

15. THE OVARIAN CYCLE OF *NATRIX RHOMBIFERA* — AN APPARENTLY GENERALIZED CYCLE OF SNAKES OF TEMPERATE LATITUDES

T. W. BETZ *

Department of Biology, Carleton University, Ottawa, Canada

Complete descriptions of ovarian morphology in reptiles are available for only a few species. However, accounts of gross ovarian morphology have been reported for *Vipera* (Loyez, 1906), *Bothrops*, *Crotalus*, *Xenodon* (Fraenkel and Martins, 1938; Fraenkel *et al.*, 1940), *Crotalus* (Tinkle, 1962), *Ophiodrys* (Tinkle, 1960), *Thamnophis* (Bragdon, 1952; Cieslak, 1945; Tinkle, 1957), *Thyphlops* (Guibé, 1948), *Enhydriana* (Kasturirangan, 1951) and *Natrix* (Loyez, 1906; Bragdon, 1952; Tinkle, 1959; Betz, 1963a). Accounts have also been reported for *Anguis*, *Lacerta*, *Platydictylus*, *Terrapene*, *Testudo*, *Crocodylus* (Loyez, 1906), *Lacerta*, *Lygosoma*, *Mabuya*, *Tiliqua* (Weekes, 1934, 1935), *Lacerta* (Hett, 1924), *Hoplodactylus* (Boid, 1940), *Zootoca* (Panigel, 1956), *Xantusia* (Miller, 1958), *Cnemidophorus* (Carpenter, 1960) and *Holbrookia* (Johnson, 1960). Others appear in the reviews of Kehl and Combescot (1955) and of Matthews (1955).

Generally the criteria for grouping the animals in these kinds of studies depend upon the size of the ovarian follicles; the size and presence or absence of corpora lutea and embryos; and the condition of the uterus.

The ovaries of mature *Natrix rhombifera* (Betz, 1963a) are elongate, thin-walled, saccular structures with an irregular, lymph-filled central cavity. They consist of a loose, semitransparent stroma in which the oval, creamy-white, relatively avascular ovocytes are seen in contradistinction to the yellow, vascular atretic follicles and corpora lutea. Each ovary is suspended by a mesovarium in the pleuroperitoneal cavity between the dorsal mesentery and the mesotubarium of the oviduct. They generally extend from the level of the oviducal infundibulum to the posterior limits of the kidneys. The right ovary is typically heavier and more anteriorly placed than the left. The length of the ovary is positively correlated with the length of the animal (Fig. 1) and longer ovaries generally have more follicles than shorter ones. The positive correlation of the length of the ovary with body length has been reported for *Natrix sipedon* (Tinkle, 1959) and for some lizards (Carpenter, 1960). The smaller ovocytes of *Natrix* are usually restricted to the lateral aspect of the ovary. The larger mature follicles are pale yellow in color. The follicles occur in four size groups: one group (I) of follicles 0.1 mm long; another group (II) 5-10 mm long; a third (III) 10-20 mm long; and a fourth (IV) 20-46 mm long. The number

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of follicles decreases as they become mature. In Missouri ovulation occurs between 15 May and 15 June as specimens caught at this time, are immediately preovular. Postpartum females are caught between 15 August and 15 September. Consequently, gestation is approximately three months long. Deviations of several weeks from the above dates are probably not uncommon. The size-frequency distribution of follicles at various times of the reproductive season indicates that the production of mature ova probably requires 2.5 years, i.e., the neonatal late summer and early fall months, followed by two full years and the spring of the third year (Fig. 2). The ovary at the end of the first year (following the neonatal fall) would contain follicles of groups I and II. At the end of the second year the ovary would contain follicles of groups I, II, and III; group II follicles of the first year have become the group III follicles of the second year; group I follicles of the first year have become the group II follicles of the second year; and a new crop of group I follicles has emerged from the germinal epithelium. Immediately prior to ovulation, in the spring of the third year, group III follicles of the second year grow rapidly and become group IV follicles. During gestation the ovary, except for corpora lutea, appears identical to the two-year-old ovary in follicular sizes. Apparently follicular growth occurs gradually over a two-year period but most of the growth occurs rapidly in the spring of the third year. The ovarian cycle is apparently annual (Fig. 2). In other forms the time required for the production of mature ova may be two years as in *Xantusia* (Miller, 1948, 1958); three years as in *Thamnophis* (Bragdon, 1952; Cieślak, 1945) and *Crotalus* (Rahn, 1942; Tinkle, 1962). Although annual ovarian cycles are commonly reported, Weekes (1934) reported that *Amphibolurus* may have two ovarian cycles a year. Also nonseasonal cycles occur in some Javanese snakes (Kopstein, 1938), house geckos (Church, 1962), and in *Lygosoma* (Baker, 1929, *vide* Miller, 1958). Yolk deposition may occur gradually during most of the year, as in *Lacerta* (Regamey, 1935), or gradually during a long growth period with a final immediately preovulatory increased rate of deposition as in *Phrynosoma* (Blount, 1929), *Hoplodactylus* (Boyd, 1940), *Hemidactylus* (Dutta, 1944), *Xantusia* (Miller, 1958), *Natrix*, and *Thamnophis* (Bragdon, 1952).

