Number 1 August 10, 1936

Editor's Note:

The publication difficulties which have lately beset all educational and scientific institutions are manifest. Coincident with reduced publication allowances and increased printing costs there has been a growth in research activity. The manuscripts submitted have far exceeded the printing budgets, necessitating the rejection or indefinite postponement of much worthwhile material. The result has been a loss to science and discouragement to the individual performing the work.

The San Diego Society of Natural History, as a partial remedy for this situation in its own case, begins herewith the publication of a third series of scientific papers to be known as the Occasional Papers. In this advantage will be taken of the newer and cheaper lithostatic process of facsimile reproduction. While not having the legibility and perfection of form of standard printing it is believed that it will be entirely satisfactory for the character of papers contemplated for this series. These will be reports primarily of interest to specialists, rather than the monographic type appearing in the Society's Memoirs or the descriptive and taxonomic papers contained in its Transactions. The two latter series will be continued as in the past.

A STATISTICAL STUDY OF THE RATTLESNAKES

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I - INTRODUCTION

Snake dens, or winter rendezvous, where numbers of snakes congregate in the autumn prior to hibernation, or emerge in the spring, are well authenticated. Amongst the many incredible tales of the serpent-tribe this, at least, has been attested by many reliable witnesses.

A number of persons, hearing of my interest in snakes, and particularly rattlesnakes, have written me of experiences with these dens. Some of these stories were no doubt true, others had grown considerably with the telling; but all lacked concrete verification.

Finally, one such letter was received October 17, 1930, from my good friend C. B. Perkins, then of Denver. In this he recounted his experiences in raiding a gathering place of the prairie rattlesnake in a prairie dog town east of Platteville, Colorado. This town he had been watching during the preceding summer and fall, and had finally been rewarded by the congregating of the snakes, of which he had succeeded in capturing a considerable number. But in its conclusion Mr. Perkins' letter differed from those previously received, for he wrote, "I am sending you today,by express, one hundred and fifty-three of these snakes." Here, at last, was what I had hoped to secure--a group of specimens from a single locality, collected within the space of a few days.

This shipment was the beginning of a series of raids on this and several adjacent prairie dog towns used by the rattlers as winter quarters, and a traffic in snakes began which did not terminate until Mr. Perkins' return to California in the spring of 1932. During this period I received, through his kindness, no less than 804 rattlers, all of which were preserved for study; and dimensional data on 57 additional specimens, which he had retained under observation alive or had sent to various scientific institutions, were made available to me. Thus, there is at hand a fairly complete statistical record of 861 specimens of the prairie rattlesnake, Crotalus confluentus confluentus, collected within a compact area and representing a complete cross-section of one rattler community.

Mr. Perkins' generosity has involved an obligation. A worker in any field of natural history invariably chafes under the handicap of lack of material; always there are questions just beyond solution because specimens from the right place, the right season, or sufficient in quantity are not at hand. But here was a series which ought to answer at least a few of the problems involving the rattlers of east-central Colorado; certainly one could not plead lack of material. They seemed to afford an opportunity to determine which of the obvious variations of the rattlers, in form and lepidosis, might be attributable to individual or sexual differences, and which to differences of species or habitat. It was hoped that these Colorado specimens (the Platteville series as they are called hereafter) would constitute a datum, or basis of comparison, for each differential character, which might be employed in evaluating the variations found in other series of the same subspecies, and thence the investigation might be extended into the other subspecies and species of the genus.

This has now been done, at least for some of the characters used in classification, and for certain morphological elements. While fundamentally it may be said that Mr. Perkins' Platteville series of confluentus constitutes the basis of these notes, corroborative data were secured from others, amongst which may be mentioned especially a series of confluentus from central South Dakota, of which 673 are in my own collection; these were secured through the courtesy of Mr. A. M. Jackley, who collected them in the field, and Mr. Howard K. Gloyd. There is likewise a series of 139 juvenile C. atrox from San Patricio, southern Texas, procured from Mr. H. J. Yoder; a series of 294 C. lucasensis brought in by Mr. Fred Lewis, from Cape San Lucas, Lower California; and a group of 244 C. c. oreganus from near Pateros, Washington, collected by P.J.Martin and others. I am also greatly indebted to many other individuals and institutions who have contributed specimens by gift or loan, so that I have been enabled to carry the investigation into all the rattlesnake species; to others I am obligated for information and data of various kinds. To all of these I hope to make acknowledgment elsewhere. Altogether scale counts and measurements have been available on more than 8000 rattlesnakes. Some 10,000 specimens have been seen alive, including all of the recognized forms except unicolor, polystictus, stejnegeri, and ravus.

This is not a monograph of the rattlesnakes, nor an attempt particularly to unravel the problem of the genetic relationships of the species. Rather it is a tracing of the trends of a number of different variables through the group, for a survey of the dispersion of characteristics of form and lepidosis constitutes the essential object of the investigation. If, thereby, relationships are indicated or determined, incidental steps toward the solution of the taxonomic problems will result; but primarily the purpose has been to ascertain the extent and equations of the variations; how they cluster about the mean; and whether they are individual, sexual, or specific. It is hoped, also, that through this study of the rattlers, some indication may be given of the general value of certain morphological characters as differential indicators amongst the snakes, particularly those which are ordinarily employed in ophidian classification. I am duly aware that this is a presumptuous program upon the part of one who has had no formal training in either statistics or herpetology.

Always the searcher hopes to find, perhaps hidden in some inconspicuous character, a definite and invariable key, distinguishing or individualizing one form from all its relatives, as if nature had written here the technical name of that form. But usually what is available is only the cumulative evidence of many characters, few of which coincide at points of divergence. Some of these may be translated into the statistics of average and correlation, and thereby serve, by weight of evidence rather than by rigid limits, to differentiate the forms. These cumulative weights are difficult to determine, and thus individual classification or group segregation becomes difficult. There is confusion between those variations produced by directional trends in form and others which are the result of individual or sexual differences. There are still other divergences, which, while definite as trends, are too unstable or too vague in value to warrant even the smallest definable distinction, that is, a division into subspecies or geographical races.

Differential characters may be of a type not describable as positive or negative, present or absent, nor in numerical or statistical form. An investigator of long experience with a certain animal, notes automatically these differences and their cumulative effectiveness, or weight; but they are difficult to explain or evaluate for the use of other workers with less acquaintance with that particular genus or family.

Thus, the large series becomes important in order that the weight and dispersion of the many characters, which in summation, constitute the basis of differentiation, can be followed through from the individual to a family or brood, thence to a localized group, then to collections of wider geographical range and varying habitat conditions, and thus to the classifications of subspecies, species, and genus. Meanwhile the parallel differences due to sex and age must be noted and correlated with the others. By such studies the values of the several variants as key or reference characters may be determined.

