TOPICAL REVIEW

A REVIEW OF ECOLOGICAL RESEARCH IN MIDDLE AMERICA

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WHEN I FIRST UNDERTOOK THE TASK OF COMPILING INFORMATION ON ECOlogical research in Middle America it seemed best to concentrate on one facet of this many-faceted science. After some time and reflection, however, I concluded that a greater service would be performed for the reader by an overview of most of the subject area encompassed by ecology. I have attempted to present this overview in the pages that follow.

The reader is warned that depth has been sacrificed for breadth and that no attempt to review all the literature has been made. To do so would require far more space than is available. Therefore it is certain that some readers will find missing what they may consider to be a specially important or interesting paper. To them I offer apology.

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Ecology as a science is virtually the child of the twentieth century although there was, to be sure, a long pre-parturitive period. Certainly man has always been an ecologist of sorts or he would have ceased to exist long ago. Ecology didn't begin with the coining of a word or the publication of a paper, i.e., an ecology understood by Amerinds existed prior to European conquest. This seems to me to be a special subject, however, and should be handled elsewhere.

The Spaniards involved in the business of conquest counted a few among their numbers who might be called naturalists. Most appear to have been earthy men bent on gain with little appreciation of the fact that a biogeographic realm new to European experience had been discovered. This is evident in their penchant for naming plants and animals after plants and animals known in Iberia. Thus the cougar, *Felis concolor*, became *león*; the jaguar, *Felis onca,* became *tigre*; a rodent, the *paca, Cuniculus* spp., became *conejo* and so on.

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Trees not bearing any particular appearance or relationship to oaks, *Quercus,* became *roble*; trees not related to the ash, *Fraxinus*, became *fresno* and so on and on. This process may have been merely an attempt to simulate the conditions of home. I suspect though that these tough warriors were just not sufficiently interested or imaginative to go to the trouble of applying new names. Of course this procedure was not followed in all cases and aboriginal names often came to be adopted. A regional variation in the use of aboriginal names exists and might bear investigation.

Some of the Spaniards were scholars and to them we owe a great deal. One of the greatest contributions made during the period of conquest was that of the great Oviedo (Oviedo y Valdez, 1851–55), who scarcely needs introduction to the readers of this review. Oviedo described in detail many of the new plants and animals of the Indies and included many data of an ethnobiological nature as well. Other chroniclers included information on the vegetation cover and the animal life, but their natural history notes were sometimes more quaint than reliable. But the Spanish government was very interested in the newly discovered biological wealth of the Americas and sought diligently for new and useful plants to be added to their materia medica for the study and use of plants was then largely the property of medicine.

An unorganized gathering of biological information characterized the first couple of centuries after conquest though there were exceptions. Among the more interesting of these were the natural history studies by the British pirate, William Dampier, who in a more enlightened age might well have occupied a professor's chair rather than the quarterdeck of a privateer. We are much indebted to Dampier for the records he kept on natural history and antropology. Similarly, Dampier's surgeon, Lionel Wafer, left an account of eastern Panama during the latter part of the 17th century that includes natural history information of great value today.

During the eighteenth century various persons undertook, often as an avocation, a fairly systematic collecting of plants and animals. A review of this period is to be found in the useful book by Chardón (1949) who discusses the naturalists working in Latin America during the 16th, 17th, and 18th centuries.

Toward the end of the 19th century, an increase in organized and systematic collections of plant and animal specimens was under way and detailed publications describing these collections were appearing. The major published work during this time was the monumental *Biologia-Centrali-Americana* (edited by Godman and Salvin) which appeared in 62 volumes (1879–1915). Many authors contributed to this work which consists of archaeological information as well as the biological information indicated in the title. Although chiefly systematic, ecological information of a general and uneven nature is in-

cluded. Despite its considerable size, this work has been overlooked by many persons who would seem to find it useful.

It may thus be noted that the groundwork for ecological studies in Middle America was laid in the period prior to the 20th century but that the synthesis of these data did not begin until the 20th century.

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The remainder of this review deals with the 20th century. Individual topics are treated separately to prevent confusion.

BOTANICAL AND ZOOLOGICAL COLLECTING

The collecting efforts that characterized a majority of the biological investigations of the 19th century continued well into the 20th. Indeed the task continues and a large percentage of papers on biological subjects relating to Middle America is still of a systematic nature. These publications are so numerous that it is unnecessary to offer even a synoptic listing here. Since many of the papers on biological subjects also contain ecological information, a few of the more representative will be discussed later.

One might conclude that by this date little new information on animals and plants remains to be collected in Middle America, but the opposite is true. Large geographic areas have been missed entirely or have been only briefly checked by zoologists and botanists.

Some of these areas, such as high ridges and mountain tops, are of great ecological and biogeographical interest. The lack of data extends even to the animals and to a somewhat lesser extent to plants that are often considered to be well known. The detailed distribution of many of these forms is not known because collecting has not been adequate.

The current preoccupation in biology with research in molecular biology—a preoccupation that sometimes assumes the proportions of a fad—means that in the future fewer competent persons will be available to perform the needed collecting job. Unfortunately, *collector* has become a tainted epithet in certain biological circles. This is ridiculus because a collector must be a good scientist. But the lure of the laboratory and DNA will, I believe, diminish the already too thin ranks of field biologists, the collectors now working in Middle America.

