S-NA- New Orleans]

TULANE STUDIES IN ZOOLOGY

Volume 4, Number 3 October 31, 1956

AN OUTLINE FOR THE STUDY OF AN AMPHIBIAN LIFE HISTORY

FRED R. CAGLE,
DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY,
NEW ORLEANS, LOUISIANA

TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY is devoted primarily to the zoology of the waters and adjacent land areas of the Gulf of Mexico and the Caribbean Sea. Each number is issued separately and contains an individual study. As volumes are completed, title pages and tables of contents are distributed to institutions exchanging the entire series.

Manuscripts submitted for publication are evaluated by the editor and by an editorial committee selected for each paper. Contributors need not be members of the Tulane University faculty.

Manuscripts should be submitted on good paper, as original typewritten copy, double-spaced, and carefully corrected. Two carbon copies in addition to the original will help to expedite editing and assure more rapid publication.

An abstract not exceeding three percent of the length of the original article must accompany each manuscript submitted. This will be transmitted to *Biological Abstracts* and any other abstracting journal specified by the writer.

Separate numbers or volumes may be purchased by individuals, but subscriptions are not accepted. Lists of papers published will be mailed on request. Authors may obtain copies for personal use at cost.

Address all communications concerning exchanges, manuscripts, editorial matters, and orders for individual numbers or volumes to the editor. Remittances should be made payable to Tulane University.

When citing this series authors are requested to use the following abbreviations: *Tulane Stud. Zool.*

Price for this number: $0.40.

George Henry Penn, *Editor*
Meade Natural History Library,
Tulane University,
New Orleans, U. S. A.

Assistant to the Editor:
Don R. Boyer

AN OUTLINE FOR THE STUDY OF AN AMPHIBIAN LIFE HISTORY

FRED R. CAGLE,
Department of Zoology, Tulane University, New Orleans, Louisiana

The life histories of many amphibians remain unknown and much of the information in the current literature cannot be used in synthesis because it is vaguely presented or lacks supporting data (Cole, 1954a). The renewed interest in natural history and the extensive use of amphibians in experimental biology demand an attempt to formulate an outline suggestive of needs, problems and procedures in life history investigations.

Often the experimental biologist's knowledge of the animal as it exists in nature has been inadequate as a basis for evaluation of his experimental results. The laboratory worker is sometimes not cognizant of the need of ecologic information and his interpretations are thus limited. The present pattern of training biologists often fails to provide the essential background relating to the entire organism or population. Rarely does the physiologist, the embryologist, the taxonomist or the geneticist utilize the potentialities of the study of the organism under natural conditions.

The ecologist or the systematist does not often utilize the techniques of the laboratory. He is sometimes unaware of knowledge reported by his laboratory-centered colleague, or of information on the anatomy, physiology, genetics or embryology of the animals involved. Yet his investigations often lead to the laboratory where, under conditions of control and experiment, he may hope to resolve the problems developed in the field. Often he must face an attitude of his experiment-minded colleague suggesting that the field observations explain nothing. The general physiologist insists on the need for a second step, the endocrinologist a third, and biochemist a fourth—each believing an answer resides in his realm although the totality of the knowledge is essential.

The wide breach between the laboratory researcher and the field researcher has been infrequently closed. The herpetologist can contribute much to the narrowing of the gap by broadening the scope of his investigations and his bibliographic research. More than 2800 serials contain information potentially pertinent to herpetology. The herpetologist cannot depend on any one or a series of abstract journals.

The biologist is confronted by a great mass of statistical theory and extensive debate about the application of statistics to ecological problems. Statistics has corrupted as well as benefited biology. Often the use of statistical procedures has contributed little and the development of statistical theory has overshadowed the addition of new biological knowledge. The "research" in natural history may be grouped into three categories: (1) general observations that present no new ideas or conclusions; (2) documented observations brought into sharp focus and used to develop generalizations; (3) investigations placing primary emphasis on the elaboration of observations through the application of statistical techniques (Packer and Pearson, 1952).

The herpetologist studying the life history of an amphibian should be cognizant of the relation of his research to broad ecological concepts. The natural history stage is thus essential to studies of population processes and interspecies reactions which are, in turn, essential to the analysis of the whole eco-system and the physico-chemical interpretation of the biodemographic picture (Elton and Miller, 1954).

The need for a reexamination of the standards and customary procedures in natural history investigations on reptiles has been previously stressed (Cagle, 1953). This annotated outline is an attempt to ascertain the ideal requirements in an investigation of the life history of an amphibian. The references cited were selected because of their value as guides to the literature on a particular topic or because they present new knowledge, approaches, or techniques.

I. *What are the morphologic characteristics of the population to be studied? Were the data reported 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?

Information must often be discarded by subsequent workers because the author failed to indicate clearly the characteristics of the individual or population studied. Description must thus be such that any investigator can recognize the population or source of a sample regardless of changes in nomenclature.

B. What morphological features discerned by the investigator are pertinent to the generic and familial level of classification? to the group phylogeny?

Features of the internal anatomy have been generally utilized at these and higher levels of classification. The autecologist often is led to explore the anatomy of the organism he is concerned with and should be aware of the possible biologic and phylogenetic significance of the structure he observes. Studies of anatomy should not be foreign to his interests (Theron, 1952). He must be particularly cognizant of those researches useful in evaluating taxonomic characters (Serafínski, 1955; Balinsky, 1955).

C. What other names have been attached to the population?

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

A representative series supporting the description given should be deposited in a suitable public museum collection. Failure to do this is almost characteristic of ecological, physiological and anatomical investigations; yet the conclusions submitted are often not acceptable because of questionable identification of the material on which they were based. Much of the experimental research utilizing amphibian larvae is deceiving as investigators have depended on biological supply houses to provide material. Often such shipments have been composite collections of several species. Deposited specimens provide a basis for permanent verification of identification.

E. 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 (1952b) 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. Simpson (1944) has stressed the concept of the hypodigm and the difficulties involved in the use of a preserved sample to represent the attributes of a population. 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. The presence of natural hybridization in populations and its influence on variations in ecology and morphology must be recognized (Moore, 1944, Blair, 1951, Volpe, 1953; Ruibal, 1955).

1. What changes in color intensity, in pattern or morphology occur from hatchling (birth) to old age? Are there any correlated sex differences? How are these changes related to taxonomic investigations?

   The analysis of color and color patterns is of particular importance in the study of amphibians. The consideration of the cause of variations in color patterns prior to their use in systematics is necessary but often ignored. The utilization of such characters should rest on an understanding of the chemical and physical bases of color (Kreig and Forster, 1937; Juszczyk, 1952) as well as an appreciation of their functional value (deRuiter, 1956). Meristic characters, widely used in zoogeographic studies, may have phenotypical relation to environmental factors

(Ernst, 1952). Phenocopies of widely distributed forms of fishes may be produced in the laboratory (Tåning, 1952).

2. What variation in physiological characters is associated with the morphological variation?

   Exploration of intraspecific, physiological variation has provided clarification of problems in evolution. The need for physiological study of variation is stressed by Prosser (1955).

3. Is the variation correlated with differences in the external environment? With a gradient in the external environment? Is the variation due to differences in genotypes or does it reflect the responses of a specific genotype to different environments?

   Investigators 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 investigators suggest that some of the characters considered to be of taxonomic importance are merely phenotypic modifications (Rostand, 1951).

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

   Although absolute size may not be a satisfactory taxonomic character for amphibians, genetic differences in potential natural longevity or growth potentials may be reflected in differences in maximum sizes between populations (Moriya, 1954).

5. 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). 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.

6. What are the principal differential growth changes in each sex? How are these changes related to the major phases of the life history? Do they vary geographically or seasonally?

