from South Africa constitutes a separate species, *Acomys selousi* (Verheyen et al., 2011). *Acomys spinosissimus* feeds on grass and seeds, but also supplements its diet with insects (Mills and Hes, 1997). Spiny mice breed during spring and summer, which coincides with the rainy season in its habitat and both sexes are reproductively regressed during the dry autumn and winter months (Medger et al., 2012b; Medger et al., 2010). To compare the effects of photoperiod and food availability on the reproductive physiology of male *A. spinosissimus*, we compared changes in body mass, mass of fat deposits, testicular histology, and levels of faecal androgen metabolites of males that received *ad libitum* food with that of food restricted males. Simultaneously, we subjected the males in both food groups to LD or SD photoperiods. Based on the findings of Medger et al.

(2012a), we predicted reduced reproductive activity under SD photoperiods and with food restriction in both SD and LD photoperiods.

Twenty-four male spiny mice (body mass (mean \pm SE): 21.1 \pm 0.5g, range: 18.0-27.0g) were collected during May and July of 2011 from Goro Game Reserve (22°58'S, 22°59'S, 29°25'E, 29°24'E) in the Limpopo Province of South Africa. Animals were trapped overnight with Sherman live traps (H. B. Sherman Traps, Inc. Tallahassee, Florida, U.S.A.) baited with a mixture of sardines, peanut butter and oats. Male spiny mice were housed individually with water and mouse pellets (Unitrade Three t/a Die Klein Kooperasie) available *ad libitum*. The animals were kept at controlled temperature (25°C) with a SD photoperiod of 10h light and 14h dark for 40 days to induce gonadal regression. Individual food intake was determined during the last week of this initial period. Thereafter, males were randomly assigned to one of four experimental treatments (n=6 per treatment). The males remained under SD, or they were exposed to a LD photoperiod of 14h light and 10h dark. For each photoperiodic treatment, males were either fed mouse pellets *ad libitum* (non-restricted) or food intake was restricted by 10% of the individual food intake determined at the beginning of the experiments (restricted). Males were weighed at the beginning, three times per week during, and at the end of the eight week experimental period. Restricted males that lost more than 20% of their body mass during the experiment were fed *ad libitum* until they regained their initial mass (2-4 days). Faecal samples were collected every second day throughout the experimental period to monitor alterations in faecal androgen metabolite (fAM) concentrations. On sampling day, faeces were collected every two hours over a six hour period, starting at 07h30 a.m. Faecal samples were frozen at -30°C immediately after collection and stored until analysis. fAM concentrations were determined using an epiandrosterone enzyme immunoassay first described by Palme and Möstl (1993), and validated for

spiny mice in de Bruin *et al.* (2014). Inter- and intra-assay coefficient of variation (%) was 12.98-14.72 % and 8.64-10.05%, respectively. All males were sacrificed after the experiment, and the fat between the shoulder blades, base of the back as well as lining of the gut (body fat) and the fat around the testes was dissected out, dried and weighed. The testes were dissected out, fixed in Bouin's solution for 24h and stored in 70% ethanol. The length and width of the testes was measured to calculate the volume (mm^3) using the formula for an ellipsoid, $V = 4/3\pi ab^2$ (a – length, b – width). Histology of the testes and measurements of seminiferous tubule diameters (ST) were done as described in Medger *et al.* (2012b). General linear models (GLM) were used to compare testes volume, ST, body and testes fat mass between the photoperiod (LD and SD), and food restriction treatments (non-restricted vs. restricted). Body mass was included as a covariate in all GLMs. Body mass and fAM concentrations were analysed using mixed models with individual as subject. Photoperiod, food restriction and measuring time were included as factors. A normal distribution was used for body mass and a gamma distribution with log-link function for fAM concentration. All analyses were followed by least significant difference pairwise comparison post hoc tests. Statistical analyses were done using IBM SPSS 23 (IBM Corporation 1989, 2015). The results are presented as mean \pm standard error (SE) and significance is assumed at $p \leq 0.05$.

