Geographic Variation in Ovarian Cycles and Clutch Size in Cnemidophorus tigris (Teiidae)

Abstract. *Ovarian cycles and individual reproductive potentials of* Cnemidophorus tigris *in Colorado and Texas were studied by counts and measurements of yolked ovarian follicles, corpora lutea, and oviducal eggs. Colorado lizards lay one clutch averaging 3.4 eggs annually between May and August; Texas lizards average two clutches, each averaging 2.2 eggs, between April and mid-August.*

Geographic variation in reproductive activity has been recognized, mainly by inference, in North American lizards of several families. In species with extensive latitudinal ranges, several clutches of eggs may be produced annually in the southern part of the range; only a single clutch in the northern part (*1*). There is also evidence that the average number of eggs in each clutch is greater in the northern part of the range of a species (*2*). The relation of these two variables in a single species has not been established, nor has the importance of this variation in the adaptation of populations of a species been generally recognized. Our studies reveal significant geographic variation both in number of clutches per season and in average number of eggs per clutch within the range of *Cnemidophorus tigris* (*3*).

Cnemidophorus tigris ranges from southeastern Oregon well into northern Mexico, occurring in all the major deserts of North America. One of us (C.J.M.) studied populations of *C. t. septentrionalis* in Colorado National Monument, Mesa County, Colorado (*4*); the other (G.A.H.) studied *C. t. marmoratus* near Kermit, Winkler County, Texas (*5*). These study areas are about 950 km apart, near the northeastern and southeastern limits of the range of the species. Each of us took weekly samples of female lizards through two complete activity seasons (1962–63 in Colorado; 1963–64 in Texas) and determined ovarian cycles, clutch size, and reproductive potential from counts and measurements of yolk-filled ovarian follicles (Fig. 1), oviducal eggs, and corpora lutea (178 in Colorado; 257 in Texas) in reproductive lizards.

In Colorado, *C. tigris* leaves hibernation around 1 May, and mature females are active for 75 to 90 days each summer. Enlarged ovarian follicles (3 to 4 mm in diameter) are visible at emergence; 20 to 25 days later the enlarged follicles begin vitellogenesis and are ready for ovulation within 20 days, when 11.5 to 12.0 mm in diameter. After fertilization and shell deposition the oviducal eggs are laid—all within 2 weeks of ovulation. The median date of egg-laying in 1962 was 21 June. The corpora lutea disappear immediately after ovoposition, and the ovaries remain inactive (all follicles less than 2 mm in diameter) for the remainder of the season.

In Texas, the season of major activity starts in early April, although a few individuals may be active in February and March. Mature females become fully active before the end of April, remaining so until mid-August. Newly emerged females have enlarged ovarian follicles which start yolk deposition immediately and reach ovulatory (maximum average) size by 21 May. After ovulation, a second series of follicles begins vitellogenesis and reaches ovulatory size in approximately 30 days. The percentage of females with oviducal eggs or corpora lutea (indicating very recent laying) also shows bimodal distribution, with maxima about 21 May and 21 July. These data indicate that the Texas females lay two clutches of eggs each season. After the second clutch is laid, the corpora lutea disappear and the ovaries become quiescent.

The size of yolk-filled follicles at ovulation (10 to 11 mm in Texas; 11.5 to 12 mm in Colorado) and the size of the mature eggs (9 to 10 by 17 to 20 mm in Texas; averaging 9.8 by 18.5 mm in Colorado) are similar in the two populations.

In lizards the fact that clutch size is frequently correlated with body size (*6*) has obscured geographic variation in the clutch size of species with geographic variation in body size (*7*). The average clutch size in lizards from Colorado and Texas was calculated on the basis of yolked ovarian follicles, corpora lutea, and ovarian eggs. Independent calculations of average clutch size in these three ways produced no significant differences in result. In Colorado, 1st-year reproductive females average 2.9 eggs per clutch, older females lay an average of 3.9 eggs per clutch; the overall mean is 3.4 eggs. In other words, 1st-year females lay three eggs; older ones lay four. In Texas, 1st-year females average 2.1 eggs per clutch; older lizards average 2.8; the overall mean is 2.2 eggs, and the individual mean reproductive potential is 4.5 eggs per annum. This geographic variation cannot be explained on the basis of disparity in body size in the two populations, since the size of adult females and size-class distribution are approximately the same in the two areas.

