

Many temperate zone reptiles exhibit discrete annual reproductive cycles, with reproductive activities restricted to the spring and summer months (Fitch, 1970). Behavioral, histological and physiological aspects of the reproductive cycle have been well studied in the European viper *Vipera berus* (Nilson, 1976, 1980, 1981; Saint Girons, 1976) and lizard *Lacerta vivipara* (Courty and Dufaure, 1979; Xavier, 1982; Bauwens and Verheyen, 1985). These species, which cohabit over extensive parts of their enormous ranges, have similar male reproductive cycles. Males of both species typically emerge from hibernation about three weeks before the females. During this period males exhibit intense spermiogenetic activity ("spring spermiogenesis"). Following emergence of the adult females, males start mating upon the completion of spermiogenesis. Testes volume decreases rapidly after the termination of the mating period. Following a resting period, a new spermatogenetic cycle starts in June or July. Spermatocytogenesis is completed at the onset of the hibernation period.

In individual male *Vipera berus* (Nilson, 1980), and several closely related species (Saint Girons, 1980), the onset of mating activities coincides with the completion of the first annual or spring molt. This "pre-nuptial" molting is highly synchronized among individuals and has been suggested to be the event that triggers mating activities (Nilson, 1980).

During a study examining the timing of female reproductive activities in a field population of *Lacerta vivipara* (Bauwens and Verheyen, 1985), we noted a synchronized spring molting in male lizards at the onset of the mating period. Based on these observations we hypothesized that, as in *V. berus*, spring shedding would coincide with the onset of mating activities in individual male *L. vivipara*. We here report and discuss results of a behavioral test of this hypothesis.

Tests were performed while conducting a mark-recapture study in a 62 x 41 m study plot located in the national nature reserve "de Kalmthoutse heide" (Kalmthout, 51°25'N, 4°25'E, prov. of Antwerp, Belgium). Lizards were captured by hand, marked individually (permanently by toe-clipping, temporarily with nail polish) and released after noting identity, sex, snout-to-vent and tail length, weight, reproductive characteristics and molting status.

We conducted behavioral tests to examine sexual activities of adult male lizards during the period 5 April-16 April 1980. An adult male was selected at random from the population and placed in an outdoor test vivarium (60 x 40 cm). After 5 min, an adult female was introduced and the lizards' behavior was observed during a 5 min test period from behind a blind. After the experiment lizards were released at the site of capture.

Male *L. vivipara* initiate courtship, without exhibiting preliminary courtship displays, by running towards a female and attempting to obtain a mouthhold on her flank, neck or tail (see Verbeek, 1972; Bauwens et al., 1987, for detailed accounts on mating behavior in this lizard). The role of the female is entirely passive during this initiation phase. Moreover, we have previously evidenced that the release of courtship behavior in males is independent of the female's reproductive state (Bauwens et al., 1987). The behavioral response of the male was scored either as "neutra," in case the female lizard was not courted

Synchronization of Spring Molting with the Onset of Mating Behavior in Male Lizards, *Lacerta vivipara*

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TABLE 1. The number of male *L. vivipara* showing "neutral" or "approach" behaviors towards an introduced female, as a function of the males' molting condition. All tests were performed within 3 days before or after the shedding date.

	Response of male	
	Neutra!	Approach
Pre-molt	17	0
Molting	12	1
Post-molt	2	23

within 5 min, or as "approach," when the male initiated courtship by running towards and biting the female on her flank, neck or tail. When the male maintained the mouth-hold and attempted to initiate copulation, the lizards were separated and the trial was terminated.

Experimental males were assigned to one of three categories, according to their shedding status at the day of the trial:

pre-molt: the lizard's coloration, especially that on the belly, is masked by a dull greyish opacity. During the last 1-2 days prior to molting, the colors again become more transparent, but the presence of the old epidermal layer above the new one can be detected by palpation.

molting: skin flakes are present on various parts of the body.

post-molt: evidenced by the bright coloration of the skin which becomes apparent upon completion of shedding, and the loss of paint color marks.

