



Nocturnalism--The Development of a Problem

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NOCTURNALISM—THE DEVELOPMENT OF A PROBLEM

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CONTENTS

	PAGE
INTRODUCTION	487
RHYTHMS OF THE ENVIRONMENT	487
THE NOCTURNAL ENVIRONMENT	488
THE NOCTURNAL PORTION OF A COMMUNITY	490
ADJUSTMENTS OF NOCTURNAL ANIMALS	500
SLEEP OR ITS PHYSIOLOGICAL EQUIVALENT	507
ENVIRONMENT AND ACTIVITY	509
PERIODISM AND ACTIVITY	512
ARHYTHMIC ACTIVITY	518
THEORETICAL DISCUSSION OF THE GENERAL PROBLEM	521
BIBLIOGRAPHY	525

NOCTURNALISM—THE DEVELOPMENT OF A PROBLEM

INTRODUCTION

The object of this paper is to integrate certain points of view and bodies of information into a general picture of nocturnalism. By nocturnalism is meant those general or specific activities initiated by, or enduring at night. In this report the term nocturnal refers to the night and diurnal to the day. Limiting the meaning of these two terms in this fashion avoids the confusion caused by using "diurnal" to mean both the normally illuminated portion as well as the twenty-four hour cycle.

Co-ordinated information concerning nocturnal animals has been sadly lacking in the past. Taxonomists have usually concerned themselves with an accurate diagnosis of a species' structural characteristics and usually have not recorded the time of day or night at which the form was active. Indeed, from the very nature of biological investigation, they did not possess this information. Naturalists reported sporadically the general activity period of animals, especially of birds and mammals; unless the observers were taxonomically expert in the group being observed, the activity was spoken of in very general terms indeed. Physiologists have noted the occurrence of certain functions or activities of nocturnal animals, and have described the conditions under which such internal reactions have been observed or elicited. Generally these physiological findings are part of a special problem, and too often are unknown to ecologists. Furthermore much of this information concerns common laboratory animals, under more or less unnatural surroundings, or which have their routine activities controlled or affected by man.

Within recent years several literature reviews and general accounts have appeared which have touched upon the nocturnal problem more or less closely. All of these have been timely, and have rendered the writer's task more feasible. Among these may be noted an account of the characteristics of nocturnal animals (Crawford 1934); the phenomena associated with sleep (Polimanti 1911, Fiebrig 1912, Pieron 1913, Rau and Rau 1916, Kleitman 1929); periodic physiological processes which appear to be more or less inherent in organisms (Richter 1927, Hoagland 1935, Welsh 1938).

In preparing this paper I have received the helpful criticism of three of my friends, Professors J. W. Buchanan, Alfred E. Emerson, and Karl P. Schmidt.

RHYTHMS OF THE ENVIRONMENT

Apparently certain important astro-physical forces, the natures of which are at present incompletely understood by astronomers, have induced a rhyth-

mic (as opposed to arhythmic) and dynamic (as opposed to static) environment on the earth surface. This rhythmicity is demonstrated by an almost infinite series of phenomena. For example, the sunspot cycle is rhythmic and Clements (1938) finds that this cycle can be correlated with annual rainfall. Study of the annual growth rings of trees has given evidence for cycles of climate within the last few thousand years (Huntington 1914, Douglass 1928). A great deal of information has been compiled concerning geological rhythms of erosion and deposition (Wanless 1938). Within these larger cycles are smaller rhythmic periods generally correlated as to climate with the more comprehensive rhythms, but specifically modified by latitude and having a complete cyclic character within themselves. Yearly rhythms are recognized by their seasonal meteorology on the one hand, and by recurring biological events which are to a certain extent catalogued, understood, and predictable.

In temperate regions, where the annual cycle is well defined, there are many well-known annual environmental adjustments; for example, hibernation, aestivation, and migration. Correlated with the annual rhythm of physical influences (for example, the length and amount of daylight, Park 1931, Clarke 1938), there is a definite seasonal succession of organisms within a given community (Clarke and Zinn 1937, Park 1930, Pearse 1926, Shelford 1913, Welsh 1935). Photoperiodism with particular reference to the relative lengths of day and night has been studied in relation to plant and animal adjustments to the annual cycle (Garner and Allard 1920, Kellerman 1926, Rowan 1926, Schick 1932).

Within seasonal rhythms are lunar rhythms which affect the height of tides, producing the unusually high spring tides when the pull of the sun and moon are in conjunction or opposition, and the neap tides when the moon is in its first or third quarter. Associated with these lunar tidal rhythms are rhythms of reproductive activity, the lunar periodicities of certain marine polychaetes (Lillie and Just 1913, Mayer 1908, Treadwell 1915, Pearse 1926, pp. 126-127). Thomson (1911) finds a correlation between the amount of river plankton and the phases of the moon, and freshwater rhythms are discussed by Shelford (1918, pp. 42-43). It must also be remembered that the rhythmic ebb and flow of tides is of great general importance to the marine littoral community (Keeble 1910). In some cases tidal rhythm apparently is not a causal agent, as in the lunar swarming of the prawn, *Anchistiooides antiguensis*, where feeding habits and growth are important in determining periodism (Wheeler and Brown 1936).

THE NOCTURNAL ENVIRONMENT

In the preceding pages certain environmental rhythms and associated biological periodicities have been cited briefly. The twenty-four hour rhythm of day and night is of particular interest here, and must be discussed more

extensively. The most obvious and basic difference between day and night is the nearly qualitative fluctuation between light and darkness. In polar regions there is a long period of continuous illumination and an equally long period of continuous darkness; in equatorial regions day and night are quite constant in their duration throughout the year, virtually twelve hours of light and twelve hours of darkness. Between these two extremes the duration of daylight varies regularly with season and latitude.

In addition to this regular variation of daylight and darkness, daylight also varies regularly in intensity through the day and this daily march of light intensity has been measured extensively. The literature upon this measurement, and the measurement of daylight in the Chicago Area has been re-reviewed (Park 1931). Light intensities at dawn and dusk for clearings and forests have been given for northern Indiana (Park and Strohecker 1936). Similarly, the measurement of daylight intensity in the tropics has been re-reviewed, and intensities recorded in the dry season of the Panama Canal Zone by Allee (1926). Also daylight intensity in the wet season of the Panama Canal Zone has been measured (Park 1938, Park, Barden, and Williams 1940) in connection with nocturnal studies. These and numerous additional reports give a clear picture of an important factor in the twenty-four hour cycle. Many influences modify daylight intensity (Clayden 1925, Humphreys 1920, Kimball 1924, Pulling 1919, Park 1931). Consequently, there is a relatively constant absence of sunlight at night, and a regularly varying but easily modifiable daylight through the day.

Usually air temperature varies directly with daylight intensity, as does the rate of evaporation, as a rule; relative humidity varies inversely with air temperature, so that these important influences are intimately associated with light. Day is relatively variable while night is relatively constant; day may be characterized by relatively high air temperature and rate of evaporation, and relatively low humidity. Conversely night has relatively low temperature and rate of evaporation, and high humidity. This discussion of diurnal and nocturnal physical conditions is over-simplified and obvious, but has been restated here since it emphasizes the fundamental dissimilarity of the two periods of the twenty-four hour cycle, and consequently focuses attention upon the adjustments necessary for life under such a varying system.

Dawn and dusk are the two periods of the cycle when these differences become reduced; these are the periods when a far-reaching change in the activity of the great majority of animals and the green plants is initiated. These changes are of two general types, changes in the physiological activity of protoplasm, and changes in the ecological activities of the whole organism. Such changes may be directly induced by changes in the environment, or may be the result of more or less specific and deeply seated rhythms acting with, but not induced by, the varying external conditions. These phenomena will

be repeatedly discussed in the course of this article. The nocturnal environment has been described beautifully by Von Humboldt (1850, pp. 198-199) for the Orinoco rain forest and that of the British Guiana rain forest by Beebe (1925) among others, for tropical waters (Beebe 1928, pp. 75-97) and deserts (Beebe 1932). In these accounts the change from day to night is described; the importance of this change has been previously discussed in relation to tropical animals (Haviland 1926, Park 1938, Visher 1923).

Bayliss (1924, p. 548) has stated that the "whole existence of living organisms on the earth depends on the receipt of radiant energy from the sun." When it is remembered that the photosynthetic processes of plants are possible only in light, and that this essential chemical conversion takes place, therefore, during the day, the magnitude of this typically diurnal activity makes the biological differential between day and night more impressive. Day, then, becomes the period when the base of the world's food-chain is reconstituted. In general, animals are either diurnal or nocturnal, and it becomes expedient to examine nocturnal animals at this point.

THE NOCTURNAL PORTION OF A COMMUNITY

Although it has been recognized for a long time that a nocturnal fauna may be varied and numerous, no general analysis of the ecology of nocturnal animals has been made. Such desirable information is still lacking for a variety of reasons, among which the following are perhaps most significant: (1) lack of specific ecological data on the periods of activity of animals of many groups, (2) the difficulty of obtaining information concerning the activity of endoparasites, protozoans, and other types of animals under normal conditions of illumination, and (3) the planktonic forms generally must adjust to the constant pull of gravity, and consequently many adaptations to maintain stratal position may be superimposed upon the normal pattern of activity.

Despite these handicaps knowledge of nocturnality of aquatic animals and internal parasites is steadily increasing. Thus planarians are said to be more active at night than by day (Ward and Whipple 1918, p. 328); certain species of *Filaria* are active in the peripheral blood stream at night where they are taken up by their host mosquitoes, and are deep in the vertebrate hosts by day (Bouvier 1922, Elton 1927, Rivas 1920, pp. 409-415). Many marine annelids are active at night (Lillie and Just 1913, Mayer 1908, Polimanti 1911, Scott 1909, Treadwell 1915). Some Arbacias capture prey at night (Parker 1932) and another echinoderm, *Thyone briareus*, is reported by Stier (1933) to have the frequency of "locomotor" waves increased in number during the winter months, between 4:00 P.M. and 1:00 A.M. Polimanti (1911) found cephalopods to be more active at night in the Naples aquarium. Many crustaceans are nocturnal; for example, crayfishes (Newcombe 1929,

Roberts 1936, Turner 1926, Szymanski 1918), lobsters (Herrick 1909), crabs (*Menippe mercenaria*, cf. Boone 1930); prawns (Welsh 1935); amphipods (*Haustorius arenarius*, cf. Dennell 1933).

There is a well-known migration of plankton through twenty-four hour cycles, especially demonstrated for fresh-water crustaceans (Juday 1904, Welch 1935, pp. 226-35) and for marine crustaceans (Easterly 1919, Clarke and Zinn 1937). Information gathered by Juday (1921) shows that fly larvae (*Corethra punctipennis*) spend the day in the mud at the bottom of lakes, and rise to the surface at night. Nocturnal activity of fishes in general is greatly in need of exact investigation. Recently Spencer (1939) has made a start in this phase of the problem. A number of elasmobranchs (Polimanti 1911), conger eels, and silurids (Polimanti 1911; Forbes and Richardson 1908) are largely nocturnal. Experimental data upon the activity of tadpoles is needed. The aquatic *Necturus* and the giant salamander of China and Japan are nocturnal (Boulenger 1930). Among aquatic reptiles, the Crocodilia are all largely nocturnal (Regan 1937, Walls 1934), although individuals often sun themselves and may even feed by day occasionally.