LIFE ZONE INVESTIGATIONS

C. Hart Merriam published in 1894 and 1898 his well known papers on the life zone concept that he originated and applied to agriculture in the United States. Biologists in the U.S. were fairly quick to adopt the model and apply it

to many parts of the country. Merriam's scheme, it will be recalled, was based upon certain (incorrect) ideas about temperature and plant growth. This aspect of the life zone idea was later to be discarded by biologists, but they, as well as geographers and others, found that the descriptive regionalizing of plant and animal associations was useful if employed at an elementary level.

The first notable application of the life zone concept in Middle America was by a mammalogist, Goldman, who included a map and a discussion of life zones in a paper on the mammals of Panama (1920). Goldman did not employ Merriam's temperature valutes; only the descriptive approach was followed. Goldman recognized three major zones for Panama, viz., Lower Tropical Zone, Upper Tropical Zone, Temperate Zone. He divided the Lower Tropical Zone into two sub units, viz., Arid Lower Tropical Zone and Humid Lower Tropical Zone. Although no climatic data are included to support these divisions, Goldman alluded to differences in seasonal rainfall and to the "refreshing influence" of heavy dews in the Humid phase. The use of the adjective *arid* is unfortunate as the areas so designated are in fact *Aw* (Tropical Savanna) in the Köppen classification of climates. An indication that the area has a seasonally reduced quantity of precipitation would be more accurate. A recent paper (1966) by Sexton and Heatwole on an aspect of Panamanian herpetology recognizes this ambiguity. The authors use the terms *seasonally humid zone* and *prehumid zone* to represent the arid and humid divisions of Goldman. Goldman's scheme was followed uncritically by others. For example, Aldrich and Bole (1937) employed it in an area of western Panama, and Breder (1946) used the scheme for a part of eastern Panama. In both cases, the term arid was used in *Am* climates (tropical monsoon climate in the Köppen system).

Another shortcoming of Goldman's map, which illustrates the then existing state of geographic knowledge of the isthmus, is the failure to show that a large portion of the Azuero Peninsula has a long rainy season as well as elevations above 5,000 feet. Similar errors occur elsewhere on the map.

Other authors writing on different elements of the Middle American fauna have attempted to describe life zones without the aid of maps, and with regard to their ecological content these efforts have been for the most part naive. Biologists were apparently aware that a life zone approach was limited chiefly to descriptive uses and did not lead to the insights desired of ecology. The implication, however, is not that the life zone idea is dead.

Holdridge has given the concept new life by proposing a life zone system that is becoming widely known as the Holdridge System. This scheme suffers from many of the defects inherent in the Merriam model concerning quantitative criteria. Holdridge employs a little more arithmetic than Merriam but the same kinds of errors are present. Space does not permit a lengthy description or critique of the Holdridge system so only a brief summary will be attempted. The

reader is referred to the following publications for more detail: Holdridge (1947, 1957, 1959, 1960), Holdridge and Budowski (1956) and Tosi (1964).

Unlike the Merriam scheme, Holdridges' system focuses on the distribution of forest formations—animals do not directly enter into the construct. The term *natural life zone* (are there unnatural life zones?) is given to the model by Tosi, one of the principal followers of Holdridge. The chief error of the Holdridge system is the use of a value called the *mean annual biotemperature.* Data from standard weather shelters are employed and to quote Tosi the mean annual biotemperature "may be calculated by dividing the sum of mean positive daily temperatures (anything above 0 degrees Centigrade) in degrees Centigrade by the total number of days of the year. . . . The concept of biotemperature was one of the key innovations in the development of Holdridge's model." Averaging numerical data that are measures of environmental parameters does not seem to be good ecology or good biology. Over three decades ago (1934) Taylor drew the attention of all ecologists to the importance of identifying and considering the unusual environmental event in his restatement of Liebig's Law of the minimum. It seems to me to be a little grandiloquent to call the mean of a mean a biotemperature. It assumes, among other things, that infinitely more is known of plant ecology and physiology than is actually the case. In addition to the temperature problem, one must draw attention to the use of the day number of the Gregorian calendar; the ignoring of edaphic factors (with the exception of obviously flooded land) and the variations in runoff and cutoff of precipitation; the use of data from standard weather shelters (I know of no organisms that characteristically live within a little white louvred box one and one-half meters above the ground); the ignoring of the fact that even the temperature records, such as they are, are too sparse for most of the humid tropics to make the system workable even as an arithmetic exercise; the all but total ignoring of anthropogenetic factors in plant and soil cover. The system is not predictive as the authors of a recent ecology text book have stated (MacArthur and Connell, 1966). For who dares to suggest that ecology has advanced so far that a few temperature and rainfall data are sufficient to predict what lies on the other side of the hill?

Tosi (1964) suggests that there had been a "gap in interdisciplinary communication" since it seemed to him that geographers and others had been bedazzled by the offerings of Thornthwaite (1948) and had overlooked the offering of Holdridge. This is hardly the case. This reviewer and a number of his colleagues have been aware of the Holdridge model for well over a decade. We have not employed it in our investigations because of some of the problems set forth above.

