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Temperature and Water Conditions Mediate the Effects of Day Length on the Breeding Cycle of a Sahelian Rodent, *Arvicanthis niloticus*

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ABSTRACT

Laboratory studies of variations in testicular activity (testicular weight and plasma testosterone concentration) were carried out on two populations of *Arvicanthis niloticus*, a Sahelian rodent that displays the particularity of being able to breed in the dry season. The animals were captured during phases of sexual activity or inactivity and were maintained in the laboratory for 50 days under humid conditions (water-rich diet, 90% atmospheric relative humidity) or dry conditions (water-deficient diet, 20% atmospheric relative humidity) and at low temperatures (20–25°C) or high temperatures (30–35°C).

The results show that humid conditions or low temperatures stimulate testicular activity in *Arvicanthis niloticus* whereas dry conditions or high temperatures inhibit breeding. 1) Humid conditions coupled with low temperatures caused the most marked stimulation of testicular activity and maintained sexual activity at its highest level. 2) Humid conditions coupled with high temperatures, or dry conditions coupled with low temperatures, brought about mild sexual activity in animals that were sexually inactive and a regression of testicular weight and plasma testosterone in animals that were sexually active at the beginning of the experiment. In the latter, the results show that testicular activity was maintained and animals remained capable of breeding. 3) High temperatures and dry conditions inhibited short-day gonadal stimulation. On the other hand, in animals maintained under humid conditions or at low temperatures, gonadal stimulation occurred only under a short photoperiod. In animals captured in Burkina Faso, the gonado-facilitating effect of low temperature and humidity, observed in animals maintained on a short-day regimen (11L:13D), was considerably weaker in animals maintained on a long-day regimen (12.5L:11.5D).

The results are discussed in relation to the annual cycle of testicular activity in *Arvicanthis niloticus* living in natural habitats. These findings show that annual variations in day length play an important role in controlling testicular activity in this species but that ambient temperature and water conditions are also involved in controlling the length of the breeding period.

INTRODUCTION

It has long been thought that reproductive function in animal species living in dry intertropical regions is exclusively controlled by rainfall [1–3]. However, it has recently been shown that in 6 of 7 species of Sahelian rodents studied, seasonal variations in day length (though limited at a latitude of 14°N) are involved in the control of annual variations in testicular activity and that this phenomenon depends on a circadian cycle of photogonadosensitivity [4].

Among rodents whose breeding is controlled by seasonal variations in day length, one species—the Nile grass-rat (*Arvicanthis niloticus*), which inhabits humid areas in the region of Oursi (14°N, Burkina Faso)—can breed in the dry season and is thus an exception [5]. We have shown that in *A. niloticus* [6], the daily cycle of photosensitivity is characterized by a privileged phase. In animals captured in habitats with a Sahelian climate (Oursi, Burkina Faso) in which food supplies fluctuate with the seasons, this phase begins 11 h 30 min after dawn; in contrast, in animals from another African region with a Sahelian climate (Bamako, Mali) in which food supplies are constant throughout the year, the photosensitive phase starts 12 h 15 min after dawn. Thus in these two populations, one from Burkina Faso and the other from Mali, inhibition of gonadal activity was caused by day lengths of more than 11 h 30 min in one population and more than 12 h 15 min in the other. This phenomenon was observed as soon as light coincided with the photosensitive phase [4]. The fact that the photosensitive phase starts 12 h 15 min after dawn in the Malian population and 11 h 30 min after dawn in the Burkina Faso population allowed us to explain the earlier regression in the Malian population, which lives in a habitat with seasonally fluctuating food supplies [6, 7]. A study of seasonal variations in the immunoreactivity of LHRH fibers projecting into the external median eminence also showed that in Burkina Faso habitats under human influence (villages, nomad camps, intensively cultivated areas in wet locations), constant food supplies were capable of inducing—as in the case of Malian populations—more lasting stimulation of the LHRH hypothalamic system [8].

