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AN OUTLINE FOR THE STUDY OF A REPTILE LIFE HISTORY

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The renewed interest of biologists in natural populations, the development of the new systematics, population genetics, biodemography, and biosociology, i.e. of bionomics, or ecology in the broadest sense, has brought demands for detailed information on life histories of animals. The herpetologist is thus obligated to reexamine many of the standards and customary procedures in natural history. Renewed emphasis is also being placed on the organization of the knowledge comprised in natural history. Investigations in autecology (the ecology of the individual or of the individual species) are aimed toward the development of significant generalizations and principles. The modern systematist should not and must not divorce his thinking from ecology; the ecologist must not ignore systematics. While condemning the ecologist for ignoring systematics, the systematist has often been guilty of ignoring ecology. There is an urgent need for men thoroughly trained in the techniques of both ecology and systematics, men who can accelerate the trend toward a blending of these fields.

The investigator interested in reptilian populations finds but few studies of the bionomics of reptiles that meet critical standards. He finds an assortment of fragmentary facts that are difficult if not impossible to integrate, and often immediately require the test of repetition. It may be pointed out that repetition of field observations in a critical spirit may be fully the equivalent of experimental test. There seems to be a need for a statement of minimum requirements of information basic to the formulation of suggestions for a systematic approach to research on natural populations.

Perhaps the best test of significance of an observation in "natural history" is one similar to the test for the adequate description of a species or subspecies. Does the observation reflect an attribute of a given population? Is it reported in such a fashion that it may be integrated with other observations to state such an attribute? Or, has the research merely reported an aberrant or extreme behavior pattern, an anomalous situation, or such fragmentary data that it fails to express any particular fact as an attribute of a population?

What information is required in a definitive life history investigation? Ideally? What, practically, can the investigator hope to contribute? In what areas of biology may his data be applicable? What are the prevalent fallacies in life history analyses? Some attempt is made here to indicate limits and to designate specifically the obligation of the student interested in natural populations of reptiles. Many of the techniques developed by the ichthyologist, mammalogist and ornithologist may well be utilized by the herpetologist. There is an urgent need for the development of new techniques of research and for new applications of old ones. The herpetologist does not have the equivalent of the procedure of the ichthyologist for determining the age and growth of an individual by the examination of the growth lines of scales; nor does he have the trapping procedure for systematic sampling as used by the mammalogist, or the activity recording techniques developed by the ornithologist. Equivalents of these techniques are among our greatest needs. All of the needs for herpetological investigation cannot be enumerated in this paper, nor can all of the techniques developed in other fields be mentioned, but the bibliography is intended to provide suggestions and a key to the vast literature.

The herpetologist concerned with the study of a single form cannot hope to explore intensively all of the questions presented in the following discussion, but his awareness of the problems and of the need for information will permit him to make observations that otherwise might not be recorded. A serious report on a life history should be the result of a planned, long term research project. Such a report will integrate all of the minor elements of the topic to be gleaned from the literature with the more directed accumulation of planned observations of the author. The investigator, through proper planning, may maintain several such research programs. The outline that follows is purposely elaborated; and it includes much detail that may appear unnecessary to my colleagues; but it is directed to the students of the future who may be approaching similar problems from both the ecological and the systematic side. An early and comparable effort to systematize studies in life histories that has had a long usefulness is the summary of Walter P. Taylor (1919). Fitch (1949) presents many valuable suggestions for the student interested in natural history.

This paper is the outgrowth of an outline for the study of a reptile life history prepared originally under the direction of Dr. Norman E. Hartweg, University of Michigan. Its development has been encouraged by the critical and generous comments of Mr. Karl P. Schmidt, Chicago Natural History Museum. I am indebted to Mr. Roger Conant, Philadelphia Zoological Garden and Mr. Arthur Loveridge, Harvard University for their suggestions. The group of graduate students in herpetology at Tulane University has been a constant source of stimulating challenge in the preparation of this report. Mr. A. H. Chaney, Mr. Robert Gordon, Mr. Paul Anderson and Mr. Richard Johnson have been of particular aid.

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I. *What are the morphologic characteristics of the population to be studied? Is action taken to insure that the data reported are* *obtained only from individuals of the genus, species or subspecies intended to be studied?*

A. What is the taxonomic status of the population? What are the diagnostic features? How are these related to the formal description of the species or subspecies? Are these sharply or only obscurely characterized?

These data are of extreme significance. Excellent information must often be discarded by subsequent workers because the author has failed to indicate clearly the taxonomic characteristics of the population studied. Description must thus be such that any investigator can recognize the population regardless of changes in nomenclature.

B. What other names have been attached to this population?

C. What samples of the population were collected and preserved and where are they deposited? Museum numbers?

A representative series supporting the description given must be collected and deposited in a suitable museum collection. Failure to do this is almost characteristic of ecological investigations, yet the conclusion submitted are often not acceptable because of questionable identification of the material on which they are based.

D. What variation is observed in the individuals composing the population? Of what is this variation a reflection? Precise analysis and explanation of individual variation is an obligation. Dice (1952) points out that few museums have adequate storage or curatorial facilities to retain the large number of specimens necessary for the analysis of variation in local populations. The investigator must often utilize materials that cannot be available to future workers; his responsibility is thus multiplied. Through such studies associated with field investigations we may hope to accumulate the data basic to systematic studies at the intraspecies level.

1. What changes in color intensity, in pattern, or morphology occur from birth to old age? Are there any correlated sex differences? How are these changes related to taxonomic investigations? The limited information available on ontogenetic changes in "characters" has resulted in much confusion in taxonomy. The trend in herpetological research toward thorough analysis of such changes promises the development of a basis for substantial clarification of the status of many forms (Oliver, 1951).

