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Circadian rhythm of photosensitivity and the adaptation of reproductive function to the environment in two populations of *Arvicanthis niloticus* from Mali and Burkina Faso

B. Sicard*, D. Maurel‡, F. Fuminier* and J. Boissin

Laboratoire de Neurobiologie endocrinologique, URA CNRS 1197, Université de Montpellier II, Place Eugène Bataillon, F-34095 Montpellier Cedex 5, France

Summary. Previous studies have shown that there is a circadian rhythm of photosensitivity in different rodent species of the Sahel (Burkina Faso) and that, despite the low amplitude of seasonal variations in daylength, the photoperiod may control reproductive function. The present investigation of *Arvicanthis niloticus* provides additional support for this hypothesis. Populations of *Arvicanthis niloticus* from two regions at the same latitude 1000 km apart but with different climates were studied. Oursi, Burkina Faso, has an arid climate (annual rainfall 315 mm) and Kamalé, Mali has a wetter climate (annual rainfall 1114 mm). The circadian rhythm of photosensitivity had the same features in both populations, involving inhibition of testicular activity, but the photosensitive phase began 11 h 30 min after dawn in the population from Burkina Faso and 45 min later in that from Mali. Comparison of these results with the annual variation of daylength showed that the photoperiod inhibits the reproductive activity of *A. niloticus* from April to December in Burkina Faso and only from mid-May to mid-August in Mali. The population of *Arvicanthis niloticus* living in an environment with a large and seasonally stable food supply (Mali) thus has a longer reproductive period. This corroborates results from field studies on annual variations of population density.

Keywords: circadian rhythm; rodents; photosensitivity; testes; *Arvicanthis niloticus*

Introduction

Little is known about the environmental control of seasonal sexual cycles in rodents of hot desert regions (review in Bronson, 1989). Testicular endocrine activity has been studied in this respect only in the sand rat (*Psammomys obesus*) and desert gerbil (*Gerbillus gerbillus*). These studies show that in the sand rat the onset of testicular endocrine activity is concomitant with the highest temperature and decreasing daylength (summer) (Khammar & Brudieux, 1986), but with the lowest temperature and increasing daylength (winter) in the desert gerbil (Khammar & Brudieux, 1987). The existence of a circadian rhythm of photosensitivity implicating photoperiodism in the regulation of sexual activity has been demonstrated in six species of Sahelian rodents in northern Burkina Faso (Sicard *et al.*, 1988). The rapid multiplication of one of these species, *Arvicanthis niloticus*, always has dramatic economic effects because of crop damage. *Arvicanthis niloticus* has a circadian rhythm of photosensitivity: during the first phase light stimulates testicular activity and during the second phase the coincidence of daylength with the photosensitive phase has a gonadoinhibitory effect (Sicard *et al.*, 1988).

*Present address: Centre de Mammalogie, ORSTOM, Ouagadougou, Burkina Faso.
‡Reprint requests.

In view of the circadian rhythm of photosensitivity demonstrated in *A. niloticus* and the possible role it might play in the photoregulation of reproduction, we determined whether two populations of *A. niloticus* living more than 1000 km apart differed with regard to testicular photosensitivity. One population was from the region of Oursi (Burkina Faso) and the other was from the region of Kamalé (Mali). These two regions were selected because they have the same latitude but differ climatically owing to the eastward shift of the pluviometric and thermal equators. By studying populations living under different climatic conditions, we could examine the role of the circadian rhythm of photosensitivity in adapting reproduction to the correspondingly different seasonal variations of food supply in the two biotopes.

Materials and Methods

Animals

Arvicanthis niloticus were captured using traps (Chauvency, France, CNRS licence) with bait consisting of peanuts mixed with peanut butter in two geographically distinct regions of West Africa, namely the region of Oursi (14°N) in the Sahelian zone of Burkina Faso and the region of Kamalé (13°N) in the Sudanese zone of Mali. The animals were captured in November and December 1989. This period of the year corresponds to the seasonal resumption of sexual activity in this species as demonstrated in the male (testis weight and plasma testosterone concentration, Sicard *et al.*, in press). During the reproductive period, the male population is composed of 20% young, 10–30% subadults or sexually inactive adults and 50–70% sexually active adults. The last group, selected according to their body weight (> 80 g) and the scrotal position of the testis, were placed in individual cages upon arrival in the laboratory (Centre de Mammologie, ORSTOM, Ouagadougou, Burkina Faso). They were fed *ad libitum* with rodent granules and highly succulent cucumbers. The same number of animals (36) from Mali and Burkina Faso were subjected to experimental photoperiods corresponding to the circadian rhythm of photosensitivity (asymmetric skeleton photoperiods).