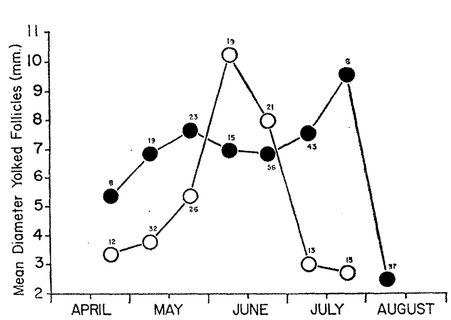

Fig. 1. Seasonal change in mean diameter of yolked ovarian follicles in *Cnemidophorus tigris* from Colorado (open circles) and Texas (solid circles); samples are lumped at 15-day intervals.

Compression of the reproductive function of *C. tigris* into a single cycle annually is probably a direct response to the shortened season of activity in the northern part of its range. Frost-free days average 218 in Winkler County, Texas; only 154 in Mesa County, Colorado. The short growing season and the severe winters in Colorado combine to reduce the amount of food available for early-emerging lizards and thus delay the start of vitellogenesis. Moreover, the earlier frosts in the fall in Colorado would prevent survival of hatchlings emerging in late August from a second clutch of eggs. If one assumes approximately equal longevity in the two areas, the greater number of eggs per clutch in the Colorado populations may have evolved as compensation for the climatically enforced single-broodedness. Judged from its great geographic range, local abundance, and competitive fitness, *C. tigris* is a successful species; this success may partly result from adaptability of the reproductive function.

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References and Notes

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4. Supported by NSF through a summer fellowship and by grant G-21903 to T. P. Maslin, Univ. of Colorado Museum.
5. Supported by NSF grant GB-13608 and AEC grant AT-40-1-2673 to D. W. Tinkle at Texas Technol. College.
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Quantitative Growth of the Mathematical Literature

Abstract. *Since 1868 the number of mathematical publications per year (measured by counts of titles abstracted) has grown from about 800 to 13,000 at an average continuous compound rate of about 2.5 percent per year, doubling about four times a century. Deviations from the exponential curve are clearly related to war, depression, and recovery. If the total number of publications prior to 1868 is estimated by extrapolating from the curve of annual output, the cumulative grand total of mathematical titles grows from 41,000 in 1867 to 419,000 by the end of 1965. Deviations from an exponential growth of 2.5 percent per year are negligible except for two "pauses" during world wars, after which the observations continue parallel to the theoretical curve. The well-known hypothesis of exponential growth of the scientific literature is strongly confirmed but at a rate less than half that found by Price and other investigators. The discrepancy appears to be due to the failure of previous studies to take into account the titles published before the beginnings of the time series used.*

There is overwhelming evidence that scientific literature increases exponentially (for examples, see *1–3*). Yet in spite of the existence since 1868 of at least one journal abstracting "all" mathematical titles, published data on the mathematical literature are lacking (*4*). Figure 1 shows the annual output of mathematical titles as measured by complete counts of author indexes (jointly authored papers counted only once) in the *Jahrbuch über die Fortschritte der Mathematik* for 1868 through 1940 and in the *Mathematical Reviews* for 1941 through 1965 (*5*). Because of delays in publication and abstracting, differences between nominal and actual dates of publication, and other random factors, the dating of a title is subject to significant errors. Hence we have plotted a 5-year moving average located at the middle year. The interruptions of steady growth are clearly related to the two world wars and the great depression of the 1930's. It is interesting to note that the wars produced almost equal minima, and that recoveries occurred at the same absolute linear rates, as indicated by the parallel straight lines. The break with linear recovery around 1957–1961 was due to a failure of abstracting to keep up with the literature (*6*).

