

# Regulation of male prolactin levels in an opportunistically breeding species, the African striped mouse

J. Raynaud<sup>1</sup> & C. Schradin<sup>2,3</sup>

<sup>1</sup> Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

<sup>2</sup> Université de Strasbourg, IPHC-DEPE, CNRS, Strasbourg, France

<sup>3</sup> School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

## Keywords

reproduction; social flexibility; testosterone; paternal care.

## Correspondence

Julien Raynaud, Animal Behaviour Group, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland. Tel: +0041 (0)44 635 52 85; Fax: +0041 (0)44 635 54 90  
Email: julien.raynaud@ieu.uzh.ch

Editor: Virginia Hayssen

Received 28 November 2012; revised 28 February 2013; accepted 11 March 2013

doi:10.1111/jzo.12040

## Abstract

The timing of reproduction of many species depends on seasonal changes in prolactin secretion. Photoperiod coincides with annual seasonal changes and typically regulates prolactin secretion. However, when environmental conditions are unpredictable, other ecological factors may contribute to prolactin regulation. In African striped mice (*Rhabdomys pumilio*), males show seasonal changes in reproduction and in prolactin levels, but unexpected increases of food availability out of the regular breeding season can also induce reproduction. We measured prolactin levels in free-ranging male African striped mice during three periods: (1) the natural breeding in spring with increasing photoperiod; (2) the natural non-breeding season in summer (dry season) with decreasing photoperiod; and (3) during two summers with unexpected rainfall inducing breeding in the population. Here, we report that breeding males showed increased prolactin levels when they were breeding independently of increases and decreases in day length. Also, we found a positive correlation ( $P = 0.05$ ) between the availability of food plants and prolactin levels. Changes in prolactin levels in opportunistically breeding species like the African striped mouse are not strictly regulated by photoperiod, but seem to respond to cues from food availability.

## Introduction

Prolactin is well known for its essential role in the reproduction of males and females (Nelson, 2005). Many species show increased prolactin secretion during the breeding season (Curlewis, 1992). Photoperiod typically regulates this hormone secretion (Goldman, Song & Bartness, 2009), i.e. the ratio of hours with daylight to the hours of darkness; and whether this ratio is currently increasing (i.e. winter to mid summer) or decreasing, prolactin levels increase when day length increases, which coincides with reproductive periods in long-day breeders (Hall, Harvey & Chadwick, 1986; Curlewis, 1992; Sharp, Dawson & Lea, 1998; Johnston, 2004; Sharp, 2005; Paul, Zucker & Schwartz, 2008). For instance, experimental decrease of day length resulted in a decrease in blood prolactin levels in prairie voles, *Microtus ochrogaster* (Smale, Nelson & Zucker, 1988); golden hamster, *Mesocricetus auratus* (Steger *et al.*, 1983); and Soay rams, *Ovis aries* (Lincoln, McNeilly & Cameron, 1978). These changes in prolactin secretion mediate necessary physiological and behavioural changes between seasons (Wingfield, 2008). Up-regulation of prolactin secretion can activate reproduction by stimulating follicle-stimulating hormone release (Steger *et al.*, 1983) and reducing sensitivity of gonadotropin release to negative tes-

tosterone feedback, which is essential for annual reactivation of gonadal activity (Bartke, 2004). High prolactin levels are also associated with parental care in birds and mammals (Buntin, 1996; Schradin & Anzenberger, 1999).

The photoperiodic regulation of prolactin is advantageous to time physiological and behavioural changes related to reproduction (Curlewis, 1992). In predictable environments, increased day length predicts when environmental conditions (food, water and temperature) are optimal for breeding. Thus, the increase of prolactin secretion can occur in advance enabling an optimal start of reproduction (Wingfield, 2008). If changes in environmental conditions are, however, unpredictable, photoperiodic cues cannot indicate when future necessary resources for breeding will be available. Under these environmental conditions, food, water and temperature may play a more important role in the regulation of prolactin secretion (Dawson, 2008). The zebra finch, *Taeniopygia guttata*, an opportunistic breeding species living in arid habitat, has increased prolactin levels outside of the breeding season, when food and water availability favour reproduction (Christensen & Vleck, 2008). Similarly in California mice, *Peromyscus californicus*, experimental changes in day length and food availability did not influence prolactin levels, but water availability did (Nelson, Gubernick & Blom, 1995). Such studies, nevertheless, are

scarce and which environmental factors modulate prolactin secretion in opportunistically breeding species is still unclear.