The periods of activity and inactivity of amphibious and terrestrial animals are much better known than wholly aquatic species. When the large number of species already described by taxonomists is realized, and this number is compared with the number of species, the activity of which has not been recorded, it will be understood that sweeping generalizations on activity patterns are unsafe. In fact one of the functions of this paper is to emphasize the lack of even the simplest data on the problem of nocturnalism and diurnalism. In Table 1 a relatively brief digest of the predominantly nocturnal animals is presented. The animals selected are chiefly North American, and it is obvious that the contents of Table 1 could be greatly expanded. These animals are representatives of four large phyla, of which the last two, the arthropods and vertebrates, have been most carefully studied with respect to their activity. The largest class of animals, the insects, has the largest number of known nocturnal species. Again, the table does not do justice to the partially nocturnal species. For example, many normally diurnal birds (warblers, thrushes, vireos, órioles, tanagers, etc., Pearson *et al.*, 1936) migrate by night, and horses and cattle may feed at night during hot, dry weather. Extensive treatment of species which are in part nocturnal and in part diurnal would be interesting but impracticable in the present paper.

Table 1 shows that the truly social animals are not often nocturnal. The majority of the species cited are solitary, although certain of them form place aggregations at feeding grounds (Aradus, Boletotherus, Hoplocephala) or gather under loose bark (Parcoblatta, Brontes, Laemophlaeus) or form sleeping aggregations (bats), or hibernating aggregations (Crotalidae), or feed in packs. Consequently there are relatively few typically gregarious nocturnal forms, e.g. elephants, the carabid beetle, *Calathus gregarius*, and the

TABLE 1. AMPHIBIOUS AND TERRESTRIAL NOCTURNAL ANIMALS

Animal	Distribution	Authority for Data
Annelida: OLIGOCHAETA Earthworms.....	General; subterranean.....	Szymanski 1918, Walton 1928, Stephenson 1930, Regan 1937
Mollusca: GASTROPODA Terrestrial snails in general.....	General; vegetation.....	Van Cleave 1931, Boycott 1934
Anguispira alternata.....	Forests of Deciduous region of North America.....	Park, Lockett, & Myers 1931, Park and Strohecker 1936
Polygyra thyroidus.....	As above.....	Park and Strohecker 1936
Slugs in general.....	General; vegetation.....	Gerhardt 1933, 1934, Zolk 1932
Agriolimax campesris.....	N. A. Deciduous forests.....	Park and Strohecker 1936
Limax maximus.....	European, introduction into North America.....	Allard 1931a
Philomycus carolinensis.....	N. A. Deciduous forests.....	Park, Lockett, & Myers 1931
Arthropoda: Onychophora Peripatus and allied forms.....	General, discontinuous, great pre- ponderance in rain forests.....	Regan 1937
DIPLOPODA Spirobolus marginatus.....	N. A. Deciduous forests.....	Park 1935, Park and Strohecker 1936
SCORPIONIDA.....	General, especially sand desert and rain forest.....	Regan 1937
SOLPUGIDA Solpugo.....	Arid and semi-arid areas.....	Schwarz 1893
ARANEIDA Amaurobius bennetti.....	North America.....	Park, Barden and Williams, 1940
Clubiona pallens.....	North America.....	Park and Strohecker 1936
Clubiona riparia.....	North America.....	Ibid.
Coras medicinalis.....	North America.....	Ibid.
Ctenus sinuatus.....	Panama rain forest.....	Park 1938
Ctenus w-notatus.....	Panama rain forest.....	Ibid.
Cupinius foliatus.....	Panama rain forest.....	Park and Strohecker 1936
Dolomedes tenebrosus.....	North America.....	Park 1938
Lycosa tristani.....	Panama rain forest.....	Hingston 1920
Orb-weaver.....	India.....	Park 1938
Paradosenus nigricans.....	Panama Canal Zone.....	Park and Strohecker
Schizocosa crassipes.....	North America.....	Park 1938
Sericopelma rubronitens.....	Panama Canal Zone.....	Park 1938
Trechalea magnifica.....	Panama Canal Zone.....	Park 1938
Wala mitrata.....	North America.....	Park and Strohecker
Xysticus ferox.....	North America.....	Park and Strohecker
INSECTA (see Kennedy 1928)		
ORTHOPTERA Ceuthophilus latens.....	North America.....	Turner 1915, Park and Strohecker
Gryllus asimilis.....	North America.....	Lutz 1932
Gryllus domesticus.....	North America.....	Lutz 1932
Oecanthus niveus.....	North America.....	Allard 1930
Parcoblatta pennsylvanica.....	North America.....	Park and Kelter 1932, Park and Strohecker
Periplaneta americana.....	North America.....	Haber 1920
Stenopelmatus.....	North America.....	Lutz 1932
HETEROPTERA Aradus crenatus.....	North America.....	Park and Strohecker
Aradus implanus.....	North America.....	Ibid.
Aradus quadrilineatus.....	North America.....	Ibid.
Meneclis insertus.....	North America.....	Ibid.
NEUROPTERA Vermileo comstockii (larvae).....	North America.....	Wheeler 1930
LEPIDOPTERA Deilephila euphorbiae.....		Bugnion and Popoff 1914

TABLE 1 (*Continued*)

Animal	Distribution	Authority for Data
<i>Lasiocampa</i>	General.....	<i>Ibid.</i>
Noctuidae.....	General.....	Brower 1930, Park and Strohecker, Stanley 1932, Williams 1935
Saturniidae.....	General.....	Bugnion and Popoff 1914
Moths (Heterocera).....	Largely nocturnal.....	Rau and Rau 1929
COLEOPTERA		
<i>Allobates pennsylvanicus</i>	North America.....	Park and Strohecker
<i>Agathidium</i>	North America.....	Park, Lockett and Myers
<i>Amblycheila</i>	North America.....	LeConte and Horn 1883, Riley Packard <i>et al.</i> 1878
<i>Amphasia interstitialis</i>	North America.....	Park and Keller
<i>Boletotherus cornutus</i>	North America.....	Park, Lockett and Myers, Park and Keller, Park and Strohecker
<i>Brontes dubius</i>	North America.....	<i>Ibid.</i>
<i>Calathus gregarius</i>	North America.....	<i>Ibid.</i>
<i>Carabus granulatus</i>	North America.....	Oertel 1924
<i>Chlaenius aestivus</i>	North America.....	Park and Strohecker
<i>Chlaenius nemoralis</i>	North America.....	Park, Lockett and Myers
<i>Chlaenius sericeus</i>	North America.....	Park and Keller
<i>Cis fuscipes</i>	North America.....	Park and Strohecker
<i>Cleotus aphodioides</i>	North America.....	<i>Ibid.</i>
<i>Clivinia impressifrons</i>	North America.....	Park and Keller
<i>Conosoma crassum</i>	North America.....	Park, Lockett and Myers, Park and Strohecker
<i>Cotinis nitida</i>	North America.....	Hintze 1925
<i>Dendroides bicolor</i>	North America.....	Park, Lockett and Myers
<i>Diaperis maculata</i>	North America.....	Park and Strohecker
<i>Enoclerus nigripes</i>	North America.....	<i>Ibid.</i>
<i>Erchomus ventriculus</i>	North America.....	<i>Ibid.</i>
<i>Euferonia stygica</i>	North America.....	Park, Lockett and Myers
<i>Galerita janus</i>	North America.....	<i>Ibid.</i> , Park and Strohecker
<i>Geopinus</i>	North America.....	Chapman, Mickel, Parker, Miller and Kelley 1926
<i>Glischrochilus fasciatus</i>	North America.....	Park and Strohecker
<i>Glischrochilus sanguinolentus</i>	North America.....	<i>Ibid.</i>
<i>Harpalus caliginosus</i>	North America.....	Park, Lockett and Myers
<i>Hoplocephala bicornis</i>	North America.....	Park and Strohecker
<i>Laemophlaeus fasciatus</i>	North America.....	<i>Ibid.</i>
<i>Laemophlaeus testaceus</i>	North America.....	<i>Ibid.</i>
<i>Leiodes blanchardii</i>	North America.....	Park, Lockett and Myers
<i>Leptostylus aculifer</i>	North America.....	Park and Strohecker
<i>Megalodacne heros</i>	North America.....	Park, Lockett and Myers, Park and Sejba 1935, Park and Strohecker
<i>Melanodrya striata</i>	North America.....	<i>Ibid.</i>
<i>Melanotus communis</i>	North America.....	<i>Ibid.</i>
<i>Melanotus decumanus</i>	North America.....	<i>Ibid.</i>
<i>Meracantha contracta</i>	North America.....	Park, Lockett and Myers
<i>Omus</i>	North America.....	LeConte and Horn 1883
<i>Ontholestes cingulatus</i>	North America.....	Park, Lockett and Myers
<i>Oryctes</i>	North America.....	Bugnion and Popoff 1914
<i>Patrobus longicornis</i>	North America.....	Park and Keller 1932
<i>Penthe obliquata</i>	North America.....	Park and Strohecker
<i>Penthe pimelia</i>	North America.....	<i>Ibid.</i>
<i>Phengodes</i>	North America.....	Barber 1905
<i>Phenolia grossa</i>	North America.....	Park, Lockett and Myers
<i>Philonthus cyanipennis</i>	North America.....	<i>Ibid.</i>
<i>Photinus</i>	North America.....	Mast 1912, Williams 1917, McDermott 1917, Hess 1920, Allard 1931, Rau 1932, Buck 1935, 1937, 1937a, Barnes 1919

TABLE 1 (*Continued*)