Climatic conditions

The two regions (Oursi, Burkina Faso and Kamalé, Mali) are characterized by a Sahelian climate (Table 1). In both regions, the mean monthly temperatures are quite similar with two annual maxima, in April–May and October. The mean monthly rainfall is always higher in Mali than in Burkina, and total annual rainfall is 1114 mm in Mali and 315 mm in Burkina. The rainy period is characterized by a mean monthly rainfall equal to or greater than 50 mm which permits the growth of the vegetation and lasts from May to October in Mali and from June to September in Burkina.

Table 1. Meteorological data recorded in Bamako (Mali) and Oursi (Burkina Faso). Means (with SEM) of monthly rainfall and temperature have been calculated according to studies of Moniod *et al.* (1977) and Brunet-Moret *et al.* (1986) for 15 years

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mali	Rainfall (mm)	1	0	4	15	68	146	234	338	213	65	10	0
	(SEM)	0·6	0	2·5	6	12	18	21	32	15	13	5	0
	Temperature (°C)	25·4	27·9	31·1	32·9	32·8	29·3	27·3	26·6	27	27·8	26·9	25·6
	(SEM)	3·7	3·9	3·7	3·8	3·6	3·1	2·9	3·0	2·8	3·1	3·0	2·9
Burkina	Rainfall (mm)	3	0	0	6	25	51	98	72	53	12	0	0
	(SEM)	1·9	0	0	2	12	11	15	13	9	7	0	0
	Temperature (°C)	25	28	31·4	34·5	35·5	33·3	30·7	29·3	30·3	32	29·2	26
	(SEM)	3·3	3·4	3·6	3·5	3·3	3·2	2·9	3·2	2·8	2·9	3·2	3·0

Experimental schedule

Animals were divided into six groups (groups 1–6) of 12 animals each (six from Burkina Faso, six from Mali) and subjected to the various experimental photoperiodic conditions described below. The total photoperiod was 8 h

light:16 h dark. The 8 h light period was divided into a main photofraction of 7 h 30 min and a secondary photofraction of 30 min interrupting the 16 h dark period at different times after the onset of the main photofraction: 9 h 45 min in group 1, 10 h 30 min in group 2, 11 h 15 min in group 3, 12 h 00 min in group 4, 12 h 45 min in group 5 and 13 h 30 min in group 6 (Fig. 1). Since the two regions are at approximately the same latitude, annual variations of daylength at Oursi (11 h 09 min–12 h 52 min) and at Kamalé (11 h 11 min–12 h 49 min) are nearly identical. The photoperiods used with groups 3, 4 and 5 were chosen to coincide with the minimal, mean and maximal daylengths at the capture site (Fig. 1). At the beginning of the experiment, all animals were subjected to cardiac puncture under equithesin anaesthesia (350 µl (100 g body weight)$^{-1}$). After 45 days, animals were subjected to the same puncture and killed. Plasma was stored at −25°C until assay.