On the basis of the observation that in *Arvicanthis niloticus* food supplies are capable of modifying the characteristics of the photoperiodic control of breeding, we were led to consider the effect of two other environmental factors on the control of the cycle of testicular activity, i.e., temperature and water conditions. We studied the combined effects of these two factors (high or low temperatures, abundant or limited water conditions) on variations

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in testicular weight and plasma testosterone concentrations. The study was carried out on animals captured in sexually active or inactive phases and in habitats with seasonally constant (Mali) or fluctuating food supplies (Burkina Faso).

MATERIALS AND METHOD

Animals and Captures

Arvicanthis were captured in two types of habitat: the first having abundant and constant food supplies throughout the year (banks of the Niger around Bamako, 13°N, Mali; Sahelian climate) and the second having abundant but seasonally variable food supplies (fields of millet, sorghum, and clay lowlands around Oursi, 14°N, Burkina Faso; Sahelian climate). Animals captured in the stable habitat were bigger, darker, and less aggressive than those captured in fluctuating habitats. However, cytogenetic studies carried out by Volobouev et al. [9] have shown that both populations belong to the species *Arvicanthis niloticus* Thomas 1925.

The animals were captured through use of Chauvancy traps (CNRS license) baited with peanuts and peanut butter. Captured animals were weighed, sexed, and classified (juveniles, sub-adults, and adults) on the basis of their size and weight. Male sexual activity was assessed by testis size and position (scrotal or abdominal). The testes of sexually active males are in the scrotal position, and their development can be verified by palpation [7]. Trapping campaigns were carried out in August during the hot humid season (period 1, sexually inactive phase) and in December during the cold dry season (period 2, sexually active phase) [7].

Experimental Protocol

Immediately after their arrival in the laboratory, the animals (n = 145) were classified into three main divisions (Fig. 1). The animals captured in Mali were all maintained on a short-day regimen, 11L:13D. Animals captured in Burkina Faso habitats with seasonally fluctuating food supplies formed the other two divisions. Animals in one division were maintained on a short-day regimen (11L:13D) and the others on a long-day regime (12.5L:11.5D). This subdivision was carried out for the following reason. An outbreak of *A. niloticus* that occurred in Burkina Faso in 1986 [7] resulted from a lengthening of the breeding period, i.e., the population continued to breed throughout the year during both short-day and long-day periods. Thus in an attempt to explain this reproductive phenomenon, we decided to maintain the animals from Burkina Faso (and only these animals) in two different photoperiods that occur naturally at the latitude where the animals were captured, i.e., a short photoperiod of 11L:13D and a long photoperiod of 12.5L:11.5D.

In each of the three divisions, animals were maintained under two types of water conditions and two different temperatures for a period of 50 days. To simulate the rainy season, the animals were placed in special cages with a double enclosure [10] that allowed the maintenance of constant high relative humidity (70–90%), and water-rich food (cucumber) was supplied ad libitum. To simulate the dry season, the animals were maintained in open enclosures with a relative humidity of no more than 20%, and water-rich food was rationed (5 g per animal). Both types of cages were placed in temperature-controlled rooms (low temperatures, 20–25°C; high temperatures, 30–35°C).

The following treatment numbering system was used to distinguish the four possible combinations of the two types of water conditions and temperatures: group 1, humid conditions and low temperature; group 2, humid conditions and high temperature; group 3, dry conditions and low temperature; group 4, dry conditions and high temperature. Within each group there were two subgroups: I (animals captured during the sexually inactive phase) and A (animals captured during the sexually active phase).

At the beginning of the experiment, 5 individuals chosen at random from each group (control I and control A) were killed. After 50 experimental days, all animals in all groups were killed. Autopsies were performed between 0900 h and 1500 h, and the testicles were removed and weighed. Testicular weight is expressed in mg/100 g of body weight (mg/100 g BW). Blood samples were stored at −20°C until analysis.