This involves also a study of the relative stability of characters. Large series make it possible to determine averages of the numerical data with relatively small probable errors of the mean, that is, the errors inherent in random sampling. Having determined these, as well as the dispersions of the variates, we may next check the significance of the differences (for various characters) between two groups, such as members of the same subspecies from different geographical locations, or ecological niches, to see how far divergence has gone and which characters show the highest degree of plasticity or mobility, and which, conversely, of stability. These data in turn should aid in the evaluation of subspecific and specific differences, thus indicating, by composite weight, relationships and the validity of taxonomic separation; for it would seem that differences in stable characters should be given more weight in judging species differences, than deviations in characters shown to be unstable within a species.

In discussing the interrelations and variations of a genus, either the characters, or the species may be treated consecutively. In many instances both methods are desirable, since only by this means are the relative values of the differences clearly evident; this, however, involves much duplication. In the present notes the character, rather than the species, is taken as the unit, the investigation being carried forward under such subjects as length, weight, head and tail proportions, fangs, venom, rattles, hemipenes, scale counts, etc. In each case some attempt is made to tabulate the variations by species; but the corollary presentation, that is, a listing of characters under each species with a complete species description, is, for the present, omitted.

For purposes of clarity a list of the species and subspecies considered valid is presented below:

1. Crotalus durissus durissus Linné, 1758.
   Central American Rattlesnake

2. Crotalus durissus terrificus (Laurenti), 1768.
   South American Rattlesnake

3. Crotalus unicolor de Jeude, 1887.
   Aruba Island Rattlesnake

4. Crotalus basiliscus (Cope), 1864.
Mexican West-Coast Rattlesnake

5. Crotalus enyo (Cope), 1861.
Lower California Rattlesnake

6. Crotalus molossus molossus Baird and Girard, 1853.
Northern Black-tailed Rattlesnake

7. Crotalus molossus nigrescens Gloyd, 1936.
Southern Black-tailed Rattlesnake

8. Crotalus adamanteus Beauvois, 1799
Eastern Diamond Rattlesnake

9. Crotalus atrox Baird and Girard, 1853.
Western Diamond Rattlesnake

10. Crotalus tortugensis Van Denburgh and Slevin, 1921.
Tortuga Island Diamond Rattlesnake

11. Crotalus lucasensis Van Denburgh, 1920.
San Lucan Diamond Rattlesnake

12. Crotalus ruber Cope, 1892.
Red Diamond Rattlesnake

13. Crotalus exsul Garman, 1883.
Cedros Island Diamond Rattlesnake

14. Crotalus scutulatus (Kennicott), 1861
Mohave Rattlesnake

15. Crotalus confluentus confluentus Say, 1823.
Prairie Rattlesnake

16. Crotalus confluentus nuntius Klauber, 1935.
Arizona Prairie Rattlesnake

17. Crotalus confluentus abyssus Klauber, 1930.
Grand Canyon Rattlesnake

18. Crotalus confluentus lutosus Klauber, 1930.
Great Basin Rattlesnake

19. Crotalus confluentus concolor Woodbury, 1929.
Midget Faded Rattlesnake

20. Crotalus confluentus oreganus Holbrook, 1840.
Pacific Rattlesnake

21. Crotalus mitchellii mitchellii (Cope), 1861
San Lucan Speckled Rattlesnake

22. Crotalus mitchellii pyrrhus (Cope), 1866.
Southwestern Speckled Rattlesnake

23. Crotalus mitchellii stephensi Klauber, 1930
Panamint Rattlesnake

24. Crotalus tigris Kennicott, 1859.
Tiger Rattlesnake

25. *Crotalus cerastes* Hallowell, 1854.
Horned Rattlesnake; Sidewinder

26. *Crotalus polystictus* (Cope) 1865.
Mexican Lance-headed Rattlesnake

27. *Crotalus horridus horridus* Linné, 1758.
Timber Rattlesnake

28. *Crotalus horridus atricaudatus* Latreille, 1802.
Cane-brake Rattlesnake

29. *Crotalus lepidus lepidus* (Kennicott), 1861.
Eastern Rock Rattlesnake

30. *Crotalus lepidus klauberi* Gloyd, 1936.
Green Rock Rattlesnake

31. *Crotalus triseriatus triseriatus* Wagler, 1830.
Mexican Spotted Rattlesnake

32. *Crotalus triseriatus pricei* Van Denburgh, 1895.
Arizona Spotted Rattlesnake

33. *Crotalus stejnegeri* Dunn, 1919.
Long-tailed Rattlesnake

34. *Crotalus willardi* Meek, 1905.
Ridge-nosed Rattlesnake

35. *Sistrurus ravus* (Cope), 1865.
Mexican Ground Rattlesnake

36. *Sistrurus miliarius miliarius* (Linné), 1766.
Carolina Ground Rattlesnake

37. *Sistrurus miliarius barbouri* Gloyd, 1935.
Southeastern Ground Rattlesnake

38. *Sistrurus miliarius streckeri* Gloyd, 1935.
Western Ground Rattlesnake

39. *Sistrurus catenatus catenatus* (Rafinesque), 1818.
Eastern Massasauga

40. *Sistrurus catenatus tergeminus* (Say), 1823.
Western Massasauga

It is to be expected that some of the above may be segregated into additional subspecies as further studies by workers in this field are carried forward. Also changes in names may be found to be necessary, as is indicated by studies in nomenclature which the writer now has under way.

In the presentation of some of the statistical data I have made some segregations between geographical groups of the same subspecies where there is a possible (or incipient) race not yet accorded recognition, as, for instance. Coronados Islands *oreganus*. Also, certain of the large series already mentioned are occasionally shown separately in order that the dispersion of characters in territorially restricted groups may be presented.

The order of publication of the several subjects discussed in this series is without logic or significance. Each is more or less complete in itself and publication will depend on the completion of the necessary data and the publication program of the San Diego Society of Natural History.

In the course of these investigations, new facts have already come to light on certain taxonomic problems of the rattlers. These have resulted in the description of new subspecies, or the reviving of forms previously thrown into synonymy. As these papers have appeared in other publication series the references are given here.

1930 New and Renamed Subspecies of Crotalus confluentus Say, with remarks on Related Species. Trans. S.D. Soc. Nat. Hist., Vol.6, No.3, pp.95-144, plates 9-12, map. Describes C.c.lutosus, C.c.stephensi (now considered C.m.stephensi), C.c.decolor (synonym for C.c.concolor Woodbury), C.c.abyssus. Discusses C.scutulatus, C.c.confluentus, C.c.mitchellii, and C.c.oreganus.

