

THE REGULATION OF THE REPRODUCTIVE CYCLE  
IN *PODARCIS S. SICULA* RAF. (REPTILIA LACERTIDAE):  
INFLUENCE OF THE REFRACTORY PERIOD  
ON THE SPRINGTIME TESTICULAR ACTIVITY \*

F. ANGELINI, V. BOTTE and R. BOSCHI

Istituto di Istologia ed Embriologia dell'Università di Napoli  
Istituto e Museo di Zoologia dell'Università di Napoli

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In lizards living in temperate regions, the reproductive cycle is controlled by a continuous interaction between an « endogenous rhythm », environmental temperature and photoperiod (see FISCHER, 1968a, 1968b, 1968c, 1969, 1970a, 1970b, 1970c, 1974; ANGELINI & GALGANO, 1969; LICHT et al., 1969; LICHT, 1971, 1972a, 1972b; ANGELINI et al., 1975, 1976a).

Between mid to late summer and late autumn, a *refractory period*, linked to the « endogenous rhythm » intervenes. During this period, the gonad becomes refractory to the stimulating effects of high temperatures, and these are no longer able to support complete spermatogenic activity in the male, vitellogenetic processes in the female and gonadal endocrine activity in both sexes (LICHT et al., 1969; FISCHER & EWALD, 1972; ANGELINI et al., 1975, 1976a, 1976b; BOTTE et al., 1978). The refractory period, which naturally disappears in late autumn (Fig. 1), is physiologically important for the prevention of reproduction in the months immediately preceding the cold season, when embryo development and the survival of new-born lizards would be difficult. The duration of the refractory period can be modified, within certain limits, by manipulation of environmental temperature and photoperiod (LICHT et al., 1969; FISCHER, 1974; ANGELINI et al., 1975, 1976b). Moreover, recent studies have shown that in female *Podarcis s. sicula* Raf., from the middle of the refractory period (September), constant relatively high temperatures can prolong gonadal insensitivity to thermal stimuli for many months, so

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as to completely inhibit ovarian development in the next spring (ANGELINI et al., 1978a; BOTTE et al., 1978).

This last phenomenon suggests the possibility of a mechanism which synchronizes the whole reproductive cycle during the refractory period. Refractoriness might have the function of « programming » the following springtime cycle, and thus its physiological importance would go beyond the simple inhibition of the reproductive processes during autumn.

In order to verify this hypothesis we have examined the effects of photo-thermal manipulation, for varying periods from September, on the behaviour of the gonad in the following months and, above all, during the normal reproductive season.

### MATERIALS AND METHODS

Adult specimens of *Podarcis s. sicula* Raf. (Reptilia Lacertidae), captured in the neighbourhood of Naples (Acerra) towards mid-September, were transferred, after some days of acclimatization, into temperature and humidity controlled terraria, where it was possible to control the photoperiod. A total of 20 male and female lizards were kept in each terrarium. They were fed on larvae of *Tenebrio molitor* L. and *Sarcophaga carnaria* L., supplemented with fresh vegetables, *ad libitum*. The mortality rate was very low, except for some cases hereinafter reported.

At various times after the beginning of the treatment, 4-5 males and as many females were sacrificed. The animals were weighed, their gonads removed and weighed.

The gonads were then prepared for histology by fixation in Stieve's fluid. The epididymes were removed from the males and the development of the femorale pores checked. The oviducts were removed from the females.

The various experimental treatments are summarized in Table 1. In short-term experiments (21 and 41 days), at the end of the treatment the lizards were transferred to normal environmental conditions, where they were kept until the following reproductive season.

In this paper, we report the results obtained with the males. Those concerning females were reported in a different paper (Botte et al., 1978).

Spermatogenic activity was evaluated on the basis of a detailed histological study of the different stages of the germ cells present in the seminiferous tubules, according to methods previously reported by other authors (GÀLGANO & D'AMORE, 1954; ANGELINI & PICARIELLO, 1975), who have studied for years the development of the natural spermatogenic cycle in *Podarcis s. sicula* Raf., living in the neighbourhood of Naples.