Hormone Assay and Statistical Analysis

Plasma testosterone concentrations were determined by RIA (RIA Kit, Biomérieux, Craponne, France) according to a method previously used with other wild mammal species [11] and validated for this rodent. The results, corrected for recovery (consistently > 90%), are expressed as ng or pg testosterone/ml of plasma. Coefficients of variation within and among assays were 7.8 and 14.3%, respectively. Sensitivity, i.e., the smallest detectable quantity of hormone, was 7.5 pg testosterone/tube. Different volumes of plasma (0.20, 0.25, 0.30, 0.35, and 0.50 ml) were assayed. The plotted values form a straight line ($r = 0.994$) fitted by the equation $y = 1.49x + 0.046$. All results are expressed as means ± SEM, and significance was calculated by ANOVA followed by Student's *t*-test.

RESULTS

Arvicanthis Captured in Habitats with Stable Food Supplies (Mali)

Testicular weight (WT) and plasma testosterone concentrations (T) measured at the beginning of the experiment were significantly lower ($p < 0.001$) in animals captured during the sexually inactive phase (control I) than in those captured during the breeding period (control A). After 50 days of maintenance in humid conditions and low temper-

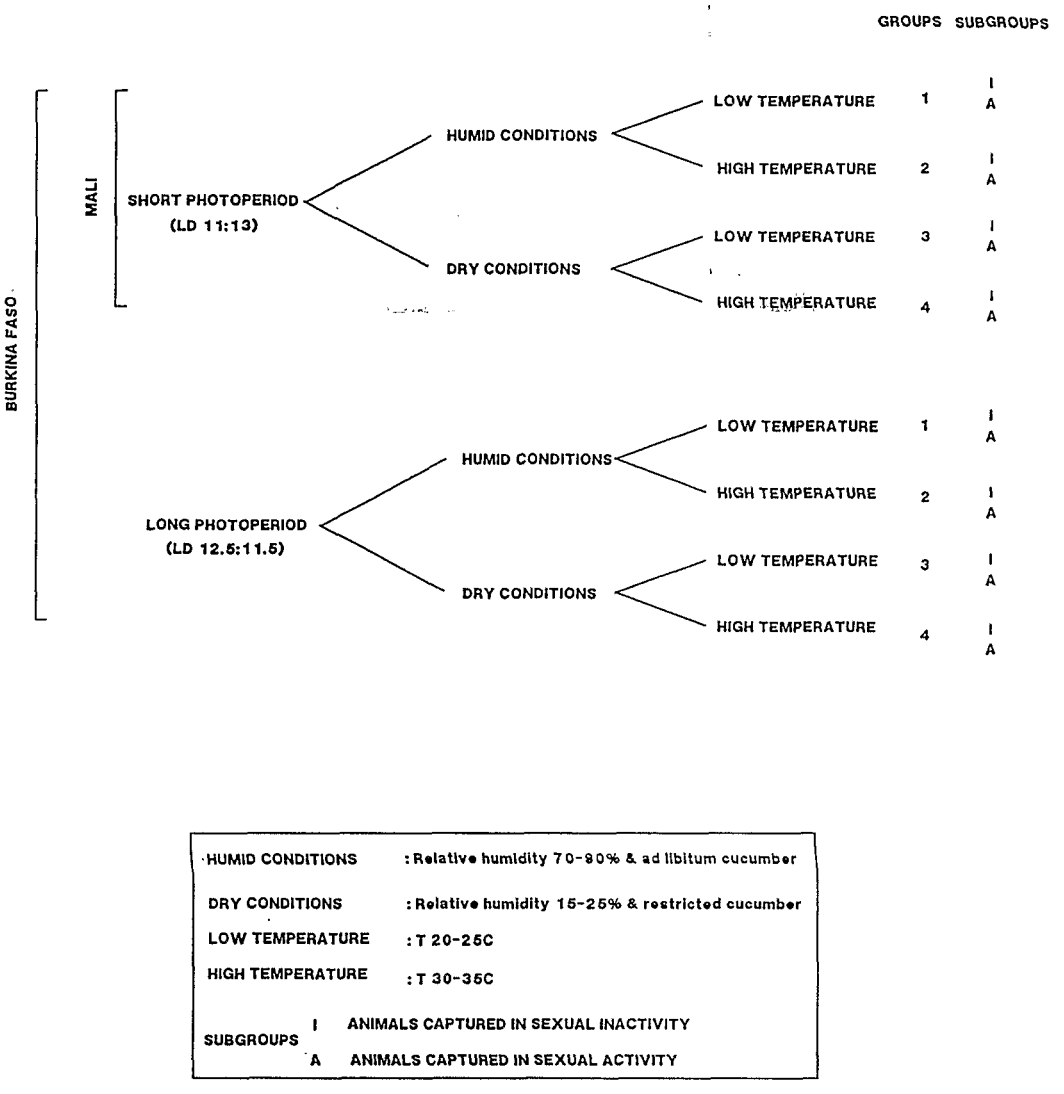

FIG. 1. Experimental protocol. Animals were captured in Malian habitats, which have constant food supplies throughout the year, and in Burkina Faso habitats, where food supplies are seasonal. Adult males captured in August were sexually inactive (subgroup I), whereas animals captured in December were sexually active (subgroup A). At the beginning of the experiment, five animals selected at random in each of the subgroups were