Body mass was similar for all males at the start of the experiment ($21.3 \pm 0.5\text{g}$; $p > 0.80$). There was no effect of photoperiod on body mass at the end of the experiments (SD: $21.5 \pm 0.9\text{g}$; LD: $20.3 \pm 0.7\text{g}$; $p > 0.26$, $F_{1,40} = 0.52$, $p = 0.47$), but food restricted males weighed significantly less ($19.4 \pm 0.7\text{g}$) than non-restricted males ($22.4 \pm 0.7\text{g}$; $p = 0.006$, $F_{1,40} = 4.96$, $p = 0.03$). Overall, none of the main factors, two-way interactions with photoperiod or the three-way interaction were significant ($F_{1,40} \leq 3.50$, $p \geq 0.07$). Body mass was positively correlated to body fat mass and the mass of fat

around the testes ($F_{1,19} \leq 3.50$, $p < 0.001$). Body and testes fat mass was comparable for all four treatments at the end of the experiments ($F_{1,19} \leq 1.36$, $p \geq 0.26$). Testicular volume and ST were not significantly affected by body mass ($F_{1,19} \leq 1.16$, $p \geq 0.29$). Both testicular variables were significantly larger in LD (volume: $155.1 \pm 11.5 \text{ mm}^3$, ST: $197.4 \pm 4.2 \mu\text{m}$) than SD animals (volume: $116.3 \pm 11.5 \text{ mm}^3$, ST: $170.8 \pm 4.2 \mu\text{m}$, $F_{1,19} \geq 5.51$, $p \leq 0.03$). However, this difference seems driven by food restriction ($p \leq 0.001$), as males that received *ad libitum* food showed no photoperiod-related differences in testicular variables ($p \geq 0.09$; Fig. 1). When photoperiod was not taken into account, there was no difference in testes volume or ST between food restricted (volume: $147.3 \pm 19.1 \text{ mm}^3$, ST: $183.8 \pm 5.9 \mu\text{m}$) and non-restricted males (volume: $124.1 \pm 6.2 \text{ mm}^3$, ST: $184.4 \pm 5.8 \mu\text{m}$; $F_{1,19} \leq 1.64$, $p \geq 0.22$). Under SD, however, food restriction resulted in a slight but non-significant reduction of testes volume and ST ($p = 0.33$, Fig. 1). Surprisingly, under LD photoperiods, testes volume was larger in food restricted than non-restricted males ($p \leq 0.006$, Fig. 1A), but not the ST ($F_{1,19} = 3.44$, $p = 0.08$; Fig. 1B). Overall, fAM concentrations were significantly higher in LD ($1.8 \pm 0.1 \mu\text{g/g DW}$) than in SD males ($1.4 \pm 0.1 \mu\text{g/g DW}$, $F_{1,111} = 19.61$, $p < 0.001$), but there was no significant difference in fAM concentrations between food restricted ($1.7 \pm 0.1 \mu\text{g/g DW}$) and non-restricted males ($1.5 \pm 0.1 \mu\text{g/g DW}$, $F_{1,111} = 2.51$, $p = 0.12$). Under LD, fAM concentrations were higher in restricted than in non-restricted males ($p = 0.03$), but there was no such difference under SD photoperiods ($p = 0.92$; Fig. 2). The interaction of photoperiod and food restriction showed a trend ($F_{1,111} = 2.98$, $p = 0.09$), with fAM concentrations being significantly higher under LD than SD in food restricted males ($p < 0.001$), and a trend for higher fAM concentrations in non-restricted males ($p = 0.06$; Fig. 2). Mean fAM concentrations increased throughout the study period and were significantly higher at the end than the beginning of the experimental period ($p \leq 0.008$; $F_{1,111} = 3.41$, $p = 0.004$).