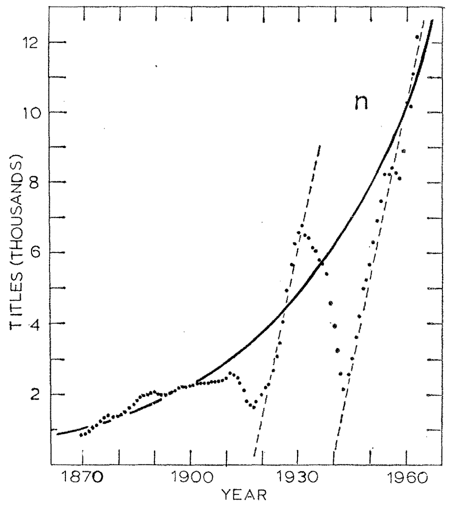

Fig. 1. Five-year centered moving average of the annual number of abstracts 1868–1965. The smooth curve n is given by Eq. 1 in the text. The broken lines suggest parallel linear growth in the postwar periods.

The smooth curve in Fig. 1 is the exponential

$$n = 1400\, e^{0.025(t\,-\,1880)} \qquad (1)$$

chosen to achieve close fit during the "normal" years prior to the first world war and to pass through what appear to be middle points of the war-induced oscillations (*7*).

Because of the violent oscillations in the war periods, Fig. 1 is hardly conclusive evidence for exponential growth, but it is essential to our main purpose of analyzing the growth of the cumulative total of mathematical titles. We could obtain cumulative totals by simply summing the successive yearly counts graphed in Fig. 1, but this would underestimate the total by ignoring the literature prior to 1868. To avoid this pitfall we estimate the cumulative total through 1867 by assuming that the annual output is given approximately by the smooth curve, that is, by Eq. 1. This gives an estimate of 41,000 titles through 1867 (*8*). We then obtain the cumulative totals by adding to 41,000 the successive annual numbers of titles shown in Fig. 1. These points are plotted in Fig. 2 together with the corresponding theoretical curve

$$N = 56{,}000\, e^{0.025(t\,-\,1880)} \qquad (2)$$

The fit in Fig. 2 is extraordinarily close, and deviations are clearly due to the two world wars, which appear to postpone growth rather than to alter its character or rate. These findings strongly support those of Price for physics (*1*, pp. 102–104; *2*, pp. 17–19). On the other hand, the rate of growth found here is only about half that found by Price. On the basis of data from several fields he conjectured "It seems beyond reasonable doubt that the literature in any normal, growing field of science increases exponentially, with a doubling in an interval ranging from about ten to fifteen years" (*1*, footnote, pp. 102). Such a doubling interval corresponds to an annual increase of from about 7 to 5 percent, whereas we have found here for mathematics an annual increase of about 2.5 percent and doubling about every 28 years.

Before jumping to the conclusion that mathematics has a different growth rate than other sciences, note that although Price speaks of "the literature" as though he were referring to the total literature, his data are actually for the literature in each field after a certain time, in each case the beginning of an abstracting service: 1900 for physics, 1908 for chemistry, 1927 for biology, and 1940 for mathematics (*2*, p. 10). Figure 3 shows the effect of similarly ignoring the mathematical literature prior to the various dates. The straight line is the semilogarithmic graph of the exponential curve of Fig. 2 and Eq. 2.

The curves P, B, and M are obtained by ignoring the literature prior to 1900, 1920, and 1940. Of course, all these curves will eventually approach parallelism with N, but up to 1950 they seem to be straightening out at much smaller doubling periods and much higher rates of growth. By ignoring the prior literature we have obtained growth rates comparable to those of Price. Indeed, curves P, B, and M look very much like his curves