killed to serve as controls (control I and control A). The other animals were maintained for 50 days in a controlled experimental environment (humid or dry conditions, high or low temperatures). *Arvicanthis niloticus* from Mali were maintained under a photoperiod of 11L:13D. Those from Burkina Faso were maintained under photoperiods of 11L:13D or 12.5L:11.5D. After 50 days, all animals in all groups were killed.

atures, the WT and T of initially sexually inactive animals (group 1I) were comparable to those of initially sexually active animals (group 1A). Values measured after this marked increase were identical to those measured in the sexually active controls killed at the beginning of the experiment (control A).

After 50 days of maintenance in humid conditions and high temperatures (groups 2I and 2A) or in dry conditions and low temperatures (groups 3I and 3A), the WT and T of animals captured during the sexually inactive phase (group 2I and 3I) were identical to those of initially sexually active animals (group 2A and 3A). These values were significantly lower ($p < 0.01$) than those of sexually active controls (control A) and significantly higher ($p < 0.05$) than those of sexually inactive controls (control I).

Finally, after 50 days of maintenance in dry conditions and high temperatures, the WT and T of animals captured during the sexually inactive phase (group 4I) were identical to those of animals captured during the sexually active phase (group 4A). They were comparable to those of animals in a sexually inactive phase at the beginning of the experiment (control I).

These results are summarized in Figure 2. It appears that in *A. niloticus* captured in Mali, the combined effects of