Holdridge has had an opportunity to diffuse his system through his work

as a forester for various governmental agencies in Middle America. Thus his reports and maps are known to many planners in that area but have not had a wide circulation elsewhere. Two exceptions may be noted: Holdridge and Budowski (1956) and Holdridge (1962). The former is a forestry survey of Panama, the latter a similar survey of Honduras. The system makes no provision for the inclusion of grasslands and the results are maps that often show what Holdridge predicts should be in a given region rather than what is in fact there. I do not cavil at attempt to reconstruct past vegetation cover or even to project it into the future—this is an important ecological task (see for example the important paper on Cuban vegetation by Waibel, 1943, which represents an attempt to employ place names to reconstruct vegetation circa 1511 A.D.). But Holdridge does not make clear to the reader that many of the vegetation types ("life zones") mapped are only his prognostications of what an area might be expected to support if left completely undisturbed for a sufficiently long period. The failure to do so is, to say the very least, misleading to the unwarned reader.

Holdridge's model has been increasingly utilized in tropical America. A notable example is to be found in a work on the birds of Costa Rica by Slud (1964). Employing a map by Holdridge of Costa Rica (contained in a report not seen by me) Slud constructed a "Life-zone or plant formation may (provisional)" for Costa Rica. Ten forest types are recognized but no provision for grasslands is included. In parts of southwest Costa Rica we find the designation *moist forest* where presently there are extensive grassy areas with scattered fire-resistent shrubs. Most of Guanacaste Province is mapped as dry forest though grasslands and *scattered* trees predominate over much of the area. Of what current ecological use are such maps when they do not show what is extant? Is it erroneous to characterize such efforts as *a priori* ecology?

Several efforts have been directed toward making a classification of the vegetation of Middle America and adjacent regions. In many respects, of course, Holdridge has done just that, and this may be the part of his work that will persist and be used. More detailed attempts were made by Beard (1944, 1953, 1955) whose classification schemes are widely known. Beard's studies are based on very extensive field research, but he too tends to ignore or underevaluate the anthropogenetic factor. He has also been rather welded to the climatic concept, an ecological oversimplification in considerable vogue, which presents more problems than it solves.

Vegetation maps of varying quality covering parts of the Middle American region have been published. Only a few will be mentioned here. One is a map of the vegetation of Nicaragua (scale unfortunately small in the published version) by Taylor (1963). Taylor found a close correlation between vegetation zones and the length of the dry season. He also emphasized the importance of fire in the savanna areas. Another is a map of vegetation zones in Mexico by

Leopold (1950 and reprinted 1959). The units employed are physiognomic. The map gives almost no consideration to man-altered vegetation over large areas of Mexico and is therefore a little like the maps of Holdridge. Judging from the map alone, for example, one would never conclude that the Yucatan area had been occupied by shifting cultivators in large numbers with attendant forest alterations.

A somewhat different effort is represented in a paper (1950) by Carr who attempted a preliminary classification of animal habitats in Honduras. Although no maps accompany the work, there are several good diagrams, well written descriptions, and well chosen photographs of vegetation types. In addition to the lack of a map, the chief criticism is of his too-cautious approach to the question of anthropogenetic factors. A useful sketch map of the phytophysiognomy of southwest Guatemala has been provided by McBryde (1945). Though not an example of fine cartography, this map shows what the author actually found growing in the area. In 1957 Holdridge published a paper on the vegetation of mainland Middle America listing descriptive categories with no map or diagrams.

A recent attempt to describe the vegetation of mainland Middle America is represented in a paper by Wagner (1964). The map accompanying the text is drawn at a disappointingly small scale. Fortunately a detailed text with good photographs accompanies the map. For Mexico, Tamayo has summarized many phytogeographic data and has described biogeographic and forestry zones in text and atlas (1962). A *pot pourri* of plant geography and ecology awaits the reader of a volume devoted to plant science in Latin America in the Chronica Botanica series edited by Verdoorn (1945). Although often exasperating because of the lack of organization, this volume contains a great deal of valuable information particularly for areas not previously mapped or otherwise described by competent observers. One of the most detailed maps of a large area in Middle America to be published recently is contained in a land-use survey of British Honduras (Romney, ed., 1959). The maps, published as two sheets, are titled "natural vegetation map." Only oblique attention is given in the text to the probable ecological consequences of ancient and prolonged human use of the land. The term "natural vegetation," which comes so easily to the pen, is surely one of the most abused terms employed in this and many other regions.

Relatively few efforts have been made to regionalize the Middle American area in terms of the fauna alone. One recent attempt must be noted. Ryan (1963) formulated a scheme of biotic provinces for Central America based on mammalian assemblages and distributions. Although Stuart (1964) in a footnote, says that this paper "will remain a classic in the field of regional geography of Central America," I believe that Ryan's approach is not particularly useful. He attempts his regionalization from too narrow a base, viz., the numerical

assemblage of mammalian taxa without recourse to historical and recent ecological factors involved in the regional patterns he describes. The method appeals chiefly, I believe, because it is numerical and suggests that some kind of meaningful analysis has been accomplished. Ryan's approach is interesting but I doubt that it has become a classic.