   Failure to recognize differential growth has led to 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. The investigator must be aware of the statistical hazards of expressing differences in terms of ratios. The review of Marr (1955) on the use of morphometric data should be consulted.

Terentjev (1943) found a temporary acceleration of growth in the hind limbs of male frogs (*Rana ridibunda*) wtih the attainment of maturity. Variation of proportions in correlation with distribution is often evident (Schmidt, 1938; Blair, 1941; Hairston, 1949; Schuster, 1950; Dely, 1952; Mecham, 1954; Snyder, 1956).

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. These data may then, in connection with other information, form the basis for the statement of a supposed "true range." The range definition should indicate the distribution of existing populations (Grobman, 1950). Analysis of distribution should be sufficiently detailed to provide a basis for detection of the actual pattern. Whenever feasible, the pattern of occurrences of mature adults during the breeding season should be contrasted with occurrences at other times. The problems of determining allopatry and sympatry should be considered (Cain, 1953).

The herpetologist has not made sufficient use of the occurrence of amphibian larvae in determining distribution patterns. This, a reflection of the difficulty of identification of larvae, emphasizes the need for further researches on larval forms. Much pertinent information has been published by experimental embryologists and morphologists. The work of Lieberkind (1937) is useful in evaluation of mouth parts and adhesive organs.

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; Hairston, 1949; Dice, 1952b; Smith, 1952). It is especially important to note that the limiting factors may be entirely different on the various borders of the range of a species (Schmidt, 1950). Bannikov (1943) found that the northern limits of distribution of *Rana ridibunda* were determined by the lengths of the periods of hibernation and development; the southern limits by the temperature range in which the animal could be active. Cei (1947) found a correlation between the reproductive habits of *Rana temporaria* and its ability to live at high altitudes. Strűbing (1954) reports data on temperature responses. Bullock (1955) supports the thesis that many poikilotherms are, within limits, relatively independent of temperature in nature. Explanation of the range should be related to the paleontological history, but this is rarely possible.

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

1. What is the significance of temperature and humidity?

a. What are the annual temperature and rainfall cycles?

b. 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 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).

c. Does temperature summation (heat summation) affect the distribution of the species investigated?

2. Do physiographic features determine the range?

C. What is the principal habitat? Marginal habitat?

Any habitat is difficult to describe. Rarely it is possible to utilize published descriptions to obtain comparative information. The difficulties and some suggestions are ably described by Elton and Miller (1954).

1. Are microclimates of significance? throughout the range? at the periphery? (Geiger, 1950; Diem, 1951).

The tendency for many amphibians to occur in small populations in a restricted area suggests the significance of specific knowledge of microclimates. Often the usual, general descriptive data are an unsatisfactory basis for explaining occurrence (Marshall and Buell, 1955).

Knowledge of cyclic changes in metabolic rates are of importance in evaluating the influence of the microclimate (Vernberg, 1951).

2. What vegetational types characterize the habitat? Is any particular plant or groups of plants always associated with the habitat? How does our knowledge of the biology of the plant aid in understanding the occurrence of the amphibian?

3. Do size, age or sex groups tend to occupy different

habitats? Do they characterize specific parts of the range?

Juvenile amphibians often select a habitat different from that occupied by adult forms (Anderson, 1954). This has caused some confusion in the studies based on sampling procedures not recognizing this situation. Hairston (1949) demonstrated a correlation between altitude and size in *Desmognathus.* Margalef (1955) reviews relationships between temperature and size.

4. Does the animal have an innate habitat recognition mechanism? Is the mechanism of significance in restricting distribution or in controlling migration?
5. What behavioral traits are associated with the preferred microenvironment or change in the microenvironment?

   Variation in factors of the microenvironment may bring about substantial responses in behavior characteristic of the species (Thorson and Svihla, 1943; Sealander, 1953; Bogert, 1952). Cohen (1952) has described the varying reactions of 3 species of salamanders to dehydration. Test (1946) studied the reaction of a salamander to light and contact.
6. What are the principal adaptations advantageous to the animal in its optimum habitat?

D. What are the principal barriers to movement between populations?

Amphibians tend to occur in local colonies. Some forms are narrowly adapted and are found only under a specific complex of conditions. Barriers insignificant to other vertebrates may restrict population expansion (Stebbins, 1954).

E. What are the principal means of dispersal?
1. What extrinsic factors are involved in dispersal?
2. What intrinsic factors are involved in dispersal?
   a. What is the extent of individual mobility? Age or sex differences in mobility?
   b. What is the extent of larval adaptability? Significance in dispersal?

      Those forms having aquatic larval stages tend to be more generally dispersed than those with terrestrial stages. Larvae or adults may be dispersed by flood waters; such dispersal may be the primary mechanism.
   c. Do group movements occur? extent? seasonal?

F. What isolating mechanisms prevent gene interchange between the populations of the form studied and related forms?

Hybrid inviability, hybrid sterility, gametic isolation, sexual isolation, seasonal isolation, ecological isolation and geographic isolation have been reported as occurring in amphibia (Pariser, 1932; Hamburger, 1936; Lantz, 1939; Chen-Chao-Hsi, 1940; Moore, 1944; Volpe, 1952; Kawamura, 1953; Moriya, 1954; Blair, 1955). The field observer, if cognizant of knowledge gained from hybridization experiments, can supplement our knowledge of isolating mechanisms. Field investigations are essential to determine the operation of laboratory-observed mechanisms in natural populations (Twitty, 1955).

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

A knowledge of the structure and dynamics of the local population is essential to systematic studies. Studies usually will include an undisturbed population for observation, another for the tracing of marked individuals, and a third as a source of samples.

The mark-release-recovery technique provides information on many problems. Tattooing, tagging, and scarring have been useful in marking; the best method appears to be toe-clipping (Raney and Lachner, 1947; Hendrickson, 1954; Stebbins, 1954).

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 populations. Estimates of the relation of sex ratios to natality should be based on the relative frequency of sexually active individuals. Sex identification is frequently reported without reference to the criteria used. What are these criteria? Secondary sex characters? Gonad conditions? If dissected, on what basis was sex determined?

2. What is the sex ratio in juveniles? in larvae? in 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 amphibians forbids the successful completion of such tables. An attempt to collect data basic to the estimation of survivorship curves should be made (Chitty, 1952).

5. What are the major predators? Is predation pressure a significant factor in annual and long-term cyclic changes? In determining selection pressure? What is the relation of loss from predation to population density?

B. What long-term cyclic changes occur in the composition of the local populations? Do random oscillations occur? What is the cause of such cycles or random oscillations? Is exhaustion of the adrenopituitary system a factor as has been demonstrated for some mammal populations?

No specific information on population cycles or random oscillations is available for amphibians, yet these animals are potentially useful in the study of such changes and their basic causes. Sufficient general information is available to suggest rapid extreme changes susceptible to more precise measurement than most bird or mammal populations (Lynn and Wachowski, 1951; Cole, 1954b; Errington, 1954; Frank, 1954).

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

Adequate local sampling may provide a basis for obtaining answers to such questions. It has been demonstrated that substantial differences may be present in the composition of local populations. Comparison of population samples must be tempered with an awareness of the difficulties of obtaining such a sample. Series of specimens preserved in museum collections are rarely unbiased samples of natural populations. The student should note particularly those few long-term or intensive studies in local areas (Pacaud, 1951).

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 populations. Information of particular value in estimating populations from recovery of marked specimens is given by Ricker (1948) and Leslie (1952).

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

B. What is the relation of density of the form studied to that of other amphibians inhabiting the area?

C. Does the individual animal or the mated pair occupy a home range, activity range, or center of activity (Hayne, 1949)? Territory?