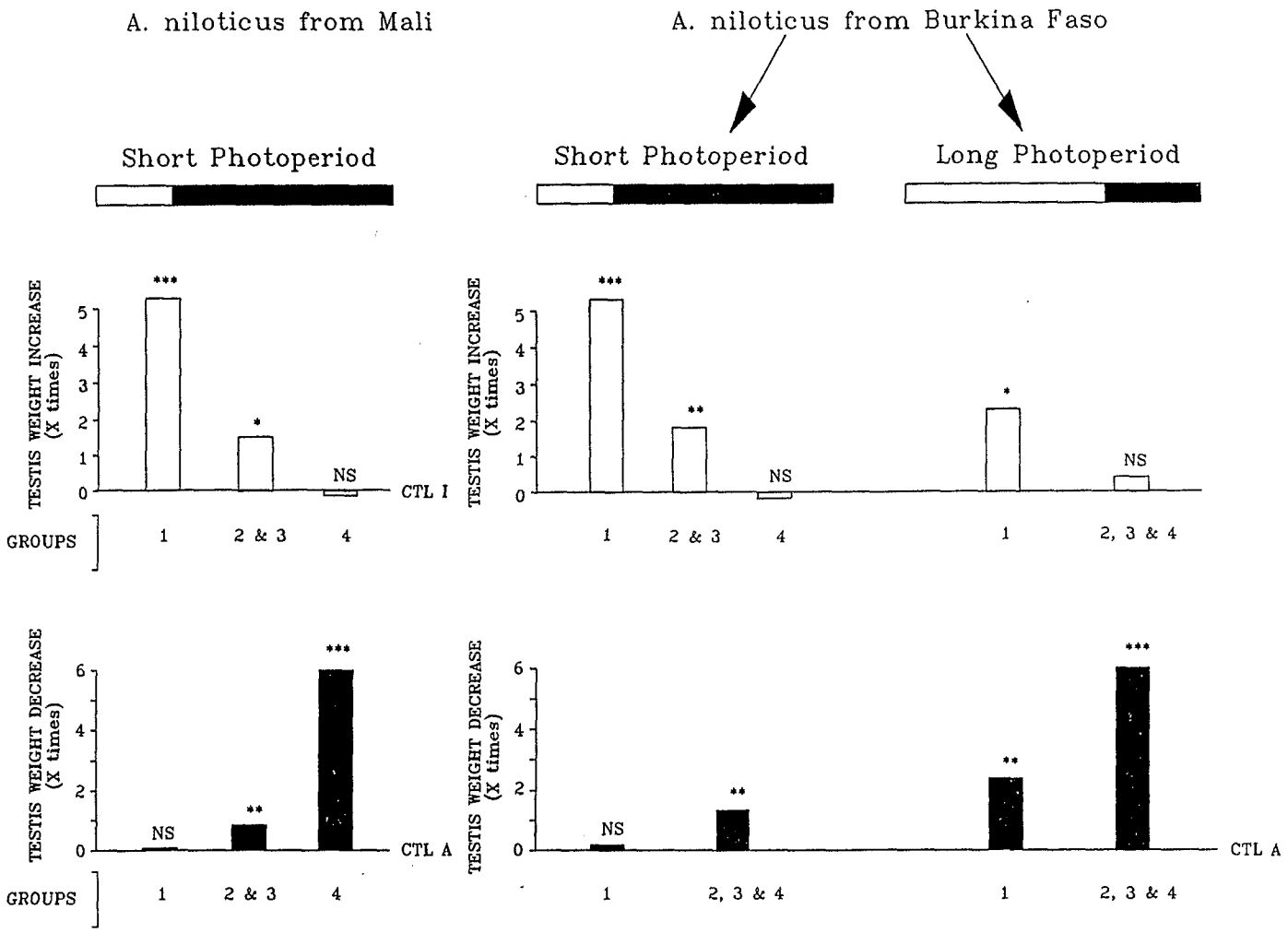

FIG. 2. Rate of testis weight variation in *Arvicanthis niloticus* after animals were maintained for 50 days under different experimental conditions. Three overall divisions of individuals were distinguished: 1) individuals captured in Mali and maintained under short days (11L:13D); 2) those captured in Burkina Faso and maintained under short days (11L:13D); 3) those captured in Burkina Faso and maintained under long days (12.5L:11.5D). Each division comprised four groups maintained under different temperature and water conditions: group 1, humid conditions and low temperatures; group 2, humid conditions and high temperatures; group 3, dry conditions and low temperatures; and group 4, dry conditions and high temperatures. Individuals in each group were classified into two subgroups depending on whether they were captured in their natural habitat during the phase of sexual inactivity (subgroup I) or of sexual activity (subgroup A). In each subgroup, the growth rates and rates of testicular weight decrease were calculated with reference to initial data obtained from sexually inactive or active controls. Subgroups with equivalent responses were distinguished. NS: nonsignificant; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

high or low temperatures with humid or dry conditions induced changes in testicular activity as follows. 1) Low temperatures associated with humid conditions resulted in a marked increase in the testicular activity of initially sexually inactive animals (group 1I) and did not affect the testicular activity of animals that were sexually active at the beginning of the experiment (group 1A). 2) High temperatures associated with humid conditions caused a moderate renewal of sexual activity in animals captured during the sexually inactive phase (group 2I) and a moderate regression in the testicular activity of animals already sexually active (group 2A). 3) Similar results were obtained in animals captured during phases of sexual inactivity or activity and maintained at low temperatures with dry conditions (groups 3I and 3A). 4) High temperatures associated with dry conditions did not stimulate testicular activity in initially sexually inactive animals (group 4I) and caused a marked regression in initially sexually active animals (group 4A).