In the present paper, changes in the gonadal weight as an index of spermatogenic activity (gonosomatic index) have not been considered. In fact, an effective correlation between increase in weight and a more active spermatogenesis was observed only in some cases (multiplication of spermatogonia and increase in primary spermatocytes).

### RESULTS

*Controls.* In the males of this group there was a normal recrudescence of spermatogenesis between the second 10 days of March and the end of April (Fig. 1), when spermiohistogenesis and spermiation had become

Table 1.

*Experimental maintenance conditions of adult specimens of Podarcis s. sicula Raf.*

No. of animals	♀ ♀	♂ ♂	Beginning of experiments	Length of treatment	Thermal regime*	Photoperiod**
40	20	20	Sept. 24	21 days	28 °C const.	dark
40	20	20	»	»	»	short
40	20	20	»	»	»	long
40	20	20	»	41 days	»	dark
40	20	20	»	»	»	short
40	20	20	»	»	»	long
40	20	20	»	10 months	»	dark
40	20	20	»	»	»	short
40	20	20	»	»	»	long
40	20	20	»	10 months	28 °C fluct.	dark
40	20	20	»	»	»	short
40	20	20	»	»	»	long
40	20	20	»	41 days	ambient	dark
40	20	20	»	»	»	short
40	20	20	»	»	»	long
40***	20	20	»	10 months	»	ambient

\* The thermal regimes were: 28 °C *const.* = constant temperature of 28 °C  $\pm$  1; 28 °C *fluct.* = 28 °C from 7 to 17 hr and environmental temperature for the remainder of the day; *ambient* = environmental temperature of the terraria, practically corresponding to the natural one.

\*\* The photoperiods were, *dark* = the terraria were lighted for 15 min at noon for cleaning and feeding; *short* = 8 hours' lighting from 8 to 16; *long* = 16 hours' lighting from 4 to 20; *ambient* = natural lighting.

\*\*\* These lizards represent the controls. The pattern of their cycle was periodically compared with that of lizards living in the field. No remarkable differences have been observed, even if springtime spermatogenesis was a little more active in the animals living in the field.

intense. The gonad remained active up to mid-late July, when the summer crisis rapidly occurred with the maximum degeneration of many germ cells, except for primary spermatogonia and Sertoli cells.

The epididymal cycle showed no difference with that observed in nature. The epididymis attained maturity in the 1st week of April and was active until mid-late July.

*Animals kept at a constant temperature of 28 °C, with different photoperiods, for 21 days.* The results of these treatments are summarized in Fig. 2. Only the animals kept in the dark (LD : 0-24) or with a long photoperiod (LD : 16-8) survived until the following summer. In treatments with a short photoperiod (LD : 8-16), the animals inexplicably