Animal	Distribution	Authority for Data
<i>Photuris pennsylvanica</i>	North America.....	McDermott 1917, Hess 1920
<i>Phyllophaga</i>	North America.....	Schwarz 1893, Forbes 1907, 1916, Davis 1916, Sanders and Fracker 1916, Park and Strohecker
<i>Pinacodera limbata</i>	North America.....	<i>Ibid.</i>
<i>Platynus hypolithos</i>	North America.....	Park, Lockett and Myers
<i>Poecilus lucublandus</i>	North America.....	Park and Keller
<i>Promecognathus laevissimus</i>	North America.....	Garnett 1920
<i>Pterostichus adoxus</i>	North America.....	Park, Lockett and Myers, Park and Strohecker
<i>Serica parallela</i>	North America.....	<i>Ibid.</i>
<i>Serica sericea</i>	North America.....	<i>Ibid.</i>
<i>Staphylinus violaceus</i>	North America.....	Park and Keller
<i>Tenebroides corticalis</i>	North America.....	Park and Stohecker
<i>Tenebroides laticollis</i>	North America.....	<i>Ibid.</i>
<i>Tetracha</i>	North America.....	Blatchley 1910
DIPTERA		
<i>Tipuloidea</i>	North America.....	Rogers 1933
	Great Britain.....	Robertson 1939
HYMENOPTERA		
For numerous references see.....		Rau 1938
<i>Halictus galpiniae</i>	Panama Canal Zone.....	Rau 1935
<i>Megacilissa yarrowii</i>	Panama Canal Zone.....	<i>Ibid.</i>
<i>Megacilissa matutina</i>	Panama Canal Zone.....	<i>Ibid.</i>
<i>Megacilissa exima</i>	Panama Canal Zone.....	<i>Ibid.</i>
<i>Xylocopa rufescens</i>	Panama Canal Zone.....	<i>Ibid.</i>
<i>Sphecodogaster taxana</i>	North America.....	Graenicher 1911
Vertebrata: Amphibia		
SALIENTIA See....		
<i>Alytes obstetricans</i>	Europe.....	Park, Barden and Williams 1940
<i>Bufo</i>	General.....	Boulenger 1938 Noble 1931, Crawford and Jones 1933, Boulenger 1938, Higginbotham 1939
<i>Centrolene fleischmanni</i>	Panama Canal Zone.....	Park 1938
<i>Engystomops pustulosus</i>	Panama Canal Zone.....	<i>Ibid.</i>
<i>Hyla granosa</i>	British Guiana.....	Crawford and Jones 1933
<i>Hyla marmorata</i>	British Guiana.....	<i>Ibid.</i>
<i>Leptodactylus pentadactylus</i>	Panama Canal Zone.....	Park 1938
<i>Rana sylvatica</i>	North America.....	Allen 1901
CAUDATA		
Generally nocturnal		
<i>Plethodon cinereus</i>	North America.....	Park, Lockett and Myers
<i>Salamandra maculosa</i>		Boulenger 1938
<i>Triturus viridescens</i>	North America.....	Pike 1886, Park, Lockett and Myers
REPTILIA		
Desert species in general. See.....		Klauber 1939
<i>Arizona elegans</i>	North America.....	Walls 1934
<i>Coleonyx variegatus</i>		Walls 1934
<i>Crotalus cerastes</i>	North America.....	Mosauer 1936
<i>Gekkonidae</i> (largely).....	General.....	Noble and Bradley 1933 , Walls 1934a, Regan 1937, Park 1938, Boulenger 1938
<i>Heloderma suspectum</i>	North America.....	Walls 1934
<i>Hypsiglena ochrorhynchus</i>	North America.....	<i>Ibid.</i>
<i>Phyllorhynchus decurtatus</i>	North America.....	<i>Ibid.</i>
<i>Sphenodon punctatum</i>	New Zealand.....	<i>Ibid.</i> , Regan 1937
<i>Trimorphodon vandenburgi</i>	North America.....	Walls 1934
Xantusiidae (largely).....		Walls 1934a

TABLE 1 (*Continued*)

Animal	Distribution	Authority for Data
AVES		
Aegothelidae (Owlet-nightjars).....	Australia, Tasmania, New Caledonia New Guinea, Moluccas.....	Regan 1937
Caprimulgidae (Nightjars).....	World save for New Zealand and Pacific Islands.....	Regan 1937, Boulenger 1938, Stülken and Brüll 1938
Tinamous.....	Panama Canal Zone.....	Park 1938
Nyctibiidae (Potoos).....	Tropical America.....	Regan 1937
Podargidae (Frogmouths).....	Tropical Asia and Australia.....	Regan 1937
Strigiformes (Owls) largely.....	General.....	Montgomery 1899, Vanderplank 1934, Regan 1937, Boulenger 1938, Park 1938
Steatornithidae (Oil-bird).....	Trinidad to Peru.....	Regan 1937
MAMMALIA (see Table 2)		
MONOTREMATA		
Echidnidae.....	Australia, Tasmania, Papua.....	Regan 1937, Boulenger 1938
Ornithorhynchidae.....	Boulenger 1938
MARSUPIALIA		
Caenolestidae (Sooty Selva).....	Colombia, Ecuador.....	Regan
Dasyuridae ("Tasmanian "Wolf") (DASYURES).....	Tasmania.....	<i>Ibid.</i>
Didelphyidae (Opossums).....	Australia.....	<i>Ibid.</i>
Marmosa isthmica.....	Americas.....	Gregory 1936, Enders 1935, Regan 1937, Park 1938
Phalangeridae.....	Panama Canal Zone.....	Park, Barden and Williams 1940
Phascolarctidae.....	Australia, Celebes, New Guinea.....	Regan, Boulenger
Potoroinae (Macropodidae).....	Tasmania, Australia.....	Regan, Boulenger
AUSTRALIAN MAMMALS	Australia.....	Regan
INSECTIVORA		
Shrews and Moles..... (generally nocturnal, but with numerous exceptions)	General.....	Bachman 1837, Shull 1907, Roosevelt 1910, Boulenger, Hamilton 1939
DERMOPTERA		
Cobegos (Flying Lemurs).....	Boulenger
TUBULIDENTARA		
Aard Varks (Orycteropidae).....	Africa.....	Boulenger
HYRACOIDEA		
Hyraxies (Dassies, etc.)..... (insufficient data for any positive state- ment: some species apparently noc- turnal, others possibly diurnal)	Africa.....	Roosevelt 1910, Boulenger
EDENTATA		
Dasyurus novemcinctus fenestratus.....	Panama Canal Zone.....	Park 1938
Myrmecophaga tridactyla	Central and South America.....	Regan
RODENTIA (could be greatly extended)		
Apodemus sylvaticus.....	England.....	Elton, Ford, Baker 1931
Arvicantis.....	Africa.....	Roosevelt 1910
Cuniculus paca virgatus.....	Panama Canal Zone.....	Allee 1926a
Dasyurus helukus.....	Africa.....	Roosevelt 1910
Dasyprocta punctata isthmica.....	Panama Canal Zone.....	Allee 1926a
Dendromys nigrofrons.....	Africa.....	Roosevelt 1910
Dipodillus harwoodii.....	Africa.....	Roosevelt 1910
Epimys (s.s.).....	Africa.....	Roosevelt 1910
Gerbillus.....	Africa, Asia.....	Boulenger
Glaucomys volans volans.....	North America.....	Walls 1931, Gregory 1936
Graphiurus parvus.....	Africa.....	Roosevelt 1910
Hystricidae (Porcupines) and ERYTHOZONTIDAE (Porcupines).....	Africa, India, Americas.....	Gregory 1936, Boulenger
Microtus..... (conflicting data on the American and British species)	North America, England.....	Hamilton 1937, Davis 1933, Gregory 1936, Hatfield 1935, 1940
Mus (generally nocturnal).....	Africa, Europe, North America.....	Szymanski 1918a, Roosevelt 1910, Snell, <i>et al.</i> 1940

TABLE 1 (*Continued*)

Animal	Distribution	Authority for Data
<i>Oenomys hypoxanthus bacchante</i>	Africa.....	Roosevelt
<i>Ondatra zibethica</i>	North America.....	Gregory 1936
<i>Peromyscus</i> (generally nocturnal).....	North America.....	Johnson 1926, Behney 1936, Gregory 1936, Park and Strohecker
<i>Rattus</i> (generally nocturnal).....	General.....	Szymanski 1918, Richter 1922, 1927, Richter and Wang 1926, Browman 1937
<i>Springhaas</i> (<i>Pedetes surdaster</i>)	Africa.....	Roosevelt 1910
<i>Tatera potthae</i> and <i>Tatera varia</i>	Africa.....	Roosevelt 1910
<i>Thamnomys</i>	Africa.....	Roosevelt 1910
CARNIVORA		
Generally nocturnal: <i>Felidae</i>	General.....	Boulenger
<i>African long-eared fox</i>	Africa.....	Roosevelt 1910
<i>Cryptoprocta ferox</i>	Madagascar.....	Boulenger
<i>Hyaena</i>	Africa.....	Roosevelt 1910
<i>Leopard</i>	Africa.....	Roosevelt 1910
<i>Lion</i> (usually).....	Africa.....	Roosevelt 1910
<i>Lynxes</i>	Europe, Asia, Africa, North America.	Boulenger
Skunks and Weasels (partially)..... (<i>Mephitis</i> , <i>Mustela</i> , etc.)	North America.....	Gregory 1936
<i>Octocyon virgatus</i> (Great-eared fox).....	Africa.....	Roosevelt 1910
<i>Potos flavus</i> (Kinkajou).....	Central America.....	Boulenger
Raccoons.....	North America.....	Schmidt 1934, Gregory 1936
<i>Puma</i> (usually).....	Americas.....	Park 1938
Badgers (partially).....	North America.....	Gregory 1936, Boulenger
Foxes (largely).....	North America.....	Gregory 1936
UNGULATA		
<i>Hydropotes inermis</i> (Chinese Water Deer).....	China.....	Boulenger
<i>Elephas africanus</i> (African elephant).....	Africa.....	Roosevelt 1910
Elephants (general).....	Africa, Asia.....	Clark 1914
<i>Hippopotamus amphibius</i>	Africa.....	Roosevelt 1910, Regan, Boulenger
Tapirs.....	Malay, Borneo, Sumatra, Central and South America.....	Regan
<i>Tayassu pecari spiradens</i> (White-lipped peccary)	Panama Canal Zone.....	Park 1938
Tragulidae (Chevrotains).....	West Africa, India, East Indies, Burma, Philippines.....	Regan
CHIROPTERA		
Bats (generally nocturnal, with a very few exceptions; chiefly crepuscular-auroral).....	General.....	Moffat 1905, Seton 1909, Roosevelt 1910, Warren 1910, Willey 1904, Sherman 1929, Ratcliffe 1932, Gregory 1936, Enders 1935, Borell 1937, Griffin and Welsh 1937, Boulenger 1938
LEMUROIDEA		
<i>Aye-aye</i> (<i>Daubentonia madagascariensis</i>).....	Madagascar.....	Boulenger
<i>Galago</i>	Boulenger
True lemurs (largely nocturnal with a few exceptions).....	Madagascar, India, Ceylon, S. E. Asia.	Boulenger
<i>Tarsius spectrum</i>	Malay, Celebes.....	Boulenger
PRIMATA		
<i>Atous</i> (Night monkey).....	Nicaragua to Amazon and eastern Peru.....	Enders 1935, Boulenger 1938

mycetophagous erotylid beetle, *Megalodacne heros*. The absence of social nocturnal animals, and scarcity of gregarious nocturnal species will be discussed later.

Nocturnal forms do not have any general feeding pattern, and the animals listed include herbivores, carnivores and omnivores. Apparently the ability to find and eat the specifically acceptable foods is not limited by the habit of nocturnalism.

Nocturnal species occur throughout the metazoan phyla which have been investigated for activity periods, and it may be concluded, therefore, that nocturnalism is a general tendency. Further, nocturnal animals are found in all basic feeding categories, are seldom gregarious and never strictly social, with the possible exception of a few ants which are said to be chiefly nocturnal.

What is the proportion of nocturnal to diurnal species in ecological communities? The answer to this question cannot be given at the present time because no one community has been thoroughly analysed with this in mind. An attempt has been made, using the mammals of two distinct areas, both of which have been studied thoroughly and the habits of the mammals observed. This comparison is presented in Table 2.