Arvicanthis Captured in Habitats with Seasonally Fluctuating Food Supplies (Burkina Faso)

In this population, as in the population captured in Mali, WT and T at the beginning of the experiment were significantly lower ($p < 0.001$) in animals captured during the sexually inactive phase (control I) than in animals captured during the breeding period (control A).

Short photoperiod (Table II). After 50 days of maintenance under a short photoperiod with humid conditions

TABLE 1. Combined effects of temperature and water conditions on testicular activity in *Arvicanthis niloticus* captured in Mali and maintained under short days (11L:13D).*

Testicular activity	Initial state	Controls	Group 1	Group 2	Group 3	Group 4
WT (mg/100 g BW)	I	391 ± 70	2515 ± 310	1106 ± 170	923 ± 223	424 ± 83
	A	2487 ± 340	2356 ± 215	1348 ± 188	1120 ± 175	347 ± 72
T (pg/ml)	I	322 ± 23	762 ± 136	446 ± 31	457 ± 50	296 ± 40
	A	735 ± 83	730 ± 40	508 ± 35	510 ± 95	250 ± 80

*WT and T were measured at the beginning of the experiment (controls) in animals that were initially sexually inactive (subgroup I) or sexually active (subgroup A), and after 50 days during which the animals were reared under different experimental conditions (group 1: humid conditions and low temperatures; group 2: humid conditions and high temperatures; group 3: dry conditions and low temperatures; group 4: dry conditions and high temperatures).

and low temperatures, the WT and T of animals that were sexually inactive at the beginning of the experiment (group 1I) were not different from those of animals that were initially sexually active (group 1A); these values were comparable to those for controls that were sexually active at the beginning of the experiment (control I).

After 50 days of maintenance in humid conditions and high temperatures, the WT and T of animals captured during the sexually inactive phase (group 2I) were identical to those of animals initially sexually active (group 2A). These values are significantly lower ($p < 0.01$) than those of controls captured during the sexually active phase (control A), and significantly higher ($p < 0.01$) than those of initially sexual inactive controls (control I).

After 50 days of maintenance in dry conditions and low temperatures, the WT and T of initially sexually inactive animals (group 3I) were significantly lower ($p < 0.05$) than those measured in initially sexually active animals (group 3A). The values for groups 3A, 2I, and 2A were identical, and those for group 3I were significantly higher ($p < 0.05$), than those for sexually inactive controls (control I).

After 50 days of maintenance in dry conditions and high temperatures, the WT and T of animals captured during the sexually inactive phase (group 4I) were significantly lower ($p < 0.01$) than those of animals sexually active at the beginning of the experiment (group 4A), and were comparable to those of sexually inactive controls (control I). Nevertheless, the treatment caused a regression of testicular activity (group 4A vs. control A).

Long photoperiod (Table III). After 50 days of maintenance under a photoperiod of 12.5L:13.5D in humid conditions coupled with low temperatures, the WT and T of initially sexually inactive animals (group 1I) were comparable to those of initially sexually active animals (group 1A). These values were significantly lower ($p < 0.001$) than those of sexually active controls (control A), but significantly higher ($p < 0.05$) than those of sexually inactive controls (control I).

In animals maintained in humid conditions and high temperatures (group 2), or in dry conditions and low (group 3) or high temperatures (group 4), the WT and T of initially sexually inactive animals (groups 2I, 3I, 4I) or initially sexually active animals (groups 2A, 3A, 4A) were all comparable. They were identical to those measured in sexually inactive controls (control I) and significantly lower ($p < 0.01$) than in initially sexually active controls (control A).