1930 Differential Characteristics of Southwestern Rattlesnakes Allied to Crotalus atrox. Bull. Zool. Soc. S.D., No.6, pp.1-72, plates 1-6, maps 1-3. Discusses atrox, tortugensis, lucasensis, ruber, exsul, and scutulatus.

1931 Crotalus tigris and Crotalus enyo, Two Little Known Rattlesnakes of the Southwest. Trans. S.D.Soc.Nat. Hist., Vol.6, No.24, pp.353-370, plate 23, map. Discusses these and related species.

1935 A New Subspecies of Crotalus confluentus, the Prairie Rattlesnake. Trans. S.D.Soc.Nat.Hist., Vol.8, No.13, pp.75-90, plate 8, map. Describes C.c.nuntius.

1936 Crotalus mitchellii, The Speckled Rattlesnake. Trans. S.D.Soc.Nat.Hist., Vol.8, No.19, pp.149-184, plates 19-20, figs.1-3, map. Discusses C.m.mitchellii, C.m.pyrrhus, and C.m.stephensi.

II - SEX RATIO IN RATTLESNAKE POPULATIONS

It has been my experience in examining preserved specimens of rattlesnakes contained in museum collections, to find a rather marked predominance of males. This condition applies to practically all species; and where sufficient specimens are at hand from different areas to afford a representative figure, the same situation will be found to exist in each separate area.

Table 1 shows the sex ratios by species of 8240 rattlers which were investigated. The 233 specimens of which the sex was not recorded represent heads, skins, embryos, and similar specimens of which the sex was indeterminate, together with some of which the sex was not noted. Subspecies are segregated only in the cases of *confluentus* and *mitchellii*; of the others not enough specimens are available to warrant separation for this particular study.

The table shows a numerical superiority of the males in all but one species. Where the available number of a species is sufficiently large to afford representative samples, say 100 or more, it will be observed that the sex ratio varies from 1.1 to 1.6 in favor of the males, the average being 1.3. Only three forms fall beyond this range; *horridus* is conspicuously low, and *nuntius* and *pyrrhus* unusually high. So consistent are these results there can be no doubt that the males collected outnumber the females.

Various explanations may be suggested to account for this unbalance of the sexes. There may be more males born than females, or there may be a higher mortality amongst the females. Again, since these figures merely indicate accumulations in collections, they may not be representative of the true situation in the wild, but rather show that females are less often captured than males. This, in fact, would be expected on the assumption that the males are less careful of concealment when searching for females in the spring mating season; or the females may be more secretive when heavy with eggs, and thus less often captured.* But a somewhat opposing theory would suggest that the females, if less active, would be more subject to capture and destruction.

We may check the original sex ratio by an investigation of broods at birth. Records are available of 56 broods, 15 subspecies being represented. These broods contained 463 young snakes, or an average of 8.3 per brood, the minimum being 2 and the maximum 18. Some had been born, others were unborn embryos. The sex can be determined in 453 young and it is found that there are 213 males and 240 females, or a male ratio of 0.89. Even allowing for errors in sexing these juvenile specimens, which, with the exception of the embryos (these have the male organs extruded), are more difficult to sex than adults, the result is conspicuously different from the general average shown in Table 1.

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* Dr. F. N. Blanchard informs me that the latter is not true in certain genera of snakes which he has investigated.

Table 1

SEX DISTRIBUTION

Species or Subspecies	Males	Females	Uncertain	Total	Ratio M/F
Durissus	59	54	7	120	1.19
Unicolor	1			1	--
Basiliscus	48	44	2	94	1.19
Enyo	39	22		61	1.77
Molossus	159	120	8	287	1.33
Adamanteus	26	16	12	54	1.62
Atrox	399	284	38	721	1.40
Tortugensis	21	7		28	3.00
Lucasensis	198	149	2	349	1.33
Ruber	154	118	16	288	1.31
Exsul	17	4		21	4.25
Scutulatus	234	143	20	397	1.64
Confluentus	1105	964	20	2089	1.15
Nuntius	122	63	3	188	1.94
Abyssus	18	12	2	32	1.50
Lutosus	229	157	7	393	1.46
Concolor	13	9		22	1.45
Oreganus	795	594	28	1417	1.34
Mitchellii	57	29	6	92	1.97
Pyrrhus	133	60	16	209	2.22
Stephensi	42	23	4	69	1.83
Tigris	26	15	6	47	1.73
Cerastes	180	140	6	326	1.29
Polystictus	9	8	1	18	1.12
Horridus	66	106	1	173	.62
Lepidus	90	71	2	163	1.27
Triseriatus	101	80	11	192	1.26
Stejnegeri	3			3	--
Willardi	15	13	4	32	1.15
Ravus	10	1	3	14	10.00
Miliarius	116	104	7	227	1.11
Catenatus	57	55	1	113	1.04
Total	4542	3465	233	8240	1.31

In addition to these broods, we have available several series of young of the year. Some of these were collected in raids on dens and are typical of young snakes going into their first hibernation or emerging therefrom. Others are groups of young just after birth but which could not be included amongst the single broods, since the mothers had not been segregated and the young therefore were all mixed together. Also there is a series of <u>oreganus</u> from San Diego County, California, where for some years I have been collecting juveniles for study. Included in this lot are all available specimens under 400 mm. in length, mostly collected in the autumn, but a few in the spring. All are young of the year. It may be assumed that they are in much the same category as a brood; there has not yet been an opportunity for any destructive or other selective forces or habits to cause an artificial sex ratio.

In the following summary the broods previously mentioned are also included:

	Males	Females	Ratio M/F
Sinaloa series of <u>basiliscus</u>	10	14	0.71
Mendocino series of <u>oreganus</u>	12	15	0.80
Smith-Dunkle series of <u>nigrescens</u>	44	39	1.13
San Patricio series of <u>atrox</u>	77	62	1.24
Jackley series of <u>confluentus</u>	80	72	1.11
Platteville series of <u>confluentus</u>	123	106	1.16
San Diego series of <u>oreganus</u>	102	107	0.95
Total, - - - -	448	415	1.08
56 Assorted broods	213	240	0.85
	661	655	1.01

From these figures it will be observed that there is a slight predominance of males amongst the young of the year. This almost balances the excess females in the broods so that when we combine the young from all sources, totaling 1316 snakes, there is almost exact equality, the male excess being only one per cent. Having in mind the variations to be expected in sampling of this kind, we feel there is every reason to believe that the sexes are born in equal numbers.