TABLE 2. COMPARISON OF THE MAMMALIAN FAUNAS OF A TEMPERATE DECIDUOUS FOREST WITH A TROPICAL RAIN FOREST REGION WITH RESPECT TO PERIOD OF ACTIVITY OF SPECIES AND SUBSPECIES

Order	CHICAGO AREA (Data from Gregory 1936)			BARRO COLORADO ISLAND, PANAMA CANAL ZONE (Data from Enders 1935)		
	Total	Diurnal	Nocturnal	Total	Diurnal	Nocturnal
	1	0	1	5	0	5
Insectivora.....	4	2	2	0	0	0
Chiroptera.....	7	0	7	10	0	10
Carnivora.....	15	0	11	9	4½	4½
Primates.....	0	0	0	4	3	1
Rodentia.....	20	12	8	16	6	10
Ungulata.....	2	1½	½	5	2	3
Edentata.....	0	0	0	5	2	3
Total, Subspecies.....	49	19½	29½	54	17½	36½
Total, Percentages.....	100	39	61	100	31	69

The most important point which emerges from this comparison (Table 2) is that the general ratio of nocturnal to diurnal species is constant for two widely different geographic areas. Further, it appears that nocturnal mammals form some two thirds, and diurnal mammals average about one third of the species under consideration. The experience of the author in these two areas has been fairly extensive and he believes that the data are reliable. The table does not include some eight species of mammals which undoubtedly roamed over the Chicago Area in the past; also there are numerous mammals

which are found in Panama, but have not been recorded from the Barro Colorado preserve. Both regions have been carefully studied by many biologists and consequently one is led to believe that these general percentages of nocturnal and diurnal components are to be expected in the great majority of mammal surveys. Whether the ratio of two-thirds nocturnal to one-third diurnal will hold for other classes of animals in these communities, or hold for the partial or total populations of different types of communities, is not definitely known. Prairies may have a higher diurnal, and sand deserts a higher nocturnal percentage, but little may be gained at this time by speculation.

Such a comparison is unsatisfactory since the analysis of only one class of animals tends to make the result faunistic rather than ecological. If the stomach contents of the carnivores among these mammals could be analysed also on the basis of activity pattern, a far more accurate picture could be obtained. Other groups are predominantly diurnal, for example, birds. Little is known regarding the activity of the myriads of mites and minute insects inhabiting the floor mold of steppe and forest. The complete activity analysis of any community food-chain, although greatly to be desired, has not yet appeared. Therefore it is not usually possible to state whether a nocturnal carnivore preys upon other nocturnal species, or whether it kills diurnal species while the latter are sleeping, or if both types of potential food are eaten in a definite ratio. Where the feeding on sleeping diurnals could be demonstrated, it might suggest a definite advantage for nocturnal carnivorism, since sleeping prey may have a raised sensory threshold.

In addition to this lack of specific and reliable information upon the activity patterns of the majority of species of animals, there are other ways in which the status of the nocturnal problem is confused and unsatisfactory. Among these is the significance of observational data upon the activity patterns of marine animals confined in aquaria as described by Polimanti (1911). Again the records of capture of insects at lights or light-traps need careful interpretation based on previous knowledge of the activity patterns of these species, since both nocturnal and diurnal animals may upon occasion come to light (Bodenheimer 1934, Cook 1930, Frost 1915, Hayward 1930, Houghton 1905, Howard 1899, Obyrne 1930, Reaumur (Bouvier 1922), Rockwood 1925, Scott 1932, Stanley 1932, and Williams 1935). Good recording light-traps, however, have been devised recently (Williams and Milne, 1935) and much better data can be expected in the future if such work is continued, for example that of Robertson (1939).

Roosevelt (1910) expressed the view that in areas where game was hunted persistently, many of the larger animals persecuted tended to become nocturnal, whereas these species were often diurnal in regions not hunted over by man.

It is also possible that the abundance or scarcity of food may alter the normal activity pattern. Environmental changes associated with change in altitude may affect the activity pattern of certain animals. Roosevelt (1910) found that the harsh-furred mouse (*Lophuromys aquilus*) of British East Africa was usually nocturnal in the lowland brush, but became diurnal in the cold, foggy uplands.

The particular weather of a given twenty-four hour cycle may affect the activity of both diurnals and nocturnals (Allard 1930, Juday 1904, Peckham and Peckham 1898, Zolk 1932). This aspect of the problem should be carefully investigated. The general picture is commonly known. Thus Park, Lockett and Myers (1931) found that many diurnal beetles (Mordellidae, Coccinellidae, anthocalous Cerambycidae) have their nightly period of inactivity on flowers or foliage prolonged on overcast days; and the strictly nocturnal rodent, the Springhaas (*Pedetes surdaster*), may be observed to be in activity on dark days (Roosevelt 1910). The Springhaas, in common with many other rodents, lives in burrows in the soil, and further is gregarious in the inactive diurnal period. This brings to mind another question, namely, how do the diurnal occupants of deep soil burrows and other dark, diurnal inactivity niches become sensible of the gradual change from day to night, or conversely, how can sleeping nocturnals perceive through their sensory system the change between day and night? In the case of the green tiger-beetle (*Cicindela sexguttata*), which passes the night inactive beneath the bark of fallen logs on the forest floor, temperature and changes in relative humidity may have been the determining influences (Park, Lockett and Myers 1931). Again, the sidewinding rattlesnake (*Crotalus cerastes*), which is nocturnal but inhabits the burrows of kangaroo rats during the day, presents the same general problem, and Mosauer (1936) also finds that the stimulus causing the snake to emerge on the surface after dark is probably thermic. This is a perplexing question which requires experimentation on many animals; we will return to this general problem later in a discussion of environmentally induced versus endogenous activity. These and many other questions are awaiting analysis.

The nocturnal habit offers definite advantages. In the first place there is the performance of certain activities at night by diurnal species. Such activities would be more easily disturbed during the day, for example, the box turtle (*Terrapene carolina*) is, according to Allard (1935), diurnal save for the period of oviposition, the female laying her eggs at night. While many turtles lay their eggs by day (especially early in the morning) there are exceptions (Cutright 1940, p. 225). It is notable that the sea turtles are essentially nocturnal in their oviposition.

Again, where the constituents of a community are not all active at the same time, and are divided into regularly nocturnal and diurnal faunas, there is an obvious reduction of direct competition or overcrowding of herbivores

for food. This cleavage in activity of the community has been demonstrated (Chapman, Mickel *et al.* 1926, Carpenter 1938, Park, Lockett, and Myers 1931, Park and Strohecker 1936), and apparently is quite general for sand areas, temperate deciduous and tropical rain forests, and meadows. A cleavage in activity has been demonstrated also for large game mammals (Roosevelt 1910) and for the flight of minute insects (McClure 1938).

The carnivorous habit would be less hazardous and a similar reduction in direct competition would result if nocturnal carnivores preyed on sleeping diurnal animals, as has been suggested by Borradaile (1923), and Clark (1914), and demonstrated for certain nocturnal carabid beetles attacking sleeping butterflies by Floersheim (1906).

In addition to competition for food, there is competition for shelter. It is probably a general rule that as habitat niches increase in a series of communities, their availability is competed for directly or indirectly, and if the species population increases at the same time, niche availability would be increased by alternate occupation of the same niche by diurnal and nocturnal species. This has been demonstrated in certain cases; thus in Ceylon certain palms are used as roosts for crows at night, and fruit-eating bats occupy these roosts by day (Willey 1904).

Two additional advantages which may be mentioned here are more directly associated with the nocturnal physical environment, that is the higher relative humidity at night would tend to reduce the rate of evaporation and consequently conserve water in many forms, chiefly Peripatus, terrestrial snails, and amphibians (Crawford 1934). Second, odors may penetrate more readily, and sounds travel more rapidly, in damp air according to Crawford (1934).

It has been shown that there is a large and diversified nocturnal fauna, and that there are certain advantages in the differential distribution of activity within the community. If this is so, the large nocturnal faunas must have certain adjustments which enable them to live and multiply in their normally darkened and relatively constant environment.

ADJUSTMENTS OF NOCTURNAL ANIMALS

With a few exceptions, the adjustment of animals to nocturnalism reported thus far are morphological and physiological adaptations of the visual sense and the development of luminescent organs. In view of what has been stated previously concerning the essential differences between day and night, this is understandable. The probability must be considered that many other structural, functional and ecological adjustments are made by nocturnal species, and that investigation of this aspect of the problem will repay the necessarily sustained effort. This phase of nocturnalism has been recently reviewed (Crawford 1934) so that a detailed analysis is unnecessary. However, there are several features which need discussion.

Years ago Verrill (1897) wrote:

Although much has been written regarding the protective and imitative colors and forms of various animals as seen by daylight, very little attention has been paid to their protective colors as seen by moonlight, twilight and starlight, when large numbers of species of small mammals and fishes, and numerous insects are most active in search of food, and most of the large carnivorous and insectivorous species are abroad in search of their prey.

The problem of protective coloration is not new, and has been discussed by biologists, pro and contra, for many years. However, within the last few years exact ecological experiments have been carried out upon mammals (Benson 1933), fishes and birds (Sumner 1934, 1935, 1935a) and upon insects (Isely 1938), the results of which show a positive protective value for certain species' coloration against their normal background coloration with respect to predation. These were largely diurnal experiments. It may be profitable, at this time, to revive Verrill's question as to the protective coloration of nocturnal animals. If precise experimental work demonstrated a positive value for nocturnal species, the problem would be greatly broadened, as well as an important adjustment for nocturnal animals added. Such an attack must be carefully planned. Not only the general objection of the protective-coloration theory must be met (Carpenter 1937, Shull 1936, 1937) but the additional problem of visual acuity and perception must be contended with. Many nocturnal species are carnivorous, and can see at night, but color vision of nocturnal animals has not been experimentally worked out and consequently, the problem remains a fruitful one. The excellent studies of Walls on nocturnal optical equipment has given a start, and experiments with such types as owls and mice, using the Sumner-Isely techniques, would be very illuminating. Nocturnal color vision must be proven by the careful quantitative pattern established by Brown (1937) for the large-mouth black bass, although such hue perception appears possible if Walls' physiological theory of the vertebrate retina is accepted (1934).

Entirely novel data have been supplied by Vanderplank (1934) which bear upon this phase of the problem. Using the tawny owl (*Strix aluco*), Vanderplank found that at night considerable terrestrial radiation of infra-red rays was present, and postulated that the owl nocturnal vision was chiefly a utilization of infra-red radiation. This was demonstrated by experiment: living animals which served the owl for food (beetles, frogs, toads, mice and rats) all were found to emit infra-red radiation; an owl could not locate dead mice or bits of horse meat in the dark, but if these dead tissues were illuminated with infra-red rays, an owl quickly found and ate them. Hence it appears that the food of owls emit infra-red rays as a consequence of metabolism, and that the owl locates its food and sees at night by means of a nocturnal vision in which infra-red radiation is utilized. These data of Vanderplank bring an entirely new interpretation to the problem of nocturnal vision and protective coloration at night.

Finally, many animals adjust to day and night by change in color. Thus rhythmic color change, correlated with day and night, has been found in such diverse forms as crustaceans (Gamble and Keeble 1900, Menke 1911), insects (Schleip 1910), fishes (Young 1935), and toads (Slome and Hogben 1929). This phenomenon appears to be widely spread but sporadic, and found in both terrestrial and aquatic, invertebrate and vertebrate animals. The physiological nature of these periodic changes in color has been recently examined by Welsh (1938), but the nocturnal adjustment involved remains to be proven by careful investigation of color vision of predators and the protective value of the color change, before these rhythmic changes can be listed as definite adaptions for survival at night.