Thus, in *A. niloticus* captured in Burkina Faso, the combined effects of low or high temperatures, humid or dry conditions, and short or long photoperiods on testicular activity can be summarized as follows. 1) Under the short photoperiod, low temperatures and humid conditions induced testicular activity in animals captured during the sexually inactive phase (Fig. 2B, group 1I); this environment maintained testicular activity in animals captured during the sexually active phase (Fig. 2B, group 1A). Under the long photoperiod, with the same temperature and water conditions, the stimulation of testicular activity was weaker (group 1I in Fig. 2C vs. group 1I in Fig. 2B) and testicular regression was more marked (group 1A in Fig. 2C vs. group 1A in Fig. 2B). 2) Under the short photoperiod, with high temperatures and humid conditions or with low temperatures and dry conditions, testicular activity was induced in

TABLE 2. Combined effects of temperature and water conditions on testicular activity in *Arvicanthis niloticus* captured in Burkina Faso and maintained under short days (11L:13D).*

Testicular activity	Initial state	Controls	Group 1	Group 2	Group 3	Group 4
WT (mg/100 g BW)	I	371 ± 120	2381 ± 383	1276 ± 183	791 ± 117	311 ± 70
	A	2420 ± 320	2367 ± 310	1237 ± 150	1240 ± 175	937 ± 140
T (ng/ml)	I	0.5 ± 0.1	2.4 ± 0.4	1.3 ± 0.2	0.9 ± 0.1	0.5 ± 0.1
	A	3.0 ± 0.3	2.5 ± 0.5	1.5 ± 0.2	1.4 ± 0.1	1.4 ± 0.5

*WT and T were measured at the beginning of the experiment (controls) in animals that were initially sexually inactive (subgroup I) or sexually active (subgroup A), and after 50 days during which the animals were reared under different experimental conditions (see *legend* of Table 1).

TABLE 3. Combined effects of temperature and water conditions on testicular activity in *Arvicanthis niloticus* captured in Burkina Faso and maintained under long days (12.5L:11.5D).*

Testicular activity	Initial state	Controls	Group 1	Group 2	Group 3	Group 4
WT (mg/100 g BW)	I	371 ± 120	1187 ± 263	654 ± 150	603 ± 99	341 ± 63
	A	2420 ± 320	1050 ± 225	707 ± 180	430 ± 171	420 ± 115
T (ng/ml)	I	0.5 ± 0.1	1.5 ± 0.2	0.8 ± 0.2	0.7 ± 0.1	0.5 ± 0.1
	A	3.0 ± 0.3	1.3 ± 0.2	0.9 ± 0.1	0.8 ± 0.2	0.5 ± 0.2

*WT and T were measured at the beginning of the experiment (controls) in animals that were initially sexually inactive (subgroup I) or sexually active (subgroup A), and after 50 days during which the animals were reared under different experimental conditions (see *legend* of Table 1).

animals captured during the sexually inactive phase (Fig. 2B, groups 2I and 3I) but was less marked than in group 1I. In animals that were sexually active at the beginning of the experiment these conditions induced greater regression (Fig. 2B, group 2A and 3A vs. group 1A). The long photoperiod reduced the stimulation observed in animals of groups 2I and 3I and increased the regression observed in groups 2A and 3A. 3) In animals maintained at high temperatures under dry conditions, and under short or long photoperiods, no stimulation was observed in individuals that were initially sexually inactive (group 4I in Fig. 2, B and C), and the largest decrease in testicular activity was observed in individuals that were initially sexually active (group 4A in Fig. 2, B and C).

DISCUSSION

These data confirm previous results showing that in *A. niloticus* the length of the photoperiod controls the regression of testicular activity [4, 6], i.e., long photoperiods inhibit testicular activity. Thus, *A. niloticus* appears to display a photosensitivity similar to that described in "short day" mammals in temperate climates [12]. These results also show that temperature and water conditions can modify the photoperiodic control of sexual activity. In both populations of rodents, experimental conditions that combined low temperatures and abundant water conditions clearly resulted in the most marked stimulation of testicular activity. The same conditions resulted in the highest continuing level of sexual activity. Nevertheless, the facilitating effect of a cool, humid environment was maximal only in the short photoperiod, as shown by the results obtained in animals captured in Burkina Faso and maintained in photoperiods of 11L:13D and 12.5L:11.5D. These results also show that experimental conditions combining high temperatures and dry conditions inhibited the gonadal stimulation observed during the short photoperiod. Results obtained in other experimental groups of animals from both Mali and Burkina Faso tend to show that the inhibition caused by a hot and water-deficient environment is the result of the combined effects of high temperature and dry conditions. The inhibiting effect of high temperatures in *Arvicanthis* has already been suggested by Neal [13], who observed in this species at latitude 0°11'N (Meru National Park, Kenya) that the end of seasonal reproduction coincided with maximal annual temperatures (end of the dry season). In many rodent species in temperate regions, it has been shown that the autumn drop in temperature potentiates the gonadal inhibition induced by short days [14]; but at low altitudes, Ghobrial and Hodieb [15] have reported that low temperatures facilitate the induction of *Arvicanthis* breeding.