The African striped mouse, *Rhabdomys pumilio*, is a seasonally breeding species with geographic variations in South Africa; breeding occurs in summer for 4–6 months in summer-rainfall areas, whereas breeding occurs in spring for 3–4 months in winter-rainfall areas (Schradin, 2005). In winter-rainfall areas, breeding males show the highest prolactin levels in spring when day length increases and significantly lower prolactin levels in summer when day length decreases, suggesting a photoperiodic control of prolactin secretion (Schradin, 2008). African striped mice from winter-rainfall areas, however, breed in summer after exceptional rainfalls, which increase food availability (Schradin, unpublished data). To our knowledge, this offers a unique opportunity to test whether photoperiod or food availability is more important in the regulation of prolactin levels in a free-ranging opportunistically breeding mammal species.

## Materials and methods

### Study area

The study site was located on Goegap Nature Reserve (41.56°S, 1.60°E) in South Africa and consisted of 20 ha. The vegetation type is Succulent Karoo (Cowling *et al.*, 1999). The field site was around a dry riverbed and the vegetation was characterized by the evergreen succulent shrub, *Zygophyllum retrofractum*. Sandy patches get more frequent the larger the distance from the dry riverbed, and, especially here, annuals (wildflowers and succulents) grow in spring. These plants are especially palatable for striped mice and are a major food source for them in spring (Schradin, 2005; Schradin & Pillay, 2006).

### Trapping and marking of animals

African striped mice were trapped in their nests by using metal live traps similar to Sherman's traps (26 × 9 × 9 cm) baited with a mixture of bran flakes and salad oil. Mice were trapped twice every month, each time for 3 days. Mice were permanently marked using numbered metal ear tags (National Band and Tag Co., Newport, KY, USA). Additionally, each individual was dyed for visual identification with a mark on the pelage (Rapido, Pinetown, South Africa). Reproduction was assessed by the presence of pups in the family group of breeding males. Groups were monitored additionally by radio tracking at least one breeding female per group. During the breeding season, breeding males also carried radio collars (for details see Schradin, König & Pillay, 2010).

### Blood samples and hormones assays

Sixty blood samples were taken from 48 adult breeding males: 12 samples from 10 males in spring 2009 (8 September–3 December), 22 samples from 19 males in summer 2009 (3 March–30 May) and 9 samples from 9 males in summer 2011

(12 February–6 April; both summers, i.e. in 2009 and 2011, with reproduction); 17 samples from 14 males in summer 2010 (4th February–20th May; summer without reproduction). Among the 48 adult breeding males, we collected a unique blood sample for 37 males. For seven males, blood samples were taken twice in the same season of the same year; for three males, blood samples were taken twice in two different seasons; for one male, blood samples were taken three times; two samples were taken in the same season of the same year and one was taken in another season. To avoid pseudoreplication, we used 'male identity' and 'year' as random factors in our statistical analysis (see data analyses). Blood samples were collected in the morning (6:00–8:00 AM) when individuals emerged from their nest, controlling for possible circadian rhythms of hormone release. Mice were anaesthetized with diethyl ether, and a blood sample of 500 µL was collected from the sublingual vein (Heimann, 2006) within less than 3 min, thereby controlling for possible corticosterone effects on prolactin levels (Schradin, 2008). After 1 h, blood samples were centrifuged two successive times for 10 min. The resulting serum was frozen in aliquots of 60 µL for prolactin assays. We used a commercial kit from SPIbio (A05101, rat prolactin) validated by Schradin (2008). The intra- and inter-assay coefficients of variation were 14.57 and 13.38%.