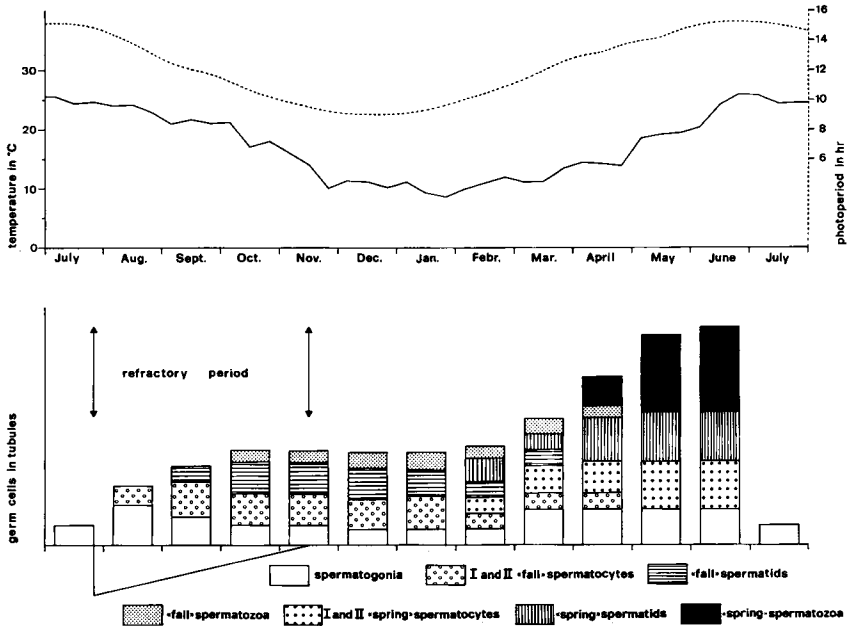
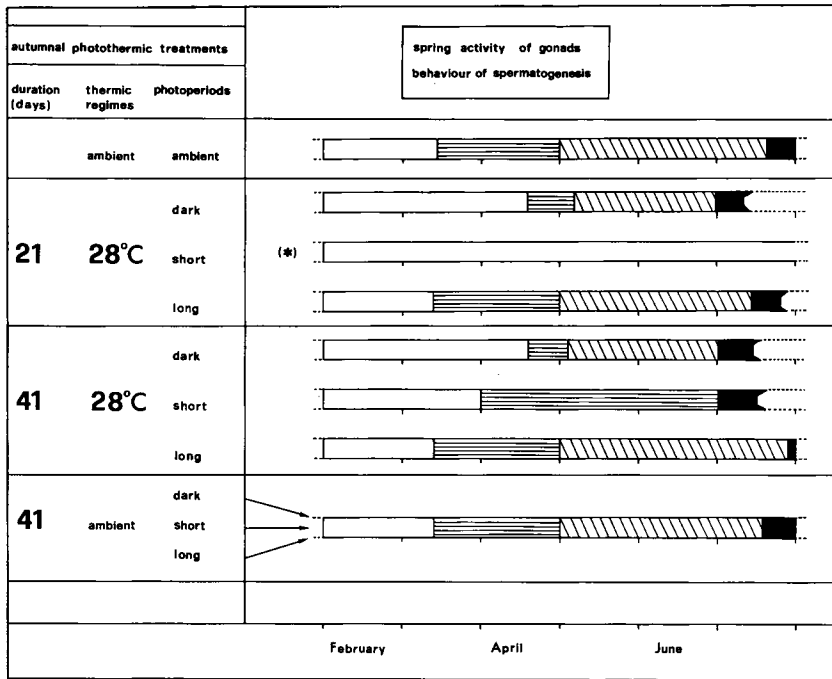


Fig. 1. — The upper half of the figure shows the annual pattern of environmental temperature (continuous line) and day length (hours of light: dotted line) in the area from which the animals were collected. The lower half of the figure depicts the differential behaviour of spermatogenic cell types during the year. The refractory period is shown by a triangular area (in the lower left hand border) which indicates that the highest intensity of this period occurs in late July and diminishes gradually, ending in November.

died before the following spring, without showing any recrudescence of the gonads in the few specimens surviving.

At the end of the 21 days, when the animals were to be transferred to environmental conditions, a slight stimulation of the first stages of spermatogenesis was observed in the testis, accompanied by degeneration of some spermatids and secondary spermatocytes. These degenerative phenomena were more evident with short photoperiod, a little less marked with the long one, whereas total darkness somewhat limited them (ANGELINI, in preparation).

In the spring, recrudescence of the gonads took place at the same time as in the controls with a long photoperiod, some weeks later in the dark (late April). In both cases the intensity of spermatogenesis did not markedly differ from that of the controls. Some degenerative phenom-



stasis      recrudescence      full activity      crisis

Fig. 2. — A schematic representation of the effects of autumnal photo-thermal treatments of lizards on the successive spring-earlysummer testicular activity. Open columns indicate stasis; horizontal lines indicate recrudescence of spermatogenesis and oblique lines, maximal spermatogenetic activity. Black areas show the crisis. The group indicated by an asterisk had a very high mortality rate (almost 75%) between February and March.

ena were observed in the germ cells (above all spermatids), particularly in the group kept in the dark. On the whole, spermiogenesis and sperm release were good, as well as the development of the epididymis and of the other secondary sexual characteristics. The gonad was active until late June in the animals kept in the dark and until mid-July in those kept with a long photoperiod.