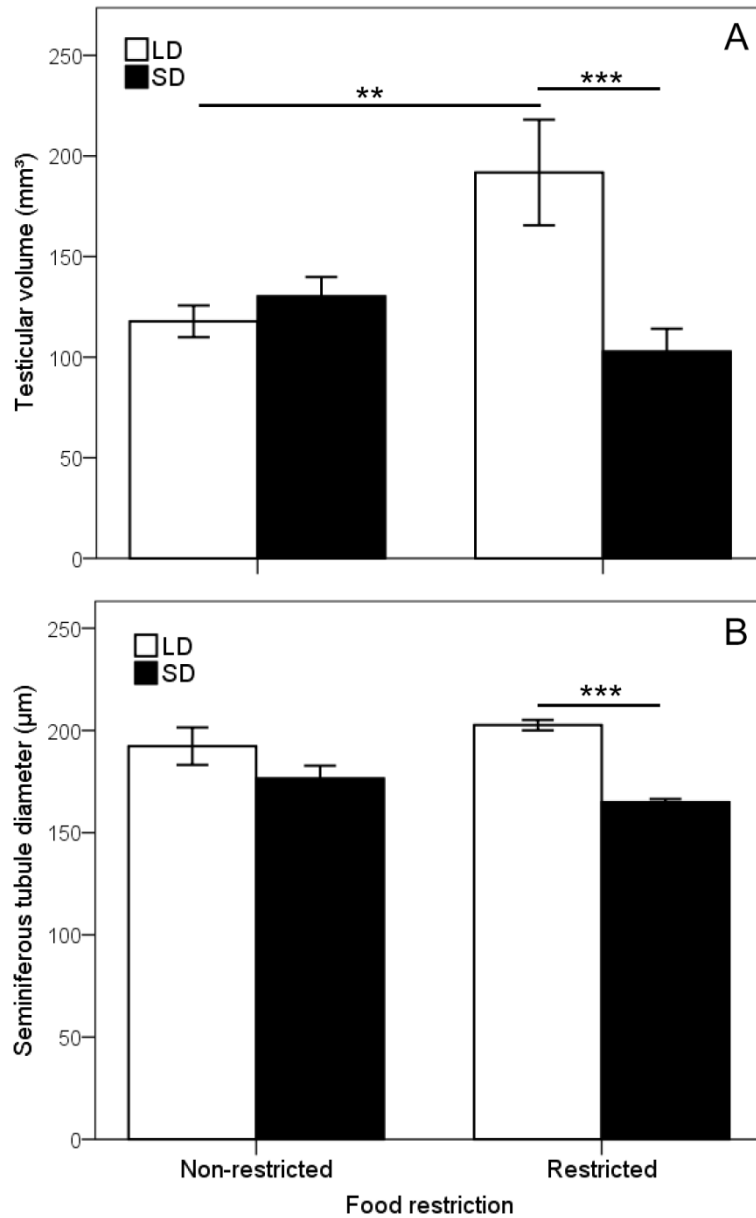


Figure 1. Testicular volume (mm³) (A) and seminiferous tubule diameter (μm) (B) of male spiny mice (*Acomys spinosissimus*) that were exposed to a long-day (LD) or short-day (SD) photoperiod and were restricted by 10% from individual total food intake (restricted) or were not restricted (non-restricted). Values are mean ± SE. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