A total of 55 tests were conducted with 36 individual males (23 males tested once, 7 in two molting categories, 6 in three shedding classes). As we frequently recaptured all males that were used in the trials, their shedding dates were known exactly, and the judgment of their shedding status was unequivocal. Only trials performed within 3 days before or after the shedding date of a male were considered. This period is considerably shorter than the ca. 1 month interval between successive molts of males. It is unlikely that the males' behavior was affected by the females' shedding status, as they completed their first annual molt during the first half of June (ca. 2 months after conducting the tests).

Our results (Table 1) evidence a clear-cut association between molting status and mating activities (log-likelihood ratio test: $G = 54.364$, 2 df, $P < 0.001$). All males that were tested in both pre- and post-molt status ($N = 10$) switched from "neutral" to "approach" behavior following shedding (McNemar test for the significance of changes: $X^2 = 8.100$, 1 df, $P < 0.005$). We observed striking qualitative change of the males' behavior upon completion of shedding. Pre-molt males showed no interest in the female, even at close proximity (both sexes often basked side by side). In contrast, most post-molt males ran towards and vigorously pursued the female when she fled, within 30 sec after her introduction in the test cage. We conclude that the onset of sexual behavior coincides with the completion of the first annual ecdysis in male *L. vivipara*.

A synchronized shedding of males at the start of the mating period has also been observed in several other species of *Lacerta* and *Podarcis* that were maintained in outdoor enclosures (B. Langerwerf, pers. comm.). This observation suggests that an association between shedding and the onset of male mating activities is widespread in Lacertidae.

The observations of molting coinciding with the onset of sexual behavior in male lizards and snakes (Nilson, 1980; Saint Girons, 1980), and of sloughing in female snakes at or shortly before egg laying (Millichamp, 1977; Saint Girons, 1980) suggest that certain endocrine mechanisms affect both reproductive physiology and ecdysis. Several findings support this hypothesis. Hormones from the thyroid and pituitary glands are known to affect the shedding cycles in reptiles (Millichamp, 1977). It has been shown that thyroidectomy decreases or even causes cessation of molting in several lizards, including *L. vivipara* (Drzewicki, 1926; Eggert, 1936; Maderson, 1966; Lynn, 1970). Although the role of thyroid hormones in reptilian reproduction remains unclear (Duvall et al. 1982), thyroidectomy has, either directly or indirectly, some striking effects on gonadal structure and sexual behavior in male *L. vivipara* (Eggert, 1937).

The simultaneity of molting and the onset of sexual activities may well serve some biological functions. In snakes, sloughing facilitates the release of pheromones through the skin, resulting in an increased attraction of recently molted females (Kubie et al. 1978) and males (Andr n, 1982) to conspecific males. We speculate that the chemoreceptive detection of conspecific male lizards, which has been demonstrated in various species (Duvall, 1979; Cooper and Vitt, 1984a, b), might be enhanced following shedding.

A second factor that might be important is the increase in brightness of color and pattern in recently molted reptiles. In many agamid, iguanid and lacertid lizards, the males possess conspicuous pigmentation on the flanks, head or throat. These color markings are involved in sex recognition (Kramer, 1937; Kitzler, 1941; Ferguson, 1966) and in female choice of males (Crews, 1975; Sigmund, 1983). Although sexual dichromatism is rather inconspicuous in *L. vivipara*, color pattern has been shown to be functional in sex recognition by males (Bauwens et al., 1987). We suggest that the increased brightness of the coloration upon shedding might accentuate some features of the male color pattern and hence the distinction between male and female coloration. This might facilitate the recognition of potential partners by mate-searching males.

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LITERATURE CITED

- ANDR N, C. 1982. The role of the vomeronasal organs in the reproductive behavior of the adder *Vipera berus*. *Copeia* 1982:148-157.
- BAUWENS, D., K. NUIJTEN, H. VAN WEZEL, AND R. F. VERHEYEN. 1987. Sex recognition by males of the