Territorial behavior in amphibians has been reported by Martof (1953) and Test (1954). Lutz (1954) suggested that *Elosia* has "an incipient notion of territory."

1. What is the size of the home range and of the territory?

The statistical concept of home range that includes the definition of "activity loci," a "center of activity," "recapture loci," a "recapture center" and "recapture radii" may be applied to studies of amphibians movements (Dice and Clark, 1953). Knowledge of the comparatively restricted home ranges of most amphibians is of importance to the systematist and ecologist (Kalela, 1954).

a. What features of the habitat may influence the extent of the territory or home range?

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

A measurement of the tendency to form pairs or small groups is essential to population studies directed toward evaluation of gene flow. Clark and Evans (1955) discuss the problem of spacing between neighbors.

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 (Stebbins, 1954). Griffin (1952) discusses radioactive tagging, a technique potentially useful in establishing the contribution of a group of larvae to an adult population.

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?

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

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

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?

The age at which an animal begins to reproduce is one of the most significant characteristics of a species, but is frequently not recorded (Cole, 1954). Investigators often fail to indicate what they mean by sexual maturity. Care must be exercised that the criteria for maturity are defined. In amphibians these may concern the presence of oviducal eggs in females, or of ovarian follicles of a specified size, or ovaries of a specified weight or volume. 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.

The development of neoteny among some groups of salamanders (perennibranchs, newts, ambystomids, and plethodontids) furnishes a possible evolutionary advantage in reproduction. The question of the processes leading to the evolution of neotenic forms is unanswered (Kezer, 1952; Toivonen, 1952).

No adequate techniques are available for determining the age of an individual amphibian. 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. Similar procedures have been applied to amphibians with varying success. Senning (1940) found that rings in some skull elements were useful in estimating age of *Necturus*. The study of marked and released specimens has yielded the best growth data (Raney and Lachner, 1947; Highton, 1956). The analysis of size groups (frequency-modes) has been useful in estimating age (Force, 1933; Blanchard and Blanchard, 1931).

1. When are the secondary sex characters developed? What is the relation of time of their appearance to the potentiality of sexual functioning?

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?

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 significance of this period in the total annual activity cycle?

The annual sexual cycles of many species have been studied and this phase is the best known aspect of amphibian biology (Cheng, 1932; Galgano, 1947; Cei, 1949; Miller and Robbins, 1954). Bullough (1951) discusses breeding. Marshall and Coombs (1952) in discussing the lipoid changes in the gonads of birds suggest avenues of research. The breeding period is usually considered as that 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 "ready for deposition" or "enlarged ova" was collected on a given date. Yet this is not clearly indicative of the time when eggs may be deposited or the young borne. Each investigator should insure preciseness of definition. Jameson (1955) states "Only the observance of deposition or of freshly laid eggs can accurately delimit the times of actual breeding." Forms of the same general region may exhibit quite different sexual cycles. Caruso (1949) points out that *Hyla raddiana* of Northern Argentina has continuous reproductive activity, but *Phyllomedusa sauvagi* of the same region breeds only during rains and the secondary sexual characters develop only at that time.

The specific factors stimulating breeding are unknown. The hormone reflex generally involved is known but the conditions releasing the reflex are but vaguely indicated for amphibians.

a. What is the relation of the "calling" of anurans to breeding activities? What factors initiate the calling response?

Confusion of periods in which individuals were calling with the breeding period has been frequent. There may be no correlation between these periods other than that the calling period includes the breeding season.

The function of the anuran voice is not clear. The use of the voice may result in aggregations essential to reproduction. Jameson (1955) believes the call is used to establish home sites, attract and stimulate the female and win sex recognition. The specific functions of the call differ in various anurans. Thus in some species aggregations occur prior to the initiation of calling. Differences in call characteristics may be of great importance in speciation of some groups. Blair (1955) has demonstrated the value of the "Sona-Graph" in the analysis of calls.

b. What is the relation of the development of secondary sex characters to the breeding season? Does the presence of the secondary sex characters indicate that individuals are prepared for reproduction?

Miller and Robins (1954) point out that the development of the secondary sex characters of the male *Triturus torosus* begins 4-6 weeks before expulsion of sperm from the testis, and that males remaining in the water after the breeding season retain the secondary sex characters.

c. What is the relation of the breeding migration to egg deposition? What factors initiate the breeding migration?

A complex of interrelated factors, usually relative humidity, temperature, precipitation or flooding variously stimulates the breeding migration when the physiological condition of the amphibian is appropriate (Blanchard, 1930; Baldauf, 1953). Storm and Pimentil (1954) outline a procedure for making a census of amphibians moving to ponds.

2. What correlation is there between courtship, copulation or amplexus, 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 populations. The fact that many amphibians have external fertilization, may produce several broods after a single fertilization, or may be parthenogenetic suggests that unbalanced sex ratios may be of but scant consequence (Angel and Lamotte, 1944). Hermaphroditism in anurans is reviewed by Ponse (1951). Population density may markedly affect breeding success.

a. What is the method of sex recognition?

Differing reactions of the female and male anurans to amplexus (Aronson, 1944), differences in structure (Hinsche, 1926), differences in call (Blair, 1955) are some of the established bases for identification. Olfaction appears to function in sex recognition in plethodontid salamanders.

b. 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. Too, behavior patterns associated with reproduction are of value in tracing phylogenies (von Wahlert, 1952).

(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?

(6) Is a spermatophore formed? If so, what is its structure and relation to the courtship pattern?

c. What is the pattern of amplexus?

d. When does ovulation occur? What is the stimulus required to initiate ovulation?

(1) Is courtship and/or amplexus essential to ovulation? to egg deposition?

Amplexus or courtship may be essential in some species (Bragg, 1941; Anderson, 1954) but not in others (Noble and Aronson, 1942).

(2) Can a female continue to produce offspring for a prolonged period after a successful courtship?

Baylis (1940) kept a spotted salamander isolated in captivity and observed that a brood of larvae was produced in May, 1937 and another in April, 1939, an interval of nearly two years. Is this an example of delayed fertilization or parthenogenesis? Angel and Lamotte (1947) suggest the occurrence of parthenogenesis in *Nectophrynoides occidentalis.* Stebbins (1954) reported that *Ensatina* retained spermatozoa for at least one month.

3. How many eggs or young are produced in each group?

   Some investigators have depended solely upon counts of ovarian eggs or of eggs found in clutches. Both procedures are subject to substantial error as the worker can but rarely be confident that no eggs have been previously deposited, that ovulation is completed or that two or more females have not utilized the same nest (Wood, 1953). 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 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 makes it exceedingly difficult to utilize much of the published data on reproductive capacity as bases for estimates of natality. Although it is often assumed that larger females deposit a larger number of eggs, this generalization is not adequately supported. Too, there may be a correlation between the number of ovarian follicles and size yet no correlation between the number of eggs deposited and/or hatched and female size. Wood (1953) indicated this situation in *Hemidactylium scutatum.*

   b. Is there a correlation between reproductive capacity and the condition (stress) in previous generations?

      The possibility of the condition of one generation affecting breeding success in subsequent generations has been suggested (Chitty, 1952). No information is available for amphibians.

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, egg mass or larva at deposition?

1. How do the egg or egg clusters vary in size and volume?
2. Is there any correlation in size, number and/or volume and size or age of females?

   Racial studies involving egg size must recognize the possible correlation between body size of females and egg size. As body size variation often is clinal, egg size may be expected to be so. Moriya (1954) reports such correlation and racial variation.
3. Is there a correlation between yolk quantity and the pattern of development? Between yolk quantity and number of eggs?

   The trend in the anurans from the microlecithal to the macrolecithal egg is associated with a reduction in the number of eggs. *Sminthillus* lays a single, large egg; *Eleutherodactylus,* 20-25 large eggs; North American ranids may lay several thousand small eggs.
4. What changes occur in size and weight of eggs and capsules during development?