2. Is the variation correlated with differences in the external environment?

With a gradient in the external environment? Is the

the variation due to differences in genotypes or does it reflect the responses of a specific genotype to different environments?

Investigations often query the status of the variation described but do not perform the simplest of experiments aimed at evaluating the genotypic flexibility of the organism studied. Some investigations suggest that some of the characters considered to be of taxonomic importance are merely phenotypic modifications (Fox, 1948). It is essential to the systematist that he determine whether variations are the result of heredity or environment or both.

3. What are the ontogenetic changes in mass as expressed by measurements or weight? What is the maximum size attained? Sex differences?

   Although absolute size is not an acceptable taxonomic character for poikilothermic vertebrates, genetic differences in potential natural longevity or growth potentials may be reflected in differences in maximum sizes between populations (Lagler and Applegate, 1943).

   What procedures were used in mensuration? Weighing?

   Care must be used to insure adequate mensuration practices and to insure that the investigator clearly reports his procedures (Simpson and Roe, 1939; Cazier and Bacon, 1949). Much confusion has been caused by misunderstandings resulting from failure to specify the methods followed. The significance of the limits of error in such data should be borne in mind. When measurements are accurate only to millimeters, proportions calculated to three decimal places give a false aspect of accuracy of the data.

4. What are the principle differential growth changes in each sex? How are these changes related to the major phases of the life history?

   Failure of the systematist to recognize the presence of differential growth has led to the erroneous use of proportions. If detailed quantitative studies cannot be made, the investigator should, as a minimum, designate the gross changes in proportion. This is a particularly acute problem in poikilothermic vertebrates (Hersch, 1941).

II. *What is the geographic range?*

The range should be expressed first in terms of museum specimens or records of authorities. All questionable records should be deleted. The range definition should indicate the distribution of existing populations (Grobman, 1950). These data may then, in connection with other information, form the basis for the statement of a supposed "true range".

A. What are the factors limiting the range?

These must be considered in terms of the ecological data assembled during the progress of the investigation with particular reference to the total knowledge of the ecological valence of the animal and possible barriers to dispersal (Darlington, 1948; Cowles and Bogert, 1944; Dice, 1952). It is especially important to note that the limiting factors may be entirely different on the different borders of the range of a species (Schmidt, 1950).

B. What physiographic and climatic factors are characteristic of the range?

1. What are the annual temperature and rainfall cycles?
2. What are the mean annual, minimum and maximum temperatures in the warmest and coldest parts of the range?

   Whenever feasible, temperature and rainfall data collected by the investigator in the areas of intensive study should be utilized. Of necessity, the investigator must often use meterological and climatological temperatures, but their interpretation should be based on the data of the researcher (Baum, 1950).
3. Does temperature summation (heat summation) affect the distribution of the species investigated?

C. What is the principal habitat? Marginal habitat?

1. Are microclimates of significance? throughout the range? at the periphery of the range? (Geiger, 1950; Diem, 1951).
2. What vegetational types characterize the habitat?
3. Do size or age groups tend to occupy different habitats?
4. Does the animal have an innate habitat recognition mechanism? (Svärdson, 1949; Tinbergen, 1948).

III. *What is the age and sex composition of a local population?*

A. What annual changes occur in the composition of a local population?

1. What is the sex ratio in mature individuals during the breeding season? How does this change during a single year?

   Sex ratios are often reported without reference to maturity or to the breeding season although radical changes do occur in some reptile populations. Estimates of the relation of sex ratios to natality should be based only on the relative frequency of mature individuals (Forbes, 1940; Cagle, 1948).

Sex identification is frequently reported without reference to the criteria used. What are these criteria? Secondary sex characters? Gonad condition? If dissection, on what basis was sex determined?

2. What is the sex ratio in juveniles? At birth? In progressive age groups?
3. What annual changes occur in the ratio of juveniles to adults? What is the potential contribution from "young of the year" to the adult segment of the population?
4. Can an ecological life table be constructed?

   The difficulty of determining mortality rates in most reptiles forbids the successful completion of such tables yet an attempt to collect data basic to the estimation of survivorship curves should be made (Deevey, 1947).
5. What are the major predators? Is predation pressure a significant factor in annual and long term cyclic changes? What is the relation of loss from predation to population density? (Errington, 1946).

B. What long-term cyclic changes occur in the composition of the local population? What is the cause of such cycles? Is exhaustion of the adreno-pituitary system a factor as has been demonstrated for some mammal populations? (Christian, 1950; Elton, 1942).

C. Do local populations differ in composition? If so, what is the basis of such differences?

Adequate local sampling provides a basis for obtaining answers to such questions. It has been demonstrated that substantial differences may be present in the compositions of local populations. Comparison of population samples must be tempered with an awareness of the difficulties of obtaining such samples. Series of specimens preserved in museum collections are rarely unbiased samples of natural populations. The student should note particularly those few long-term studies in local areas (De Haas, 1941).

D. Does the individual animal or the mated pair occupy a home range (or activity range as defined by Carpenter, 1952). Territory?

1. What is the size of the home range and of the territory?
   a. What features of the habitat may modify the size?

b. What is the relation of the size of the territory or home range to density?

c. Does the individual have homing ability? If so, what are the mechanisms involved in orientation?

The recovery of marked individuals in short-term and long-term studies will provide information on these questions. A wide variety of methods have been used for the marking of reptiles: metal bands or plates (Wickham, 1922); scale clipping (Blanchard and Finster, 1933; Conant, 1948; Fitch, 1949); plate notching (Cagle, 1939); tattooing (Woodbury, 1948); branding (Woodbury and Hardy, 1948); painting (Cagle, 1946). Trapping and other special collecting procedures are described by Dargan and Stickel (1949), Lagler (1943a). The calculation of size of home range from trapping results is discussed by Hayne (1949) and Stickel (1950). Stickel and Cope (1947) summarize information on home ranges. Schaefer (1941), Bailey (1952) and Leslie (1952) discuss the estimation of size of animal populations by marking experiments.