*Animals kept at a constant temperature of 28 °C, with different photoperiods, for 41 days.* The results are summarized in Fig. 2. When the animals were to be transferred to environmental conditions, the same changes in spermatogenesis were observed in the testis as had been seen in the previous group.

The next spring, in the animals kept in the dark, the development of spermatogenesis was similar to that of the animals treated for 21 days. With a long photoperiod, the spermatogenetic activity was more intense and lasted longer than in the controls (late July). Spermiohistogenesis, spermiation and epididymal development were more apparent in the dark.

With a short photoperiod the recrudescence occurred a little later than in the controls, spermatogenesis was not very active and the development of the epididymis and of the other SSC (secondary sexual characteristics) relatively insufficient. A real period of full spermatogenesis was lacking, spermiation being poor or absent. The crisis set in at the end of June.

*Animals kept at a constant temperature of 28 °C, with various photoperiod, for 10 months.* The animals were killed at various times throughout the treatment. In the first weeks of treatment, a stimulation of the autumnal spermatogenesis was observed with all three photoperiods, if compared to the controls (Fig. 3). It took place earlier with a long photoperiod, followed by the short one and, finally, by the dark, and consisted of a marked increase in the first stages of spermatogenesis (spermatogonia and primary spermatocytes); on the contrary, the stimulatory effects on the last stages of spermatogenesis were more limited and different with the various photoperiods (Fig. 3). Compared with the controls, there was an increase in the production of spermatozoa, which were evacuated only in small numbers into the epididymal ducts. The epididymis showed a low stimulation, nor was there an increase the other SSC. In all the groups, after some weeks, the testis showed degenerative signs (« fall crisis ») similar to those typical of the summer crisis. Such degenerative phenomena appeared in mid-October with a short photoperiod, in mid-November with the dark and only in January with a long photoperiod. The « fall crisis » was very apparent with the short photoperiod; in the seminiferous tubules only spermatogonia and Sertoli cells remained. The degenerative phenomena were, on the contrary, more limited with long photoperiod and just decernable with the dark.

After the « fall crisis » the gonad remained unchanged until the next spring. Only in the animals treated with a short photoperiod did we observed in November a production of various primary and secondary