Atretic follicles are hyperemic and more flaccid than developing follicles. The yolk is more fluid and paler than in developing follicles. The follicle wall is thin, fragile and easily broken. Follicles of all sizes in various stages of atresia are commonly present. As atresia proceeds (as seen in selected stages) the follicles become progressively smaller, more hyperemic, and the yolk more pale, more fluid, and diminished in amount. Eventually the corpus atreticum is replaced by stromal tissue leaving an indefinite, variously persistent scar. Atresia probably accounts for the decrease in the number of follicles as they mature. Also any follicles of group IV that are not ovulated undergo atresia. It is not uncommon to find ovaries during early pregnancy with large group IV atretic follicles. Follicular atresia is common in most reptiles and has been reported by Mingazini (1893), Dubisson (1905), Loyez (1906), Boyd (1940), Bragdon (1946, 1952), Bretschneider and Duyvene de Wit (1947), Miller (1948, 1958), and Altland (1951).

Occasionally irregularly shaped, creamy-white, viscous masses of ectopic yolk material occur both in the coelom and in the ovarian stroma. These masses are of the same consistency irrespective of their size. Apparently the ectopic yolk masses in the coelom or ovarian stroma are from burst atretic follicles. The shape and size would depend on the space available among the viscera or follicles

and the amount of yolk in the follicle at the time of bursting. The position of the masses would depend on the site of rupture of the follicle wall. Judging from the amount of yolk usually present in these masses, bursting atresia is more common in large follicles, probably because of the greater thinness and fragility of their walls. These ectopic yolk masses are apparently quickly reabsorbed since they do not occur in the preovulatory females but only in pregnant and early postpartum females. Bursting atresia has also been reported in *Thamnophis* (Bragdon, 1952). One factor which is a source of error in studies of reproductive cycles which are based only on gross morphology is that follicles which have just begun to undergo atresia could easily be miscounted as growing follicles. However, the two types of follicles are easily distinguished from each other on a histological basis (Betz, 1963b).

The corpus luteum of the first month of gestation is pale yellow. The surface is indented by a puckered umbilicus which may contain a transient ectopic blood mass. The gland is approximately 10-12 mm long. The shape is essentially oval but is variable and depends on the space available between the adjacent developing or atretic follicles. The gland is placed well within the ovarian stroma and does not appreciably project from the surface of the ovary. The gland is more vascular than the developing follicles but less so than well-advanced atretic follicles. There is a 1:1 correspondence between the number of corpora lutea and the number of embryos or yolk masses in the uterus. It is common to find a disparity between the number of corpora lutea in the ovary of one side and the number of conceptuses in the uterus of the same side which is probably due to the extrauterine migration of ova to the contralateral uterus as reported by Legler (1958).

During the second month of gestation the corpus luteum is darker yellow, smaller (5-7 mm) and the umbilicus and ectopic blood mass are not present. In the last month of gestation the corpus luteum is deep yellow and less than 5 mm long. The corpora lutea usually degenerate rapidly; in the two- or three-week postpartum animal they are small (1 mm), orange patches in the ovarian stroma. Usually by the following spring all traces of the glands have disappeared as evidenced by a general lack of these structures in the preovulatory females; however, occasionally the scars persist until the next spring. Corpora lutea have been described for oviparous, ovoviviparous, and viviparous species of reptiles (Lucien, 1903; Hett, 1924; Weekes, 1934, 1935; Fraenkel and Martins, 1938; Kasturirangan, 1951; Bertin, 1952; Amoroso, 1955; Miller, 1958). The length of time that the corpora lutea are maintained can be positively correlated with the egg-retaining habits of a species (Miller, 1958). In oviparous and ovoviviparous species, a corpus luteum develops which begins to regress before oviposition occurs (Weekes, 1934; Rahn, 1938; Harrison, 1948). In most viviparous forms the length of gestation is two to three months. Typically the corpora lutea begin to regress during the last third of gestation (Weekes, 1934; Cieslak, 1945; Miller, 1948; Bragdon, 1952), but in some species regression is not apparent until after parturition (Rahn, 1938, 1939, 1942).