Coming now to the adults, we may next determine whether the discrepancy between the sexes is a real one or whether it is due to those circumstances of life function and habit which lead to the more ready capture of the males. If the latter be the case, the sexes should be found in more nearly equal numbers after the time of year of active sexual function. Thus the season of retirement or hibernation should offer a clue, and we are led to consider the Platteville series as they enter and issue from hibernation. For all specimens exceeding 400 mm. in length we have the following situation:

Season	Males	Females	Ratio M/F
Spring	104	98	1.06
Autumn	228	195	1.17
Grand Total	332	293	1.13

We see that, although there is a rather definite predominance of males, it is not nearly so pronounced as in the case of the specimens listed in Table 1, where the sex ratio, exclusive of the young already considered, is 1.40 in favor of the males.

In the Jackley series there were 552 adolescents and adults; of these there were 292 males and 260 females, a sex ratio of 1.12. These also represent autumn and spring collections about hibernating retreats. It will be observed that this agrees closely with the Platteville figure.

It may be suggested that sex characteristics might still be effective in causing a selection of snakes about hibernating dens, particularly in the spring, for the more active and ardent males might be more ready to come out daily for the first warmth of the season. This may partly account for the statistics of certain smaller spring raids on dens as indicated in the following schedule:

24 _C_._c_._lutosus_ (15M, 9F) taken by E. Raymond Hall May 22, 1929, 5½ Mi. SW.of Osceola,Nevada.

24 _C_._c_._lutosus_-_oreganus_ intergrades, (16M, 8F) taken by A. L. Hagar, 16 Mi. WNW. of Council,Idaho, May 21, 1932.

23 _C_._c_._lutosus_ (11M, 12F) taken by C.B.Perkins 10 Mi. NW. of Abraham, Utah, May 12, 1929. (6 on a succeeding date).

225 _C_._c_._oreganus_ (131M, 94F) taken by P. J. Martin and others, 6 Mi. N. of Pateros, Washington in May.

Here we have a total of 298 snakes with 173 males and 125 females, a ratio of 1.38, which is as high as the general average of Table 1. However, it is important to observe that in two instances (including the last) there was a conscious selection of the larger specimens, thus procuring more males. Deliberate selection of this kind must be guarded against in such studies or the results will be distorted. Also the raids should be made on several consecutive days (as was the case in the Platteville and Jackley series) or a difference in activity may affect the relative numbers of each sex secured.

Certain figures are at hand which indicate that there is a real seasonal difference in the frequency of capture of the sexes. In San Diego County records are available of 123 adult specimens of _oreganus_. We find that the sex ratio of the spring specimens (31 males, 23 females) is 1.35, while for the summer and autumn specimens (June to December) it is 2.29, there being 48 males and only 21 females.

Similarly, in a group of 122 adult C. scutulatus from Arizona, the spring ratio (18 males, 16 females) is 1.12, while the summer-autumn ratio (61 males, 27 females) is 2.26.

In a collection of 99 adult C. atrox from Arizona the spring ratio (15 males, 14 females) is 1.07 and the summer-autumn ratio (44 males, 26 females) is 1.69.

There is in these figures a rather definite indication that in the spring mating season there is a slight predominance of males; later in the summer, as the females become increasingly heavy with young, they seek seclusion and are not so often collected, hence at this time the males more strongly predominate.

Whether there are any species differences in sex ratio cannot be conclusively determined from the figures of Table 1, since the species which differ greatly from the mode are not represented in sufficient numbers to prove the point. It is possibly significant that all three of the mitchellii subspecies and their near relative, tigris, have abnormally high male ratios; it will be interesting to see if this holds for larger series. The low figure for horridus is somewhat more doubtful.

It may be noted that the only two exclusively island species (except unicolor, of which only one specimen was available), that is, tortugensis and exsul, have very high ratios of males to females, 3.00 and 4.25 respectively. Yet Coronados Islands oreganus, the only other form of which more than 10 island specimens are available, has an unusually low ratio, there being 11 males and 20 females, a ratio of 0.55. Evidently these rather small island series have been affected by the season of collection; at least we are not yet in a position to conclude that island sex ratios differ from those existing in mainland races.

Returning to a discussion of the 56 broods it may be stated that they vary in size from 2 to 21. A test for the significance of correlation between size of brood and percentage of males indicates that there is none--at least it is not shown in this relatively small number of broods. It is true that the only three broods of a single sex (with 2, 3,and 4 individuals respectively) have all females, but I do not consider this more than a result of chances in sampling. To prove anything on this point would require a large number of broods of a single species, since it is known that the size of the brood varies both with the size of the individual mother and the average size of the species, smaller races having smaller broods.

An attempt was made to check the sex distribution against a point binominal curve of equal sex distribution by allocating broods regardless of size to the percentage distribution of an 8-unit litter, this being the average size. But the method is of doubtful validity and the number of broods too small and too varied in size really to prove (as the results seem to indicate) that broods run somewhat higher in unbalanced distributions than is to be expected on the theory that the sex of each individual is the result of pure and independent chance. The following table contains the distribution:

M/F	8/0	7/1	6/2	5/3	4/4	3/5	2/6	1/7	0/8
Theoretical frequency	0.2	1.8	6.1	12.2	15.3	12.2	6.1	1.8	0.2
Actual frequency	0.0	4.0	6.0	10.0	12.5	7.0	8.0	5.5	3.0

If we concede a numerical inferiority of the males in the ratio of .47 to .53 (as indicated by the broods but not by the other young of the year) we have a somewhat closer agreement between the theoretical and actual distributions:

M/F	8/0	7/1	6/2	5/3	4/4	3/5	2/6	1/7	0/8
Theoretical frequency	0.1	1.2	4.8	10.8	15.2	13.7	7.4	2.5	0.3
Actual frequency	0.0	4.0	6.0	10.0	12.5	7.0	8.0	5.5	3.0

But the unbalanced broods are still high at the expense of the more evenly distributed; that is, the 7/1, 6/2, 2/6, and 1/7 broods are all well above the expected frequency.

Taking all of these data into consideration I am of the opinion that the following conclusions may be drawn with respect to the sex ratio amongst the rattlesnakes:

1. The sexes of rattlesnakes are born in approximately equal numbers.

2. There is a slightly higher mortality amongst the females which leads to an excess amongst adult males of about 10 per cent above the females.

3. Owing to the greater activity of the males, particularly in the summer and early autumn when the females are heavy with young, collectors capture more males than females, so that the adult males in collections average about 40 per cent in excess of females.