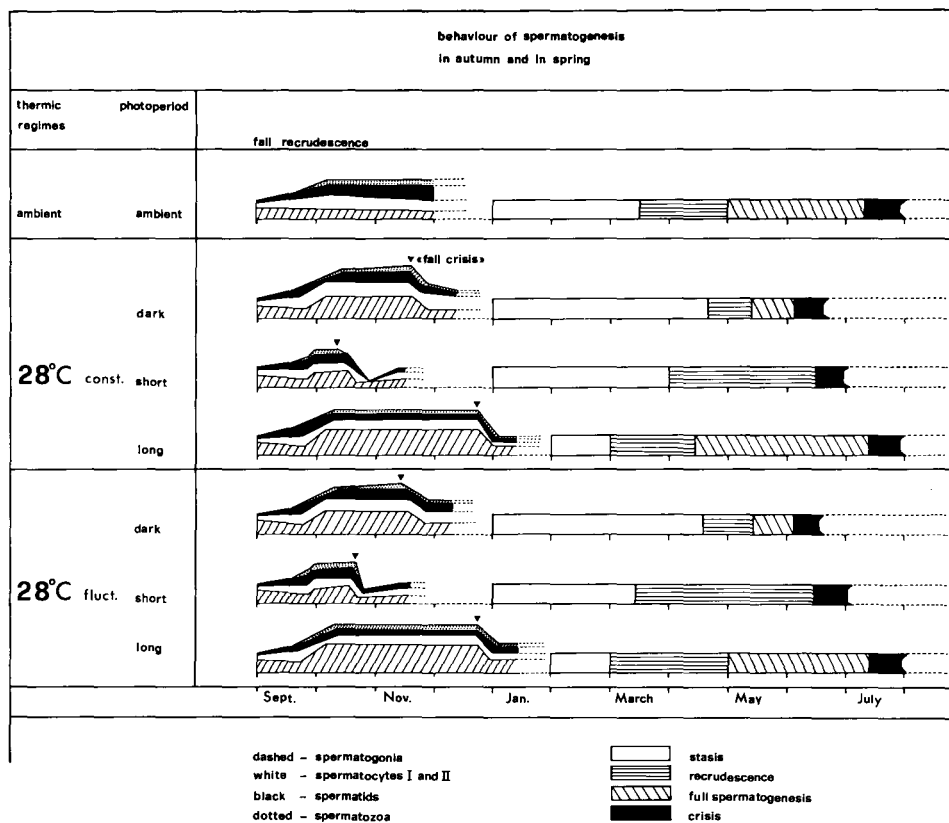


Fig. 3. — A schematic representation of the effects of the long-term treatment of autumnal lizards under free-running constant (28 °C const.) and fluctuating (28 °C fluct.) experimental conditions. On the left of the figure the different photo-thermal treatments are summarized; in the middle is shown the differential behaviour of autumn germ cells with these treatments. The right of the figure depicts the effects of the same experimental conditions on the successive spring-earlysummer testicular activity.

spermatocytes and some spermatids before a kind of stasis occurred in this group.

The next spring, the gonad began to develop again only at the end of April in the dark, at the end of March with a short photoperiod and considerably earlier (late-February to early-March) with the long one (Fig. 3). Spermatogenesis (up to round spermatids) was as active as in the controls with a long photoperiod and in the dark but, very poor, on the contrary, with a short photoperiod. Spermiohistogenesis and spermiation were intense in the dark, less marked with a long

photoperiod and just evident with the short one, where there was an absence of a real period of « full spermatogenesis ». The development of the epididymis and of the gonadal interstitial tissue was remarkable in the lizards kept in the dark, almost normal with the long photoperiod and scarce with the short one. In all cases there was a sperm evacuation, that was minimal with short photoperiod.

The gonad remained active for some weeks and the summer crisis occurred in late May in the dark, in June with the short photoperiod and in mid-July with the long one.

*Animals kept under fluctuating thermal regimes, with different photoperiods, for 10 months.* The animals were killed at various times as in the previous group. In autumn, a slight stimulation of spermatogenesis, with a pattern similar to that described for the previous group, was observed with all photoperiods (Fig. 3). Spermiohistogenesis, spermiation and epididymal development were more apparent.

In this group, too, a « fall crisis » was observed after stimulation. It occurred earlier in darkness and with the short photoperiod. The degenerative phenomena were considerably more intense with the short photoperiod.

In the spring, the gonadal recrudescence was hastened by the long photoperiod, deferred by darkness and occurred at the same time as in the controls with the short photoperiod. The spermatogenetic activity up to round spermatids appeared normal with darkness and the long photoperiod, rather limited with the short one. Spermiohistogenesis, the development of the epididymis and of the interstitial tissue were very apparent in the dark, normal with long photoperiod and poor with the short one. In the group treated with a short photoperiod a real « full spermatogenesis » was absent, spermiation, too, was poor.

The springtime activity of the gonad lasted some weeks, ending with the summer crisis, which was early in the dark (late May), followed by the short photoperiod (early July) and by the long one (mid-July).

*Animals kept at environmental temperature, with different photoperiods, for 41 days.* In this group the spring recrudescence of the gonad, spermatogenetic activity and epididymal development showed no differences as compared to the controls (Fig. 2).