It is significant of the rapid and diverging growth of the general problem that quite recently Buck (1937a) found that both sexes of the firefly, *Photinus pyralis*, had a color vision extending from at least 5600 A (in the green) to at least 6900 A (deep red). Leaving this general problem for further research, there are a number of nocturnal adjustments which have been described, and certain of these are summarized in the following table (Table 3). From the examples listed, it will be noted the large number and great diversity of adjustments for nocturnal vision. In view of the general absence from the literature of parallel and numerous adjustments of other senses for nocturnalism, it appears that either the visual sense was the most easily adapted, or that the ability to see at night was of first importance to nocturnal animals. The latter is the more probable explanation.

It is quite obvious that fireflies see at night, and that they flash synchronously under certain conditions (Craig 1917, Hess 1920). Buck (1935) was able to induce this synchronous flashing experimentally, to demonstrate that vision was involved (1937), that sex attraction of males flashing in response to the flashing female was a basic causal influence, and that these females were probably acting as "leaders" (Hess, Buck) in the gathering. Therefore the luminescent organs, visual perception and mating appear to be ecologically interrelated in the fireflies. From the literature several interesting correlations can be drawn concerning these nocturnal beetles, and comparative data are given in Table 4. The information presented has been drawn from numerous studies upon the super-family Cantharoidea (Allard 1931, Balduf 1935, Barber 1905, Barnes 1919, Buck 1935, Fabre 1909, Hess 1920, Hudson 1891, McDermott 1910, 1911, 1912, 1914, 1917, Mast 1912, Williams 1917, and observations of the writer). Although the table could be greatly extended, the data presented demonstrate that the diurnal species lack photogenic organs, or possess them in a rudimentary condition while nocturnal species have photogenic organs in varying degrees of perfection. The majority of the nocturnal photurids exchange flashes between the two sexes as a definite nocturnal adjustment to mating. This presumably places a premium upon vision and ability to reach the female, and we find that the males tend

TABLE 3. ADJUSTMENTS OF NOCTURNAL ANIMALS

Nature of Adjustment	Animals Involved	Relevant Literature
Mating adaptation as a photogenic function of	Fireflies (Photuridae) Chiefly <i>Photinus pyralis</i>	Buck 1937, 1937a Folsom 1922 Hess 1920 Mast 1912 McDermott 1911, 1917 Williams 1917
Abdominal luminescence:		
Thoracic luminescence:	Elateridae <i>Pyrophorus noctilucus</i>	Dubois 1886 Bouvier 1922
Nocturnal Visual Adaptations		
Invertebrates		
Periodic migration of the	Crustacea (Decapoda)	
(a) Distal (iris) pigment of compound eyes, to assume a day and a night position:	<i>Macrobrachium olfersii</i> <i>Macrobrachium acanththurus</i> <i>Palaemonetes vulgaris</i> <i>Latreutes fucorum</i> <i>Leander tenuicornis</i> <i>Anchistiooides antiquensis</i>	Welsh 1930 Welsh 1930a Welsh 1935 Welsh 1936
(b) Proximal (retinal) pigment	<i>Cambarus virilis</i> <i>Latreutes fucorum</i> <i>Leander tenuicornis</i> <i>Penaeopsis goodei</i>	Bennett 1932a Welsh 1935
(c) Reflecting (tapetal) pigment	<i>Latreutes fucorum</i> <i>Leander tenuicornis</i> <i>Anchistiooides antiquensis</i> <i>Cambarus</i> <i>Homarus</i>	Welsh 1932 Welsh 1935 Welsh 1936 Welsh 1938 Welsh 1938
Periodic migration of the distal (iris) pigment of compound eyes, to assume a day and night position:	Insecta (Lepidoptera) <i>Plusia gamma</i> , a noctuid moth	Kiesel 1894 Demoll 1911, 1917
	Nocturnal lepidoptera	Horstmann 1935
Structure and function of the reflecting layer (tapetum); and of the several optic adjustments in general:	Insecta (General) (Moths) <i>Sphinx</i> <i>Bombyx</i> <i>Deilephila euphorbiae</i>	Comstock 1924 Imms 1924 Bugnion & Popoff 1914
	(Coleoptera) <i>Oryctes rhinoceros</i>	
Size of facets of eye:	(Hymenoptera) Nocturnal Bee (Ephemerida)	Graenicher 1911
Size of Ocelli	Certain mayflies Nocturnal Hymenoptera	Sharp 1918 Rau 1935
Vertebrates		
Differential change in the length of rods and cones between day and night:	Fishes (Siluridae) <i>Ameiurus nebulosus</i>	Welsh and Osborn 1937
Differential migration in the retinal pigment between day and night:	Reptilia (Crocodilia) <i>Alligator mississippiensis</i>	Laurens and Detwiler 1921

TABLE 3 (*Continued*)

Nature of Adjustment	Animals Involved	Relevant Literature
Presence of a Tapetum lucidum: (or functional equivalent)	Pisces (Elasmobranchii in part) Reptilia (Crocodilia) Mammalia (General) (Marsupials) Opossums in general (Chiroptera) Fruit bats (Carnivora) Many species of nocturnal cats (Ungulata) Elephants	Walls 1938 Walls 1938 ^t Hertwig 1912 Pennington 1935 Walls 1938 Enders 1935 Crawford 1934 Walls 1938 Walls 1938 Walls 1938 Crawford 1934 Walls 1938
Lens of eye Yellowish in diurnal forms as opposed to colorless in crepuscular and nocturnal forms:	Reptilia (Snakes of nocturnal habits) <i>Arizona elegans</i> <i>Trimorphodon vandenburghi</i> <i>Phyllorhynchus decurtatus</i> <i>Hypsilema ochrorhynchus</i> Mammalia (Nocturnal rodent) Flying Squirrels (<i>Glaucomys volans</i>)	Walls 1931, 1934 Walls 1931
"Spectacle," a horny delamination or homologue of the palpebral complex associated with certain forms of both crawling and nocturnal habits:	Reptilia Many nocturnal snakes Lizards Gekkonidae Xantusiidae Pygopodidae	Walls 1934a
Histological structure of the retina: nocturnality associated with preponderance of rods over cones, to the pure rod retina:	Reptilia Rhynchocephalia <i>Sphenodon punctatum</i> Lacertilia <i>Heloderma suspectum</i> <i>Xantusia riversiana</i> <i>Coleonyx variegatus</i> Opnidia <i>Rhinocheilus lecontei</i> <i>Arizona elegans</i> <i>Trimorphodon vandenburghi</i> <i>Phyllorhynchus decurtatus</i> <i>Hypsilema ochrorhynchus</i>	Walls 1934
	Boidae in general Viperidae in general Crotalidae in general	
	Mammalia Chiroptera (Bats)	Walls and Judd 1933 Crawford 1934
	Nocturnal Primates	Woollard 1927

¹Walls does not cite a tapetum lucidum for birds. However the eyes of owls and nighthawks glow strongly in the beam of a night lamp, and the histology of the eyes of nocturnal birds should be investigated in this regard. Dr. Walls has recently informed me that the *lamina vitrea* is the layer which reflects light and is the functional equivalent in this respect of the tapetum lucidum in nocturnal birds.

TABLE 3 (*Continued*)

Nature of Adjustment	Animals Involved	Relevant Literature
Clear cornea	Typical nocturnal vertebrates	Walls and Judd 1933
Large eyes, absolute size or relatively to their diurnal allies:	Majority of nocturnal birds	Crawford 1934
	Nocturnal mammals	Kahmann 1930
Vertically elliptical pupil:	General Reptilia Rhynchocephalia <i>Sphenodon punctatum</i> Lacertilia <i>Xantusia riversiana</i> <i>Coleonyx variegatus</i> Gekkonidae largely nocturnal Thecadactylus rapicaudus	Mann 1931 Mann 1931 Walls 1934 Walls 1934 Barbour 1926 Mann 1931 Walls 1934 Park 1938 Evans 1936
	Ophidia Boidae generally Viperidae generally Crotalidae generally <i>Trimorphodon vandenburghi</i> <i>Phyllorhynchus decurtatus</i> <i>Hypsiglena ochrorhynchus</i> Crocodilia Mammalia Nocturnal cats in general (Many species)	Pope 1937 Mann 1931 Walls 1934
Infra-red vision	Tawny Owl (<i>Strix aluco</i>)	Vanderplank 1934

to have larger eyes and better developed powers of flight. Culmination is reached in both the phengodid and the phorurid families, in which there are apterous and larviform females with brilliant luminescence and large-eyed, winged males with generally smaller and less brilliant photogenic organs. Confirmatory evidence is found in the nocturnal bee (*Sphecodogaster texana*), where the pollen is gathered from flowers from after sunset until ten o'clock at night. Females of this bee are flightless and have normal eyes, whereas the males are good night flyers and large facets characterize their eyes (Graenicher 1911). Again, in the photurid (*Pyropyga fenestrata*) the adults are diurnal and lack functional photogenic organs, while the carnivorous larvae are nocturnal and possess well-developed luminescent powers. The possession of photogenic organs by photurid larvae requires further investigation as to its significance.

Courtship, fighting patterns and other aspects of behavior have been correlated with nocturnality of geckos (Noble and Bradley 1933, Evans 1936) so that mating behavior and nocturnalism offer research opportunity with vertebrate as well as invertebrate animals.

TABLE 4. CORRELATION OF CERTAIN PHYSIOLOGICAL AND ECOLOGICAL FUNCTIONS IN CANTHAROID BEETLES

Taxonomic Group	Activity	Feeding	LUMINESCENCE		WINGS	
			Male	Female	Male	Female
I. CANTHARIDAE...	Diurnal (Adults)	Carnivorous and Herbivorous	Absent	Absent	Present	Usually present
II. LYCIDAE.....	Diurnal	Herbivorous (Larvae xylophagous)	Absent	Absent	Present	Present or larviform and apterous
III. DRILIDAE..... Drilus Malacogaster	Diurnal?	Adults? Larvae feed on snails	Absent	Absent	Present	Larviform and apterous
IV. PHENGODIDAE... Phengodes Zarhipis	Nocturnal	Carnivorous	Absent	Present	Present	Larviform and apterous
V. PHOTURIDAE.... (Lampyridae, s.s.)		(Larvae feed chiefly on snails)				

DETAILS OF ADULT PHOTURIDS

	Activity	FEMALE		MALE	
		Metawings	Luminescent Organs	Metawings	Luminescent Organs
Pyropyga fenestralis..... (larvae.....)	Diurnal	Present	Absent	Present	Absent
Ellychnia corrusca.....	Nocturnal	Absent	Present	Absent	Present)
Lucidotata atra.....	Diurnal	Present	Vestigial	Present	Vestigial
Photuris pennsylvanica.....	Chiefly diurnal	Present	Poorly developed	Present	Poorly developed
Photinus	Nocturnal	Present	Present	Present	Present
consanguineus					
pyralis					
marginellus, etc.					
Pyractomena	Nocturnal	Present, but fly seldom; (P. castus only crawl)	Present, usually average smaller than males	Present, fly very well as a rule	Present, usually average larger than females
Luciola lusitanica					
Lampyris noctiluca					
Pelania mauritanica					
Microphotus angustatus					
Phausis					
Phosphaenus hemipterus					
Lamprophorus tenebrosus					

Although the nocturnality of bats has long been known, and their marked agility in the air has been substantiated, the recent observations of Borell (1937) appear to necessitate further research upon the adjustments of these usually nocturnal forms in their nightly search for food. Borell found that bats could be easily obtained by stretching wires over a water tank, when the

bats coming in, presumably to drink, were unable to avoid the wires and fell into the water!