To summarize this section, it should be clear that many attempts have been made to regionalize Middle America through use of ecological and/or taxonomic criteria. So far, the attempts that have employed environmental measurements of parameters such as temperature and precipitation have fallen far short of what is required. Most successful are schemes that are purely or chiefly descriptive. Yet it should be stressed that what is required are efforts to achieve sound eco-regional divisions founded upon meaningful quantitative data. It is suggested that application of systems theory in analyzing these ecosystems will ultimately produce the sound generalizations that have thus far eluded our efforts.

ENVIRONMENTAL MEASUREMENT

Fundamental to the study of ecology are measurements of relevant environmental elements such as macro and microclimates, soil elements, and hydrographic measurements. These studies are not yet sufficiently advanced in Middle America.

In the study of macroclimates we encounter what at first glance appears to be an abundance of data. Most abundant are precipitation data with temperature data lagging rather far behind. Still greater is the dearth of data on atmospheric humidity, radiation, soil temperatures.

Apparently the easiest weather instruments to read and maintain are nonrecording rain gauges, which may explain why they are more abundant than even simple max-min thermometers. Before we congratulate ourselves on these apparent riches, however, let us examine briefly the question of reliability of the rainfall records. Rain gauges must be set up in situations where there is no 'shadow' cast by trees or buildings or other interfering elements. They should not be placed in an atypical terrain situation unless a particular atypical situation is being studied. Unfortunately, a large share of the rainfall records in Middle America relate to instrument sites chosen for ease of access to the person having to keep the record rather than for sound ecological criteria. These station sites also tend to "wander" during a long time span even though the same station name may be employed throughout the period of record. An additional problem is that of possibly well-meant falsification of data when someone neglected to read the rain gauge and guessed the quantity of rain that fell. The falsification is sometimes but not always obvious. Unless automatic rain gauges are used,

only gross daily amounts of rainfall are available and the ecologically significant feature of how much rain fell in a given rainfall is lost. The daily sums are usually added as monthly totals and these are the values one most often encounters. Whatever value this data may have for descriptive climatology it falls short of what is required for meaningful ecological application. Furthermore, the plethora of rainfall data is more apparent than real. Very large areas have no records at all or records of a duration too short to be of more than limited use. Probably no record of less than 15 years is particularly meaningful. One of the persistent illusions in geographical-ecological circles is that the individual elements of the microclimates of the humid tropics are so unvarying that very short weather records are significant. This is untrue. When tropical precipitation is subjected to careful analysis, it is possible to discern significant variations in diurnal and nocturnal quantities of rainfall, the appearance of little "dry seasons" in the midst of wet seasons, the amounts of rain that occur during individual rainfall periods, and so on. The most advanced description of Central American rainfall available is by Portig (1965). He has recognized some of the problems associated with traditional descriptions and offers more sophisticated statistical treatment. He errs, however, when he suggests that we have a fairly good knowledge of the amounts of rainfall in Central America. We do not.

Data on atmospheric temperatures are scarce and most of those that are available have but limited ecological application because they are not obtained from situations in which most plants and animals are found. The data are usually confined to maximum and minimum values both of which are often averaged. This is of little ecological value. What is needed are recording thermometers (or manually recorded thermometers if the man-power is available) operating over long periods of time. They should be set up in habitats occupied by plants and animals (including man). Among the foremost fables of our time are the numerous published maps showing mean monthly or annual isotherms curving their sinuous paths over our region. These lines often rely more upon the clairvoyance of a cartographer than upon the existence of temperature data.

The measurement of atmospheric humidity has scarcely begun as a standard practice in much of this region. In terms of the ecologically crude data obtained from rain gauges and max-min thermometers set up in standard weather shelters, it would be no difficult task to obtain relative humidity data with a sling psychrometer. Perhaps it is just as well that this kind of measurement has not been attempted on a large scale as the chances for error are great. If the device is not slung fast enough or long enough an inaccurate reading will result. If the same elevation above the ground is not employed each time an observation is made the record becomes meaningless. The instrument is in any case passed through too much air to yield significant data. Recording hygrographs have

given only indifferent results. Most of these instruments are operated by a wind-up clock mechanism that may not function properly in constant high absolute humidity. The graph paper is usually very unstable dimensionally in humid tropical conditions. The ink is often very hygroscopic causing the pen trace to smear and be illegible. The recent availability of thermistor thermometers and sophisticated recording devices (the latter can be set up as much as several thousand feet from where the sensors are placed) may provide the tools necessary to obtain the required temperature and humidity data (the thermistor bulbs can be made to function as wet bulb thermometers). The usual humidity value one encounters in published sources is relative humidity. When this is presented without a simultaneous temperature reading it is of little or no value for ecological purposes. A more meaningful value is the vapor pressure deficit which, contrary to warnings in the past (see Leighly, 1937 for this view; see also Schulz, 1960, who shows that this is a meaningful value in the humid tropics), is obtainable and is of ecological significance.