III. BIRTH RATE

Age Classes - Platteville Series:

The Platteville, Colorado, series of *Crotalus confluentus confluentus* offers an opportunity to make approximations of the birth rate of this species of rattlesnake, based on the numbers of eggs found in the females. Also, as all the snakes were collected when entering or issuing from hibernation, and without conscious selection as to size, it may be assumed that we have an average sample of all population elements. We can therefore determine the proportion of juveniles remaining at the first hibernation.

A statistical presentation of the data available is given in Table 2. These data represent a study of 841 out of 861 snakes comprising the Platteville series; egg records were not available on twenty.

These 841 specimens may be segregated as follows:

	Males	Females	Total
Juveniles (0 - 399 mm.)	123	106	229
Adolescents (400 - 579 mm.) . . .	41	44	85
Adults (580 mm. or over)	285	242	527
Total	449	392	841

The reason for dividing the adolescents from the adults at 580 mm. will appear hereafter.

Since these specimens were collected at the beginning or end of the hibernating season, the series may be considered as representing a single period in the life cycle, this being one during which the adult females should be carrying eggs.

Life Curve Summary:

Before presenting the birth rate calculations it will be advisable to consider the probable life curve of the species. As our specimens represent only a single period we must draw our conclusions in part from related forms. From San Diego County there are available numbers of *Crotalus confluentus oreganus* and *Crotalus ruber*, collected at various times throughout the year, all months being represented. From these we are able to plot approximate growth curves and draw the following conclusions:

1. Young rattlesnakes are born in the early autumn, in most areas in September or early October.

2. Females go into their third hibernation (at an age of about 26 months), carrying developing eggs; fertilization occurs in the spring and the first brood is born about the time the mother snake has completed her third year of life.

Table 2. Females with Eggs. Platteville Series

Size-Class	Number of Gravid Females	Percent Distribution of Gravid Females	Females without Eggs	Total Females	Gravid Females in Percent of Total Females	Total Eggs	Eggs per Batch Max.	Eggs per Batch Min.	Average Eggs per Batch	Average Eggs per Female	Distribution of Total Eggs in Percent
570-9	0	0	8	8	0	0	0	0	0	0	0
580-9	1	0.7	15	16	6	9	9	9	9.0	0.6	0.5
590-9	1	0.7	10	11	9	7	7	7	7.0	0.6	0.4
600-9	1	0.7	7	8	13	8	8	8	8.0	1.0	0.5
610-9	3	2.0	12	15	20	13	5	4	4.3	0.9	0.7
620-9	2	1.3	10	12	17	15	9	6	7.5	1.3	0.9
630-9	1	0.7	5	6	17	6	6	6	6.0	1.0	0.3
640-9	6	4.0	3	9	67	62	13	6	10.3	6.9	3.5
650-9	8	5.4	7	15	53	68	11	7	8.5	4.5	3.8
660-9	7	4.7	2	9	78	65	12	7	9.3	7.2	3.7
670-9	6	4.0	6	12	50	61	12	8	10.2	5.1	3.5
680-9	5	3.4	1	6	83	50	12	8	10.0	8.3	2.8
690-9	3	2.0	3	6	50	30	11	9	10.0	5.0	1.7
700-9	6	4.0	2	8	75	57	11	8	9.5	7.1	3.2
710-9	7	4.7	0	7	100	79	16	9	11.3	11.3	4.5
720-9	8	5.4	2	10	80	87	15	6	10.9	8.7	4.9
730-9	13	8.7	1	14	93	146	15	8	11.2	10.5	8.3
740-9	10	6.7	0	10	100	136	17	10	13.6	13.6	7.7
750-9	13	8.7	1	14	93	164	16	9	12.6	11.7	9.3
760-9	9	6.0	0	9	100	117	15	9	13.0	13.0	6.6
770-9	8	5.4	2	10	80	115	21	5	14.4	11.5	6.5
780-9	3	2.0	2	5	60	40	14	13	13.3	8.0	2.3
790-9	8	5.4	0	8	100	128	18	12	16.0	16.0	7.2
800-9	6	4.0	0	6	100	100	19	14	16.7	16.7	5.7
810-9	4	2.7	2	6	67	55	18	10	13.7	9.2	3.1
820-9	3	2.0	0	3	100	48	17	14	16.0	16.0	2.7
830-9	1	0.7	0	1	100	16	16	16	16.0	16.0	0.9
840-9	2	1.3	0	2	100	32	16	16	16.0	16.0	1.8
850-9	3	2.0	0	3	100	41	15	11	13.7	13.7	2.3
860-9	1	0.7	0	1	100	12	12	12	12.0	12.0	0.7
Total	149	100.0	93*	242*	62	1767	21	4	11.9	7.3	100.0

* Exclusive of 570-9 mm. class

This appears to be the typical life cycle, but there may be deviations. There seem to be well authenticated instances of snakes mating in the summer; and in the late spring some young have been found which were so small in size as to lead to the suspicion that they could not have been born in the autumn, but probably appeared subsequent to the hibernating season. Of course these statements have reference to snakes under natural conditions; the effect of captivity on growth and development is so material that it is doubtful whether observations on captive specimens are of much value in determining growth and maturity curves.

Fertility Statistics - Platteville Series:

Returning to the Platteville series of confluentus, we find the smallest female with developing eggs to be 588 mm. long, and that egg bearing continues up to the largest size reached by the females (863 mm.) The smallest true adults may therefore be considered to be about 580 mm. in length; however it will be noted from the sixth column in Table 2, showing gravid females in per cent of total females, that comparatively few of these small females are fertile, the figure averaging less than 20 per cent up to 640 mm. At this point there is a sharp increase in fertility to somewhat in excess of 50 per cent. Thus, we may conclude that the length-range of 580 to 640 mm. contains some large adolescents as well as some small adults; this is probably the range in which the large year-old snakes overlap the small two-year-olds. Above 640 mm. the fertility rate increases rapidly until it approaches 100 per cent in the largest sizes, as illustrated in Fig. 1. It is clear that with gravid females well over 50 per cent in all these larger sizes, it is proven (as would be expected) that young are normally borne annually.

The distribution of gravid females amongst the size groups is indicated in the third column of Table 2, and by the solid line in Fig. 2, in which the results have been generalized by smoothing out the fluctuations produced by the individual points. It will be observed that there is first a minor peak at 650 mm. followed by a principal peak at 750 mm. It is presumed that the first peak is the result of an advance to the adult stage of a group of adolescents, slightly more than two years old, while the second peak comprises the females which have reached full adult growth; the latter probably includes individuals from a number of successive annual classes.* The distribution of gravid females differs from that of total females primarily in the sharpness of the two peaks; the spread of total females indicating a more even distribution. This would tend to confirm the presumed overlapping of adolescents one year old with the lagging adults of the preceding year.