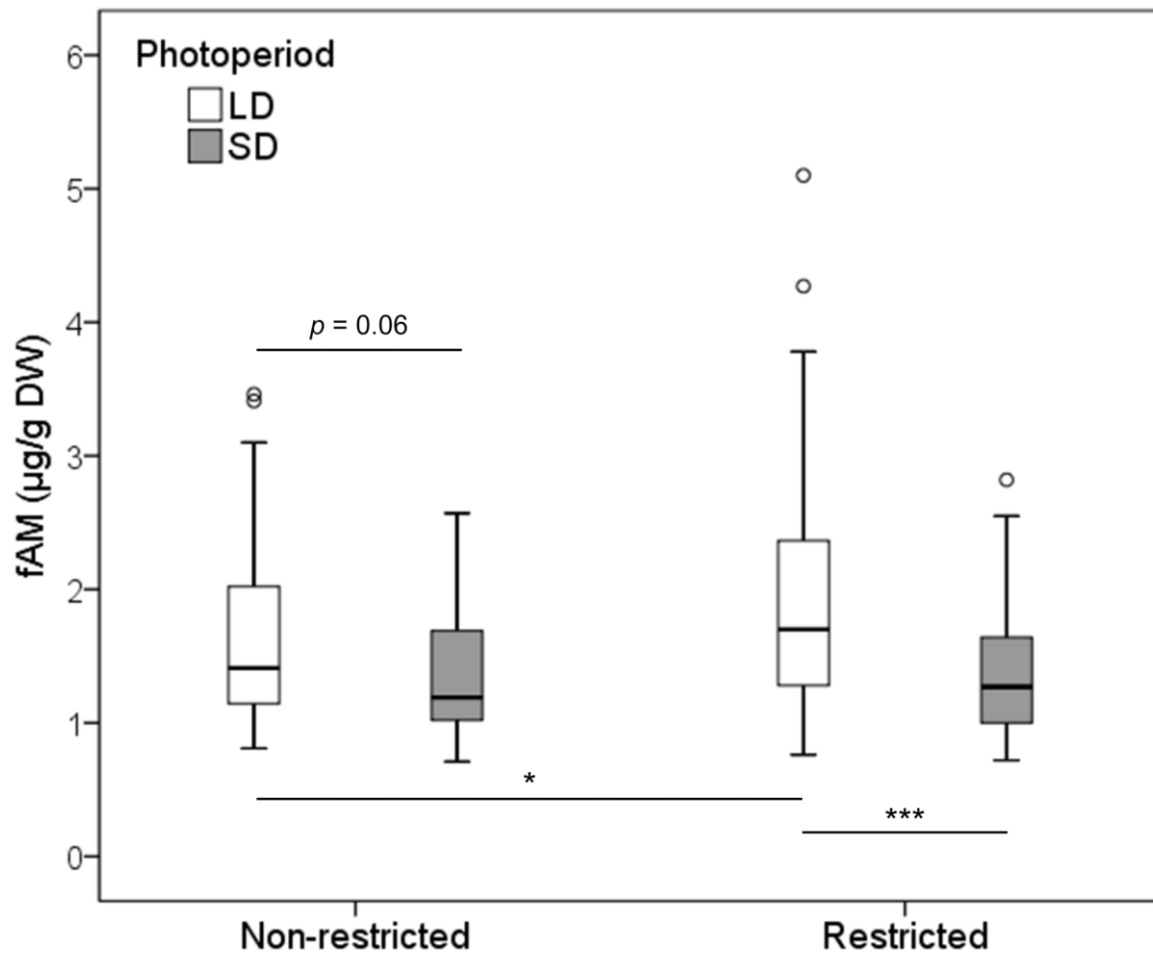


Figure 2. Box-plots showing faecal androgen metabolites (fAM; µg/g dry weight) measured in male spiny mice subjected to long-day (LD) and short-day (SD) photoperiods and *ad libitum* food (non-restricted) or restricted food supply by 10 % of total individual food intake (restricted). * $p \leq 0.05$, *** $p \leq 0.001$

The lack of a photoperiod effect on reproduction of non-restricted males and the large increase of reproductive activity of restricted LD males were very surprising and contrary to our predictions. The findings seemingly contradict the findings of Medger et al. (2012a), who found a clear effect of photoperiod on reproductive activity of male spiny mice with SD photoperiods reducing gonad size and androgen concentrations. A possible explanation for this might be that Medger et al. (2012a) used a more distinctive light-dark cycle of 16 h dark and 8 h light for SD and vice versa for LD. In addition, the exposure to the different photoperiods was shorter in Medger et al. (2012a) with 10 weeks against 14 weeks exposure in the present study. It is possible that the less pronounced light-dark cycle (10h light:14h dark) may not have been a strong enough signal for reproductive suppression. However, this appears unlikely as, for example, golden spiny mice (*Acomys russatus*) decrease testicular activity at the same SD photoperiod (Wube et al., 2008). In addition, the photoperiod used in the present study is more similar to the photoperiod in the natural environment. If this photoperiod would be insufficient to regulate reproductive activity, it would be more likely that *A. spinosissimus* are non-photoresponsive. Thus the longer exposure to a SD photoperiod in this study may better explain the lack of a photoperiodic response. Many small mammals exhibit spontaneous recrudescence of the gonads with prolonged exposure to SD photoperiods. For example, after initial reproductive inactivity, development of gonads is similar to LD levels after 26 to 30 weeks under SD photoperiods in hamster (Nelson and Zucker, 1987), white-footed mice (*Peromyscus leucopus*) (Johnston and Zucker, 1980) and field voles (*Microtus agrestis*) (Grocock, 1980). Fourteen weeks under a SD regime appears too short for recrudescence to have occurred in the spiny mice, but the animals were caught in May and July and as such already experienced natural SD photoperiod prior to being

housed in the laboratory. However, further studies are needed to determine if and when 'spontaneous' recrudescence occurs in *Acomys*.