The multiplicity of problems involved in animal orientation are ably discussed by Fraenkel and Gunn (1940).

2. Is the territory selected by the male, female or both? Do both sexes participate in its defense?

a. What are the characteristic behavior patterns used in defense of territory?

Lowe and Norris (1950) summarize the reports of aggressive behavior in snakes.

b. What is the chief stimulus to maintenance of territory?

c. Is the territory maintained throughout the year or or only during short periods?

Nice (1941) presents a classification of the types of territoriality.

IV. *What is the density of the population?*

There should be more than a vague estimate of density expressed as rare, common or abundant. The objective should be to gain a measure of the number of individuals in a given area expressed in terms clearly defined by the investigator. The use of the concepts of abundance, and relative apparent abundance as suggested by Marr (1951) is recommended. The method selected for this determination of abundance must rest on the knowledge of the ecological requirements of the individual. Kendeigh (1944) provides a suggestive review of the procedures for measurement of bird population. Andrushko (1936) suggests techniques suitable for some species. A summary of methods is presented by Thomas Park (1950). Information of particular value in estimating populations from recovery of marked specimens is given by Ricker (1948), Jackson (1939) and Bailey (1952). This procedure has been applied to reptiles by several authors (Cagle, 1950; Fitch, 1949; Stickel, 1950).

A. What is the relation of density to the questions posed in sections I, D and III A to D (Blair, 1951)?

B. What is the relation of density of the form studied to that of other reptiles inhabiting the area? (Fitch, 1949; Cagle, 1950; Cagle and Chaney, 1950).

V. *What is the potential reproductive capacity? What is the relation to realized reproductive performance? What are the best measures of natality?*

A. At what age and/or size does the animal become sexually mature?

1. When are the secondary sex characters developed? What is the relation of time of their appearance to the potentiality of sexual functioning? (Regamey, 1935)
2. What cyclic changes occur in secondary sex characteristics?
3. What is the relation of age of attainment of maturity to the annual reproductive cycle?

   Investigators often fail to indicate what they mean by sexual maturity. Care must be exercised that the criteria for maturity are defined. In reptiles these may concern the presence of oviducal eggs in females, of corpora albicantia, of ovarian follicles of a specified size or ovaries of a specified weight or volume (Altland, 1951). In males a specific stage of spermatogenesis, a specified testicle weight or volume in relation to an indication of total body mass or the presence of motile sperm may be useful (Cieslak, 1945; Cagle, 1944; Risley, 1938; Fox, 1952). No adequate techniques are available for determining the age of an individual reptile. The procedures used by Bryuzgin (1939) should be further explored. Bryuzgin concluded that rings discernible in cleared skull bones of snakes could be used to determine age.

B. What is the total period of reproductive activity in the life of an animal?

1. Does the annual reproductive potential remain the same, decrease or increase with age?
2. When does senility occur?
3. What is the ecological longevity?

C. What is the annual realized reproductive performance?

1. What is the annual period of reproductive activity in females? in males? What is the relation of this period to the total annual activity cycle?

   Baker (1947) discusses the causes of breeding seasons. Volsøe (1944) describes seasonal fluctuations in the reproductive system. Kendeigh (1941) summarizes information on the relation of length of day to gonad development. This period is usually considered as that period in which the females are "carrying" young or are laying eggs. Much confusion has resulted from failure to delimit this period. Thus it may be stated that a female having eggs in the oviduct was collected on a given date. Yet this is not clearly indicative of the time when eggs may be deposited. Each investigator should insure preciseness of definition. Writers frequently use the presence or absence of oviducal eggs to delimit the season but this can lead to potential errors if not weighed properly. Eggs may be retained in the oviducts for long periods (Cagle and Tihen, 1948).

2. What correlation is there between courtship or copulation and ovulation? What is the significance of the sex ratio and population density in relation to annual realized reproductive performance?

   These are little-explored areas in herpetology yet important ones if we are to arrive at an understanding of those factors controlling changes in reptile populations. The fact that some reptile females may bear young or deposit fertile eggs after as long as eight years after copulation suggests that unbalanced sex ratios may be of but scant consequence. The unverified yet not disproven statement that single or successive copulations are essential to stimulate ovulation indicates the importance of a favorable sex ratio. The work of Darling (1938), Vogt (1942), Errington (1946) and others has suggested that population density may markedly affect breeding success.

   a. What is the pattern of courtship?

      Exploration of the courtship patterns with emphasis on interspecies differences promises to yield much of value in explaining the development of physiological isolation. Noble and Bradley (1933) furnish many suggestions for procedure and interpretation. Cagle (1950) describes differences in the courtship pattern between two species of the genus *Pseudemys.* Davis (1936) summarizes the literature for snakes; Gloyd (1947) suggests additional problems; Greenberg (1945) summarizes the knowledge of courtship in the family *Iguanidae*.

(1) How does it differ from that of related forms?

(2) What advantages in reproduction are provided by the courtship pattern?

(3) What selective factors function in courtship?

(4) What secondary sex characters are of most significance in courtship?

(5) What senses are involved in courtship? (Noble, 1937)

b. What is the relation of courtship drives to aggregation? (Finneran, 1949).

c. When do ovulation and fertilization occur?

(1) What is the fertilization rate? The relation of successful courtship and copulation to fertilization rate?

(2) Is copulation essential to ovulation? to egg depositions? (Woodward, 1933).

3. How many groups of young (eggs) are produced each year?

This question must usually be answered by the examination of ovaries from chronological samples taken during the breeding season so that progressive changes in number and size of ovarian follicles or total volume or weight may be reported. Too, examinations of the ovaries of females at the end of the reproductive period may yield counts of ovulation points (corpus luteum or corpus albicans) (Samuel, 1952).