Columns 7 to 11 present the egg statistics in terms of total eggs, and minimum, maximum, and average eggs per gravid female; also the average eggs per female, whether or not gravid. The same data are set forth completely in Table 3. It will be noted that the eggs comprising a clutch vary in

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*There are no further peaks because the individual dispersion in size amongst the adults more than counterbalances the gradually increasing average size of successive age-classes.

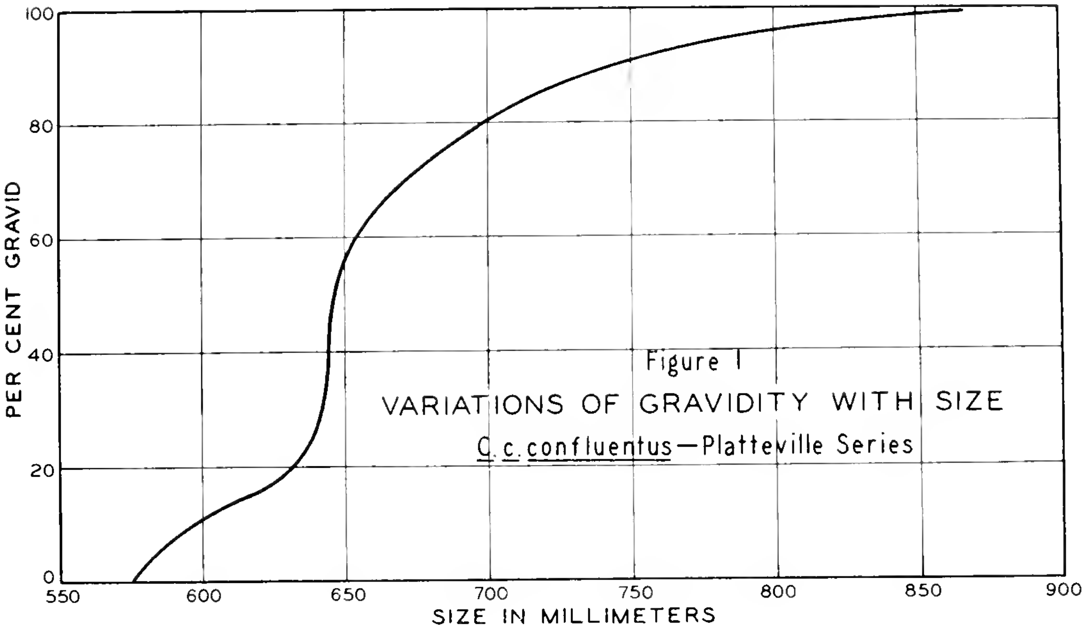
Figure 1
VARIATIONS OF GRAVIDITY WITH SIZE
C. c. confluentus—Platteville Series
PER CENT GRAVID
SIZE IN MILLIMETERS
0
20
40
60
80
100
550
600
650
700
750
800
850
900

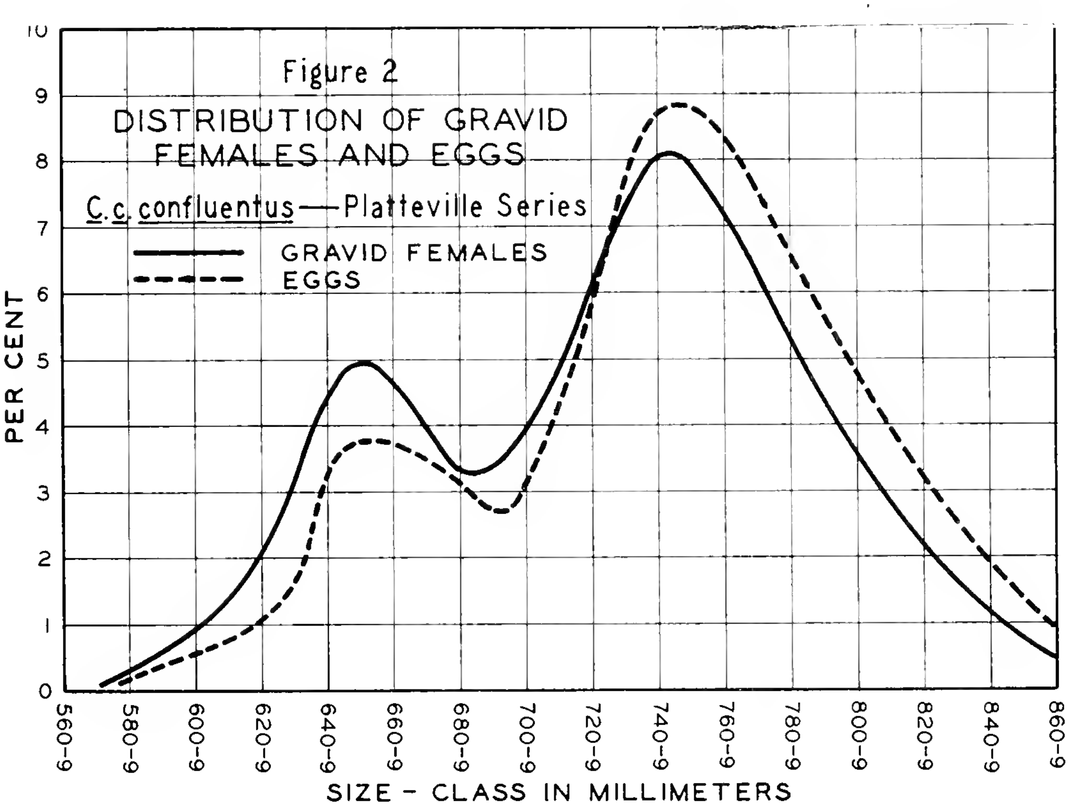
Figure 2
DISTRIBUTION OF GRAVID FEMALES AND EGGS
C. c. confluentus—Platteville Series
GRAVID FEMALES
EGGS
PER CENT
SIZE - CLASS IN MILLIMETERS
0
1
2
3
4
5
6
7
8
9
10
560-9
580-9
600-9
620-9
640-9
660-9
680-9
700-9
720-9
740-9
760-9
780-9
800-9
820-9
840-9
860-9