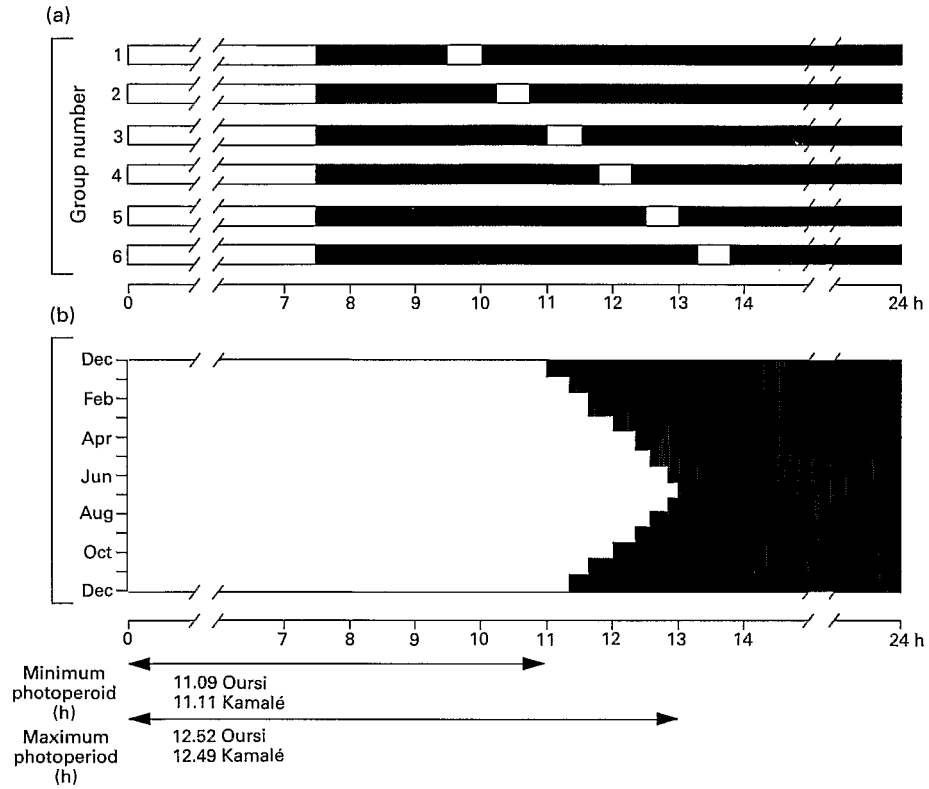

Fig. 1. (a) Experimental schedule of asymmetric photoperiods 8 h light:16 h dark applied to the six groups of *Arvicanthis niloticus*. The light phase consisted of a main photofraction of 7 h 30 min and a secondary photofraction of 30 min interrupting the 16 h dark period at different times after the onset of the main photofraction (group 1: 19 h 45 min; group 2: 10 h 30 min; group 3: 11 h 15 min; group 4: 12 h 00 min; group 5: 12 h 45 min; group 6: 13 h 30 min). The timing of secondary photofractions corresponds to the annual variations of light and dark phases at the latitude of the capture sites. (b) Annual variations of daylength at the latitude of the capture sites at Oursi (Burkina Faso) and Kamalé (Mali). (□) light, (■) dark.

Hormone assay

Plasma testosterone concentrations were determined by radioimmunoassay (RIA Kit, Biomérieux, France) according to a method previously used with other wild mammal species (Maurel *et al.*, 1981), and validated for this rodent. The results, corrected for recovery (consistently >90%), are expressed as ng or pg testosterone ml^{-1} plasma. Coefficients of variation within and between assays were 7·9 and 13·8%, respectively. Sensitivity, i.e. the smallest detectable quantity of hormone, was 8 pg of testosterone per tube. Different volumes of plasma (0·20, 0·25, 0·30, 0·35 and 0·50 ml) were assayed. The plotted values gave a straight line ($r = 0{\cdot}988$) fitted by the equation $y = 1{\cdot}58x \pm 0{\cdot}045$.

Statistical analysis

Results are expressed as means ± SEM and significance was calculated by ANOVA followed by Student's *t* test.

Results

Testosterone concentrations of plasma measured at the beginning of the experiment were 3·0 ± 0·1 ng ml^{-1} in the population from Burkina Faso and 390 ± 20 pg ml^{-1} in that from Mali (Fig. 2). After 45 days in the experimental photoperiod, no statistically significant variation of plasma testosterone levels was observed in groups 1, 2 or 3, either in animals from Mali (group 1: 379 ± 55 versus 451 ± 56 pg ml^{-1}; group 2: 429 ± 54 versus 454 ± 41 pg ml^{-1}; group 3: 390 ± 23 versus 429 ± 82 pg ml^{-1}) or from Burkina Faso (group 1: 3·0 ± 0·1 versus 3·4 ± 0·3 ng ml^{-1}; group 2: 3·0 ± 0·1 versus 3·3 ± 0·2 ng ml^{-1}; group 3: 3·1 ± 0·1 versus 3·4 ± 0·2 ng ml^{-1}). In contrast, a statistically significant decrease was observed in plasma testosterone levels of animals from Burkina Faso in group 4 (1·31 ± 0·22 versus 2·85 ± 0·1 ng ml^{-1}, $P < 0·001$), group 5 (0·28 ± 0·02 versus 3·25 ± 0·12 ng ml^{-1}, $P < 0·001$) and group 6 (0·29 ± 0·04 versus 3·20 ± 0·15 ng ml^{-1}, $P < 0·001$). Animals from Mali showed a comparable decrease only in group 5 (323 ± 24 versus 425 ± 35 pg ml^{-1}, $P < 0·05$) and group 6 (282 ± 7 versus 375 ± 21 pg ml^{-1}, $P < 0·01$).