Even such generally adjusted forms as men, which are essentially neither diurnal nor nocturnal in the strict sense of the word, have some adjustment for nocturnal conditions, as has been shown by Cobb (1923, 1923a) in a study of dark adaptation with reference to night flying of aeroplanes.

Before turning to the subject of nocturnal activity *per se*, there is a very important biological adjustment which must be examined briefly.

SLEEP OR ITS PHYSIOLOGICAL EQUIVALENT

Although certain animals are reported in more or less continuous activity, as are larvae of the noctuid moth, *Anticarsia gematilis* (Watson 1916) and the oyster (Nelson 1921), others are said to be normally active for only a small fraction of the twenty-four hour period, as are certain Phasmidae (Annandale 1902, Schmidt 1919). The majority of metazoans have more or less regular periods of activity and recuperation. Generally these periods alternate rhythmically under normal conditions, following a species pattern with individual variation. The necessity for protoplasmic rehabilitation following photoplastic activity is a thoroughly grounded physiological principle, and similarly activity of the organism, in its search for food, must be followed by inactivity and rest.

In a discussion already too long, the author does not propose to review the literature upon sleep. This has been done by numerous investigators (Polimanti 1911, Werner 1911, Fiebrig 1912, Pieron 1913, Rau and Rau 1916, Rau 1938, Kleitman 1929, Park, Lockett, and Myers 1931, Laird and Muller 1930). The unsatisfactory state of information upon sleep must be reaffirmed. It is especially unsatisfactory with regard to a general theory which will explain sleep of organisms as a whole. The long continued and brilliant attack upon the physiology of mammalian sleep by Kleitman and his co-workers (Kleitman 1923, 1925, 1928, 1929, 1932, 1933, 1933a, 1937, 1939, Lee and Kleitman 1923, Reed and Kleitman 1925) has given a precise experimental picture of recuperation in dogs and men; their results should apply, in general, to higher vertebrates. Conklin (1927), Laird and Muller (1930), and Freeman (1935) have, with others, studied sleep in man from a psychological point of view. Conklin summarizes:

Sleep may be said to be an instinctive mechanism with its own special neuron pattern activated by a great variety of stimuli, according to the experience of the individual. It is facilitated by relaxation and reduction in the number and strength of sensory stimuli as well as by the presence of limited amounts of fatigue substances in the body.

Pieron (1913) finds that sleep is a suspension of those sensory-motor activities which bring the individual into relation with its environment, and which

is accompanied by a characteristic diminution of muscle tonus, loss of equilibration, reduction of spontaneous activity, elevating the threshold of irritability, and absence of critical reactivity. Kleitman (1933) found sleep to be a habit depending upon the cerebral cortex for its development, demonstrated by his previous work on decorticated dogs, and states that the twenty-four hour variation in sleep and activity of the organism is one of several periodic variations which show a twenty-four hour rhythm; further, Kleitman views the sum total of these rhythmic variations, including sleep and activity, as manifestations of a twenty-four hour rhythm in organisms which have adjusted their lives to the alternation of day and night. He finds in man a diurnal variation of speed and accuracy of performance, and a variation in body temperature and excretion of phosphates. These day-night variations he finds may be a consequence of a diurnal-nocturnal rhythm in tonicity of the skeletal musculature, and the latter variation is held to be probably responsible for the development and persistence of the sleep habit.

Kleitman (1929) in a theoretical and summarizing paper found sleep to be an easily reversible inactivity of the cerebral cortex due to a break between the cortex and other parts of the nervous system, this break resulting from a marked decrease in the number of afferent impulses. He believes that sleep is due to fatigue of the neuro-muscular mechanism concerned in the maintenance of muscular tonus. In this theory of sleep, Kleitman excludes hypnosis, narcosis, and coma.

Now when an examination of the literature upon sleep in insects is made, it is found that many insects, especially in the order Hymenoptera, have a normal inactive period characterized by a marked rigidity. In fact, many are inactive, with their legs and body rigid, and grasping a twig, leaf or stem by the mandibles alone (cf. literature cited by Rau and Rau 1916, and Rau 1938). Other insects do not have this rigid inactive condition.

Fiebrig (1912) in a critical review, compared insect sleep with sleep of vertebrates and found both groups have in common (1) relative inactivity while asleep, (2) raised threshold of irritability among other resemblances; but the rigid condition of the insect muscles, while asleep, he held to be analogous to the condition of humans when under hypnosis. Pieron (1913) went further in that he separated sleep of invertebrates and even some fishes from the sleep of mammals, regarding the sleep of the former to be nothing more than comparative immobility depending upon external influences.

When the many theories of sleep are considered, a number of which have been discredited, we are impressed with, first of all, a lack of agreement upon what sleep consists of. Thus sleep is instinctive according to some and habitual according to others; it is rigidly limited to the very highest vertebrates, or a general response. Some years ago at a symposium on sleep at the Biology Club of the University of Chicago, the material presented was confined to such mammals as dogs and men. In the discussion which fol-

lowed on sleep in general, the physiologist Ralph Lillie stated that at least we could consider sleep in the broad sense as a general anesthesia. This is one of the very few general ideas concerning sleep that have come to the author's attention.

The word "sleep" appears to include a considerable variety of physiological states which may not be comparable. My own position is that we do not gain by limiting sleep to mammals until the problem has been experimentally exhausted, and the problem will not be exhausted by working only with one group of animals. Rather we must attack the rigid sleep of certain insects by the same refined physiological techniques employed with mammals, and review or investigate the inactive states of animals from protozoans to higher vertebrates. Again, how is rigid insect sleep to be understood by comparing it with death-feigning (letisimulation) of insects or hypnosis of other animals if letisimulation and hypnosis are not thoroughly understood. Recent data by Payne (1937) on death-feigning in insects should be followed up by an extensive and intensive exploration of insect sleep.

Finally, we should note that protoplasm is a labile and dynamic system, highly irritable, highly specific but having certain general properties. Activity followed by inactivity may be looked upon as a general protoplasmic phenomenon, and recuperation of the body as a whole would seem to be inactivity at a quantitatively different level of organization. Naturally, as the organism becomes more complex, the pattern of sleep will change but if it is said that mammalian sleep differs qualitatively from, say, insect sleep, then must we not say that mammalian activity, and consequently muscle physiology, is also unrelated in the two groups? We are hardly in a position to say this at the present time, and when nocturnal activity is discussed in the following pages it should be kept in mind that inactivity is a normal correlative of activity.

ENVIRONMENT AND ACTIVITY

Since irritability is a quality of protoplasm we would expect the dynamic environment to elicit a wide variety of protoplasmic responses. This is substantiated by the large literature upon behavior (Jennings 1906, Loeb 1918, Mast 1911). However, since periodism is to be discussed presently, certain environmental stimuli must be spoken of at this time. Some of these have been noted previously, for example lunar periodicity and the relative length of the day and the night. Other effects are so thoroughly known that not more than passing reference is necessary, viz. the involved relation of radiant energy to the endocrine and sexual cycle of birds and mammals (cf. J. Benoit, T. H. Bissonnette, L. G. Brownman, E. W. Dempsey, M. Hill, F. H. A. Marshall, C. R. Moore, W. Rowan and others).

In the previous review of nocturnal animals the effect of local weather upon species activity was discussed. In this discussion light intensity ap-

peared to be an important influence in these and many similar observations. The nocturnal activity of the wood mouse (*Apodemus sylvaticus*) is partially controlled by light (Elton, Ford, and Baker 1931); the diurnal wren (*Troglodytes musculus*) and diurnal bees (*Trigona mosquito*) of the Panama Canal Zone were shown by Lutz (1931) to have their activity pattern partially modifiable by light intensity. In polar regions where, save for the spring and autumnal periods, there are long continuous stretches of darkness or light, the influence of light is less obvious. Elton (1927) finds that the species of polar areas are largely diurnal animals and Hesse (1924) states that bees work in the illuminated arctic period. Pearse (1926) notes that polar Eskimos have highly irregular periods of activity and recuperation.

Under laboratory conditions of continuous illumination, Warren and Scott (1936) found that hens lay continuously, whereas eggs are laid only in daytime under normal alternation of day and night.

Generally light and temperature operate together under normal conditions; their effects are partially compound and must be carefully separated. Chapman (1923) found that the leaf-mining beetle (*Taphrocerus gracilis*) was positive to light at high field temperatures, flying when stimulated, whereas the species became negative to light at low field temperatures and upon stimulation folded the appendages and fell to the ground or into the axils of the leaves where they were inactive. In the laboratory under controlled conditions, Chapman found that the beetles could be brought into the light by increasing the temperature and made to retire by lowering the temperature. Their response to light and temperature, then, regulates their twenty-four hour activity cycle, and affords an excellent example of environmental control of poikilothermal forms.

Chapman and co-workers (1926) carefully studied the daily emergence and activity of a number of insects forming part of a Minnesota sand dune community and found that the night sand fauna differed from the day sand fauna, the change in activity of the inhabitants being closely correlated with change in temperature; similarly Park and co-workers (1931) found an apparent correlation between the rhythmic change in temperature, light, relative humidity and rate of evaporation and the change in activity of diurnal and nocturnal animals of an Ohio beech-maple forest community.

Body temperature is obviously correlated with air temperature in poikilothermal species and temperature is an important influence of animal activity. Simpson and Galbraith (1905) and Wetmore (1921) found that normally diurnal birds and normally nocturnal birds had opposite body temperature curves, the body temperature of each type coinciding with the periods of rest and activity. Hilden and Stenbäck (1916) confined birds in a dark room and regulated their activity by artificial illumination. By this technique they were able to reverse the body temperature rhythm. The importance of temperature with regard to reptile activity has been demonstrated by Mosauer

(1936), and is being pursued, notably by Raymond B. Cowles at Los Angeles.

Moisture is well established as a critical environmental influence; the enormous literature is ably summarized elsewhere (Chapman 1926, Elton 1927, Shelford 1913). Boycott (1934) found that relative humidity was influential in determining field activity of snails, and Rogers (1933) states that crane-flies (*Tipuloidea*) are nocturnal or crepuscular but believes this to be a response to a favorable ratio between humidity and rate of evaporation. Shelford (1914, 1914a) has previously demonstrated the rate of evaporation to be of great importance in regulation of activity and Necheles (1927) found that a relative humidity of between 75 percent and 85 percent was favorable for the activity of mosquitoes, these animals retiring during the day to avoid the low humidity and high rate of evaporation.