4. How many young (eggs) are produced in each group? Some investigators have depended solely upon counts of oviducal eggs or of eggs found in nests. Both procedures are subject to substantial error as the worker can but rarely be confident that no eggs have been previously deposited, that ovluation is completed or that two or more females have not utilized the same nest. Counts of ovulation points are usually more acceptable. Certainly the typical extreme variation in number of eggs and young produced emphasizes that little significance may be attached to many of

the literature reports of the number of young in single females or nests. Counts of young present in the uteri of viviparous or ovoviviparous forms possibly provide the most reliable criteria of clutch size. (The terms, viviparous and ovoviviparous, have been used in varied ways in herpetological literature. It is suggested that the term, ovoviviparous, be restricted to describe a situation in which the developing young gains no sustenance from the female).

a. Is there a correlation between reproductive capacity and size or age? How is this related to estimates of natality in local population?

The large difference in reproductive capacity between small and large females make it exceedingly difficult to utilize much of the published data on reproductive capacity as bases for estimates of natality.

VI. *What are the major factors controlling the relation of the number of surviving young to the number of eggs or young produced by females?*

A. What are the characteristics of the egg at deposition?

1. How do the eggs vary in size, volume and weight in each clutch?

The irregular shape of most reptile eggs reduces the value of measurements of length or width reported without volumes (Lynn and Brand, 1945).

2. Is there any correlation in size and/or weight and size of female?

3. What changes occur in size and weight of eggs during incubation?

The weight and volume of eggs change much and irregularly with age and the environment. Cunningham and Hurwitz (1936) reported that eggs increased as much as 60% in weight during incubation. Data on reptile eggs are of little value unless they are accompanied by statements as to their age and conditions under which they were incubated. The statistical treatment (Edgren, 1949) does not remedy this discrepancy.

4. In what stage of development is the egg at deposition?

a. Does this stage of development vary with the time eggs are retained in the oviducts? If so, how does this influence the incubation period?

b. How is the stage of development related to the egg size and weight?

B. Where and in what manner are eggs deposited?
   1. Is a nest constructed?
      a. What factors determine the nest site?
      b. How is the nest constructed?
      c. What is the relation of choice of nest site and construction to potential survival of young?
      d. What is the behavior pattern of the female constructing a nest? What features are of survival importance?
      e. Does the female use the same nesting site for subsequent clutches? in subsequent years?
   2. Does the female remain with the eggs? return to them? What is the relation of female behavior to survival potential of young? of the females?
      a. Does the female "defend" the eggs?
      b. Does the female contribute "heat" to incubation?

         These questions cannot be answered on the basis of single observations. Behavior of reptiles is sufficiently variable that repeated observations are essential to description of behavior patterns. In most situations the investigator can gain but restricted field data on these questions and is compelled to study captive specimens as a basis for evaluation of field-collected data (Noble and Mason, 1933).

C. What factors determine incubation rates?
   1. What is the period of incubation? in field nests? in the laboratory?
      a. What is the relation of temperature levels or changes to incubation time? of degree-hour to incubation time? (Cunningham, 1939).
      b. Are differences in incubation time between clutches of eggs related to egg-deposition (sequence in oviducts; time of retention in oviducts; quality of shell deposited)? Observers frequently do not state incubation periods in degree-hours and do not provide their criteria for "hatching". The extreme difficulty of evaluating much of the published material makes it unavailable for coherent treatment.

         It is not usually possible to observe the deposition of reptile eggs and the incubation period must be expressed as the interval between the laying of the last egg and the hatching of the last egg. This procedure is usually followed in reporting the incubation time of bird eggs (Skutch, 1950). Although reptiles typically deposit an entire brood over a short period as compared with birds, the total time required to deposit a brood is often significant in relation to the incubation period. The incubation time should be expressed in terms of days and hours or degree-hours.

2. How sensitive are eggs to low or high temperature during the incubation period? What extremes are the eggs subjected to in the typical nest site? Potential mortality?
3. How do the hatchlings escape from the egg? What is the function of the caruncle? What mortality is involved in the process of hatching?

D. Does the female develop any particular behavior traits associated with gestation?

1. What is the period of gestation? (Bragdon, 1951).
2. What are the principle causes of mortality during embryonic development?
3. Does the female tend to select a particular type of site for the birth of the young? Relation of such selection to potential survival?
4. Describe the birth of the young.

VII. *What are the characteristics of the young? Are there any typical behavior traits? What is the relation of the behavior pattern to survival? to growth?*

A. What advantageous resources in morphology, physiology, behavior patterns do the young adults possess? (Daniel and Smith, 1947).

1. What is the amount of yolk retained? Is it utilized as a source of nourishment? How long and under what conditions will it serve to support the young?
2. How long do the young remain in the nest or with the female? What factors influence the length of this period? May young overwinter in the nest? Remain with the female for prolonged periods? What relation may this bear to survival potentialities?

B. What are the major hazards to which the young are exposed immediately after leaving the nest or the female?

VIII. *What are the characteristics of the growth curve of individuals of the local population?*

A. What is the length of the growing season?

1. What are the factors serving to delimit the growing season? Availability of food? Changes in environmental temperature? Cyclic changes independent of temperature?

Various procedures have been attempted for determining the limits of the growing season. The actual observation of initiation and cessation of growth through study of seasonal samples is best but such observations are difficult to obtain. The correlation of formation of growth rings in turtles with season has been attempted (Cagle, 1946). Too, once the minimum and maximum effective temperatures of a form are known they may be utilized to approximate the time of initiation or slowing of activity. This does not, however, necessarily define the growing season as it has been demonstrated that reptiles may become quiescent during the winter although retained at constant temperature. Evans and Hegre (1940) have suggested that some genetic time factor, distinct from the temperature factor, is operative in reptiles.