### Plant surveys

On the 15th of each month, we did plant surveys in eight plots, each of 2 × 2 m, within the home ranges of eight groups, using standard protocols (Braun-Blanquet Method; Werger, 1974), recording the number of food plant species in each plot. Monitoring plots were chosen such that the availability of ephemeral and annual plant species was recorded, which are regarded as the high-quality food sources for striped mice (Schradin & Pillay, 2006). Palatability of food plants was known from direct behavioural observations (Schradin & Pillay 2006).

### Data analyses

Statistical analyses were carried out with R 2.15.0 (R Development Core Team, 2012). Results are presented as mean ± SEM and significance was accepted at  $\alpha \leq 0.05$ . We ran two generalized linear mixed effect models (GLMMs) with a Gaussian error distribution and 'prolactin levels' as a response variable, which was square root transformed to achieve linearity of residuals. 'Male identity' and 'year' were added as random effects in the models because 12 blood samples were replicates and our field study covered 3 successive years. In a first model (GLMM1), we tested whether 'photoperiod' [time period when day length is either increasing (i.e. spring) or decreasing (i.e. summer)] and 'reproduction' influenced 'prolactin levels'. In a second model (GLMM2), we tested whether 'photoperiod' and 'food availability' influenced 'prolactin levels'. We ran two models instead of one because reproduction is highly correlated with food availability (Schradin & Pillay, 2006). We used Akaike's second-order information criteria (AICc) for small sample size to compare

the two models. To further test the effect of reproduction on male prolactin levels, we performed pairwise comparisons between 'spring', 'summer without reproduction' and 'summer with reproduction' with *post hoc* tests following the Benjamini and Hochberg method (Benjamini & Hochberg, 1995).

### Results

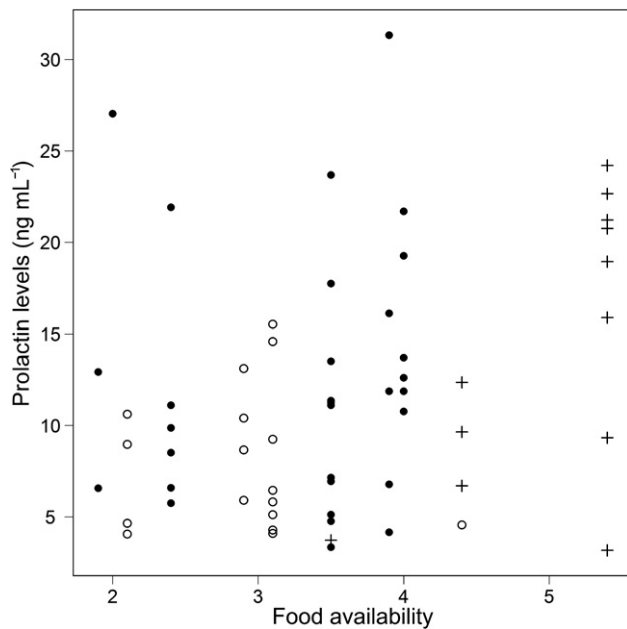
GLMM1 showed a significant effect of reproduction on male prolactin levels ( $F_{1,48.5} = 5.02$ ;  $P = 0.03$ ). In GLMM2, 'food availability' also influenced significantly male prolactin levels ( $F_{1,40.5} = 4.03$ ,  $P = 0.05$ ; Fig. 1). 'Photoperiod' did not significantly influence male prolactin levels (GLMM1:  $F_{1,57} = 0.83$ ,  $P = 0.37$ ; GLMM2:  $F_{1,33.4} = 0.00$ ,  $P > 0.99$ ). The AICc of GLMM1 was very slightly lower than the AICc of GLMM2 (172.9034 vs. 173.6545). Male prolactin levels during spring were significantly higher than those during summer without reproduction ( $P = 0.04$ ) but did not differ significantly from prolactin levels during summer with reproduction (*post hoc*:  $P = 0.47$ ; Fig. 2). Male prolactin levels during summer with reproduction were significantly higher than those during summer without reproduction ( $P = 0.04$ ).