Microclimatological investigations are not significantly advanced. The first important effort to collect microclimatic (or bioclimatic) data in this region was by Allee who 40 years ago published what are still two often cited papers (1926a, 1926b). These deal with bioclimatic conditions inside a tropical monsoon forest in the Canal Zone. The period of record is for only one dry season (1922). The fact that other ecologists still find these two papers useful is mute testimony to the fact that studies of this kind have not advanced a great deal in the intervening 40 years. A lengthier study in the same area has been undertaken by this reviewer and the data are being analyzed for future publication.

Tropical microclimatology is certainly one of the most neglected aspects of tropical ecology and offers rich rewards for the persons who turn their attention to it.

Climatic data are often included in biological papers that are otherwise chiefly systematic in content. There are many of these papers available and they are sometimes overlooked as possible sources of data. The climatic data they contain are often highly generalized but may nevertheless be the only published data available for the localities under discussion. As random examples of this kind of source the reader is referred to Duelling (1963); Slud (1960); Loock (1950).

Detailed soil studies were begun in this century but much of the region remains to be investigated by pedologists. Virtually all of the work thus far accomplished has been directed toward agricultural needs and uses. Little of this work has as yet been translated into terms that are applicable to more general ecological problems. H. H. Bennett was one of the pioneers in these investigations (see for example 1926, and 1929). Since the end of World War II there

has been much greater interest shown in these studies. Many have been assisted and directed by outside experts. A great deal of the recent work has been most ably summarized by Stevens (1964). Recent studies have concentrated on those areas in which the agricultural potential appeared to be greatest. This has usually meant that, with the exception of Mexico, the studies have been in *Aw* climatic areas. Least known edaphically are areas of *Af* climates. Banana lands are often located in areas of *Am* climates and in these cases soil investigations have usually been carried out though not always published. Panama can be mentioned as an example of the recent trends in soils investigations in Middle America. The investigations have concentrated on the agricultural and livestock areas to the west of the capital city and many maps and reports have been published. A more or less typical example of this research is by Mathews and Guzman (1955) on the soils of the Coclé Plains. This, and companion studies, display broad appreciation of ecological factors that have contributed to soil formation. Perhaps the chief fault is an under-appreciation of the importance of fire in some of the areas studied.

A soil study of Honduras has been published by the O.E.A. (see citation to Holdridge, 1962). The investigation concentrates on the areas of chief agricultural potential as presently understood. The study does not achieve the level of ecological sophistication attained by those completed so far in Panama. The government of Great Britain recently sponsored a land-use survey of British Honduras and included a detailed soil study containing two good maps (Romney, ed., 1959).

Hydrographic and limnologic investigations are in a state of infancy in this area. The best summary presently available is to be found in Tamayo and West (1964). On mainland Middle America the two areas best known hydrographically are Mexico and the Panama Canal Zone. A large amount of very elementary work remains to be done.

VERTEBRATE ECOLOGY AND ETHOLOGY

Significant work on vertebrate ecology and ethology (behavior) began in the 1930's but did not make much progress until very recently. One reason for the lack of studies may have been the difficulty of setting up long-term study projects that would not be disturbed in one way or another. Generally poor facilities have also hampered research. For a number of years the principal area in which studies on vertebrates ecology and ethology were pursued was Barro Colorado Island in the Canal Zone. This is an island measuring approximately six square miles that was created when Gatun lake was formed for the operation of the Canal lock system. The island was set aside in the 1920's as a natural re-

serve and continues to be one. The Smithsonian Institution is responsible for the administration of the facility now called the Smithsonian Tropical Research Institute.

What is often considered the classic work on the behavior of free-ranging primates was done at Barro Colorado Island by Carpenter who studied howler monkeys (1934). Also of importance in this period was a long paper by Enders (1935) on the life histories of many of the wild mammals occupying the island. The howler monkeys were again studied by Collias and Southwick who reported changes in population (1952).

In the recent and current period during which the facility has been under the directorship of Martin Moynihan, an ethologist, there has been greater emphasis given to behavioral and related investigations. Among Moynihan's contributions are works on the behavior of various neotropical birds and primates (1962, 1963, 1964). Kaufmann made the first detailed study of the interesting procyonid called the coati (*Nasua*) using the island as the study area (1962). Several graduate students are presently engaged in studies of animal behavior of native vertebrates.

Ecological studies are not well represented for other parts of Panama. Carpenter made a preliminary study of the behavior of free-ranging red spider monkeys in western Panama and adjacent Costa Rica (1935). A recent contribution to the limited store of information on the ethology of tropical reptiles and amphibians has been made by Sexton, Heatwole, and Knight for eastern Panama (1964). This paper deals with some of the relationships between structural organizations of habitats and the microdistributions of certain reptiles and amphibians.

In Costa Rica, Skutch has been publishing a series of bird studies which he calls life histories. These fall somewhere within avian ethology and though the author is not a professional biologist his work is highly regarded by many professionals. Some of the representative publications by Skutch include: a description of the quetzal bird (1940); a life history of the marbled wood quail (1947); life histories of several families of birds occurring in Central America (1954); life history of the groove-billed ani (1959).