2. What variations in length of growing season occur within the area of investigation?

   It is indicated by some researches that the time of initiation or cessation of growth may vary significantly from one local habitat or situation to another.

B. What is the annual increment (in that measure selected as the best indicator of total change in mass) during each season of the animal's life? What sex differences occur?

1. What are the factors influencing the rate of growth? (size and/or age; senility, length of growing season, social dominance).
2. What are the limits of variation in growth rates? How does growth rate affect the attainment of maturity, natality, mortality?
3. What age or size groups may be discerned? (Klau and David, 1952).
4. Is growth potentially continuous throughout the life of the individual?

C. What is the natural (ecological) longevity?

1. What longevity records are available from captive sepcimens?
2. What estimates of age may be made from the population samples (Woodbury, 1951).
3. What are the characteristics of youth, maturity, old age?

IX. *What is the annual cycle of activity and what factors exert primary influence on the cycle?* (Fitch and Glading, 1947; Oliver, 1947).

A. What is the relation of the growing season to the period (periods) of courtship, egg-deposition and birth of young?

B. What are the optimum, minimum and maximum effective body temperatures?

C. What is the seasonal cycle in diel behavior (e.g., in basking) (Girons, 1947).

D. Are the animals quiescent during any period of the year? Are aggregations formed?

1. What preparations are made for the period of quiescence?
2. Where do the animals spend the winter?
3. What environmental factors cause the initiation of quiescence? renewed activity?

   Bailey (1949) demonstrated that the plains gartersnake, *Thamnophis radix* could endure temperatures of approximately —2°C. for a protracted period.
4. What is the composition (age groups, size groups, sex ratios) of the winter aggregation?
5. What is the role of winter quiescence in limiting the geographic distribution? (Bailey, 1948).

X. *What is the diel cycle of activity?*

A. What is the role of basking in the daily cycle?

1. What determines the time of basking, the length of the period?

   Sergeev (1939) reports a close relation between environmental temperature and the period of activity. Benedict (1932) summarizes temperature relations in reptiles.
2. What is the function of basking?
   a. How is the period of basking related to rate of increase or decrease of body temperature?
   b. What is the characteristic behavior pattern in basking. How is this related to control of body temperature? (Cowles and Bogert, 1944; Gunn, 1942; Chernomordikov, 1943; Bogert, 1949).

B. Is feeding restricted to any particular part of the day? How is the feeding behavior or length of the feeding period influenced by food availability?

C. Are breeding activities (courtship; egg-deposition; birth of young) restricted to any part of the day?

D. When does the peak of activity occur in the daily cycle?

E. How is the diel (Klauber, 1939) cycle modified by weather changes, population density?

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Interspecies differences in the diel cycle of activity may affect the entire life history. Exploration of the cycle may yield the key to many of the problems presented here. Noble (1946) presents valuable information on such problems.

XI. *What are the food habits? Their relation to growth and survival?*

A. How does the animal obtain its food?

1. Can the animal pursue and catch actively moving prey?
2. What food preferences are exhibited in the field and laboratory?

B. What are the principle foods? Relation to availability?

1. What is the relative importance of the food items?
2. How do feeding habits vary during the life of the animal?
3. Is there any seasonal variation in feeding habits?

Most studies of reptile food habits have reported a high percentage of empty stomachs. It is thus essential that the investigator utilize intestinal as well as stomach contents. Too, the fecal material of many reptiles may be used. Fitch and Twining (1946) emphasize the value of scats in the determination of the food habits of snakes. The scats of lizards, particularly, are of great value in food analysis. Carpenter (1952) obtained data on food habits of snakes by forcing regurgitation. Lagler (1943b) reviews the food habits of Michigan turtles.

C. Does the animal act as a controlling or limiting predator?

XII. *Does this form exhibit any characteristic and genetically limited patterns of group behavior?*

The study of behavior under undisturbed natural conditions often yields startling information of basic importance to the explanation of population problems (Svärdson, 1949; Calhoun, 1950; Carpenter, 1950) and phylogeny (Bellairs and Underwood, 1951). Few zoologists have developed the ability to profit from the observation of field behavior patterns (Emlen, 1950). Herpetologists, particularly have not utilized this procedure.

A. Do aggregations occur? If so what are the stimuli and binding forces in aggregation? the function of the aggregation? (Noble, 1936; Allee, 1931, 1951; Greenberg, 1943.)

B. Are social hierarchies present?

1. If dominance hierarchy is present, what is the relation

to territoriality, natality? (Evans, 1938, 1951; Greenberg, 1943).

2. How does the social hierarchy affect the migrating individual? the juvenile seeking a territory?
3. Does the social hierarchy influence growth and reproductive potential? (Calhoun, 1950).

Such questions as these may be answered if some of the methods of field ornithologists be adapted. The use of blinds and optical equipment for observation will yield much of value to the interpretation of interactions. Observation towers were used to study the behavior of turtles in Illinois (Cagle, 1944; 1950). Excellent suggestions, many of which are of value to the herpetologist, are presented by Emlen (1950). The work of Evans (1938, 1951) is suggestive of problems and procedures.

C. Are there typical defensive or offensive behavior patterns? Bogert (1941) describes the "king-snake defense posture" of rattlesnakes. Mertens (1946) summarizes reports of such actions in reptiles.

LITERATURE CITED

ALLEE, W. C. 1931. *Animal Aggregations. A Study in General Sociology.* Univ. of Chicago Press, Chicago, pp. 1-431.

———— 1951. *Cooperation Among Animals.* Henry Schuman, N. Y. pp. 1-233.

ALTAND, PAUL D. 1951. Observations on the structure of reproductive organs of the box turtle. *Jour. Morph.*, 89: 599-616.