### Discussion

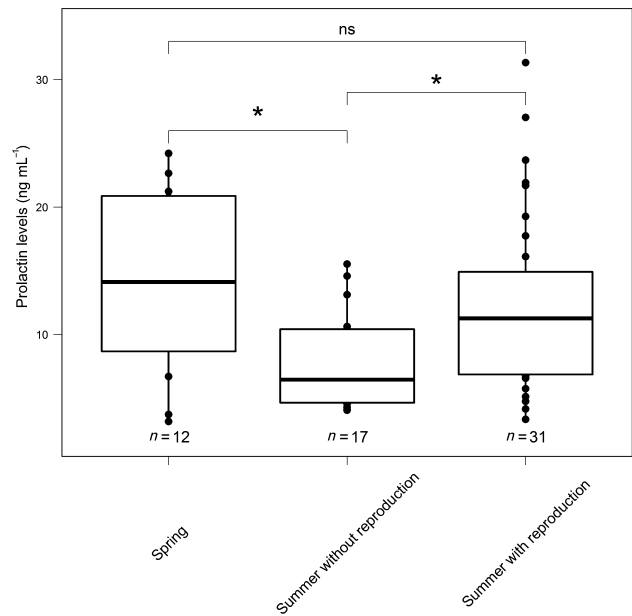
Up to date, which environmental factors influence prolactin secretion is not clear in opportunistically breeding species, that is, species coping with unpredictable changes in environ-

mental conditions (Dawson, 2008). In the present study, we demonstrated that adult breeding males, which were reproducing, had high prolactin levels independently of whether they reproduced in spring, with increasing day length, or in summer, with decreasing day length. This suggests that other factors that photoperiod must be important in the regulation of prolactin secretion in opportunistically breeding male striped mice. We found a correlation between food availability and prolactin levels, which indicates that direct cues related to reproduction might play an important role.

During the natural non-breeding season, male striped mice are non-scrotal (Schradin & Pillay 2005) and do not show spermatogenic activity (David & Jarvis, 1985), but the environmental factors regulating this regression of reproductive activity are not well understood. Neither an experimental prolonged exposure to short day length (winter) nor a natural decrease of day length induces spermatogenic regression in male African striped mice (Jackson & Bernard, 1999). Similarly, results were found in the pouched mouse (*Saccostomus campestris*) in which reproduction is not regulated by photoperiod (Bernard & Hall, 1995). In the present study, prolactin levels in reproductively active males were highly independent of whether photoperiod was increasing or decreasing, indicating that prolactin secretion might not be photosensitive or that males might have lost sensitivity to photoperiod, which is called photorefractoriness (Nicholls, Goldsmith & Dawson, 1988). In some seasonal long-day



**Figure 1** Effect of food availability on male prolactin levels (GLMM2) during spring with reproduction (normal breeding season; +), summer without reproduction (normal dry season; ○) and summer with reproduction (dry season with unexpected rainfall; ●).



**Figure 2** Comparison of male prolactin levels ( $\text{ng mL}^{-1}$ ) during spring (normal breeding season;  $14.05 \pm 2.17 \text{ ng mL}^{-1}$ ), summer without reproduction (normal dry season;  $8.01 \pm 0.92 \text{ ng mL}^{-1}$ ) and summer with reproduction (dry season with unexpected rainfall;  $12.47 \pm 1.25 \text{ ng mL}^{-1}$ ). The median is indicated by the horizontal bar inside the box, the first and third quartile by the box itself; outliers are shown by a black-filled circle. Ns, non significant;  $*P < 0.05$ .

breeding species, the breeding season ends while day length is still increasing, and photorefractoriness allows these animals to terminate reproduction before photoperiod starts to decrease. This photorefractoriness has been reported in Japanese quails, *Cortunix japonica* (Robinson & Follett, 1982; Guyomarch & Guyomarch, 1995), European starlings, *Sturnus vulgaris* (Nicholls, Goldsmith & Dawson, 1984; Dawson, 1991, Dawson 2001) and in Soay sheep, *O. aries* (Almeida & Lincoln, 1984; Lincoln, Andersson & Clarke, 2003). While we cannot exclude that photoperiod had an influence on prolactin secretion in male striped mice, in our study, photoperiod could not explain why prolactin levels were higher in summers with reproduction than without reproduction; and additional factors must be at play in the regulation of prolactin secretion.