Willis has been making a series of studies on avian behavior and has concentrated on birds that follow army ants. A representative paper treats with nesting behavior of ant tanagers in British Honduras (1961). Willis' work is principally descriptive.

Slud (1960) attempted an ecological study of birds in a moist part of northern Costa Rica. Though almost entirely of a descriptive nature and lacking adequate data on the physical environment, this paper nonetheless includes a reasoned discussion on fundamental ecological and paleo-ecological problems. It is regrettable that Slud did not follow up some of his ideas in detail in his

later work on the birds of Costa Rica which, with the exception of the included life zone map discussed above, is little more than a systematic list of birds for the Central American country.

I am aware that many if not most papers of more than a few pages that treat a facet of the recent biota of a part of Middle America also include ecological information. I have mentioned this fact above in another context. Here the matter may be dismissed by indicating that the ecological information is only rarely related to the animals or plants included in the list. The reader, it appears, is supposed to make his own do-it-himself synthesis from the sparse information. There are, to be sure, exceptions but space doesn't permit their discussion or inclusion.

An enormous amount of work remains to be done on vertebrate ecology-ethology in Middle America. Until many more studies on this subject are completed, our understanding of the operation of these ecosystems will be less than adequate and fundamental problems in animal evolution will continue to go unanswered. It might also be noted that too few of the existing studies demonstrate much awareness of the evolutionary implications of the data presented. A notable exception to this charge is the work of Moynihan.

INVERTEBRATE ECOLOGY

It is an understatement to indicate that the ecology of invertebrates has received little attention in Middle America with the exception of certain organisms, chiefly arthropods, of which some are of medical or veterinary significance.

An important center for the study of the relationship of invertebrate ecology to human and animal disease is the Gorgas Memorial Laboratory in Panama City, Panama. Though administered by the U.S. government, this organization enjoys excellent relationships with the government of Panama and the governments of neighboring countries. During the years since its establishment in 1929 many important contributions to tropical medicine have been made by the members of the staff who represent several of the biological-medical specialty areas.

As might be expected, a large share of the investigations have focused on mosquitoes since they are the principal or sole vectors of several serious febrile diseases. The bibliography of staff publications on various aspects of mosquitoes in relation to disease is too extensive even to attempt a synoptic listing and it may be a disservice to mention only a few. One of the most valuable papers, in terms of this review, is a study of tree-canopy mosquitoes by Galindo, Carpenter, and Trapido (1951). This paper also summarizes much of the known information regarding the epidemiology of sylvan yellow fever in Central America. The great weakness of the paper is the very inadequate treatment of climatic

factors, a gap that serves to emphasize comments made earlier in this review. Another paper which this reviewer found to be extremely useful treats with the abundance cycles of arboreal mosquitoes in Panama (Galindo, Trapido, Carpenter, and Blanton, 1956). This otherwise fine study suffers from an almost complete neglect of climatic data. The authors do, however, offer an apology for this omission. One does wonder how much longer these researchers are going to be able to pursue their studies without making the detailed bioclimatic studies that are so clearly needed.

Another preoccupation of this research group is the ecology of Leischmaniasis which is a fairly serious medical problem in tropical America (and elsewhere). The vectors are sandflies (*Phlebotomus* spp.), which occur abundantly in most of the region. It is strongly suspected that the disease is a zoonose (a disease transmissable between man and other vertebrate animals) but the wild animal(s) reservoirs elude positive identification. (See, for example, Hertig and McConnell, 1963 as well as each annual report of the Gorgas Memorial Laboratory, which is published as a House Document of the U.S. Congress).

Research has also been done on other arthropods by the Gorgas staff but only two examples will be mentioned here: (1) The tabanids (Diptera: Tabanidae), which are the deer flys, horse flys, and so on. These are medical and veterinary pests of a high order and the ecology of many of the medically important species has not been studied. Most of the studies to date are on the systematics of the family. (2) Insects that are vectors for Chagas' disease (or New World Trypanosomiasis) have been given significant attention but the ecology of many of the vectors (chiefly true bugs, Hemiptera, of the family Reduviidae) is little understood at present.

Cooperating with the Gorgas Memorial Laboratory is the staff of the recently established Middle American Research Unit. This group is based in the Canal Zone and is engaged in a wide range of medical investigations that of necessity includes ecological elements.

Studies on the behavior of invertebrates are still in a beginning state. Thus far the most important work has been done with army ants (*Eciton* spp. and others). The foundations for these investigations were laid by Schneirla (1933), who made his pioneer studies at Barro Colorado Island. Representative of some of the modern work on this group of insects is that of Rettenmeyer (1963) and Jackson (1953). Rettenmeyer, in the work just cited, has collected much of what is known of ant behavior in the Middle American area and also presents new data based on his extensive research. Jackson has addressed himself principally to relationships between microclimatic conditions and army ant behavior. He has presented extremely interesting and unusual bioclimatic data in this regard.