ANDRUSHKO, S. I. 1936. Methods and technique of reptilian censuses in deserts. *Probl. Ecol. Biocenol. Leningrad,* 3: 158-167 (Russian; English summary).

BAILEY, NORMAN T. 1952. Improvements in the interpretation of recapture data. *Jour. Animal Ecol.*, 21: 120-127.

BAILEY, REEVE 1948. Winter mortality in the snake *Storeria dekayi. Copeia,* 1948: 215.

———— 1949. Temperature toleration of gartersnakes in hibernation. *Ecology,* 30: 238-242.

BAKER, JOHN R. 1947. The seasons in a tropical rain-forest (New Hebrides). *Linnean Society's Journal-Zoology,* 41: 248-258.

BAUM, WERNER A. 1950. Ecological use of meteorological temperatures. *Science,* 113: 333-334.

BELLAIRS, A. d'A. and GARTH UNDERWOOD 1951. The origin of snakes. *Biol. Rev.*, 26: 193-237.

BENEDICT, FRANCIS G. 1932. The physiology of large reptiles with special reference to the heat production of snakes, tortoises, lizards and alligators. *Carnegie Inst. Wash.* 425: 1-539.

BLAIR, W. FRANK 1951. Evolutionary significance of geographic variation in population density. *Texas J. Sci.*, 3: 53-57.

BLANCHARD, FRANK N. and ETHEL B. FINSTER 1933. A Method of marking living snakes for future recognition, with a discussion of some problems and results. *Ecology*, 14: 334-347.

BOGERT, CHARLES M. 1941. Sensory cues used by rattlesnakes in their recognition of ophidian enemies. *Ann. N. Y. Acad. Sci.*, 41: 329-344.

__________ 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution*, 3: 195-211.

BRAGDON, DOUGLAS E. 1951. The non-essentiality of the corpora lutea for the maintenance of gestation in certain live-bearing snakes. *Jour. Exper. Zool.*, 118: 419-435.

BRYUZGIN, V. L. 1939. A procedure for investigating age and growth in reptiles. *Comptes Rendus (Doklady) de l'Acad. des Sciences de l' U.S.S.R.*, 23: 403-405.

CAGLE, *Fred* R. 1939. A system of marking turtles for future identification. *Copeia*, 1939: 170-173.

__________ 1944a. Sexual maturity in the female of the turtle *Pseudemys scripta elegans*. *Copeia*, 1944: 149-152.

__________ 1944b Home range, homing behavior, and migration in turtles. *Misc. Publ. Mus. Zool. Univ. Mich.*, 61: 1-33

__________ 1946. The growth of the slider turtle, *Pseudemys scripta elegans*. *Amer. Midl. Nat.*, 36: 685-729.

__________ 1948. Sexual maturity in the male turtle *Pseudemys scripta troostii*. *Copeia*, 1948: 108-111.

__________ 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). *Ecol. Monogr.*, 20: 31-54.

CAGLE, FRED R. and A. H. CHANEY 1950. Turtle populations in Louisiana. *Amer. Midl. Nat.*, 43: 383-388.

CAGLE, FRED R. and JOSEPH TIHEN 1948. Retention of eggs by the turtle, *Deirochelys reticularia*. *Copeia*, 1948: 66.

CALHOUN, JOHN B. 1950. The study of wild animals under controlled conditions. *Ann. N. Y. Acad. Sci.*, 51: 1113-1122.

CARPENTER, CHARLES C. 1952. Comparative ecology of the common garter snake *(Thamnophis s. sirtalis)*, the ribbon snake*(Thamnophis s. sauritus)*, and Butler's garter snake *(Thamnophis butleri)* in mixed populations. *Ecol. Monogr.*, 22: 235-258.

CARPENTER, C. R. 1950. General plans and methodology for field studies of the naturalistic behavior of animals. *Ann. N. Y. Acad. Sci.*, 51: 1006-1008.

CAZIER, MONT A. and ANNETTE L. BACON 1949. Introduction to quantitative systematics. *Bull. Amer. Mus. Nat. Hist.*, 93: 347-388.

CHERNOMORDIKOV, V. V. 1943. On temperature reactions of reptiles. *Zool. J. Moscow*, 22: 274-279.

CHRISTIAN, JOHN J. 1950. The adreno-pituitary system and population cycles in mammals. *Jour. Mamm.*, 31: 247-259.

CIESLAK, EDWIN S. 1945. Relations between the reproductive cycle and the pituitary gland in the snake *Thamnophis radix*. *Physiol. Zool.*, 18: 299-329.

CONANT, ROGER 1948. Regeneration of clipped subcaudal scales in a pilot black snake. *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 13: 1-2

COWLES, RAYMOND B. and CHARLES M. BOGERT 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Amer. Mus. Nat. Hist.*, 83: 265-296.

CUNNINGHAM, BERT 1939. Effect of temperature upon the developmental rate of the embryo of the diamond back terrapin *(Malaclemys centrata Lat.). Amer. Nat.*, 73: 381-384.

CUNNINGHAM, BERT and A. P. HURWITZ 1936. Water absorption by reptile eggs during incubation. *Amer. Nat.*, 70: 590-595.

DANIEL, ROBERT S. and KARL U. SMITH 1947. The sea-approach behavior of the neonate loggerhead turtle *Jour. Comp. and Physiol. Psych.*, 40: 413-420.

DARGAN, LUCAS M. and WILLIAM H. STICKEL 1949. An experiment with snake trapping. *Copeia*, 1949: 264-268.

DARLING, F. F. 1938. *Bird Flocks and the Breeding Cycle. A Contribution to the Study of Avain Sociability.* Cambridge Univ. Press, Cambridge, England, pp. 1-24.