It is abundantly demonstrated, therefore, that changes in the environment effect changes in activity, and since the larger environmental changes are rhythmic in nature it follows that a more or less rhythmic activity would result. The literature cited, however, has been concerned chiefly with study of activity through observation or indirect measurement. Direct recording of activity was studied first by Stewart (1898), Slonaker (1908, 1912) and by Szymanski (1914). Using various types of recording machines, Szymanski found (1918c) that the blow fly (*Calliphora*) was diurnal and monophasic, e.g. that the flies exhibited a major recuperative period at night and a major activity period at day; that crayfish were nocturnal and monophasic in general, the greatest activity coming between seven and nine o'clock in the evening; that earthworms were nocturnal and polyphasic, showing about four rest and four activity periods in the twenty-four hour cycle with the greatest activity falling between two o'clock in the afternoon and midnight, and that the earthworms were active about fourteen hours out of the twenty-four. He found that snails had an uneven distribution of rest and activity periods; rabbits were polyphasic, being active for about twelve hours of the twenty-four hour cycle, with from sixteen to twenty-one activity and rest periods; the domestic cat had relatively unbroken sleep at night, and a few relatively active periods at day, and this monophasic diurnality he regarded as being secondarily imposed upon it by the sleep-activity pattern of man. Szymanski (1918a) also studied white rats and found that they were typically polyphasic, with a general nocturnal tendency, and an activity of about ten hours out of the twenty-four; in the same paper he found that waltzing mice were also polyphasic, generally nocturnal, and active some fourteen hours out of the twenty-four hour cycle. Later he investigated the activity of human infants (1918b) and of men (1922); these studies will be discussed later.

When the writer (Park, Lockett, and Myers 1931) had completed the survey of a forest community at night, and found a striking coincidence between the activity and the operating environmental influences, it was realized that only the parallelism of environmental and animal activities had been

demonstrated, and if this relationship was to be further analysed, constant environmental conditions must be obtained. Consequently, a study of typical forest species under controlled surroundings was initiated to throw light upon this parallelism (Park and Keller 1932). The first species used was the common forest cockroach (*Parcoblatta pennsylvanica*), and it was found that this species tended to give maximal activity until fatigued, when held in total darkness and constant air temperature and rate of evaporation.

Recently Nielsen (1938) has studied the activity and song of three katydids (*Tettigonia viridissima*, *T. cantans*, and *Decticus verrucivorus*) by means of recording equipment. Nielsen was able to demonstrate that the activity, and to a less extent the song, was largely induced by regulation of the illumination, and in constant darkness no clear rhythm persisted. Here, as in Chapman's study with *Taphrocerus gracilis* (1923) and the forest roach, the data supported the already heavily documented conclusion that environment controlled activity and induced periodicity in many species. Other data were to follow shortly, however, to broaden the activity concept.

Although it is not safe to generalize very far, since each species of animal apparently has a specific set of physiological requirements and activity pattern, those activity patterns which are wholly or in great part regulated and induced by the rhythmic twenty-four hour day-night cycle, may be called the Exogenous Type of Activity. This is a general and collective concept, the precise limits of which are not yet defined (Park 1940a).

PERIODISM AND ACTIVITY

Not all animals have their activity so easily controlled; rather the pattern is more deeply seated, more or less regulated internally, and under constant experimental conditions tends to continue its rhythmic character. When the author was working with the forest cockroach, *Parcoblatta pennsylvanica*, he also was studying the activity of a forest fungus beetle, *Boletotherus cornutus*. This beetle is nocturnal, feeds upon fungi, especially shelf fungi (Fomes), copulates and oviposits on the fungus, and the larvae develop and pupate within the fungus. This beetle, when placed under identical conditions as the forest roach, namely total darkness, constant temperature, and constant rate of evaporation, continued to exhibit its normal nocturnal activity and diurnal inactivity. In other words, under constant conditions its activity was periodic. This is but a single example of rhythmic behavior, and a number of similar instances have been reported in recent years as given in the following table (Table 5).

From Table 5 it will be seen that periodic activity, under constant environmental conditions, has been demonstrated by investigators, working in widely separated localities, and upon a variety of animals. These animals embrace laboratory and wild stocks; individuals of both sexes, of various ages; both

TABLE 5. PERIODIC ACTIVITY OF ANIMALS UNDER CONSTANT CONDITIONS

Chronology	Animals Involved	Conditions	Literature
1917-1919....	Copepoda (<i>Acartia</i>).....	Vertical migration in constant darkness.....	Esterly (contra Franz, 1911-1913)
1918.....	White Rat.....	Constant darkness.....	Szymanski
1922.....	White Rat.....	Constant darkness.....	Richter
1925.....	<i>Cotinis nitida</i> (Larvae).....	Constant darkness and constant light	Hintze
1926.....	<i>Peromyscus leucopus</i>	Constant darkness.....	Johnson
1930.....	Japanese Waltzing Mouse.....	Constant darkness.....	Wolf
1932.....	<i>Boletotherus cornutus</i>	Constant darkness.....	Park & Keller
1932.....	<i>Stenopelmatus</i>	Constant darkness.....	Lutz
1932.....	<i>Gryllus domesticus</i>	Constant darkness.....	Lutz
1932.....	<i>Gryllus assimilis</i>	Constant darkness.....	Lutz
1933.....	<i>Thyone briareus</i>	Constant dim red light.....	Stier
1933.....	<i>Microtus</i>	Constant darkness.....	Davis
1935.....	<i>Megalodacne heros</i>	Constant darkness.....	Park & Sejba
1935.....	<i>Spirobolus marginatus</i>	Constant darkness.....	Park
1936.....	<i>Huro salmoides</i>	Oxygen consumption in constant dark	Clausen
1936.....	<i>Ameivurus melas</i>	Oxygen consumption in constant dark	Clausen
1936.....	White Rat.....	Constant darkness.....	Browman
1937.....	<i>Myotis lucifugus</i>	Constant darkness.....	Griffin & Welsh
1937.....	<i>Pipistrellus subflavus</i>	Constant darkness.....	Griffin & Welsh
1939.....	<i>Bufo americanus</i>	Constant darkness and constant light	Higginbotham
1939.....	<i>Bufo fowleri</i>	Constant darkness and constant light	Higginbotham
1939.....	<i>Peromyscus</i>	Constant light	Johnson

larvae and adults. The list includes holothurians, copepods, crickets, beetles, fishes, toads, mice, rats and bats. In certain experiments the constant conditions maintained are not sufficiently rigid to withstand criticism, but in the majority of cases light intensity was constant or constant darkness was complete, and air temperature, relative humidity and rate of evaporation were controlled.

Therefore such periodism appears to be a general response which is repeated under abnormally constant conditions. This rhythmicity is quite different from environmentally induced periodism in that the former deeply seated periodism has been shown to persist under constant conditions for from a few days in some species, to over eighteen months in others.

In order to obtain objective data on periodism, at least two essential conditions must be met. First, the animals must be under constant environmental conditions (which immediately introduces an abnormal factor since most species inhabit periodic environments). Second, recording apparatus should be used. Within recent years recording equipment has been devised. Apparatus for larger terrestrial animals (rats, mice, toads, bats), utilizing elastic bands, springs, excentric drives has been reported, sometimes incompletely (Slonaker 1908, 1912, Szymanski 1918, Richter 1922, Richter and Wang 1926, Davis 1933, Colton 1933, Durant 1935, Browman 1936, Hemmingsen and Krarup 1937, Griffin and Welsh 1937, Park 1938, Higginbotham 1939, Park and Woods 1940); for small terrestrial animals (crickets, grasshoppers, beetles) by Lutz (1932), Park (1935) and Nielsen (1938); for aquatic species (crayfish, fishes) by Spencer (1929) and Park, Roberts

and Harris (1940); and within recent years sound-recording apparatus based on the audio-frequency principle (Park 1937, Nielsen 1938) and other electrical devices (Kendeigh and Baldwin 1936, Spencer 1939, Odum and Kendeigh 1940). It is apparent that technical difficulties are being overcome.

There are other difficulties, more human and consequently less easily corrected, involved in the interpretation of the data obtained. In the first place, have we controlled the complete environment? Light and total darkness, air temperature, humidity, evaporation rate, vibration, wind movement have been held constant; recently (Horstmann 1935) the electrical changes in the atmosphere have apparently been eliminated and environmental infra-red radiation (Park 1937) removed. Food and water supply and the excessive accumulation of faeces offer no major difficulties with the newer recording equipment. Ultra-violet is not involved in totally dark cabinets and water screens. There remain cosmic rays and certain other little understood influences, for example, periodic changes in the gravitational and geomagnetic fields.

The perfect experiment has not been performed. It would include recording apparatus, the records of which are changed without disturbing the experimental animals; food and water supplies similarly handled; cabinet control of light, temperature, and humidity well within the limits of experimental error; lead walls to eliminate environmental infra-red; the whole experimental equipment operated in some deep cave (300 to 400 feet under ground) to eliminate cosmic rays; the experimental animals reared apart from their parents to eliminate direct or indirect tutoring, and reared in the experimentally constant environment to eliminate habit formation.

The writer is convinced that the periodic activity patterns demonstrated under controlled conditions are not the product of the immediate environment, but are internal and resident within the organism. Such periodic activity patterns have been placed in a second category of activity by the writer, namely the Endogenous Type of Activity. These periodic patterns have been given other names (vital rhythms, inner rhythms, internal, endogenous, inherent, innate, etc.), but the designation eventually adopted is of little consequence as long as such activity patterns are distinguished from those of the environmental type, and we differentiate between *inherited pattern* and habit (cf. Park 1940a).

Recently the training of insects, and the subsequent analysis of this habituated activity, has received renewed attention. These investigations are pertinent to the general problem since they serve to emphasize the importance of separating habit-formation from true periodicity. Following the early lead of Beling (1929) that the activity of bees appeared to have a twenty-four hour rhythm of feeding, Grabensperger (1933) found that ants and termites could be trained for a feeding rhythm of a particular temporal character. Ants appeared to be easily trained, viz. they were very plastic. Their experimental feeding rhythm would endure for nine days after the food was

removed from the feeding chamber; termites could be trained to a twenty-one hour rhythm. Grabensperger (1934, 1934a) then used a variety of chemical compounds with the food and found a number of resulting changes in the feeding pattern established experimentally. For example, using bees and wasps it was found that quinine delayed, and iodothyreoglobulin tended to accelerate the feeding time. Kalmus (1934) was able to train bees to visit a given feeding place at a certain time and found that certain influences modified the experimentally induced habit (low temperature, carbon dioxide, quinine) while others (etherization, prolonged darkening of the hive) did not appreciably affect the habit. Kleber (1935), in an ingenious paper, reported similar training of bees, and then studied the relation of the normal feeding rhythm of bees to the pollen and nectar production of a number of flowers. Kleber suggests that the normal feeding rhythm of bees may be a naturally formed activity pattern, just as the experimentally induced feeding rhythm is a humanly formed habit. All of these researches tend to differentiate between the environmental induced habit ("time sense" of certain authors, but not of all who use this term) and the internal periodic patterns which are initiated within the organism as a deeply seated response.

The distinction between exogenous and endogenous rhythms, however, must be understood. A more complete understanding will only come with continued investigation, but it seems obvious that a periodic phenomenon is either induced by the environment or is not so induced. Those patterns induced by the immediate environment are environmental, while those induced by the internal environment are internal. These patterns may be a consequence of (a) former induction by a rhythmic environment within the life of the individual, that is, habit formation, or (b) truly inherent. This question of habit *versus* inherence is an important aspect, but can be resolved by further research upon the immature or young stages of animals. Thus, in the beetle, *Boletotherus cornutus*, the beetles of one experimental series were raised from the egg stage in the fungi, in light-tight containers, and the activity pattern of these adult beetles was in general that of other beetles collected from fungi in the forest when adult (Park and Keller 1932).

