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Endocrine Events during the Life Cycle of *Lithobius forficatus* L. (Myriapoda, Chilopoda)

by

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Abstract: The endocrine signals demonstrated or inferred from natural cycles or experimental series are reviewed. All data are for the situation in Northern France, since animals are responsive to climatic conditions. — The main signals that occur in the control of molting are ecdysteroid peaks and cerebral gland secretions. In addition, an autumnal "molt-blocking factor" may occur, leading to low levels of ecdysteroids and to lack of molting. Day-length may be the main factor involved in triggering and maintenance of this phase. — During the spermatogenic cycle a winter rest period also occurs, but a minimal spermatocyte growth rate is maintained, related probably to an increase in testis ecdysteroid level. As no influence of ecdysteroid level variations were found during the period of high physiological activity, other factors may be involved in the modulation of the testis-blood barrier. — A hormonal balance between ecdysteroids and a cerebral gland factor could also be involved in regulating oocyte growth.

1. Introduction:

Lithobius, like other animals, is under the control of endocrine factors. Our purpose in this paper is to review the endocrine signals, in order to elucidate their functions during the natural life cycle, to correlate endocrine activities to external events (e.g. climatic changes), or to show how a physiological process can be controlled by the antagonistic action of two hormones (e.g. ecdysteroids and a moderating factor during oogenesis). As the life cycle of *Lithobius forficatus* is under the influence of climatic conditions, mainly temperature, all the data presented in the three next sections (molting cycle, spermatogenic cycle and oogenetic cycle) are for animals living under the rather oceanic climate of Northern France.

2. Molting Cycle:

JOLY (1966) reported that the rate of molting was not the same throughout the year. For example, the percentages were 20 % and less than 8 % in animals (maturus senior stage, VERHOEFF 1905) collected during March - April and mid-September, respectively. More recently, an experimental series performed from Sept. 20, 1985 to May 21, 1986 on 20 mature animals, kept at room temperature, fed regularly (three times a week), showed (Fig. 1) no molting during autumn and winter; the first of the five molts recorded happened only on March 31. Nevertheless, differences exist from one year to another, molting activity resuming either by early March (after a "warm" winter) or by early April (after a "cold" winter).

The first signal to be demonstrated was the moderating role of the cerebral glands (cephalic neurohemal organs), with an efficiency period (= secreting period) demonstrated experimentally

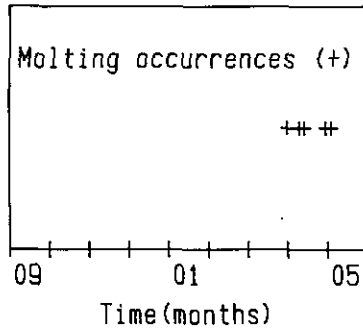


Fig. 1: Time occurrence of molts (5 molts recorded from 20 individuals) in lab conditions. Data from DESCAMPS (unpublished).

between 10 and 30 days after ecdysis (JOLY 1966). Nevertheless, the main signals of the molting cycle are the two ecdysteroids peaks (Fig. 2) (JOLY et al. 1979), corresponding most probably to the cuticular postecdysial and preecdysial syntheses, respectively. Total ecdysteroid levels, recorded from September to July (DESCAMPS et al., submitted) showed (Fig. 3) that periods of low molting rate are characterized by low ecdysteroid levels, whereas a dramatic rise in ecdysteroid content was recorded before the molting activity resumed. The low ecdysteroid levels during the winter rest period is comparable to that observed in diapausing insects, although the winter rest is not a diapause, the animals continue to eat regularly.

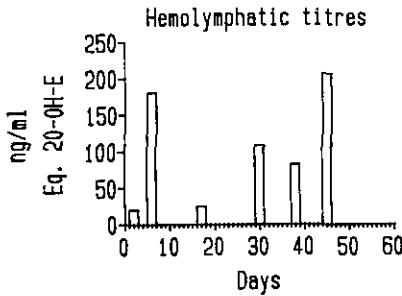


Fig. 2

Fig. 2: Hemolymphatic titres in *L. forficatus* during a molt cycle as determined by RIA. Data (values obtained from about 400 individuals) from JOLY et al. (1979). 20-OH-E = 20-hydroxyecdysone.

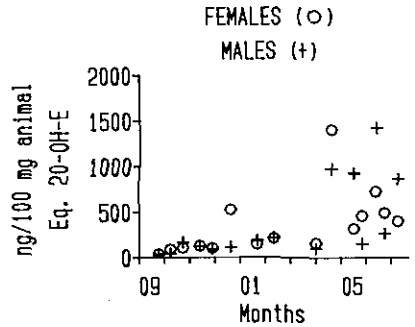


Fig. 3

Fig. 3: Total ecdysteroid levels in male and female *L. forficatus*. Each point obtained from one individual. Data from DESCAMPS et al. (in press).