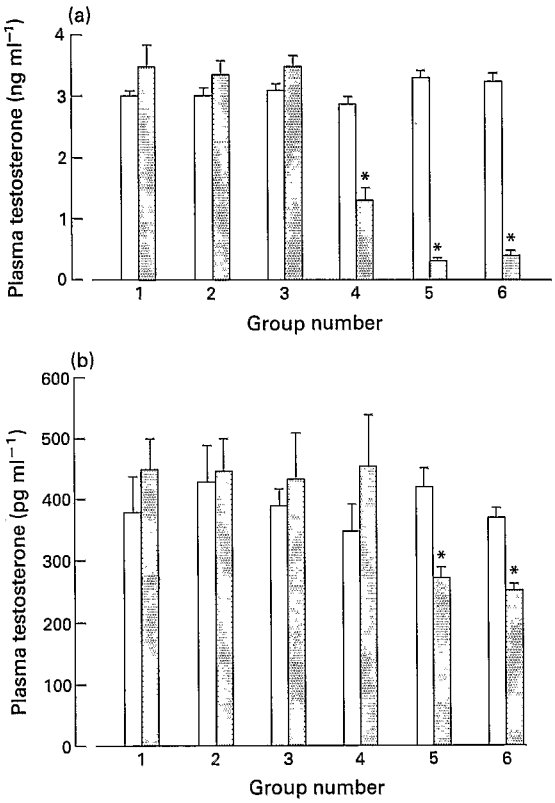

Fig. 2. Plasma testosterone (means ± SEM), in six groups of *Arvicanthis niloticus* from (a) Burkina Faso and (b) Mali, subjected to experimental photoperiods (see legend to Fig. 1). Asterisk indicates a statistically significant difference ($P < 0·01$) in the same group between the beginning (day 0 □) and the end (day 45 ▨) of the experiment.

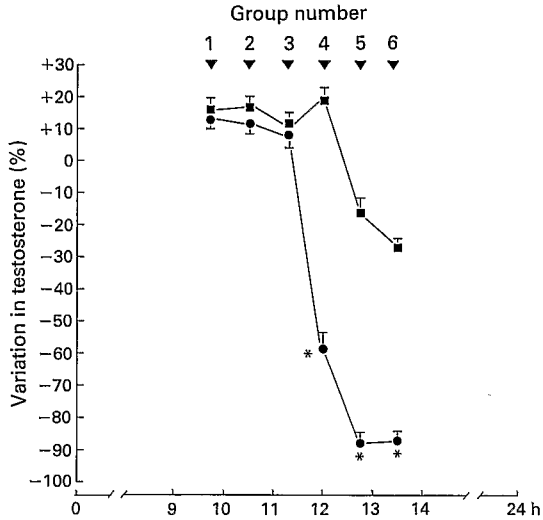

Fig. 3. Variation in plasma testosterone (between the beginning and the end of the experiment) measured in six groups of *Arvicanthis niloticus* from Mali (■) and Burkina Faso (●) subjected to experimental photoperiods (details in legend to Fig. 1). Asterisk indicates a statistically significant difference ($P < 0{\cdot}001$) in the same group between populations from the two regions.

The variation in testosterone concentration of plasma compared with initial values of animals from the same area (Mali or Burkina Faso) were similar in groups 1, 2 and 3, ranging from +10 to +15%. In group 4, the subgroup from Burkina Faso showed a clear decrease (−60%), whereas the subgroup from Mali showed an increase (+19%) comparable to that observed in the first three groups. Groups 5 and 6 showed decreases ranging from −20 to −30% in the Mali subgroup and close to −90% in the Burkina Faso subgroup.

Discussion

There were notable differences in plasma testosterone concentrations at the beginning of the experiment depending on the origin of the animals (Mali or Burkina Faso), although they were all in the sexually active phase (Sicard *et al.*, in press). The systematics of the *Arvicanthis* group are controversial; the 36 forms of *Arvicanthis* were assigned to six species by Allen (1939), and then to only four species according to Ellerman (1941). Dorst (1972) demonstrated that *A. blicki* is a separate species, whereas the successive studies of Rosevear (1969), Misonne (1971) and Corbet & Hill (1980) attribute the 36 forms of *Arvicanthis* to five species, one of which, *A. niloticus*, comprises 12 forms. Despite a slight difference in fur colour and greater aggression in the Burkina Faso form, the biometric analyses of Rousseau (1985) and the karyological analyses of Volobouev *et al.* (1988) have provided no evidence distinguishing two species, which might have explained the differences in plasma testosterone concentrations in these sexually active adults. In general, the mean concentrations of plasma testosterone are extremely variable even in closely related species of mammals (not taking into account the pulsatility that characterizes androgen secretion) with regard to the seasonal maxima measured during the period of full sexual activity. For instance, in the red fox (*Vulpes vulpes*) the maximum has been reported to be $1{\cdot}09 \pm 0{\cdot}37$ ng ml^{-1} (Joffre & Joffre, 1975) and $1{\cdot}36 \pm 0{\cdot}27$ ng ml^{-1} (Maurel & Boissin, 1981), whereas in the closely related species, the blue fox (*Alopex lagopus*), the seasonal maxima are higher, ranging from 5·3 to 12·2 ng ml^{-1} (Smith *et al.*, 1987). The white-tailed deer (*Odocoileus*