   The weight and volume of eggs and capsules may change, often irregularly, with age and environment. The reporting of egg size without reference to the age or conditions under which the eggs were retained is of scant significance. Geographic variation in egg size (Moore, 1944) suggests the necessity for review of data in relation to geographic sources of material.
5. In what stage of development is the egg at deposition?
   a. Does the stage of development vary with the time eggs are retained by the female? If so, does this influence the development period?
   b. How is the stage of development related to the egg size and volume?

B. Where and in what manner are eggs deposited?
1. What is the behavior pattern of the female? Significance?
2. Does the female remain with the eggs? return to them? What is the influence of female behavior to survival of young?
   a. Does the female or male "defend" the eggs?

      Behavior of amphibians 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. Female *Desmognathus* will oppose intrusion to the nest; adult *Cyclorhamphus* reportedly guard their spawn.

b. Do the adults contribute to the maintenance of the eggs through physical action or the contribution of substance? Does either sex "brood" the eggs?

Stebbins (1954) speculated that the female *Ensatina* may release excess water from the urinary bladder into the egg cluster. Noble (1931), Gordon (1952) and others have reported the growth of mold on the eggs in the absence of the female salamander. Many anurans retain the eggs until hatching: *Rhinoderma* in gular sac; *Nectophrynoides* is ovoviviparous; *Cryptobatrachus* on back; *Amphignathodon* in folds of skin on back.

3. Is a nest or container provided for the eggs?

The nesting habits are poorly correlated with phylogeny. Related members of the same family (especially Hylidae and Ranidae) may thus exhibit widely different habits. Too, there have been no adequate studies reporting the variation of nesting habits of any species in relation to varying environments. Foam nests occur in the Bufonidae and the Polypedatidae; eggs in basins near water occur in the Brevicipitidae and the Hylidae. The salamander, *Batrachuperus,* deposits 7-12 eggs in a well-formed egg case attached to stone.

a. What factors determine the site?

b. How is the nest or container constructed?

c. What is the relation of choice of nest site to potential survival of eggs?

Bragg and Bresler (1951) note that contamination of pools may prevent hatching of eggs (*Bufo cognatus*) and report a 34 percent hatch of one egg group.

d. Does the female use the same site for subsequent clutches? In subsequent years?

C. What factors determine development rates?

1. What is the period of development? in the field? in the laboratory?

The factors modifying rate of development are not clearly known. The toads of the genus *Atelopus* are known for rapid development (19 hours).

a. What is the relation of temperature and humidity levels or changes to development time? of degree-humidity-hours to development time?

The failure to report development time in terms of degree-hours makes extremely difficult the synthesis of published data. Too, temperature and humidity may be paired factors with neither playing a master role (Shelford and Yeatter, 1955).

b. Is there a correlation between rate of development and the nature of the egg site?

2. How sensitive are eggs to low or high temperatures during the period of development? What extremes are the eggs subjected to in the typical field site? Potential mortality?

3. What factors initiate hatching? birth?

The functioning of hatching enzymes has been described (Noble and Brady, 1933; Kawahara, 1952) but the precise mechanism is unknown. The herpetologist should report observations on fluctuation in hatching behavior and rates.

4. What is the stage of development at hatching? birth?

   a. How is the time of development related to the stage of development at hatching or birth?

   b. Is the time required for development related to the quantity of yolk retained? Significance of quantity of yolk retained?

   The apparent general trend in the anurans toward withdrawal from the water is correlated with an increase of yolk and acceleration of development. This is reflected by the novel reproductive habits in many different evolutionary lines.

   c. What are the behavior patterns and their sequence of development in larvae?

VII. *What are the characteristics of the larvae? Diagnostic features?*

1. What is the adaptive significance of the morphological features?

Cheng (1932) traces the development of reproductive organs and germ cells in tadpoles. Orton (1955) stresses the possible significance of larval adaptability in distribution.

2. What is the adaptive significance of the behavior traits?

3. What are the primary factors determining growth rate? influence of density, food, temperature, light?

Crowding is sometimes a factor (Adolph, 1931; Noble, 1931; Savage, 1935). Both temperature and food are of great importance in regulating growth (Wilder, 1924; Krohn, 1930; Gosner and Black, 1955; Snyder, 1956). Reports of growth rates should attempt to present data on such factors.

4. What are the factors apparently related to metamorphosis?
   a. Do the larvae have the potentiality of being neotenic or must they metamorphose in order to reproduce?
   b. If neotenic, is this a result of insensitivity of tissues to thyroid hormone (perennibranchid amphibian), the absence of the stimulating agent or a deficient relationship between the anterior lobe of the pituitary and the thyroid gland?

      Kezer (1952) succeeded in inducing metamorphosis in the neotenic salamanders, *Eurycea neotenes* and *E. tynerensis,* although these forms are not reported to metamorphose under natural conditions.

5. What is the size at metamorphosis? the time of metamorphosis?

   There is typically much variation in size at metamorphosis. This is related to the temperatures experienced during development, the availability of food to the larvae and other environmental factors. (Adolph, 1931; McCarrison, 1921; Tobler, 1947; Lynn and Wackowski, 1951; Snyder, 1956.) Ryan (1953) reports that *R. clamitans* vary 26-38 mm in body length at metamorphosis. The technique of Richards and Riley (1937) for study of growth of salamander larvae is useful in comparing samples.

VIII. *What are the characteristics of the young adults? 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? (Freisling, 1948).

B. What are the behavior hazards to which the young adults are exposed immediately after metamorphosis?

IX. *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. 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 (Ryan, 1953). This does not, however, necessarily define the growing season as it has been demonstrated that amphibians may become quiescent during the winter although retained at constant temperature.

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

   Some researchers indicate that the time of initiation or cessation of growth may vary significantly from one local 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 egg; senility, length of growing season, social dominance).

   Growth rates in larvae and adults are exceedingly variable. Wilder (1924) demonstrated correlation of growth rate and food finding success. Noble (1931) thought crowding restricted growth of tadpoles. Bragg (1943) thought that aggregations stimulate feeding. Climatic factors influence growth. The diet influences growth rate and body proportions. Powers (1907) found that cannibalistic *Ambystoma tigrinum* differed from non-cannibalistic salamanders in flatness of head, length of teeth and body proportions.

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?

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 specimens?

   Few records of known ages are available. Angel (1947) summarizes these. *Megalobatrachus* may live 55 to 60 years. Other salamanders have been in captivity for 30 years. Anurans have survived for 36 years.

2. What estimates of age may be made from the population samples?

   The value of size groups must be estimated for each population. Age may be determined from anatomical attributes (Senning, 1940).

3. What are the characteristics of youth, maturity, old age?

D. What is the relation of ecdysis to growth? What are the factors inducing ecdysis? How does it occur? Habits associated with ecdysis?

X. *What is the annual cycle of activity and what factors exert primary influence on the cycle?*

A. What is the relation of the growing season to the period (periods) of courtship, development of eggs and larvae?

   Related species may respond differently to similar conditions (Powers, 1933). The annual sexual cycle is often closely associated with the recent evolutionary history.

   Caruso (1949) found no difference in the cyclic gametogenetic activity of *Hyla raddiana* from the plains and mountains of northern Argentina. The ovaries were mature during all months of the year and secondary sex characters were developed throughout the year. In contrast, *Phyllomedusa sauvagi* of northern Argentina breeds only during rains and the secondary sex characters are developed only during the breeding season.