How can such a rest period be triggered? It must be pointed out that the animals can be stimulated, and the winter rest broken (at least in a significant percentage of animals if not the majority), either by removal of cerebral glands (9 molts out of 21 animals deprived of their glands; experiments performed during the period December – early February, no molt observed in the controls), or injection of ecdysteroids, or pars intercerebralis (postero-dorsal area of the protocerebrum) electrical stimulation (JOLY & DESCAMPS 1977).

The mechanism involved may be as follows: at the end of summer or beginning of autumn, under the influence of decreasing daylength or increasing night-length, a winter rest factor (WRF)

is released, most probably by the cerebral glands. Secretion by the ecdysial gland is inhibited by WRF and the ecdysteroid level decreases. The temperature has no influence, no molt or only few molts being observed, even if the lab temperature remains optimal. After a period of low ecdysteroid levels and a signal from the brain, the ecdysteroid level rises dramatically and molting resumes. What are the signals acting on the brain? Daylength may be primarily involved; but how does one explain high ecdysteroid levels recorded as early as December during a "warm" winter? Temperature may also be involved. It must be noted that during a "warm" winter, when high levels of ecdysteroids can be recorded as early as December, the molting activity does not resume at this time: February (at the earliest) or early March (generally) remains the period when the molting cycle resumes. In short, if some of the factors involved can be determined, their roles are much more complex than formerly expected.

3. Spermatogenic Cycle:

Two spermatogenic phases normally occur during the year, one in early spring and the second in late spring or early summer. If there is a "warm" winter, a third spermatogenic phase occurs at the end of winter (February) (JOLY & DESCAMPS 1969). Two spermatogenic factors stimulate spermatocyte growth: a factor released from the pars intercerebralis (p.i.) neurosecretory cells (DESCAMPS 1974), and an ecdysteroid (DESCAMPS 1981). These hormones do not work independently; in addition, a sufficient amount of p.i. factor is necessary for the stimulatory action of 20-hydroxyecdysone (20-OH-E) (DESCAMPS 1986). A cerebral gland factor counteracts the effects of the two previous hormones and moderates spermatocyte synthesis (DESCAMPS 1975).

No linkage was found between the molting cycle and the spermatogenic cycle. As ecdysteroid hemolymphatic levels fluctuate and no variation of spermatocyte growth was recorded following these periodic changes, the testis permeability may be controlled in order to regulate testis hormonal level and metabolite access to germinal cells.

It has been demonstrated (BENIOURI 1984) that 20-OH-E increases the permeability of the testis-blood barrier. In addition, a refractory period takes place during the meiotic phase (BENIOURI et al. 1983, DESCAMPS et al. 1986). Neither injection of 20-OH-E nor p.i. electrostimulation can stimulate spermatocyte syntheses during this phase. This is evidence for the action of an inhibiting mechanism, working independently of 20-OH-E and p.i. hormones, and acting either on the testis-blood barrier or on the spermatocyte hormonal receptors.

Finally testis ecdysteroid levels (DESCAMPS et al., submitted) show increased values either during the period of rapid spermatocyte growth (Fig. 4) or, but at far lower levels, during the winter rest. The latter may be related to a compensatory effect that counteracts the low ecdysteroid level recorded in the whole body and is related most likely to the maintenance of a minimal rate of spermatocyte synthesis.

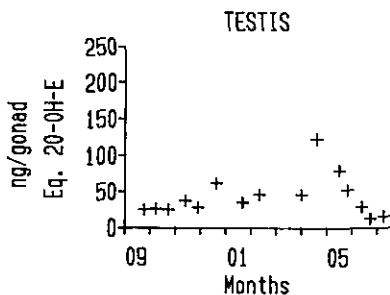


Fig. 4: Testis ecdysteroid levels in *L. forficatus*. Each point is the mean value obtained from 2 testes. Data from DESCAMPS et al. (in press).

In short, the hormonal signals controlling the spermatogenic cycle seem to be involved only in the control of cellular metabolism and in the control of the permeability barrier. No hormonal action has been reported on meiosis or spermiogenesis, except the triggering of precocious meiosis after repeated injections of 20-OH-E (DESCAMPS 1977). Nevertheless, testis ecdysteroid and the control of these compounds may complicate a rather simple scheme of hormonal action.