Male spiny mice, which were food restricted and kept under LD photoperiods, showed the largest responses in gonadal and endocrine parameters compared to any of the other groups. Further, food restricted males held under SD photoperiods showed similar reproductive responses as non-restricted males. These results were surprising as many studies have found a negative effect of food restriction on reproduction especially in SD photoperiods. Food restriction usually results in gonadal regression (Edmonds et al., 2003; Steinman et al., 2012; Young et al., 2000) and reduced spermatogenesis (Blank and Desjardins, 1984), pregnancy success (Bazhan et al., 1996), and sexual behaviour (Gill and Rissman, 1997). Most of these studies used high levels of food restriction of usually 30% and up to 50%. In comparison, the 10% food restriction used in the present study was mild. This suggests that the 10% food restriction may not have been enough to trigger a reduction in gonadal and hormonal development in SD individuals. Nevertheless, we observed that even a 10% food restriction can adversely affect the health of spiny mice, and restricted individuals also appeared to be less active than their non-restricted counterparts (R. de Bruin, personal observation). A reduction of physical activity is common in mammals, which experience increased energy demands due to reproductive activities (Speakman, 2008). Decreases in activity may have masked the effects of food restriction on reproduction in *A. spinosissimus* and may also explain how the food restricted LD individuals were capable of achieving the high reproductive activity observed in the present study. The reason for such high reproductive activity is, however, much more difficult to explain.

The terminal investment hypothesis predicts that animals should invest more into reproduction, if the chance of survival and future reproduction is low (Clutton-

Brock, 1984). Siberian hamsters (*Phodopus sungorus*), for example, delay reproductive regression, if they are immune-challenged (Weil et al., 2006). The survival prospect of immune-challenged hamsters is low and the prolonged reproductive activity may provide additional reproductive success before death (Weil et al., 2006). Similarly, the increased reproduction in food restricted LD spiny mice may provide a mechanism to ensure greater reproductive success when food is scarce and survival is likely reduced. In spiny mice, LD photoperiods are a signal for both the onset of reproduction as well as increased food availability during the warm and wet summer months (Medger et al., 2012a; Medger et al., 2010). We suggest that adverse conditions that result in low food availability during the breeding season may result in considerably reduced survival of spiny mice to the next season and as such also reduce the chance of iteroparous reproduction. Male spiny mice may, therefore, increase reproductive activity to ensure reproductive success during the breeding season even if environmental conditions are seemingly detrimental to reproduction. In addition, the mild food restriction in the present study may have aided an increase in reproduction, whereas spiny mice may not be able to compensate for more severe food restriction and would then cease reproduction. Nevertheless, the increased reproduction despite a lack of food must have severe negative effects on the animals and males must compensate for the lack of energy by adjusting their behaviour and other physiological functions. Further studies are needed to investigate how food restriction in conjunction with increased reproduction affects the behaviour and physiology of male spiny mice and how the males can consolidate the higher energy requirements of reproduction with the low food availability.

Surprisingly, fat reserves did not appear to be different between the non-restricted and restricted cohorts, although body mass was reduced in food restricted

spiny mice indicating that food restriction depleted energy reserves. The 10% food restriction may not have been enough to reduce all the fat reserves, but e.g. subcutaneous fat, which we did not measure, may have been reduced accounting for the reduction in body mass. A reduction of body mass with food restriction is expected and has also been found in a number of other small mammal species (Edmonds et al., 2003; Hamilton and Bronson, 1985; Steinman et al., 2012). As already found by the earlier study by Medger et al. (2012a), photoperiod does not affect body mass of male spiny mice. This is not uncommon in small mammals; photoperiod does not influence the body mass of California mice (*Peromyscus californicus*) (Steinman et al., 2012), gerbils and Cairo spiny mice (*Acomys cahirinus*) (El-Bakry et al., 1998).

In conclusion, 10% food restriction in conjunction with LD photoperiods results in a significant increase in reproductive activity of male spiny mice. The increase in reproduction despite reduced energy availability may be explained by the terminal investment hypothesis, suggesting that male spiny mice aim to increase reproductive success in the face of reduced survival.

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