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

   Freisling (1948) describes behavior of *Bufo viridis* in relation to temperature. Vernberg (1952) reports that *Plethodon cinereus* and *Eurycea bislineata* have highest metabolic rates at 10° C during May and June, lowest in October and November. At 1° C *Plethodon cinereus* had higher rates in October and November than in May and June. The cessation of activity at designated temperature levels has been frequently reported (Mullally, 1952; Bannikov, 1943; Bohnsack, 1952; Freisling, 1948; Marx, Metz and Kayser, 1946). Bullock (1955) discusses compensation for temperature. Incipient lethal temperatures and their relation to acclimation are known for few amphibians (Gibson, 1954).

C. What is the seasonal cycle in diel behavior?

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

   Many amphibians have periods of relative quiescence during the year. The use of the terms "hibernation" and "estivation" in designating these periods should be avoided as these words have specific physiological connotations developed through their use in the ecology of mammals.

1. What preparations are made for the period of quiescence?

   Cyclic, physiological modifications may bring about quiescence (Holzapfel, 1937). Morphological evidence derived from study of fat bodies and total weights is of concern here. Fromm and Johnson (1955) found oxygen consumption of frogs retained at constant temperature was maximum during the spring and decreased 40% in the winter.

2. Where do the animals spend the winter?

   Amphibians usually live in an environment buffered from thermal extremes. Information on the winter quarters of amphibians suggests that aquatic forms tend to aggregate while terrestrial forms remain isolated (Cagle and Smith, 1939; Bohnsack, 1952). Terrestrial forms may burrow into the ground to escape thermal extremes or drying. Cagle (1942) reported toads buried 6-20 inches in hard baked clay in October; Stebbins (1954) reported the intermittent movement of salamanders to underground retreats.

   Many amphibians have the ability to resist near-freezing temperatures during winter quiescence. Bohnsack (1952) reports that the temperature of the soil surrounding a bullfrog dropped to 23° F.

3. What environmental factors cause the initiation of quiescence? renewed activity?

   The role of paired factors as well as master factors must be considered. Biased attempts to recognize a master factor has often led to inconclusive answers for these questions.

   The significance of light cycles, especially ultra-violet, in amphibian activity has not been thoroughly explored. Researches on other vertebrates suggest the probable importance of light (Sabrosky, Larson and Nabours, 1933; Bailey, 1950).

4. What is the composition (age groups, size groups, sex ratios) of a winter aggregation?

5. What is the role of winter quiescence in limiting the geographic distribution?

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

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

B. Are breeding activities (courtship, egg-deposition) restricted to any part of the day?

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

The relation of temperature to activity was studied by Marx, Metz and Kayser (1946) who outlined techniques for recording activity and temperature simultaneously. Bannikov and Denissova (1943) demonstrated a correlation between digestion and movement from land to water in *Rana ridibunda* and found 2 peaks of activity, a nocturnal and a diurnal one.

D. How is the diel cycle modified by weather changes, population density?

Interspecies differences in the diel cycle of activity may affect the entire life history (Bannikov and Denissova, 1943; Chernomordikov, 1943). The activity threshold in relation to temperature may be characteristic of the species. Mullally (1952) points out that *Bufo boreas haplophilus* are active only when their body temperatures are greater than 3° C. Bogert (1951-2) expresses the opinion that salamanders cannot exercise control over their body temperature but that unpublished data indicate that some of the *Salientia* may do so. Exploration of the cycle may yield the key to many of the problems presented here.

XII. *What are the feeding and drinking habits of larvae, adults? Their relation to growth and survival?*

A. How does the animal obtain its food and water?

1. Can the animal pursue and catch actively moving prey? What senses are used?

2. What food preferences are exhibited in the field and laboratory?

B. What are the principal 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 food habits have reported a high percentage of empty stomachs. It is essential that the investigator utilize intestinal as well as stomach contents.

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

D. What is the significance of the food habits in determining the distribution of related forms?

Competition for food has been stressed as a limiting factor in the distribution of related species. The unlimited acceptance of Gause's hypothesis should be carefully considered (Gilbert, Reynoldson and Hobart, 1952). Although larvae of related species may live together, their food habits may be different. Inger (1956) suggests that the larvae of three species of *Rhacophorus,* living in the same pool, have different feeding habits.

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

The study of behavior under natural conditions often yields information of basic importance to the explanation of population problems and phylogeny (Freisling, 1948; Kortlandt, 1955). Few zoologists have developed the ability to profit from the observation of field behavior patterns. Herpetologists particularly have not utilized this procedure. Behavior of amphibian larvae is in many forms of great value in identification and may be used in the field and laboratory in the absence of morphological characters (Oyen, 1953).

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

B. Do group movements occur? Migration?

C. Are social hierarchies present?

1. If dominance hierarchy is present, what is the relation to territoriality, natality?
2. How does the social hierarchy affect the migrating individual? the juvenile seeking a territory? (Freisling, 1948).
3. Does the social hierarchy influence growth and reproductive potential?

D. Are there typical defensive or offensive behavior patterns? (Hediger, 1953.)

References Cited

Adams, A. E. 1940. Sexual conditions in *Triturus viridescens* III. The reproductive cycle of the adult aquatic form of both sexes. *Amer. Jour. Anat.,* 66: 235-271.

Adolph, E. F. 1931. Body size as a factor in the metamorphosis of tadpoles. *Biol. Bull.,* 61: 376-386.

Allee, W. C. 1951. *Cooperation Among Animals.* Henry Schuman, N. Y., pp. 1-233.

Anderson, Paul K. 1954. Studies in the ecology of the narrow-mouthed toad, *Microhyla carolinensis carolinensis. Tulane Stud. Zool.,* 2: 15-46

ANGEL, F. 1947. *Vie et Moeurs des Amphibiens.* Payot, Paris, pp. 1-317.

ANGEL, F. and M. LAMOTTE. 1947. Note sur la biologie d'un Crapaud vivipare, *Nectophrynoides occidentalies* Angel. *C. R. Acad. Sci. Paris*, 224: 413-415.

ARONSON, LESTER R. 1944. The sexual behavior of Anura, 6. The mating pattern of *Bufo americanus, Bufo fowleri,* and *Bufo terrestris. Amer. Mus. Novitates,* No. 1250: 1.15.

BALINSKY, B. I. 1955. Histogenetic and organogenetic processes in the development of specific characters in some South African tadpoles. *Jour. Embryol. Exp. Morph.,* 3: 93-120.

BAILEY, F. 1950. Ultraviolet boosts egg production. *Poultry Tribune,* 56: 34.

BALDAUF, RICHARD J. 1953. Climatic factors influencing the breeding migration of the spotted salamander, *Ambystoma maculatum* (Shaw). *Copeia,* 1953: 178-181.

BANNIKOV, A. G. 1943. The ecological conditions of activity of the amphibians as factors limiting the distribution of the species. *Zool. Jour. Moscow,* 22: 340-344.

BANNIKOV, A. G. and M. N. DENISSOVA 1943. Diurnal and nocturnal cycles of activity in *Rana ridibunda* Pall in southern Daghestan. *Ibid.,* 22: 33-37.

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

BAYLIS, H. A. 1940. Delayed reproduction in the spotted salamander. *Proc. Zool. Soc. London,* 109:243-246.

BLAIR, A. P. 1941. Variation, isolating mechanisms, and hybridization in certain toads. *Genetics,* 26: 398-417.

——— 1955. Distribution, variation and hybridization in a relict toad *(Bufo microscaphus)* in southwestern Utah. *Amer. Mus. Novitates,* No. 1722: 1-38.

BLAIR, W. FRANK 1951. Interbreeding of natural populations of vertebrates. *Amer. Nat.,* 85: 9-30.

——— 1955. Differentiation of mating call in spadefoots, genus *Scaphiopus. Texas Jour. Sci.,* 7: 183-188.