4. Oogenetic Cycle:

The oogenetic cycle of *L. forficatus* is characterized by two main periods of vitellogenesis: autumn, after an aestival rest period, and spring (HERBAUT & JOLY 1972). The two first hormonal influences demonstrated during the course of the oogenetic cycle were 1) the stimulating action of a p. i. factor (HERBAUT 1975) and 2) the necessary presence of the cerebral glands in order to insure a normal oogenesis. HERBAUT (1976) stated that the cerebral glands released a stimulating factor. SAREEN & ADIYODI (1983) were at odds with this explanation and were in favor of an indirect effect, via the moderating action of the cerebral glands on molting, according to a crustacean-like model.

It was more recently shown (DESCAMPS 1989) that too high ecdysteroid levels lead to the release of a moderating factor (Fig. 5). In my opinion, the cerebral glands, by the release of a moderating factor, are necessary to counteract the too high levels of ecdysteroids occurring during the course of the molting cycle. Nevertheless, ecdysteroids are necessary for oogenesis, 20-OH-E supply leading in vivo (0,2 µg and 0,4 µg per animal, Fig. 5) to increased RNA synthesis, and in vitro ($8,3 \times 10^{-7}$ M) to an oocyte membrane depolarization interpreted as a stimulating action (DESCAMPS & LASSALLE 1986).

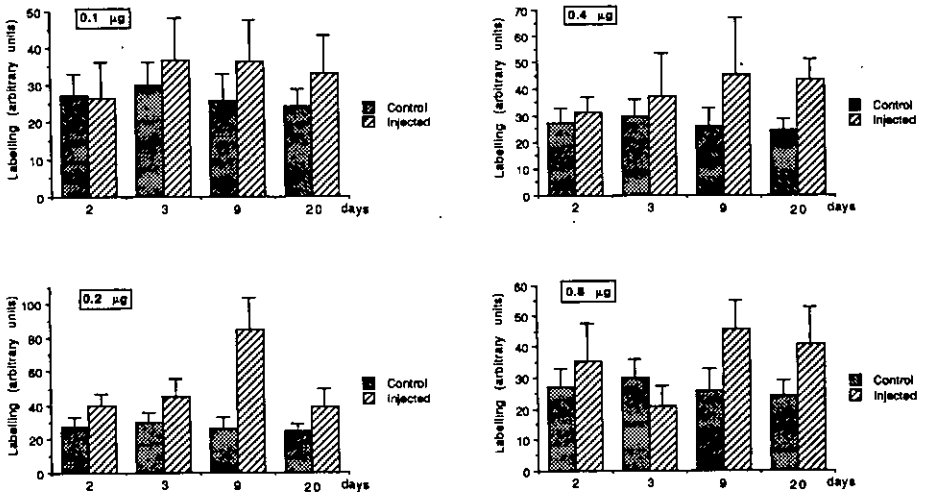


Fig. 5: Dose influence of injected 20-OH-E on uridine uptake by oocytes as shown by cytophotometric measurements on autoradiographs (mean \pm SD). In the 0,8 µg experiments a decreased level of uptake statistically highly significant (risk < 0.001) was recorded on day 3, evidence for the release of a moderating factor. Data from DESCAMPS (1989).

Finally, the rise of ovarian ecdysteroids observed during the vitellogenic phases (DESCAMPS et al., submitted; Fig. 6) are more likely to be related to the storage of ecdysteroid conjugates than to signals controlling vitellogenesis.

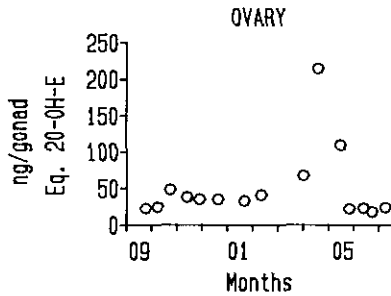


Fig. 6: Ovary ecdysteroid levels in *L. forficatus*. Each point is the mean value obtained from 2 ovaries. Data from DESCAMPS et al. (in press).

5. Conclusion:

Experimental endocrinology of Chilopoda, as summarized here, shows that the *Lithobius* model, though some years ago to be controlled very simply by the balance between two factors, one stimulating (issued from or controlled by the p.i. neurosecretory cells) and a moderating one (issued from the complex "protocerebral frontal lobe NSC-cerebral glands" has evolved toward a more elaborate system in which the origin of some of the factors is either hypothetical or unknown. Moreover, the endocrine control of oogenesis should be reinvestigated taking into account the exogenous origin of yolk proteins (e.g. vitellogenins).

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