virginianus) is another example of intraspecific variation of plasma testosterone concentrations during full sexual activity. The levels in Minnesota populations (McMillin *et al.*, 1974) were found to be $2{\cdot}1 \pm 0{\cdot}5$ ng ml^{-1}, whereas they were 15 times higher (of the order of 30 ng ml^{-1}) in Virginia populations (Mirarchi *et al.*, 1977). Consequently, under the probable hypothesis that the *Arvicanthis* individuals studied here represent two populations of the same species, and considering that the populations are located in regions with very different climates (annual rainfall 315 mm in Oursi, 1114 mm in Kamalé), it is possible that the large variability of plasma testosterone concentrations is related to environmental characteristics. The existence of a seasonal sexual cycle characterized by a resumption from November onwards (testis weight and plasma testosterone concentration) has been demonstrated in this species (Sicard *et al.*, in press). So the difference in plasma testosterone concentration noticed between the two populations is not due to the difference in the sexual state of the animals.

Given the results previously obtained in various Sahelian rodent species that showed that a photoperiod of lower duration than the one measured could trigger the resumption of sexual activity (Sicard *et al.*, 1988) we chose a main photofraction the duration of which (7 h 30 min) is lower than the minimum photoperiod in the capture area (11 h 09 min).

The present study of differences in plasma testosterone concentrations depending on the timing of photofractions shows the existence, under experimental conditions, of a daily phase during which light has an inhibitory effect on testis function in *A. niloticus*. This phase occurred 11 h 30 min after the onset of the main photofraction in animals from Burkina Faso, and 45 min later (12 h 15 min after dawn) in those from Mali. We have previously demonstrated that the photoperiod has a stimulatory effect on the induction of sexual activity in other species of Sahelian rodents (Sicard *et al.*, 1988), whereas the present results confirm that the photoperiod has an inhibitory effect on testicular activity in *Arvicanthis*. The type of photoresponse observed in *Arvicanthis* from Mali and Burkina Faso is comparable to that described in the mink, *Mustela vison*, a short-day mammal in which photoinhibition prevents the induction of testicular activity before daylength becomes shorter than 10 h (Boissin-Agasse *et al.*, 1982; Boissin-Agasse & Boissin, 1985).

According to the model of external coincidence, which is generally used to explain the synchronization of sexual cycles by photoperiods, a photodependent response is induced when daylength coincides with the phase of endogenous photosensitivity (review in Boissin & Canguilhem, 1988). Application of this model to our results shows that the testicular activity of *Arvicanthis* is blocked when daylength exceeds 11 h 30 min in Burkina Faso populations and 12 h 15 min in Mali populations. Considering the annual variations of daylength at the latitude of the capture sites (Fig. 1), the testicular activity of *A. niloticus* is inhibited from April to December in Oursi (Burkina Faso) and from mid-May to mid-August in Kamalé (Mali). Assuming that the chain reaction beginning with the perception of the photoperiod and leading to inhibition of testis endocrine function requires 30 days to become fully effective (B. Sicard & F. Fuminier, unpublished data) and if the photoperiod is the main factor controlling reproduction, the periods of sexual activity would thus extend from the end of November to the end of April in *A. niloticus* from Burkina Faso and from mid-September to mid-June in those from Mali. This experimental photobiological evidence corroborates results obtained by studying population densities during reproductive cycles of this species in the natural environment (Sicard, 1987). The reproductive period of *Arvicanthis* populations living in an environment with an abundant and seasonally stable food supply (Mali) is three months longer than that of populations living in an environment whose food supply is less abundant and more variable over the year (Burkina Faso).

Thus, adaptation, by anticipation of the reproductive function, to different conditions of food supply has been achieved in *A. niloticus* by a 45-min shift in the circadian phase of photosensitivity. Apart from elucidating mechanisms regulating the timing of reproductive cycles in Sahelian rodents, the present results indicate that *Arvicanthis* is an excellent animal model for studying genetic adaptation of populations to environmental conditions owing to the endogenous nature of the circadian rhythm of photogonadosensitivity (Boissin & Canguilhem, 1988).

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