BLANCHARD, FRANK N. 1930. The stimulus to the breeding migration of the spotted salamander, *Ambystoma maculatum* (Shaw). *Amer. Nat.,* 64: 154-167.

BLANCHARD, FRANK N. and F. C. BLANCHARD 1931. Size groups and their characteristics in the salamander, *Hemidactylium scutatum* (Schlegel). *Ibid.,* 65: 149-164.

BOGERT, CHARLES M. 1952. Relative abundance, habitats and normal thermal levels of some Virginian salamanders. *Ecology,* 33: 16-30.

BOHNSACK, KURT 1952. Terrestrial hibernation of the bullfrog, *Rana catesbeiana* Shaw. *Copeia,* 1952: 114.

BRAGG, ARTHUR N. 1941. Observations on the ecology and natural history of Anura, VIII. Some factors in the initiation of breeding behavior in Anura. *Turtox News,* 19: 10-12.

BRAGG, ARTHUR N. and JACK BRESLER 1951. Viability of the eggs of *Bufo cognatus. Proc. Okla. Acad. Sci.,* 32: 13-14.

BRYUZGIN, V. L. 1939. A procedure for investigating age and growth in reptiles. *C. R. Acad. Sci. Moscow,* 23: 403-405.

BULLOCK, THEODORE HOLMES 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.*, 30: 311-342.

Bullough, W. S. 1951. *Vertebrate Sexual Cycles.* John Wiley and Sons, pp. 1-117.

Cagle, Fred R. 1942. Herpetological Fauna of Jackson and Union Counties, Illinois. *Amer. Midl. Nat.*, 28: 164-200.

__________ 1953. An outline for the study of a reptile life history. *Tulane Stud. Zool.*, 1: 31-52.

Cagle, Fred R. and Philip E. Smith 1939. A winter aggregation of *Siren intermedia* and *Triturus viridescens. Copeia*, 1939: 232-233.

Cain, Arthur J. 1953. Geography, ecology and coexistence in relation to the biological definition of the species. *Evolution*, 7: 76-83.

Caruso, M. A. 1949. Sobre el ciclo sexual anual de algunos "Hylidae" del Norte Argentino. *Acta Zool. Lilloana*, 8: 83-103, 6 pls.

Cei, G. 1942. Intorno a un neonato di *Geotriton fuscus* Bonap. ottenuto in cattivita con cenni sul suo grado di sviluppo. *Boll. Zool. Torino*, 13: 57-63.

__________ 1942 Ricerche biologiche e superimentali sul ciclo sessuale annuo dei Tritoni alpestri *(Triturus alpestris* Laur.*)* del Trentino e dell' alto Adige. *Studi Trenteni, Trento* 2B: 189-241.

__________ 1947. Su i probabili rapporti tra le possibilità respiratorie embrionali e le caratteristiche della distribuzione altimetrica della *Rana agile (Rana dalmatina* Bonap. = *R. agilis* Schr.*). Arch. Zool. Torino*, 32: 343-364.

Cei, J. M. 1949. El ciclo sexual y el predominio de la espermatogenesis annual continua en various batracios de la region chaquena. *Acta Zool. Lilloana*, 7: 527-544, 6 pls.

Cheng, Tso-Hsin 1932. The germ cell history of *Rana cantabrigensis* Baird II. Sex differentiation and development. *Zeit. Zellf. mikr. Anat.*, 16: 592-596.

Chen-Choa-Hsi 1940. Notes on a new hybrid toad *(Bufo radei* ♀ X *Bufo asiaticus* ♂*). Chinese Jour. Exp. Biol.*, 1: 335-338.

Chernomordikov, V. U. 1943. On temperature reactions of reptiles *Zool. Jour. Moscow*, 22: 274-279.

Chitty, D. 1952. Mortality among voles *(Microtis agrestis)* at Lake Vyrnwy, Montgomeryshire in 1936-7. *Trans. Roy Soc. London*, Ser. B, 236: 505-552.

Clark, P. J. and F. C. Evans 1955. On some aspects of spatial pattern in biological populations. *Science*, 121: 397-398.

Cohen, Nathan W. 1952. Comparative rates of dehydration and hydration in some California salamanders. *Ecology*, 33: 462-479.

Cole, Lamont C. 1954a. The population consequences of life history phenomena. *Quart. Rev. Biol.*, 29: 103-137.

__________ 1954b. Some features of random population cycles. *Jour. Wildl. Mgt.*, 18: 2-24.

Darlington, P. J. Jr. 1948. The geographical distribution of cold-blooded vertebrates. *Quart Rev. Biol.*, 23: 105-123.

Dely, O. G. 1952. Examen systematique et osteo-biometrique de la *Rana arvalis* Nilss. et de la var. *wolterstorffi* Féjeráry. *Ann. Hist.-nat. Musei Nationalis Hungarici*, 3: 231-244, pls. 9-11.

Dice, Lee R. 1952a. Measure of the spacing between individuals within a population. *Contrib. Lab. Vert. Biol.*, No. 55: 1-23.

———— 1952b. *Natural communities.* Univ. Mich. Press, Ann Arbor.

DICE, LEE R. and PHILIP J. CLARK 1953. The statistical concept of home range as applied to the recapture radius of the deermouse *(Peromyscus). Contrib. Lab. Vert. Biol.*, No. 62: 1-15.

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.

ELTON, CHARLES S. and RICHARD S. MILLER 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural features. *Jour. Anim. Ecol.*, 42: 460-495.

ERNST, FRITZ 1952. Biometrische Untersuchungen an schweizerischen Populationen von *Triton alp. alpestris* (Laur.). *Rev. Suisse de Zool.*, 49: 21-476.

ERRINGTON, PAUL L. 1954. On the hazards of overemphasizing numerical fluctuations in studies of "cyclic" phenomena in muskrat populations. *Jour. Wildl. Mgt.*, 18: 66-90.

FORCE, EDITH 1933. The age of attainment of sexual maturity of the leopard frog, *Rana pipiens* (Schreiber) in northern Michigan. *Copeia,* 1933: 128-131.

FRANK, FRITZ 1954. The causality of rodent cycles in the light of recent experiments on the population of German microtines (an interim report) (in German). *Ber. Morph. u. Oekol. Tiere,* 43: 321-356.

FREISLING, JOSEF 1948. Studien zur biologie und psychlogie der Wechselkröte *(Bufo viridis* Laur*). Osterr. Zool. Z.*, 1: 383-440.

FREYTAG, G. E. and E. SUSEBACH 1948. Zweiter Beitrag zur Kenntnis des Farbkleides des Feuresalamanders *(Salamandra salamandra)* Die Weiterzucht nigrinotischer Feuersalamander. *Mitt. Mus. Nat. Vorgesch. Magdeburg,* 1: 95-120.

FROMM, PAUL O. and ROBERT E. JOHNSON 1955. The respiratory metabolism of frogs as related to season. *Jour. Cell. Comp. Physiol.*, 45: 343-359.

GALGANO, M. 1947. Il ciclo sessuale annuale in *Triturus cristatus carnifex* (Laur) II. Azione della temperatura e di altri fattori ambientale sul ciclo sessuale maschile e femminile. *Arch. Zool. Torino*, 32: 33-207.

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

GIBSON, M. BEATRICE 1954. Upper lethal temperature relations of the guppy, *Lebistes reticulatus. Canadian Jour. Zool.*, 32: 393-407.

GILBERT, O., T. B. REYNOLDSON and J. HOBART 1952. Gause's hypothesis: an examination. *Jour. Animal Ecol.*, 21: 310-312.

GORDON, R. E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). *Amer. Midl. Nat.*, 47: 666-701.