Table 3. Correlation of Egg Clutches with Size of Mother. Platteville Series

Size-Class of Mother mm.	Number of Eggs Secreted																	
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Total
580-9						1													1
590-9				1															1
600-9					1														1
610-9	2	1																	3
620-9			1			1													2
630-9			1																1
640-9					1	1	1	2		1									6
650-9				2	3	1	1	1											8
660-9				1	2	1	1	1	1										7
670-9					1	1	2		2										6
680-9					2		1		2										5
690-9						1	1	1											3
700-9					1	2	2	1											6
710-9						3			3				1						7
720-9			1			1	1	1	3			1							8
730-9					1	1	3	2	3	2		1							13
740-9							1		1	2	4	1		1					10
750-9						2			4	3	2	1	1						13
760-9						1			1	3	3	1							9
770-9		1							1	1		1	2	1				1	8
780-9										1	2								3
790-9									1			2		4	1				8
800-9											1	1		2	1	1			6
810-9							2							1	1				4
820-9											1			2					3
830-9													1						1
840-9													2						2
850-9								1				2							3
860-9									1										1
Total	2	2	3	4	12	17	10	10	23	13	13	11	7	11	3	1		1	149

number from 4 to 21, and that there is a definite tendency to increase in number per clutch as the size of the mother increases, from about 6 in the young mothers, to 15 or 16 in those of 800 to 820 mm. Beyond this a slight reduction is evident, although this cannot be considered definitely proven because of the small number of large fertile females available. The coefficient of correlation between the size of the mother and the size of the brood is found to be $+0.711 \pm 0.039$.

The total egg production curve (dash line, Fig.2) is slightly different from that showing the distribution of gravid females because of the effect of larger broods in the larger snakes (column 12, Table 2).

Taking this group of <u>confluentus</u> as a whole we find that there were 1767 eggs in 149 females, with an average of 11.85 ± 0.18 per batch. In the same size-classes there were 93 females without eggs, so that the eggs per individual of the total female population averaged 7.3. However, as has been pointed out, probably some of the 580-640 mm. snakes are only over-large adolescents. If we eliminate this group and the eggs which they produce, we find that the average eggs per female is 10.3, which should be taken as indicating the productivity of the fully adult female population, after allowing for infertile individuals.

<u>Birth Rate - Platteville Series</u>:

As 1767 eggs are produced by a population of 841 snakes of both sexes and all sizes, including juveniles (which latter at the next bearing season will be adolescents), a birth rate of 2.10 is indicated. However, this assumes that the population in the late summer will be of the same comparative composition as exists at the hibernating season; that there will be no selective losses. My experience would lead me to expect a high loss amongst the juveniles,* as compared with other elements of the population; this would tend to increase the apparent birth rate or ratio of young to the then existing population.

Of course the number of eggs found in the females does not give a true picture of the live births to be expected. Examination of the eggs discloses a number which are much smaller than their fellows of the same batch; some of these no doubt are defective. Broods born in captivity often include infertile eggs, distorted embryos, and deformed young snakes born dead or which succumb soon after birth. While these losses are probably of greater magnitude amongst captive snakes than are to be expected in nature, still there must be a considerable reduction from the egg count to live young.

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*Juveniles are more careless of concealment than adults and are preyed upon by various animals which could not successfully cope with an adult. See Klauber: Bull.Zool.Soc.San Diego, No.8, p.59, 1931.

We might hope to have some indication of the population distribution which exists in early autumn, when the young are born, in the proportion of juveniles that are present (or at least captured) at the season of hibernation. We find the ratio of juveniles to adolescents and adults to be 229 to 612, or 0.374. Out of a total population of 612 existing in September the gravid females probably numbered 114. This figure is reached by eliminating the females which, as of the succeeding hibernating season, are carrying eggs for the first time. This gives a birth rate (based on juveniles still alive and collected at hibernation) of only 2 per brood, which is decidedly too low. We are therefore forced to conclude that there is a heavy mortality of juveniles between birth and hibernation, or that there is some selective effect tending to reduce the proportion of juveniles caught when the dens are raided in the autumn and spring. Probably both factors are effective. It is not impossible that juveniles may favor individual retreats to a greater extent than adults, owing to inability to find the dens or the difficulty of traveling to them.

If we allow an average loss of three per brood for infertile eggs and defective young, we have 9 live births per brood and a birth rate of 1.65 young per unit of total population at the time of birth. Thus, for a short time in the late summer, the rattlesnake population is more than doubled, but the high mortality amongst the juveniles must soon cut this ratio extensively, so that by the time the hibernation season is at hand the juveniles already number less than the adult population, although probably not quite to the extent indicated by the juvenile proportion of 26.7 per cent found in the Platteville series. This figure of 26.7 per cent is closely approximated in each of the four separate major catches which constitute the Platteville series, so that it may be taken as a true index of the number of juveniles that stray outside of the prairie dog holes. Mr. Perkins informs me that about the same relative proportion of adults as juveniles escaped during his raids.

Selective losses are less important amongst the young in the spring season than in the autumn. If we assume that all of the snakes between 400 and 579 mm. were born the previous year, and that half of those between 580 and 639 mm. (this being the area of overlapping between the one- and two-year olds) represent last year's broods, we find that these adolescents represent 26.5 per cent of the population exclusive of juveniles; in other words, the adolescents have the same ratio to the older classes that the juveniles have to those of an age greater than themselves. This would indicate that the young hold their own in the spring.

Statistics of Jackley Series:

The Jackley series of C.c.confluentus from the vicinity of Pierre, South Dakota, also furnishes some data on the size of egg clutches; but not on birth rate or proportion of gravid females, for this series does not represent an average sample of the snake population, a full quota of juveniles not having been collected.

There are 673 snakes in the series; of these there are 107 gravid females, containing 1151 eggs. The eggs per clutch average 10.76 ± 0.21 compared with 11.85 ± 0.18 in the

Platteville series. The clutches vary in size from 4 to 20. The smallest female containing developing eggs was 683 mm. compared with 588 mm. in the Colorado specimens. The maximum was 1020 mm., but this was a rather unusual specimen, the next largest being 950 mm. The largest Platteville female was 863 mm. Thus, it will be seen that the South Dakota adult females run about 100 mm. longer than those from Colorado; however, the productivity per female does not show an increase in South Dakota over Colorado, notwithstanding the correlation between size of mother and number of eggs within each series. This correlation in the South Dakota series is $+0.704 \pm 0.046$ compared with the figure of $+0.711 \pm 0.039$ found in the Platteville group.

It should be understood that these statistics on both groups are made from counts of developing eggs. These are relatively large and yellow in color. Interspersed with them are frequently found white eggs of much smaller size which are not counted. Also, a few females are found (some clearly immature) which have only small white eggs of this type, presumably for development at some future time. These small eggs number up to 25 in a single female. They cannot be counted with great accuracy, and as neither their time of development nor the proportion that will come to maturity is known, they have been omitted entirely from consideration in the statistics herein discussed.