## DISCUSSION

The present study aims at investigating possible influences of the refractory period, other than inhibition of reproduction in unfavourable periods of the year, on the sexual cycle of *Podarcis s. sicula* Raf.



Maintenance at high, constant or fluctuating, temperatures, combined with different photoperiods, from September to November, has shown that in this stage of the refractory period, it is possible, within certain limits, to influence the gonadal activity of next spring. In particular, the lizards maintained for 21 or 41 days, from late September, at high temperatures, with long or short photoperiods or in the dark and then transferred to environmental conditions, seem «to remember» the autumnal photo-thermal experiences during the springtime recrudescence. According to these experiences they tend to regulate the beginning of spermatogenesis, its intensity and duration, as well as the endocrine activity (tested by development of the epididymis and of the femorale pores). Therefore, in animals kept in autumn for relatively short period (21 or 41 days) in the dark or with short photoperiod, always combined with high temperatures, the spring recrudescence of the gonad is deferred and its activity lasts for a rather short period, ending earlier as compared to the controls. With the long photoperiod, on the contrary, the recrudescence and duration of the testicular activity is almost the same as in the controls; only in the group treated for 41 days is the summer crisis somewhat deferred. In most cases, moreover, spermatogenesis is less active than in the controls.

Treatments with the same photo-thermal regimes as above, but carried out for long periods, show that, when the refractory period diminishes the male gonad can react to various photo-thermal combinations as it does in spring. In fact, the fall abortive recrudescence of spermatogenesis is always stimulated by high temperature, but is anticipated and lasts longer with long photoperiod; it is deferred and shorted in the dark. On the contrary, the stimulatory effects are much limited and very short with the short photoperiod. As a consequence of these stimulation, there is increased spermiogenesis in the gonad, some spermiation and, in some cases, a slight epididymal stimulation.

In this connection, it must be noted that in the lizard in autumn both the epididymis and the other SSC are less sensitive than spermatogenesis to photo-thermal changes. There are no data explaining such a difference between spermatogenetic and endocrine activities, even if it has been observed that in this period the amount of androgens required for complete epididymal development is considerably greater than in other months, at both environmental temperature or 28°C (ANGELINI et al., 1978b).

The autumnal stimulatory effects just described, are by far less intense than the spring ones. After some weeks of activity («fall recrudescence»), as found in nature at the end of the reproductive period, the gonad is affected by a crisis («fall crisis»), with more or less intense degeneration of the germ cells; in the most marked cases (short photo-

period) only spermatogonia and Sertoli cells are found in the seminiferous tubules.

The possibility of « programming » in autumn the future sexual cycle of the gonad gives the refractory period a remarkable regulatory function on the springtime reproductive activity of *Podarcis*. On the other hand, the problem of defining the physiological importance of this phenomenon arises. As from September (Fig. 1) to November average environmental temperatures are still relatively high (above 13 °C) and the day length is the same as in the normal period of springtime recrudescence (exceeding 11 hr), we should not exclude the possibility that, in autumn, the gonad is « programmed » by a particular photo-thermal combination, that, when it reappears again in spring, at the end of the semihibernation, acts as a starter for the spermatogenetic processes.

The combined action of the photoperiod and temperature in this regulatory system is shown by the frequent observation that, in a particularly cold spring, recrudescence naturally occurs later (f.i. in April) when the right thermal regime is reached, but it is more rapid, since at this time the photoperiod is longer than in March.

Our data show that the autumnal « programming » does not markedly influence the intensity of spermatogenesis and of the gonadal endocrine activity, which do not differ much as compared to the controls, except for some conditions (short photoperiod). It is undoubtedly curious that short autumnal treatments (darkness or short photoperiods, combined with high temperatures) can determine the duration of gonadal activity in the following spring, by anticipating the summer crisis.

On the basis of our experiments other observations can be made. In the long-term experiments, constant high temperature regimes stimulate the gonad less than the fluctuating ones. Similar observations were made by NOESKE & MEIER (1977) in male *Anolis carolinensis* Dum. & Bibr.