GOSNER, KENNETH L. and IRVING H. BLACK 1955. The effects of temperature and moisture on the reproductive cycle of *Scaphiopus h. holbrooki. Ibid.*, 54: 192-203.

GRIFFIN, DONALD R. 1952. Radioactive tagging of animals under natural conditions. *Ecology,* 33: 329-335.

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

HAIRSTON, NELSON G. 1949. The local distribution and ecology of the plethodontid salamanders of the Southern Appalachians. *Ecol. Monogr.*, 19: 47-73.

HAMBURGER, F. 1936. The larval development of reciprocal species hybrids of *Triton taeniatus Leyd.* (and *Triton palmatus*, Duges) x *Triton cristatus*, Laur. *Jour. Exp. Zool.*, 73: 319-373.

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

HEDIGER, H. 1953. Uber die Bezeihungen tierlicher Flucht und "Hypnose." *Arch. Neerl. Zool.*, 10: 51-64.

HENDRICKSON, JOHN R. 1954. Ecology and systematics of salamanders of the genus *Batrachoseps*. *Univ. Calif. Publ. Zool.*, 54: 1-46.

HIGHTON, RICHARD 1956. The life history of the slimy salamander, *Plethodon glutinosus* in Florida. *Copeia*, 1956: 75-93.

HINSCHE, GEORG 1926. Uber Brunst und Kopulationsreaktionen des *Bufo vulgaris*. *Zeitschr. Vergl. Physiol.*, 4: 564-606.

HOLZAPFEL, RUTH A. 1937. The cyclic character of hibernation in frogs. *Quart. Rev. Biol.*, 12: 65-84.

INGER, ROBERT F. 1956. Some amphibians from the lowlands of North Borneo. *Fieldiana-Zoology*, 34: 389-424.

JAMESON, D. L. 1955. Evolutionary trends in the courtship and mating behavior of Salientia. *Sytematic Zool.*, 4: 105-119.

JUSZCYK, W. 1952. The preservation of natural colors in skin preparations of certain amphibia. *Copeia*, 1952: 33-38.

KALELA, OLAVI 1954. Über den Revierbesitz bei Vögeln und Säugetieren als populationsökologischer Faktor. *Ann. Zool. Soc. Vanamo*. 16: 1-48.

KAWAHARA, HARUYUKI 1953. Experimental study on the hatching mechanism of amphibians, Part III: Experimental observation on the hatching enzyme. *Bull. Exp. Biol.*, 3: 1-7.

KAWAHARA, TOSHIJISO 1953. Studies on hybridization in amphibians. V. Physiological isolation among four *Hynobius* species. *Jour. Sci. Hiroshima Univ.*, Ser. B, Div. 1, 14: 1-116.

KENDEIGH, S. C. 1944. Measurement of bird populations. *Ecol. Monogr.*, 12: 67-106.

KEZER, JAMES 1952. Thyroxin-induced metamorphosis of the neotenic salamanders, *Eurycea tynerensis* and *Eurycea neotenes*. *Copeia*, 1952: 234-237.

KORTLANDT, A. 1955. Aspects and prospects of the concept of instinct (vicissitudes of the hierarchy theory). *Arch. Neerl. Zool.*, 11: 155-284.

KREIG, H. and H. FORESTER 1937. Grundregeln der Rückenziechnung bei den Anuren. *Vorläuf Mitteil. Zool. Anz.*, 119: 288-293.

KROHN, E. 1930. Futterungsnersuche an Tritonen; III. Die Veranderung des Kopfform des Teichmolches *(M. vulgaris taeniata)* infalge Muschelfleischfutterung. *Arch. Entw. Mech.*, 121: 545-597.

LANTZ, L. A. 1939. Über die Bastardierung von Kammolch mit Marmormolch. *Abh. Mus. Nat. Vorgesch. Magdeburg*, 7: 113-120.

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

LIEBERKIND, INGVALD 1937. Vergleichende Studien über die Morphologie und Histogenese der larvalen Haftorgane bei den Amphibien. *C. A. Reitzals Farlag (Kobenhavn)*, 1-80, 28 pls, 8 figs.

LUTZ, BERTHA 1954. Anfibios Anuros do Distrito Federal. *Mem. Inst. Oswaldo Cruz*, 52: 155-238.

LYNN, W. GARDNER and HENRY E. WACKOWSKI 1951. The thyroid gland and its functions in cold-blooded vertebrates. *Quart. Rev. Biol.*, 26: 123-168.

MARGALEF, RAMON 1955. Temperatura, dimensions y evolución. *P. Inst. Biol. Apl.*, 19: 13-94.

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

———— 1955. The use of morphometric data in systematic, racial and relative growth studies in fishes. *Ibid*, 1955: 23-31.

MARSHALL, A. J. and C. J. F. COOMBS 1952. Lipoid changes in the gonads of wild birds; their possible bearing on hormone production, sexual display and the breeding season. *Nature*, 169: 261-264.

MARSHALL, W. H. and M. F. BUELL 1955. A study of the occurrence of amphibians in relation to bog succession, Itasca State Park, Minnesota. *Ecology*, 36: 381-387.

MARTOF, B. S. 1953. Territoriality in the green frog, *Rana clamitans*. *Ibid.*, 34: 165-174.

MARX, C., B. METZ and C. KAYSER 1946. Le rythme nycthimeral de la temperature at de l'activite chez la Grenouille. *C. R. Soc. Biol. Paris*, 140: 609-611.

MCCARRISON, R. 1921. Observations on the effects of fat excess on the growth and metamorphoiss of tadpoles. *Proc. Roy. Soc. London*, 92: 295-303.

MECHAM, JOHN S. 1954. Geographic variation in the green frog, *Rana clamitans* Latreille. *Texas Jour. Sci.*, 6: 1-24.

MILLER, MALCOLM R. and MARILYN E. ROBBINS 1954. The reproductive cycle in *Taricha torosa* (Triturus torosus). *Jour. Exp. Zool.*, 125: 415-445.

MORIYA, KATSUTA 1954. Studies on the five races of the Japanese pond frog, *Rana nigromaculata* Hallowell I. Differences in the morphological characters. *Jour. Sci. Hiroshima Univ.*, Ser. B, Div. I, 15: 1-21, 2 pls.

MOORE, JOHN A. 1944. Geographic variation in *Rana pipiens* Schreber of eastern North America. *Bull. Amer. Mus. Nat. Hist.*, 82: 345-370.

MULLALLY, DON P. 1952. Habits and minimum temperatures of the toad, *Bufo boreas halophilus*. *Copeia*, 1952: 274-276.

NOBLE, G. K. 1927. The value of life history data in the study of evolution of the amphibia. *Ann. New York Acad. Sci.*, 30: 31-128.

———— 1931. *The Biology of the Amphibia*. McGraw-Hill Co., New York, pp. 1-517.

NOBLE, G. K. and L. R. ARONSON 1942. The sexual behavior of anura, 1. The normal mating pattern of *Rana pipiens*. *Bull. Amer. Mus. Nat. Hist.*, 80: 127-142.

NOBLE, G. K. and M. K. BRADY 1933. Observations on the life history of the marbled salamander, *Ambystoma opacum* Gravenhorst. *Zoologica*, 11: 89-132.

ORTON, GRACE L. 1955. Some aspects of ecology and ontogeny in the fishes and amphibians. *Amer. Nat.*, 89: 193-203.

OYEN, W. G. v. 1953. De determinatie van anuren-larven naar het gedrag. *Lacerta*, 1953: 73-75.

PACAUD, ANDRÉ 1951. Méthode experimentale et écologique en milieu aquatique. *Année Biol.*, 27: 545-553.

PACKER, H. P. and H. S. PEARSON 1952. The growth, survival, wandering and variation of the long-tailed field mouse, *Apodemus sylvaticus* III. Wandering power and distribution. *Biometrika*, 39: 389-442.