The results of our study show that humid conditions or low temperatures have a gonado-facilitating effect, whereas dry conditions or high temperatures have a gonado-inhibiting effect. In cases where experimental conditions combined the effects of humid conditions (gonado-facilitating factor) and high temperatures (gonado-inhibiting factor) or combined the effects of dry conditions (gonado-inhibiting factor) and low temperatures (gonado-facilitating factor), the effects obtained were comparable. In both cases, after 50 days of exposure to these conditions, a slight stimulation of sexual activity was observed in initially sexually inactive animals; and although the treatment resulted in decreased TW (900–1400 mg/100 g BW) and T in animals that were sexually active at the beginning of the experiment, the values nevertheless provide evidence that testicular activity was maintained and allowed the animals to continue breeding. Field observations [7] showed that the presence in a given environment of *A. niloticus* males with a TW of 900 mg/100 g BW is a good indication that the population is breeding, since pregnant females and juveniles were captured at the same time. Nevertheless it should be stressed that the gonadal stimulation observed in animals maintained in either humid conditions or low temperatures occurred only under the short photoperiod. This fact was confirmed in animals captured in Burkina Faso, since gonadal activity was stimulated only in those maintained under the photoperiod of 11L:13D whereas it was inhibited under the 12.5L:11.5D photoperiod.

These results can be used to explain the ecoregulation of the annual cycle of testicular activity in *A. niloticus*. In Mali and Burkina Faso, field observations have shown that breeding starts at the beginning of the cold rainy season (October) when day length is reduced to 11 h 30 min. On the other hand, testicular regression occurs when day length reaches more than 11 h 30 min in Burkina Faso and more than 12 h 15 min in Mali. In Burkina Faso, testicular activity

remains intense throughout the cold dry season (beginning of December to the end of January) and continues at the same level during the first part of the hot dry season, due to the advantageous feeding habits of this species (consumption of insects and of the bark of *Acacia seyal*, which has a high water content) [7, 16]. Testicular activity subsequently regresses due to the combined effects of the long photoperiod, high temperatures, and drought. In Mali, sexual activity continues throughout the hot dry season (beginning of February until the end of May); then testicular activity regresses during the hot rainy season (end of June, beginning of July) when day length is more than 12 h 15 min [6, 7].

It is more difficult to explain the continuation of testicular activity during the hot dry season in animals living in Malian habitats where food supplies are abundant throughout the year. It can nevertheless be noted that during the hot dry season, day length does not inhibit gonadal activity, since it is still less than 12 h 15 min [6]. In addition, the availability of water-rich food in habitats with constant food supplies throughout the year must allow *Arvicanthis niloticus* to maintain its water balance. Ghobrial and Hodieb [15] have previously proposed that water-rich food may have a facilitating effect on breeding in this species. It has been shown in many other African rodents that breeding patterns are related to the rainfall cycle [4, 17]. Investigators have shown that the rodent reproductive response to rainfall may be related to an increased water intake [18, 19] or to variations in the quality or quantity of available food [20, 21]. It should also be noted that an abundant water supply has been found [22] to be a prerequisite for successful breeding in another Sahelian rodent, *Taterillus petteri*, living in the same region but in a more arid habitat.

It would thus appear that although annual variations in day length control the annual cycle of testicular activity in intertropical regions, it is also true that in *Arvicanthis niloticus*, temperature and water conditions are involved in controlling the length of the breeding period. These two environmental factors, which vary in intensity from one year to another, are thus likely to be involved in causing outbreaks of this species in certain years.

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