Attention is drawn to the still valuable studies conducted a few decades ago in the Yucatan Peninsula by Harvard scientists under sponsorship of the Carnegie Institution of Washington. These investigations were primarily ecological although the term doesn't appear in the titles of any of the monographs I have examined and read. The single most important volume is edited by Shattuck (1933), a medical doctor. The collaborators include representatives from other fields of biology as well as from geography and the social sciences. An enormous amount of data relating to the health and living conditions in Yucatan have been brought together in this volume and the chief criticism is that no adequate synthesis was included. Of special interest are the discussions of helminth infections which pose serious problems in this region of karst forms and underground drainage.

In Puerto Rico, the excellent Agricultural Experiment Station has been a base for extensive work related principally to agriculture. Though many of the publications are not ecological in content, both the *Journal* and the *Bulletin* have published useful ecological data. An excellent example is a long paper on the economic entomology of Puerto Rico by Wolcott (1955). This contains valuable ecological information, particularly with reference to the use of DDT insecticides.

HUMAN ECOLOGY

The term human ecology has so many variations in usage that it no longer serves to identify a topic without additional definition. The usage here is in the bio-ecological sense and not in the sociological sense. It is unfortunate that sociologists did not invent a new term and thus save us all from lasting semantic confusion.

Two principal lines of investigation vis à vis human ecology in Middle America are demonstrable: (1) the study of aboriginal man with regard to his use of the environment and the potential that the environments possessed in relation to the technology of the group studied; (2) assessing the importance of man as an ecological element in the region.

(1) Kroeber made the first important attempt to relate Amerind numbers to the assumed carrying capacity of the habitats occupied. In this classic though dated work (1939, reprinted in 1963) Kroeber organized the whole of North America into regions based on an evaluation of the habitats in terms of aboriginal use patterns and practices at the time of European contact. The study is fundamentally one of aboriginal demography and the figures offered for the various regions have been increasingly revised upward in recent years. It is safe to assert that Kroeber seems to have erred on the conservative side, but his study is still a kind of bench mark and will remain so for many years to come.

The first serious challenge to Kroeber's estimations of aboriginal numbers in Mexico was raised by Cook and Simpson (1948). Further studies have appeared on this interesting and fundamental aspect of aboriginal ecology. Cook and Borah have fixed their attention on the question of population changes occurring in parts of Mexico in the years after the conquest by the Spaniards. One example is a study of population changes in central Mexico 1550–1570 (1957). Two of Cook's studies represent attempts to provide partial answers to intriguing ecological questions of pre-Columbian aboriginal ecology in central Mexico. One is an effort to relate soil erosion to population changes (1949). The ecological shock that occurred when the Spaniards introduced grazing animals is discussed in another paper (1952). This subject has not received the attention that it deserves.

Studies attempting to relate biophysical environments to the ways of aboriginal life have only recently begun. We can dismiss as of none but historical significance the facile deterministic statements that once (and unfortunately occasionally still do) colored the literature. A tragic fact is that much if not most of the data required for these studies has been forever lost because the cultures are either dead or seriously altered by centuries-long contact with Europeans. The task is now one of ecological detective work with few clues to "solve the case."

Data relating to crop yields grown under varying conditions of soil, climate, and insect pests are few. We have only vague ideas about the quantitative aspects of hunting and fishing success under different environmental and technological conditions. Our knowledge of dietary requirements is too often based upon assumptions extrapolated from studies of nonaboriginal populations. Research has too often proceeded according to dogma established by an "authority" rather than by first-hand observation and, when possible, experimentation.

Although it is now too late to obtain data from many Amerind cultures, some groups do remain and if allowances are made for acculturative phenomena, important data may still be obtained. An example is a study of certain aspects of hunting and fishing of the mainland Cuna in eastern Panama (C. Bennett, 1962). I have been told repeatedly, however, that because no theoretical problem is involved these studies are now often considered by anthropologists to be beneath the dignity of their profession. Is it possible that a false sense of dignity and sophistication may rob us of what little remains to be salvaged?

The classic question on human ecology in this region is "what caused the downfall of the Mayan civilization?" A small army of scholars has been attacking this question chiefly along ecological lines. A commonly advanced hypothesis holds that the collapse was due to soil exhaustion. This has appeared reason-

able because it has often been assumed that shifting cultivation always results in serious lessening of soil fertility and that tropical soils are usually not capable of producing sustained crop yields year after year without the addition of fertilizer.

A rather classic study of this problem was undertaken in Yucatan by Steggerda who found that much more than a decline in soil fertility is involved (1941). In an experimental plot Steggerda grew maize (*Zea*) crops that did not give the expected yield if a decline in soil fertility had been the principal ecological variable. He found that weed encroachment was a more serious problem but also discovered that other (edaphic) factors which he was not able to identify were involved. Steggerda's work is noteworthy for at least two reasons: (1) he demonstrated that grass encroachment is a serious problem for at least some shifting cultivators who do not possess the means (hoe) to rid their fields of the competing vegetation and (2) that it is possible to set up experiments to test certain hypotheses related to human ecology.

The attack on the soil question has become very sophisticated. Notable among the modern studies are those of Cowgill and Hutchinson (1963a, 1963b). These investigators have turned to careful analysis of the soils in the region of Tikal (in the Petén) in an attempt to determine whether or not the Maya did in fact destroy the ecological basis of their way of life. After detailed study, the authors conclude that this widely held position is untenable and that other hypotheses must be developed. One hypothesis has recently been offered by George Cowgill (1964) who relies not on ecological conditions but upon hypthecated political events.