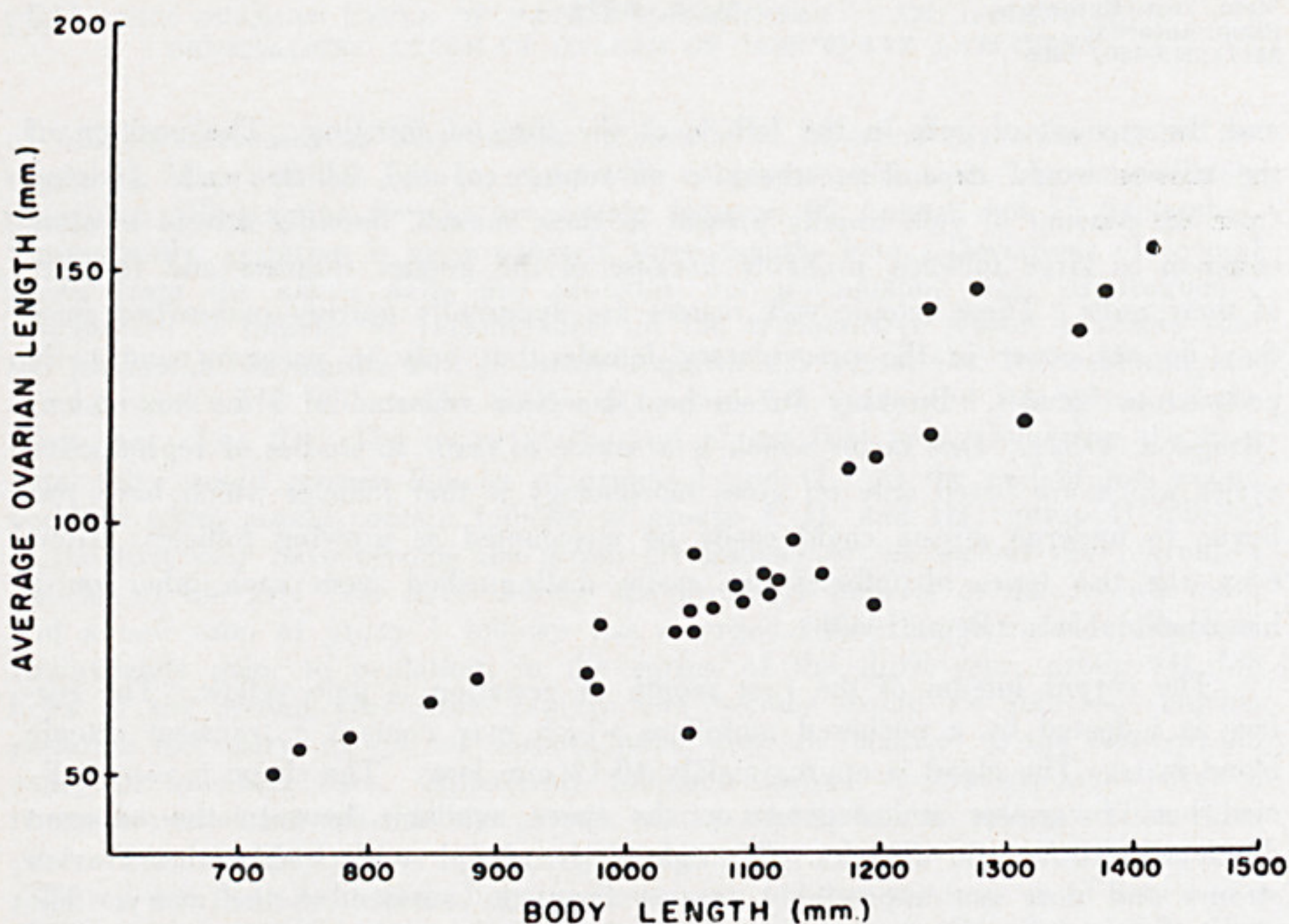


Fig. 1 — Scatter diagram of the correlation between average ovarian length with body length of *Natrix rhombifera*.