At the time of hibernation the developing eggs vary considerably in size, some typical clutches in the South Dakota series average in mm. as follows: 32 x 17, 28 x 15, 34 x 16½, 34½ x 15½, 30 x 17½, 27 x 14, 37 x 18, 30 x 14, 31 x 13, 21 x 10, 15 x 7½, 36½ x 16½, 31½ x 13. There were altogether 121 eggs in these measured clutches. These figures are to be considered only approximate as the eggs are extremely soft and flexible, hence the dimensions depend somewhat on the method of support. There is considerable variation within each clutch; for example, a clutch averaging 32 x 17 mm. varied from 36 x 19 mm. to 27 x 14 mm. The undeveloped eggs, which are white in color, vary in all sizes from mere pinheads up to about 5 mm. x 3 mm., and their segregation from the developing eggs is rarely difficult.

Egg Growth in Hibernation:

It should be noted that the fall catches were made early in October, and that the snakes issued from hibernation in mid-April. However, in each case actual preservation took place about a month later, in November or May. Measurements of a considerable number of the eggs in the Platteville series, indicate that there is little growth during the hibernating season, as is indicated by the following figures:

	Length mm.			Width mm.		
	Max.	Min.	Aver.	Max.	Min.	Aver.
Autumn - - - - - - - - - -	29	18	23.2	17	8	12.1
Spring - - - - - - - - - -	28½	18½	24.5	15½	8	12.8

The growth in each dimension during the hibernating season is thus found to average about 6 per cent. In making these measurements only normal, developing eggs were considered; the small, white non-developing eggs were omitted.

Table 4. Rattlesnake Egg Batches or Broods

Species	Number in Brood																								Total	Ave.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	30		
C. durissus												1						2		1					4	17
C. basiliscus														1										1	2	22
C. molossus			3	1	3	1																			8	5
C. adamanteus																		1							1	18
C. atrox				1	1	2	7	3	5			1						1				1	1		23	9
C. lucasensis			4	2	3	2	1	1			1	1													15	6
C. ruber					1	5	3		3		2		2												16	8
C. scutulatus					2	3	2		5		2														14	8
C.c. confluentus																										
Platteville Series				2	2	3	4	12	17	16	10	23	13	13	11	7	11	3	1		1				149	12
Jackley Series				1	4	3	6	12	15	16	9	10	10	5	8	3	3	1		1					107	11
Miscellaneous					2	2	3	4	3	6	3	1	1	1	3	4	1	2	1	1					38	11
Total confluentus				3	8	8	13	28	35	38	22	34	24	19	22	14	15	6	2	2	1				294	11
C.c. nuntius			1	1	2		1			1															6	6
C.c. abyssus						1							1												2	10
C.c. lutosus			1		1	2			2		2	1	3												12	8
C.c. oreganus	1	1	8	9	5	2	3	1	5	4	3	2	4	1											49	7
C.m. pyrrhus			1	2	1																				4	4
C.m. stephensi						1		1																	2	7
C. tigris					1																				1	5
C. cerastes							2				1	1	1			1									6	11
C. enyo						1			1																2	8
C. horridus					2	1	2	2	2	2	1	5	2	2			1								22	11
C. lepidus		1	3	1				1																	6	4
C. triseriatus			1	3	3	1	2	1																	11	5
C. willardi						1																			1	6
S. catenatus			1	1	3	2	1	2	1			1													12	7
S. miliarius											1						1								2	14
Total	1	1	23	24	36	33	37	40	59	45	35	47	37	23	22	15	17	10	2	3	2	1	1	1	515	10

I have previously mentioned the fact that the smallest fertile female in the Platteville series, has a length of 588 mm. and that the range, 580 - 640 mm. is presumed to contain half adolescents and half young adults, the faster growing members of the former class having caught up with the slower members of the latter. Attention should be called to the fact that these figures, 588 and 640 mm., have reference to young adult females at the time of hibernation; when their first broods are born in the early autumn, these individuals will have increased somewhat in length so that their differences from the average size of the adult females will be somewhat reduced. From certain rattle studies I would estimate this increase at not less than 120 mm. per snake, so that we may presume the smallest females to have a length of about 700 mm. at the time of the birth of their first broods. This refers only to the Platteville series of C.c.confluentus as found in east-central Colorado. In the Dakotas and Montana they will be about 100 mm. longer; and near Winslow, Arizona, where they have differentiated into the stunted subspecies, C.c. nuntius, they will be about 250 mm. shorter than the Colorado specimens.

Sizes of Rattlesnake Broods - Other Species:

For comparative purposes such data as are available on sizes of broods in C.c.confluentus in addition to the Platteville series, and in other species are given in Table 4. There are represented 515 egg batches or broods with an average of 9.9 young per brood.

Obviously, these data are too fragmentary to warrant extensive conclusions, since comparatively few broods are available in most species. The larger species (atrox, ruber, etc.) are probably not fairly represented, as the largest females do not ordinarily appear in collections; thus we may expect that their broods will average somewhat larger than the tabular figures would indicate. The few broods of durissus and basiliscus suggest that these large rattlers are probably prolific.

Smaller species of rattlers, as for instance, lepidus and triseriatus, have fewer young than the larger species. Stunted subspecies, such as C.c. nuntius, show the same tendency. Three batches from the stunted oreganus on Coronados Islands, averaged only 3 eggs. The embryos of these small species are both longer and heavier in proportion to the dimensions of the mother than are the embryos of the larger species; thus, there are physical limitations preventing more numerous broods in the smaller species. This fact is quite evident upon a visual inspection of full term embryos and parents, and is corroborated by measurements.

Conclusions:

1. The smallest fertile females in C.c. confluentus from Colorado are about 585 mm. long. At 640 mm. there is a sharp increase in fertility, which tends toward 100 per cent above 700 mm. These lengths are determined about 6 months prior to the birth of the initial broods.

2. The egg production curve of C.c. confluentus reaches a maximum at 750 mm., owing to the high proportion of adult females of approximately this length.

3. Broods of *C.c.confluentus* vary from about 4 to 21. There is a definite increase in number of young with the size of the mother, the coefficient of correlation being about +0.7. _ e eggs average about 11 per batch.

4. The birth rate of a rattlesnake population is about 1.65, but there is a considerable loss of juveniles between birth and hibernation, so that when the latter season arrives the juveniles number only one-quarter of the population.

5. The eggs seem to increase about 6 per cent in linear dimensions during the hibernating season.

6. Fragmentary data from species other than *C.c.confluentus* indicate that fully adult rattlesnakes normally give birth to from 3 to 20 young, the average being 10 or 11. Smaller species, such as *triseriatus* and *lepidus* tend to have fewer young, usually numbering 4 to 6.