- lizard *Lacerta vivipara*: an introductory study. *Amphibia-Reptilia*. 8:49-57.
- , AND R. F. VERHEYEN. 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. *J. Herpetol.* 19: 353-364.
- COOPER, W. E., AND L. J. VIIT. 1984a. Detection of conspecific odors by the female broad-headed skink, *Eumeces laticeps*. *J. Exp. Zool.* 229:49-54.
- , AND —. 1984b. Conspecific odor detection by the male broad-headed skink, *Eumeces laticeps*: effects of sex and site of odor source and of male reproductive condition. *J. Exp. Zool.* 230: 199-209.
- COURTY, Y., AND J. P. DUFAURE. 1979. Levels of testosterone in the plasma and testis of the viviparous lizard (*Lacerta vivipara* Jacquin) during the annual cycle. *Gen. Comp. Endocr.* 39:336-342.
- CREWS, D. 1975. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. *Anim. Behav.* 23:349-356.
- DRZEWICKI, S. 1926. Influence de l'extirpation de la glande thyroïde sur la mue du lézard (*Lacerta agilis* L.). *C. R. Séanc. Soc. Biol.* 95:893-895.
- DUVALL, D. 1979. Western fence lizard (*Sceloporus occidentalis*) chemical signals. I. Conspecific discriminations and release of a species-typical visual display. *J. Exp. Zool.* 210:331-326.
- , L. J. J. R. GUILLEITE, AND R. E. JONES. 1982. Environmental control of reptilian reproductive cycles. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 3, pp. 201-231. *Academie Press*, London.
- EGGERT, B. 1936. Zur Morphologie und Physiologie der Eidechsen-Schilddrüse. III. Über die nach Entfernung der Schilddrüse auftretenden allgemeinen Ausfallserscheinungen und über die Bedeutung der Schilddrüse für die Häutung und für die Kaltstarre. *Z. Wiss. Zool.* 148:221-260.
- , 1937. Zur Morphologie und Physiologie der Eidechsen-Schilddrüse. IV. Über den Einfluss der Schilddrüsenextirpation auf den ultimobranchialen Körper und auf die Kiemdrüsen. *Z. Wiss. Zool.* 149:280-322.
- FERGUSON, G. W. 1966. Releasers of courtship and territorial behavior in the side blotched lizard, *Uta stansburiana*. *Anim. Behav.* 14:89-92.
- FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* 52:1-247.
- KITZLER, G. 1941. Die Paarungsbiologie einiger Eidechsen. *Zeitschr. Tierpsychol.* 4:353-402.
- KRAMER, G. 1937. Beobachtungen über Paarungsbiologie und soziales Verhalten von Mauereidechsen. *Zeitschr. Morphol. Kol. Tiere* 32:752-783.
- KUBIE, J. L., A. VAGVOLGYI, AND M. HALPERN. 1978. Roles of the vomeronasal and olfactory systems in courtship behavior of male garter snakes. *J. Comp. Physiol. Psychol.* 92:627-641.
- LYNN, W. G. 1970. The thyroid. In C. Gans and T. S. Parsons (ed.), *Biology of the Reptilia*, Vol. 3, pp. 201-234. *Academie Press*, London.
- MADERSON, P. F. A. 1966. Histological changes in the epidermis of the tokay (*Gecko gecko*) during the sloughing cycle. *J. Morph.* 119:39-50.
- MILLICHAMP, N. 1977. Aspects of reptilian ecdysis. *Cotswold Herpet. Symp. Rep.* 3:42-47.
- NILSSON, G. 1976. The reproductive cycle of *Vipera berus* in SW Sweden. *Norw. J. Zool.* 24:233-234.
- , 1980. Male reproductive cycle of the European adder, *Vipera berus*, and its relation to annual activity periods. *Copeia* 1980:729-737.
- , 1981. Ovarian cycle and reproductive dynamics in the female adder, *Vipera berus* (Reptilia, Viperidae). *Amphibia-Reptilia* 2:63-82.
- SAINT GIRON, H. 1976. Les différents types de cycles sexuels des mâles chez les Vipères européennes. *C. R. Acad. Sci. Paris, Sér. D.* 282:1017-1019.
- , 1980. Le cycle des mues chez les vipères européennes. *Bull. Soc. Zool. France* 105:551-559.
- SIGMUND, W. R. 1983. Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. *J. Herpetol.* 17:137-143.
- VERBEEK, B. 1972. Ethologische Untersuchungen an einigen europäischen Eidechsen. *Bonner Zool. Beitr.* 23:122-151.
- XAVIER, F. 1982. Progesterone in the viviparous lizard *Lacerta vivipara*: ovarian biosynthesis, plasma levels, and binding to transcortin-type protein during the sexual cycle. *Herpetologica* 38:62-70.