Darkness combined with high temperatures causes, in many cases, a considerable increase in spermiogenesis and, above all, an intense stimulation of the interstitial tissue and the epididymis. A stimulatory effect on ovarian development and on the number of eggs laid during the reproductive period has been observed in other reptilian species (STEBBINS & COHEN, 1973; LEVEY, 1973; ANGELINI et al., in preparation). This phenomenon might be caused by a failure of light to stimulate the pineal gland. However, pinealectomy does not have any stimulatory effect in ovarian circannual cycle of *Cnemidoporus uniparens* Wright & Lowe (CUELLAR, 1978).

In male *Anolis carolinensis*, parietectomy does not seem to affect the spermatogenetic and endocrine activities of the gonad (LICHT & PEARSON, 1970). The same phenomena have been observed also in male

*Sceloporus occidentalis* Baird & Girard (STEBBINS & COHEN, 1973). Our preliminary observations show that in male *Podarcis s. sicula* the shielding of parietal bones causes a better and longer lasting epididymal development (ANGELINI et al., in preparation).

The photo-thermal combination of high temperature and short photoperiod is the most unfavourable one for the gonad. In the animals of these groups, spermatogenesis and epididymal development are very limited, even if accompanied sometimes by spermiation. This phenomenon can be observed both in short and long-term experiments.

To conclude, the refractory period is an important stage in the regulation of the reproductive cycle in *Podarcis s. sicula*. In fact, its function does not consist solely of inhibiting reproduction in unfavourable seasons, but also of correctly « programming » the activity of the gonad during the following reproductive period.

#### SUMMARY

From the middle of the refractory period, adult males of *Podarcis s. sicula* Raf. (Reptilia Lacertidae) were treated with different photo-thermal regimes: 28 °C, combined with darkness, short or long photoperiods. The treatments were short (21-41 days) and long (exceeding 10 months).

In both cases, in spring, recrudescence of testes occurred early after long photoperiods and was markedly delayed after darkness. In the latter case, moreover, the summer crisis is remarkably anticipated as compared to the controls. High temperatures, combined with short photoperiod, induce limited stimulatory effects on spermatogenesis with a poor development of the secondary sexual characteristics.

A comparison between the results obtained from short and long term experiments clearly show that the autumnal refractory period is of fundamental importance in the regulation of the reproductive cycle of *Podarcis s. sicula*. In fact, during this period, the gonadal activity is « programmed » and pre-arranged for the next spring reproductive period.

#### RIASSUNTO

Sono stati trattati maschi adulti di *Podarcis s. sicula* Raf. (Reptilia Lacertidae) a partire dalla parte media del periodo di refrattarietà con diverse condizioni foto-termiche: 28 °C associate rispettivamente a buio o a fotoperiodo breve o lungo. I trattamenti sono stati effettuati a breve (21 e 41 giorni) e a lungo termine (oltre 10 mesi).

In entrambi i casi si è avuto in primavera una ripresa precoce della spermatogenesi con il fotoperiodo lungo ed un evidente ritardo con il buio. In quest'ultimo caso inoltre la comparsa della regressione estiva è notevolmente anticipata rispetto ai controlli. Le alte temperature associate ai fotoperiodi brevi provocano limitati effetti stimolatori sulla spermatogenesi e scarso sviluppo dei caratteri sessuali secondari.

Dal confronto dei risultati ottenuti negli esperimenti a breve durata e a lungo termine, appare evidente che il periodo di refrattarietà è una fase fondamentale nella regolazione del ciclo riproduttivo di *Podarcis s. sicula* Raf. in quanto in esso viene probabilmente programmata ed impostata la futura attività della gonade per il successivo periodo riproduttivo primaverile.

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Address of the first author: Prof. FRANCESCO ANGELINI, Istituto di Istologia ed Embriologia dell'Università, Via Mezzocannone 8, 80134 Napoli.