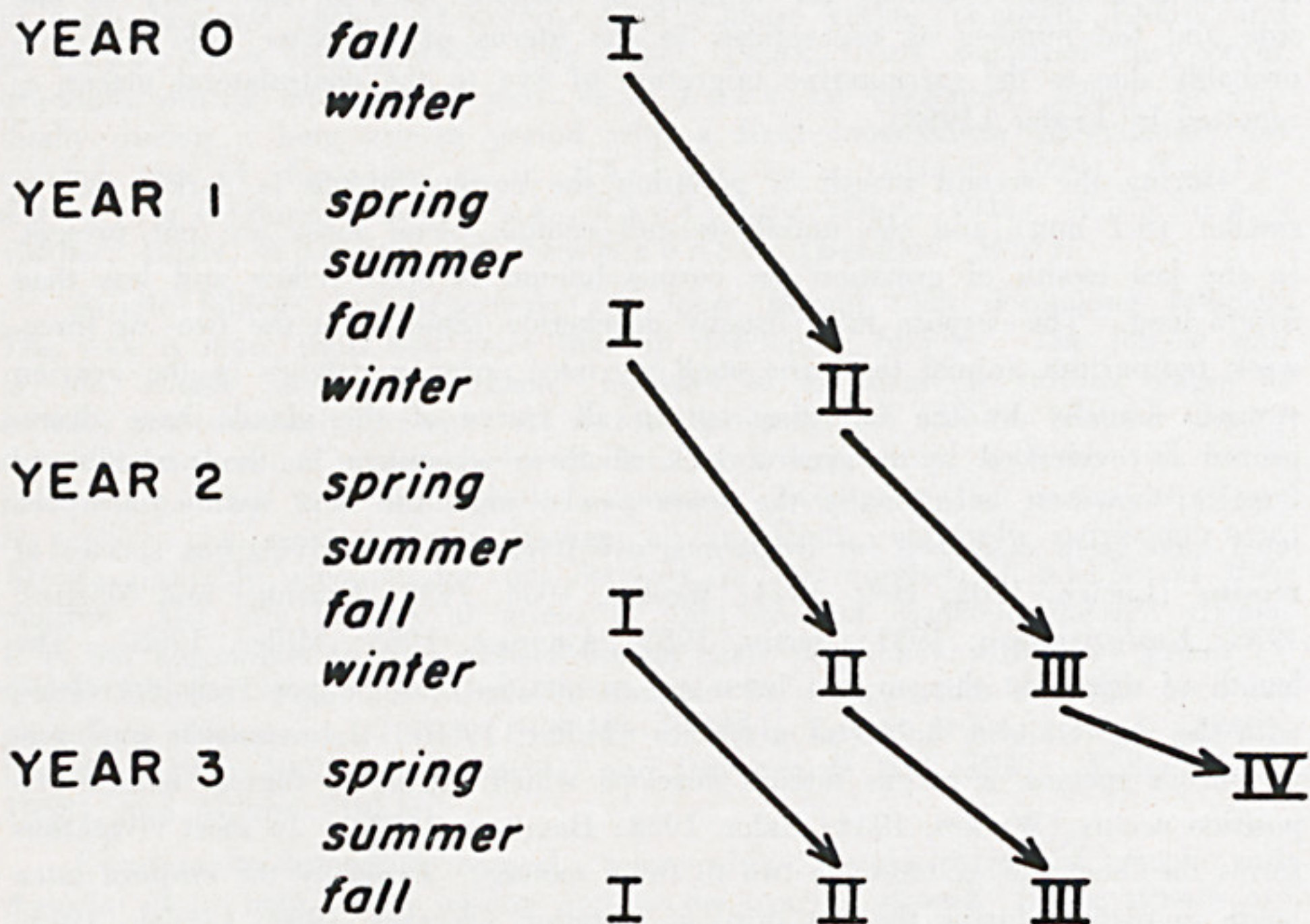


Fig. 2 — A diagram of the hypothetical sequence of follicular maturation in *Natrix rhombifera*. Roman numerals refer to follicle size groups.

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