PARISER, K. 1932. Verschiebung des Geschlechtsverhältnisses bei Künstlich erzeugten Triton - bastarden. *Biol. Zentralbl.*, 52: 654-659.

PONSE, K. 1951. La génétique du sexe chez les batraciens avec un apercu des travaux de R. R. Humphrey. *Colloques Internat. du Centre Nat. de la Recherche Sci.*, 31: 1-32.

POWERS, J. H. 1907. Morphological variation and its causes in *Ambystoma tigrinum. Stud. Univ. Nebraska*, 7: 197-224.

POWER, J. H. 1933. Physiological adaption to environment in *Rana fuscigula. So. African Jour. Sci.*, 30: 416-418.

PROSSER, C. LADD 1955. Physiological variation in animals. *Biol. Rev.*, 30: 229-262.

RANEY, EDWARD C. and ERNEST A. LACHNER 1947. Studies on the growth of tagged toads *(Bufo terrestris americanus* Holbrook). *Copeia*, 1947: 113-116.

RICHARDS, OSCAR WHITE and GORDON ARTHUR RILEY 1937. The growth of amphibian larvae illustrated by transformed coordinates. *Jour. Exp. Zool.*, 77: 159-167.

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

ROSTAND, JEAN 1951. *La Genetique des Batraciens*. Hermann et Cie. Paris, pp. 1-80.

RUIBAL, RODOLFO 1955. A study of altitudinal races in *Rana pipiens. Evolution*, 9: 322-338.

RUITER, L. DE 1956. Countershading in caterpillars: an analysis of its adaptive significance. *Arch. Neerl. Zool.* 11: 285-341.

RYAN, RICHARD A. 1953. Growth rates of some ranids under natural conditions. *Copeia*, 1953: 73-80.

SABROSKY, C. W., I. LARSON and R. K. NABOURS 1933. Experiments with light upon reproduction, growth and diapause in grouse locusts. *Trans. Kansas Acad. Sci.*, 36: 298-300.

SAVAGE, M. 1935. The ecology of young tadpoles, with special referrence to some adaptations to the habit of mass-spawning in *Rana t. tempororia. Proc. Zool. Soc. London:* 605-610.

SCHAEFER, MILNER B. 1951. Estimation of animal populations by marking experiments. *Fishery Bull., U. S. Fish and Wildl. Serv.*, 52: 191-203.

SCHMIDT, KARL P. 1938. A geographic variation gradient in frogs. *Field Mus. Nat. Hist., Zool. Ser.*, 20: 379-382.

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

SEALANDER, JOHN A. JR. 1953. Body temperatures of white-footed mice in relation to environmental temperature and heat and cold stress. *Biol. Bull.*, 104: 87-99.

SCHUSTER, O. 1950. Die klimaparallele Ausbildung der Korperproportionen bei Poikilothermen. *Abh. Senckenb. Naturf. Ges.*, No. 482: 1-89, 2 pls.

SENNING, W. C. 1940. A study of age determination and growth of *Necturus maculosus* based on a study of the parasphenoid bone. *Amer. Jour. Anat.*, 66: 483-495.

SERAFÍNSKI, WLODZIMIERZ 1955. The senescence of the brown rat (*Rattus norvegicus* Berk.) in the light of craniometry. *Acta Theriologica*, 1: 1-14.

SHELFORD, V. E. and R. E. YEATTER 1955. Some suggested relations of prairie chicken abundance to physical factors, especially rainfall and solar radiation. *Jour. Wildl.. Mgt.*, 19: 233-242.

SIMPSON, G. G. 1944. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 85: 1-350.

SIMPSON, G. G. and A. ROE 1939. *Quantitative Zoology*. McGraw-Hill, New York.

SMITH, MALCOLM 1952. The climate of the British Isles and its influence on the habits and distribution of the amphibians and reptiles. *British Jour. Herp.*, 1: 103-112.

SNYDER, RICHARD C. 1956. Comparative features of the life histories of *Ambystoma gracile* (Baird) from populations at low and high altitudes. *Copeia*, 1956: 41-50.

STEBBINS, ROBERT C. 1954. Natural history of the salamanders of the plethodontid genus *Ensatina*. *Univ. Calif. Publ. Zool.*, 54: 47-124.

STORM, ROBERT M. and RICHARD A. PIMENTEL 1954. A method for studying amphibian breeding populations. *Herpetologica*, 10: 161-166.

STRÜBING, HILDEGARD 1954. Über Vorzugstemperaturen von amphibien. *Z. Morph. u Okol, Tiere*, 43: 357-386.

TÅNING, A. VEDEL 1952. Experimental study of meristic characters in fishes. *Biol. Rev.*, 27: 169-193.

TERENTJEV, P. V. 1943. Correlations of indices of *Rana ridibunda* *Pall. Zool. Jour. Moscow*, 22: 267-273.

TEST, FREDERICK H. 1946. Relations of the red-backed salamander *(Plethodon cinereus)* to light and contact. *Ecology*, 27: 246-254.

———— 1954. Social aggressiveness in an amphibian. *Science*, 120: 140-141.

TEST, FREDERICK H. and BARBARA A. BINGHAM 1948. Census of a population of the red-backed salamander *(Plethodon cinereus)*. *Amer. Midl. Nat.*, 39: 362-372.

THERON, J. G. 1952. On the cranial morphology of *Ambystoma maculatum* (Shaw). *So. African Jour. Sci.*, 48: 343-364.

THORSON, T. and A. SVIHLA 1943. Correlation of the habitats of amphibians and their ability to survive the loss of body water. *Ecology*, 24: 374-381.

TINBERGEN, N. 1952. "Derwid" activities; their causation, biological significance, origin and emancipation during evolution. *Quart. Rev. Biol.*, 27: 1-32.

TOBLER, ALBERT 1947. Der Einfluss des Lichtausfalles auf den Ablauf der Metamorphose und auf die Gonadenentwicklung von *Triton aepestris*. *Revue Suisse de Zool.*, 54: 27-457.

TOIVONEN, SULO 1952. Ein Fall von partieller Neotenie bei *Xenopus laevis* Daudin und experimentelle Untersuchungen zu seiner kausalen Erklärung. *Arch Soc. Zool.—Bot. Fenn. "Vanamo,"* 6: 107-123.

TWITTY, VICTOR C. 1955. Field experiments on the biology and genetic relationships of the California species of *Triturus*. *Jour. Exp. Zool.*, 129: 129-147.

VERNBERG, F. JOHN 1951. The oxygen consumption of the two species of salamanders at different seasons of the year. *Physiol. Zool.*, 25: 243-249.

VOLPE, E. PETER 1952. Physiological evidence for natural hybridization of *Bufo americanus and Bufo fowleri*. *Evolution*, 6: 393-406.

__________ 1953. Embryonic temperature adaptations and relationships in toads. *Physiol. Zool.*, 26: 344-354.

VON WAHLERT, GERD 1952. On the systematic position of the salamandrid genus *Taricha* and its species. *Copeia*, 1952: 29-30.

WILDER, I. W. 1924. The relation of growth to metamorphosis in *Eurycea bislineata* (Green). *Jour. Exp. Zool.*, 40: 1-112.

WOOD, JOHN THORNTON 1951. Protective behavior and photic orientation in aquatic and larval two-lined salamanders, *Eurycea b. bislineata* x *cirrigera*. *Virginia Jour. Sci.*, 2: 113-121.

__________ 1953. Observations on the complements of ova and nesting of the four-toed salamander in Virginia. *Amer. Nat.*, 87: 77-86.

ABSTRACT

An annotated outline designed to suggest the ideal requirements in an investigation of the life history of an amphibian.