Food availability is an important factor limiting reproduction, for instance, in pine siskins, *Spinus pinus* (Watts & Hahn, 2012) and passerines (Porlier *et al.*, 2012). We found a positive correlation between the number of annual and ephemeral food plant species, which are regarded as high-quality food for African striped mice (Schradin, 2005; Schradin & Pillay, 2006), and prolactin levels, but this correlation was rather weak (Fig. 1) and only approached significance ( $P = 0.05$ ). Similarly, food supply during the winter non-breeding season increased testis and epididymis size as well as spermatogenesis activity in male striped mice (Jackson & Bernard, 2005). Together, these studies indicate that food availability might be one of the several factors influencing prolactin secretion and reproduction. Food availability is typically a function of previous rainfall (Schradin & Pillay, 2006). Water availability, humidity and barometric pressure may be other factors influencing prolactin secretion, as reported in California mice, *Peromyscus californicus* (Nelson *et al.*, 1995) and Darwin's ground finches, *Geospiza fuliginosa* (Hau *et al.*, 2004). Rainfall reliably predicts a future increase of food availability for African striped mice; but whether prolactin levels increase immediately after rainfall or only after an increase of food availability remains unknown.

Interestingly, prolactin levels can also differ between males of different reproductive tactics in house finches (Badyaev & Vleck, 2007) and in African striped mice (Schradin, 2008). Males show higher prolactin levels when they switch from a solitary non-paternal to a group-living paternal reproductive tactic during the breeding season (Schradin & Yuen, 2011). This physiological flexibility of male African striped mice suggests that prolactin has more important effects on reproductive behaviours (including paternal care) than it does on timing of reproduction *per se*. Thus, the regulation of prolactin levels appears to depend on a complex interaction between environmental factors timing reproduction (e.g. food availability) and ecological factors mediating social flexibility (i.e. population density and reproductive competition; Schradin *et al.*, 2010, 2012; Schoepf & Schradin, 2012).

Our study is a step forward to understanding the regulation of prolactin release in opportunistically breeding species. Experimental studies will be essential to demonstrate which non-photoperiodic cues are at play. As higher prolactin levels are only reported during breeding events, prolactin likely

influenced gonadal activity and paternal care (Schradin, 2008). In harsh habitats, prolactin secretion might also respond to energetic constraints due to parenting effort as in bird species (Angelier & Chastel, 2009). These hypotheses are not mutually exclusive and testing them will help to go towards a full understanding of prolactin regulation and its function in species coping with unpredictable environmental changes.

## Acknowledgements

We thank the Department of Tourism, Environment and Conservation of the Northern Cape for research permits and the manager and staff of the Goegap Nature Reserve for their support. For help in the field, we thank I. Schoepf and C. H. Yuen (Research Station Manager). We thank Prof. B. König for her support. Dr C. Bousquet and Dr C. Pryce, and two anonymous reviewers provided insightful comments on earlier drafts of this manuscript. Funding was provided by the Claraz Stiftung Switzerland. Animal ethical clearance was provided by the University of the Witwatersrand, Johannesburg, South Africa (no. 2004/87/2A, 2005/82/4, and 2006/3/03).

## References

- Almeida, O.F.X. & Lincoln, G.A. (1984). Reproductive photorefractoriness in rams and accompanying changes in the patterns of melatonin and prolactin secretion. *Biol. Reprod.* **30**, 143–158.
- Angelier, F. & Chastel, O. (2009). Stress, prolactin and parental investment in birds: a review. *Gen. Comp. Endocrinol.* **163**, 142–148.
- Badyaev, A.V. & Vleck, C.M. (2007). Context-dependent development of sexual ornamentation: implications for a trade-off between current and future breeding efforts. *J. Evol. Biol.* **20**, 1277–1287.
- Bartke, A. (2004). Prolactin in the male: 25 years later. *J. Androl.* **25**, 661–666.
- Benjamini, Y. & Hochberg, Y. (1995). Controlling the false discovery rate – a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Stat. Methodol.* **57**, 289–300.
- Bernard, R.T.F. & Hall, J. (1995). Failure of the estrous-cycle and spermatogenesis to respond to day length in a subtropical african rodent, the pouched mouse (saccostomus-campestris). *Biol. Reprod.* **52**, 1291–1295.
- Buntin, J.D. (1996). Neural and hormonal controls of parental behavior in birds. *Adv. Study Behav.* **25**, 161–213.
- Christensen, D. & Vleck, C.M. (2008). Prolactin release and response to vasoactive intestinal peptide in an opportunistic breeder, the zebra finch (*Taeniopygia guttata*). *Gen. Comp. Endocrinol.* **157**, 91–98.
- Cowling, R.M., Esler, J.J. & Rundel, P.W. (1999). Namaqualand, South Africa – an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology* **142**, 3–21.