DARLINGTON, P. J. JR. 1948. The geographical distribution of coldblooded vertebrates *Quart. Rev. Biol.*, 23: 105-123.

DAVIS, D. DWIGHT 1936. Courtship and mating behavior in snakes. *Zool. Series Field Mus. Nat. Hist.*, 20: 257-290.

DEEVEY, E. S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.*, 22: 283-314.

DE HAAS, C. P. J. 1941. Some notes on the biology of snakes and their distribution in two districts of West Java. *Treubia*, 18: 327-375.

DICE, LEE R. 1952. Quantitative and experimental methods in systematic zoology. *Systematic Zool.*, 1: 97-104.

DIEM, M. 1951. Tagesgang der relative Feuchtigkeit in der bodennahen Luftochicht in Gras und über nacktem Humus. *Arch. Meteorol. Geophys. u Bioklimatol., Ser. B*, 2: 441-447.

EDGREN, RICHARD A. 1949. Variation in the size of eggs of the turtles *Cheldydra s. serpentina* (Linne) *Sternotherus odoratus* (Latreille). *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 53: 1.

ELTON, CHARLES 1942. *Voles, Mice and Lemmings. Problems in Population Dynamics.* Oxford, pp. 1-496.

EMLEN, JOHN T. 1950. Techniques for observing bird behavior under natural conditions. *Ann. N. Y. Acad. Sci.*, 51: 1103-1112.

ERRINGTON, P. L. 1946. Predation and vertebrate populations. *Quart. Rev. Biol.* 2: 144-177; 3: 221-245.

EVANS, LLEWELLYN T. 1938. Cuban field studies on territoriality of the lizard, *Anolis sagrei. Jour. Comp. Psych.*, 25: 97-125.

__________ 1951. Field study of the social behavior of the black lizard, *Ctenosaura pectinate. Amer. Mus. Novitates*, No. 1493: 1-26.

EVANS, LLEWELLYN T. and ERLING HEGRE 1940. Endocrine relationships in turtles. *Endocrinology*, 27: 144-148.

FINNERAN, L. C. 1949. A sexual aggregation of the garter snake. *Thamnophis butleri* (Cope). *Copeia*, 1949: 141-144.

FITCH, HENERY S .1945. Notes on social behavior of the collared lizard *Copeia*, 1945: 226-230.

__________ 1949a. Outline for ecological life history studies of reptiles. *Ecology*, 30: 520-532.

——— 1949b. Study of snake populations in central California, *Amer. Midl. Nat.*, 41: 513-579.

FITCH, HENRY S. and BEN GLADING 1947. A field study of a rattlesnake population. *Calif. Fish and Game*, 33: 103-123.

FITCH, HENRY S. and H. TWINING 1946. Feeding habits of the Pacific rattlesnake. *Copeia*, 1946: 64-71.

FORBES, THOMAS R. 1940. A note on reptilian sex ratios. *Copeia*, 1940: 132.

FOX, WADE 1948. Effect of temperature on development of scutellation in the garter snake. *Thamnophis elegans atratus. Copeia*, 1948: 252-262.

——— 1952. Seasonal variation in the male reproductive system of Pacific Coast garter snakes. *Jour. Morph.* 90: 481-542.

FRAENKEL, GOTTFRIED S. and DONALD L. GUNN 1940. *The Orientation of Animals; Kineses, Taxes, and Compass Reactions.* Oxford, Clarendon Press, pp. 1-352.

GEIGER, RUDOLPH 1950. *The Climate Near the Ground.* Harvard University Press, Cambridge, Mass. pp. 1-482.

GIRONS, H. SAINT 1947. Ecologie des viperes. I *Vipera Aspis. Bull. Soc. Zool. France*, 72: 158-169.

GLOYD, HOWARD K. 1947. Notes on the courtship and mating behavior of certain snakes. *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 12: 1-4.

GREENBERG, BERNARD 1943. Social behavior of the western banded gecko, *Coleonyx variegatus* Baird. *Physiol. Zool.*, 16: 110-122.

GROBMAN, ARNOLD B. 1950. The problem of the natural range of a species. *Copeia*, 1950: 231-232.

GUNN, D. L. 1942. Body temperatures in poikilothermal animals. *Biol. Rev.*, 14: 293-313.

HAYNE, DON W. 1949. Calculation of size of home range. *Jour. Mamm.* 30: 1-18.

HERSH, A. H. 1941. Allometric growth; the ontogenetic and phyolegenetic significance of differential rates of growth. *3rd Growth Symposium*: 113-145.

JACKSON, C. H. N. 1939. The analysis of an animal population. *Jour. Anim. Ecol.*, 8: 238-246.

KENDEIGH, S. C. 1941. Length of day and energy requirements for gonad development and egg-laying in birds. *Ecology*, 22: 237-248.

——— 1944. Measurement of bird populations. *Ecol. Monogr.*, 12: 67-106.

KLAU, HELENE H. and PAUL R. DAVID 1952. The bimodality of length distribution in *Heterodon p. platyrhinos L.* and its relation to the season in which the specimens were collected. *Amer. Midl. Nat.*, 47: 364-371.

KLAUBER, L. M. 1939. Studies of reptile life in the arid southwest. *Bull. Zool. Soc. San Diego*, 14: 1-100.

LAGLER, KARL F. 1943a. Methods of collecting freshwater turtles. *Copeia*, 1943: 21-25.

——— 1943b. Food habits and economic relations of the turtles of Michigan with special reference to fish management. *Amer. Midl. Nat.*, 29: 257-312.

LAGLER, KARL F. and VERNON C. APPLEGATE 1943. Relationship between the length and the weight in the snapping turtle. *Chelydra serpentina* Linnaeus. *Amer. Nat.*, 77: 476-478.