Most investigators have accepted the view that the Maya subsisted chiefly upon maize but Bronson (1966) recently suggested that root crops may have played a greater role in the Mayan diet than has been believed. This is a very important observation since it alters many of the presently held ideas regarding food production potential in this region during pre-Columbian times.

An important preliminary attempt to arrive at an understanding of the ecological conditions prevailing when certain peoples in Meso-America made the change from food gathering to food production is represented in a paper by Coe and Flannery (1964). This is one of the few sophisticated attempts to relate paleoecology to archaeology at this particular time period. Two areas, Tehuacán in Mexico and the Ocós area of Pacific coastal Guatemala, were studied and the biotopes (the term microenvironments was used in the paper) described. The authors conclude that no sudden agricultural revolution took place as is so often stated but rather a gradual transition from gathering to agriculture.

The recently published (1964) first volume of the *Handbook of Middle American Indians* includes many chapters that are supposed to be related to the

ecological conditions encountered by Indians prior to contact (West is the editor of this first volume). Unfortunately, most of the individual contributions leave it up to the reader to do the relating. The outstanding exception is the chapter on soils by Stevens. West tried through footnotes to add ethnographic data but this unfortunately could not compensate for the lack of attention given it in the individual articles. There is sufficient material in these hundreds of pages to permit at least a preliminary synthesis of pre-Columbian Amerind ecology in Middle America if ethnographic data from other sources are collated with it.

(2) Turning now to the question of man as an ecologic agent, we encounter a most interesting and rewarding line of ecological research.

Investigations of this facet of ecology have only recently begun. The long held belief that the region has been little altered by man until very recent years has inhibited research. This myth—for myth it is—was founded only on beliefs that aboriginal man was not capable of altering his environment. A strong thread of cultural superiority and not a little ignorance of aboriginal ecology is visible in this folk-way of science. That these views were standard until fairly recently is demonstrated by many of the authors of a work on the natural history of the Americas that appeared in 1926 (Shelford, ed.). In the majority of cases the several authors describing the biota of parts of Middle America assure the reader that man has not done a great deal to alter the ecosystems ("original biota"). We are informed, for example, that "great areas of (Honduras) are absolutely primeval," that "the greater part of Costa Rica is still in a primeval and unspoiled condition," and that "much of Mexico remains in essentially primeval condition" and so on *ad infinitum.* It sometimes appears that certain American biologists have been as preoccupied with the search for a "primeval" wilderness as other persons and cultures have been preoccupied with female virginity. Or perhaps it is nothing more than the persistent cultural effect of James Fennimore Cooper on later generations of Americans? The matter does deserve investigation. If a vote were taken, it is possible that these untenable views would prove to be the more frequently held even today. Certainly an examination of Shelford's recent book (1963) will indicate that he seems not to have altered his views significantly.

A pioneer paper on the subject of man's effect on the land in this region was by O. F. Cook (1909) in which fires set by aboriginal farmers received attention. The ecological implications of Cook's paper were virtually ignored for years although now we can perceive a rapidly growing interest in this and related problems in Middle America.

Parsons (1955) drew attention to apparent relationships between man-set fires and the pine savannas of Nicaragua and Honduras. Budowski (1956) has argued that tropical savannas may be the result of repeated tree cutting and

burning by aboriginal cultivators. Sauer (1957) argued that man has long been an important factor in the ecology of Tropical America and that attention must be given to this fact when ecological investigations are undertaken in the region. Denevan (1961) has shown that fire set by man resulted in a fire "disclimax" of pine forests in upland Nicaragua. Johannessen (1963) has demonstrated how fire set by man played a major role in the development of the savannas of interior Honduras. Harris, in a broadly based study (1965), has examined many aspects of human ecology on the islands of Antigua, Barbuda, and Anguila. As a comment on one aspect of the ethology of biologists, it might be noted that one reviewer of Harris' fine monograph was upset because it had appeared in a series of geographical publications and was therefore all but "lost" to botanists.

Studies related to faunal changes caused by man have as yet received little attention. In addition to the work by Harris cited above one can mention the following: Westerman (1963) has brought together valuable information on man's impact on the wildlife of the Caribbean region. Gilmore (1950) also discussed, in a preliminary fashion, some of the possible extinctions caused by aboriginals in the same part of Middle America. Bennett (1965) has made a preliminary examination of man's effects on the zoogeography of the Panamanian isthmus. Heatwole (1966) has determined that the distribution of some of the herpetofauna of eastern Panama has been influenced by man.

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To summarize briefly, the status of ecological investigations in Middle America varies from entirely inadequate to barely adequate. Chief among the problem areas are the lack of detailed measurements and analyses of environmental elements such as air temperature, precipitation, and radiation. This is particularly true of microclimatology which has scarcely been investigated. Much more detailed attention must be given to evaluating the ecological impact of aboriginal man. Perhaps most important of all is the clear need to admit our vast ignorance about the functioning of these ecosystems and then begin work with renewed effort.

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