- Curlewis, J.D. (1992). Seasonal prolactin secretion and its role in seasonal reproduction – a review. *Reprod. Fertil. Dev.* **4**, 1–23.
- David, J.H.M. & Jarvis, J.U.M. (1985). Population fluctuations, reproduction and survival in the striped fieldmouse *Rhabdomys-pumilio* on the cape flats, South-Africa. *J. Zool.* **207**, 251–276.
- Dawson, A. (1991). The induction of photorefractoriness and molt in starlings, *Sturnus-vulgaris*, by continuous or intermittent long days. *Physiol. Zool.* **64**, 1252–1261.
- Dawson, A. (2001). The effects of a single long photoperiod on induction and dissipation of reproductive photorefractoriness in European starlings. *Gen. Comp. Endocrinol.* **121**, 316–324.
- Dawson, A. (2008). Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **363**, 1621–1633.
- Goldman, B.D., Song, C.K. & Bartness, T.J. (2009). Seasonal rhythms: seasonal hormonal changes and behavior. In *Encyclopedia of neuroscience*: 501–508. Squire, L.R. (Ed.). Oxford: Academic Press.
- Guyomarch, C. & Guyomarch, J.C. (1995). Molting cycles in european quail (*Coturnix-coturnix coturnix*) under constant photoperiodic conditions. *Biol. Rhythm Res.* **26**, 292–305.
- Hall, T.R., Harvey, S. & Chadwick, A. (1986). Control of prolactin secretion in birds – a review. *Gen. Comp. Endocrinol.* **62**, 171–184.
- Hau, M., Wikelski, M., Gwinner, H. & Gwinner, E. (2004). Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. *Oikos* **106**, 489–500.
- Heimann, M. (2006). *Development and validation of the method of sublingual blood sampling in mice and other small rodents*. PhD thesis, University of Zurich.
- Jackson, C. & Bernard, R.T.F. (1999). Short day length alone does not inhibit spermatogenesis in the seasonally breeding four-striped field mouse (*Rhabdomys pumilio*). *Biol. Reprod.* **60**, 1320–1323.
- Jackson, C. & Bernard, R.T.F. (2005). Effects of supplementary food on the winter inhibition of reproduction in male and female four-striped field mice (*Rhabdomys pumilio*). *Reprod. Fertil. Dev.* **17**, 393–400.
- Johnston, J.D. (2004). Photoperiodic regulation of prolactin secretion: changes in intra-pituitary signalling and lactotroph heterogeneity. *J. Endocrinol.* **180**, 351–356.
- Lincoln, G.A., McNeilly, A.S. & Cameron, C.L. (1978). Effects of a sudden decrease or increase in daylength on prolactin secretion in ram. *J. Reprod. Fertil.* **52**, 305–311.
- Lincoln, G.A., Andersson, H. & Clarke, I.J. (2003). Prolactin cycles in sheep under constant photoperiod: evidence that photorefractoriness develops within the pituitary gland independently of the prolactin output signal. *Biol. Reprod.* **69**, 1416–1423.
- Nelson, R.J. (2005). *An introduction to behavioral endocrinology*. 3rd edn. Sunderland: Sinauer Associates, INC.
- Nelson, R.J., Gubernick, D.J. & Blom, J.M.C. (1995). Influence of photoperiod, green food, and water availability on reproduction in male california mice (*Peromyscus-californicus*). *Physiol. Behav.* **57**, 1175–1180.
- Nicholls, T.J., Goldsmith, A.R. & Dawson, A. (1984). Photorefractoriness in european starlings – associated hypothalamic changes and the involvement of thyroid-hormones and prolactin. *J. Exp. Zool.* **232**, 567–572.
- Nicholls, T.J., Goldsmith, A.R. & Dawson, A. (1988). Photorefractoriness in birds and comparison with mammals. *Physiol. Rev.* **68**, 133–176.
- Paul, M.J., Zucker, I. & Schwartz, W.J. (2008). Tracking the seasons: the internal calendars of vertebrates. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **363**, 341–361.
- Porlier, M., Charmantier, A., Bourgault, P., Perret, P., Blondel, J. & Garant, D. (2012). Variation in phenotypic plasticity and selection patterns in blue tit breeding time: between- and within-population comparisons. *J. Anim. Ecol.* **81**, 1041–1051.
- R Development Core Team (2012). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Robinson, J.E. & Follett, B.K. (1982). Photoperiodism in japanese quail – the termination of seasonal breeding by photorefractoriness. *Proc. R Soc. Ser. B-Bio.* **215**, 95–116.
- Schoepf, I. & Schradin, C. (2012). Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*). *J. Anim. Ecol.* **81**, 649–656.
- Schradin, C. (2005). When to live alone and when to live in groups: ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784). *Belg. J. Zool.* **135**, 77–82.
- Schradin, C. (2008). Differences in prolactin levels between three alternative male reproductive tactics in striped mice (*Rhabdomys pumilio*). *Proc. R Soc. Ser. B-Bio.* **275**, 1047.
- Schradin, C. & Anzenberger, G. (1999). Prolactin, the hormone of paternity. *News Physiol. Sci.* **14**, 223.
- Schradin, C. & Pillay, N. (2005). Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. *Mammal. Biol.* **70**, 84–92.
- Schradin, C. & Pillay, N. (2006). Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behav. Ecol.* **17**, 452–458.
- Schradin, C. & Yuen, C.-H. (2011). Hormone levels of male African striped mice change as they switch between alternative reproductive tactics. *Horm. Behav.* **60**, 676–680.
- Schradin, C., König, B. & Pillay, N. (2010). Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *J. Anim. Ecol.* **79**, 515–521.
- Schradin, C., Lindholm, A.K., Johannesen, J., Schoepf, I., Yuen, C.-H., König, B. & Pillay, N. (2012). Social

- flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Mol. Ecol.* **21**, 541–553.
- Sharp, P.J. (2005). Photoperiodic regulation of seasonal breeding in birds. In *Trends in comparative endocrinology and neurobiology*: 189. Vaudry, H., Roubos, E., Schoofs, L., Fiiik, G. & Larhammar, D. (Eds). New York Acad Sciences: New York.
- Sharp, P.J., Dawson, A. & Lea, R.W. (1998). Control of luteinizing hormone and prolactin secretion in birds. *Comp. Biochem. Physiol.* **119**, 275–282.
- Smale, L., Nelson, R.J. & Zucker, I. (1988). Daylength influences pelage and plasma prolactin concentrations but not reproduction in the prairie vole, *Microtus ochrogaster*. *J. Reprod. Fertil.* **83**, 99–106.
- Steger, R.W., Bartke, A., Goldman, B.D., Soares, M.J. & Talamantes, F. (1983). Effects of short photoperiod on the ability of golden hamster pituitaries to secrete prolactin and gonadotropins in vitro. *Biol. Reprod.* **29**, 872–878.
- Watts, H.E. & Hahn, T.P. (2012). Non-photoperiodic regulation of reproductive physiology in the flexibly breeding pine siskin (*Spinus pinus*). *Gen. Comp. Endocrinol.* **178**, 259–264.
- Werger, M.J.A. (1974). On concept and techniques applied in the Zürich-Montpellier method of vegetation survey. *Bothalia* **11**, 309–323.
- Wingfield, J.C. (2008). Organization of vertebrate annual cycles: implications for control mechanisms. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **363**, 425–441.