LESLIE, P. H. 1952. Ehe estimation of population parameters from data obtained by means of the capture-recapture methods. II. The estimation of total numbers. *Biometrika*, 49: 363-388.

LOWE, CHARLES H. JR. and KENNETH S. NORRIS 1950. Aggressive behavior in male sidewinders. *Crotalus cerastes*, with a discussion of aggressive behavior and territoriality in snakes. *Chicago Acad. Sci., Nat. Hist. Misc.* No. 66: 1-13.

LYNN, W. GARDNER and THEODOR VON BRAND 1945. Studies on the oxygen consumption and water metabolism of turtle embryos. *Biol. Bull.*, 88: 112-125.

MARR, JOHN C. 1951. On the use of the terms abundance, availability and apparent abundance in fishery biology. *Copeia*, 1951: 163-169.

MERTENS, ROBERT 1946. Die Warn-und Droh-Reaktionen der Reptilien. *Abk. Senck. Naturf. Ges.*, 471: 1-108.

NICE, MARGARET 1941. The role of territory in bird life. *Amer. Midl. Nat.*, 26: 441-487.

NOBLE, RUTH CROSBY 1946. *The Nature of the Beast.* Doubleday and Co., Inc., pp. 1-224.

NOBLE, G. K. 1936. The aggregation behavior of *Storeria dekayi* and other snakes, with special reference to the sense organs involved. *Ecol. Monogr.*, 6: 269-316.

_______ 1937. The sense organs involved in the courtship of *Storeria, Thamnophis* and other snakes. *Bull. Amer. Mus. Nat. Hist.*, 73: 673-725.

NOBLE, G. K. and H. T. BRADLEY 1933. The mating behavior of lizards: its bearing on the theory of sexual selection. *Ann. N. Y. Acad. Sci.*, 35: 25-100.

NOBLE, G. K. and E. R. MASON 1933. Experiments on the brooding habits of the lizards *Eumeces* and *Ophisaurus*. *Amer. Mus. Nov.*, No. 619: 1-29.

OLIVER, JAMES A. 1947. The seasonal incidence of snakes. *Amer. Mus. Novitates*, No. 1363: 1-14.

_______ 1951. Ontogentic changes in osteodermal ornamentation in skinks. *Copeia*, 1951: 127-130.

PARK, THOMAS 1950. Chapter 18. General properties of populations. IN: *Principles of Animal Ecology*, pp. 263-271.

REGAMEY, JEAN 1935. Les caractères sexuels du Lézard *(Lacerta agilis L.) Revue Suisse de Zoologie*, 42: 87-168.

RICKER, WILLIAM E. 1948. Methods of estimating vital statistics of fish populations. *Indiana Univ. Publ., Sci. Series*, 15: 1-101.

RISLEY, P. L. 1938. Seasonal changes in the testis of the musk turtle, *Sternotherus odoratus* L. *Jour. Morph.*, 63: 301-317.

SAMUEL, MARY 1952. Histogenesis and development of the corpus luteum in *Cerberus rhyncops* (Schneider). *Jour. Zool. Soc. India*, 3: 201-310.

SCHAEFER, MILNER B. 1951. Estimation of animal populations by marking experiments. *Fishery Bull.* U. S. Fish andWildlife Service, 52 (69): 191-203.

SCHMIDT, KARL P. 1950. The concept of geographic range with illustrations from amphibians and reptiles. *Texas Jour. Sci.*, 2: 326-334.

SERGEEV, A. 1939. The body temperature of reptiles in natural surroundings. *Comptes Rendus (Doklady) de l'Acad. des Sci. de l'USSR*, 22: 49-52. (Russian).

SIMPSON, GEORGE GAYLORD and ANNE ROE 1939. *Quantitative Zoology*. McGraw-Hill Book Co., pp. 1-414.

SKUTCH, ALEXANDER F. 1950. Outline for an ecological life history of a bird, based upon the song tanager, *Ramphocelus paserinii costaricensis*. *Ecology*, 31: 464-469.

STICKEL, LUCILLE 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). *Ecol. Monogr.*, 20: 351-378.

STICKEL, WILLIAM H. and JAMES B. COPE 1947. The home ranges and wanderings of snakes. *Copeia*, 1947: 127-236.

SVÄRDSON, GUNNAR 1949. Competition and habitat selection in birds. *Oikos*, 1: 157-174.

TAYLOR, WALTER P. 1919. Suggestions for field studies of mammalian life-histories. *U. S. Dept. Agric., Circ.* No. 59: 1-8.

TINBERGEN, N. 1948. Social releasers and the experimental method required for their study. *Wilson Bull.*, 60: 6-51.

VOGT, WILLIAM 1941. A practical lizard trap. *Copeia*, 1941: 115.

__________ 1942. Informe sobre las Aves guaneras elevado a la Compania Administradora del Guano. *Bol. Comp. Admin. Guano*, 18: 3-132.

VOLSØE, H. 1944. Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L.). *Spolia Zoologica Musei. Haunienses Copenhagen*, 5: 7-172.

WICKHAM, M. M. 1922. Notes on the migration of *Macrochelys lacertina*. *Proc. Okla. Acad. Sci.*, 2: 20-22.

WOODBURY, ANGUS M. 1948. Marking reptiles with an electric tattooing outfit. *Copeia*, 1948: 127-128.

__________ 1951. Introduction—A ten-year study. A snake den in Tooele County, Utah. *Herpetologica*, 7: 4-14.

WOODBURY ANGUS M. and ROSS HARDY 1948. Studies of the desert tortoise. *Gopherus agassizii*. *Ecol. Monogr.*, 18: 145-200.

WOODWARD, S. J. 1933. A few notes on the persistence of active spermatozoa in the African night-adder, *Causus rhombeatus*. *Proc. Zool. Soc. London*, 1933: 189-190.