Again, there is the question raised by the modifiability of the true inner rhythm by the environment. The experimenters cited in Table 5 varied their investigations in a number of ways; in some cases constant darkness, constant light of various intensities, or light and dark periods of many different lengths of time were employed; the twenty-four hour cycle was reversed in other experiments, exposing the animals to a dark day and an illuminated night; similarly starvation or regular feeding; varying the temperature or varying the relative humidity, have been used in certain experiments. The details of these investigations can be learned by consulting the literature cited. From a study of these there emerges a clear conclusion: namely, that the rhythm can be modified by the environment. But this conclusion is not new. We

are unfamiliar with any protoplasmic property which may not be destroyed or altered by the environment. That protoplasm and protoplasmic rhythms are modifiable would seem to be well established and of long standing. On the other hand it appears remarkable that such rhythms can persist in the face of such abnormal conditions (cf. Park and Keller 1932, Park 1935) and the writer's view of the internal periodicities of protoplasm coincides with the observations of others. It has been repeatedly pointed out (Park 1935) that the existence of periodism of activity should not be confused with modification of the rate and character of this periodism by environment. This is obvious, since organismal periodism in the whole community must keep step with the gradual change in the environment, for example with the change in light intensity with time of year and latitude or altitude; it is suggested by the known modification of environmental influence upon activity (*vide supra*); it has recently received experimental confirmation by Johnson (1939). Johnson found that white-footed mice (*Peromyscus*) had a well-defined activity rhythm which persisted in constant conditions for eighteen months, but that the rhythm could be shifted through the twenty-four hours and that definite amounts of modification of the activity result from definite light intensities. Again, within the organism such rhythms as the beat of the reptilian heart can be experimentally altered or destroyed (Chu and Sollmann 1925, 1925a, 1925b), and this modification of activity does not cause one to assert that there is no cardiac rhythm.

There are a great many such physiological rhythms, some not as fully investigated as the cardiac rhythm, but all of interest since these periodic phenomena within the organism are partially responsible for, or arise in part from similar sources as, the ecological activity rhythm of a whole organism. Consequently study of rhythmic phenomena is one of the many fields in which both physiology and ecology can cooperate for a solution of a common problem. Such functional rhythms range from the rate of deposition of dentin and enamel in rat incisors (Schour and Hoffman 1935, 1935a; Schour and Steadman 1935) to the periodic migration of pigment in the eyes of crustaceans (Welsh 1930, Bennett 1932, *et al.*).

Thus there are many insects (certain Diptera, Lepidoptera and Hymenoptera especially) which show a remarkable constancy in the emergence of adults from the pupal cases. As with activity patterns, such emergence is characteristic of a given species, the period of the twenty-four hour cycle in which emergence occurs varying between different insects but remaining relatively fixed for members of the same species. Bremer (1926) used a variety of flies and their hymenopterous parasites, as well as a meal moth. In general he found that light was an important modifying influence. However, the meal moth (*Ephestia kühniella*), which under normal day-night sequence shows 95.3 percent emergence between 2 P.M. and 5 A.M., and only 4.7 percent emergence from 5 A.M. to 2 P.M., continued to emerge at

practically the same times when in constant darkness. Bünnig (1935) studying the emergence of *Drosophila*, found that external changes even during the early embryonic stages have little effect on the emergence rhythm, and that after fifteen generations of *Drosophila* were kept in constant light, temperature and humidity, they still exhibited the emergence rhythm. Kalmus (1935) attaches great importance to light intensity in the control of *Drosophila* rhythm of emergence, but in constant darkness obtained a relatively typical pattern.¹

Bünnig also demonstrated that the rhythm of emergence could be lengthened by lowering the temperature and shortened by increasing the temperature, as he had previously demonstrated for physiological rhythms in bean plants (*Phaseolus*), and Bünnig pointed out that this temperature control of the rhythm makes its inherent character the more obvious. Certainly these results with temperature coincide with the effect of temperature upon the velocity of cardiac and other inherent physiological phenomena.

Kalmus (1935), however, introduces a different idea from that held by the majority of workers in this field. He separates environmental and inherent patterns on the basis of velocity, thus those functions which have their velocity influenced by environmental factors he terms *allochronous*, while those which endure without such modification are called *autochronous*. Such a restriction of inherent (autochronous) rhythms would not agree with the view set forth in the preceding pages, nor with the view of many other investigators.

Horstmann (1935) kept pupae of nocturnal lepidopterans in darkness for from two to ten days prior to emergence, and when the adults emerged he found the same periodic migration of pigment in their ommatidia as that experienced in the ommatidia of normally reared forms. This, too, is a clear case of a deeply-seated physiological rhythm; however, Horstmann attributes the persistence of the pigment rhythm to a memory of the larval period, a view which cannot at present be justified by experimental data.

Within the last ten years a large body of information has been accumulated upon physiological rhythms, and the relation of the induction or maintenance and modification of these periodic phenomena to the endocrine secretions. Among numerous examples, in addition to the role of hormones in the rhythms associated with the bird and mammal reproductive systems, there is the apparently extensive control of pigment in Crustacea by secretion of hormone or hormonoid materials. This paper does not pretend to review these and other physiological rhythms. They have been given admirable at-

¹ Unpublished observations of the writer indicate the same rhythm of pupation in another fly. While studying the guests of the mound-building ant (*Formica ulkei Emery*), a number of the slug-like larvae of the syrphid fly (*Microdon*) were obtained (Park 1935) and reared to adults. These adult flies belong to an undescribed species and emergence of the adults from the puparium always took place in the night, especially the hours preceding dawn. My data on emergence, however, are observational only and are not critical in the sense that rigid experimental conditions were maintained. *Microdon* emergence, however, should be examined experimentally, especially since the pupation takes place in the relatively constant environment of the host and nest.

tention by others (Bouvier 1922, Chap. III, Richter 1927, Rau and Rau 1929, Kalmus 1935, Hoagland 1935, Hemmingsen and Krarup 1937, Jores 1937, and Welsh 1938). It should be pointed out, however, that since so many internal cycles have a secretory control, and since total activity is partially an expression of internal physiological states, inherent activity patterns are affected by these internal conditions, and later research may show that such inherent activity is induced by rhythmic secretion. On the other hand were such a direct connection between activity and secretion established, it would merely raise the question as to the nature of the stimuli which induce such periodic changes in the endocrine system.

Consequently, whether we are dealing with inherent activity, or with internal physiological cycles, the problem of the general inherited pattern of protoplasms is eventually encountered.

Before discussing the nocturnal problem as a whole, there is a third category of activity which must be examined.

ARHYTHMIC ACTIVITY

From what has been said it is clear that the generally accepted view of physiologists regarding activity and inactivity is insufficient to explain the facts accumulated, nor are ecologists in a more enlightened position. In addition to the types of activity patterns reviewed, there are other species, relatively few in number, which have no fixed pattern of activity. That is, individuals of such species satisfy their physiological requirements at any period of the twenty-four hour cycle. It follows that such species have no discernible day-night periodicity, and consequently activity tends to be distributed over day as well as night. This is not to say that individual habits may not be fixed in a given individual or group of individuals. On the other hand, in certain of these arhythmic forms a very plastic behavior has been demonstrated, and habits can be induced which give to the animal a superficial resemblance to the patterns of animals in the exogenous or endogenous categories. Close observation and controlled experiments are quite necessary to differentiate this activity type. Thus under constant conditions, the *exogenonts* are active or inactive as a group, depending upon the conditions being maintained with respect to their normal pattern; the *endogenonts* tend to maintain the activity pattern regardless of the constant conditions; the arhythmics present no group action, some individuals being in activity at any section of the twenty-four hours. It should be pointed out that such constant conditions must be held well within the limits of toleration of the species concerned.

One generalization which can be made of the arhythmic group is that they inhabit constant environments, or are social forms. Examples of this category include the cave crayfish, *Cambarus pellucidus*, the log-inhabiting,

relatively social beetle, *Passalus cornutus*, certain ants, certain termites and modern civilized man.

Results upon *Cambarus pellucidus* are so recent (Park, Roberts and Harris 1940) that no extensive comment is necessary. It was shown that under constant darkness, constant illumination of several intensities, reversed illumination, or normal day and night variation, at constant temperatures, well-fed males or females of these cave crayfishes gave an arhythmic pattern of activity. Each crayfish was active or inactive individually and independently. This species, although lacking the pigmented eyes of its epigaeous congeners, is photonegative and consequently gives a more intense record of activity in illuminated experiments, but the distribution of activity, that is, the percentage of active to inactive time, is relatively equally divided between the day and the night. Such a distribution for a species population is an index of its arhythmic nature (cf. Park 1940a).

Similarly the black passalid beetle, *Passalus cornutus*, shows a truly arhythmic activity under a wide variety of conditions varying from normal to highly abnormal environmental conditions (Park 1935, 1937), and although activity is increased under unfavorable, low relative humidities, the distribution of time active and time inactive is uniform and roughly equally divided between day and night.

The normal environments of both the cave crayfishes and log-inhabiting passalid are constantly dark, and the temperature and other conditions relatively stable and uniform, in contrast to the external environment. Both of these species have been studied by means of recording equipment under controlled conditions, and the activity analyzed for its percentage distribution over the twenty-four hour cycle. The data accumulated on the social species is more circumstantial, but never the less suggestive.

That certain species of ants have no uniform period of inactivity appears to be well substantiated. Thus McCook (1877) speaking of eastern mound-building ants observes :

ants at Camp Riddle, when observed during every hour of the night from sunset to sunrise, were found to be pursuing the very same labors in the same way, and in the same fields as during the day. The avenues, tree-paths, feeding stations, feeding grounds and hills were always thronged day and night.

This clear statement by an experienced myrmecologist regarding the normal activity pattern of *Formica exsectoides* is convincing. Parallel observations are numerous. *Lasius niger americanus* (Flint 1914), *Aphaenogaster fulva* (Park, Lockett, and Myers 1931), *Aphaenogaster fulva picea*, *Aphaenogaster tennesseensis*, *Camponotus caryae*, and *Camponotus herculeanus pennsylvanicus* (Park and Strohecker 1936) have also been observed through day and night, and species activity appears to have been constant. It is to be expected that in such species the active periods were at different times for

different individuals; probably there was greater activity during certain periods of the twenty-four hour cycle, but the distribution of active to inactive periods appears to resemble, very closely, that of passalids and cave crayfish. Flint's observations (1914) were substantiated (Park and Strohecker 1936), these "corn field ants" appearing at observation stations at all times of the day and night. Seeman (1928) found that *Crematogaster lineolata* worked through the night, even during rain and thunder storms, while *Formica pallide-fulva* he found more active by day than at night. This same arhythmicity was found by Schneirla (1938) for the army ant, *Ecton hamatum* in the Barro Colorado rain forest. Schneirla found that during the nomadic phase of colony activity there was vigorous raiding throughout the day with morning and afternoon peaks of activity, and the raiding was usually continued during the night, but less vigorously; during the statary phase the army ants raided much less vigorously during the day, and nocturnal raiding was weak or absent. Mallis (1938) observing army ants in California found this same nocturnal raiding taking place, so that it appears that many ecologically different ants, belonging to widely separated taxonomic categories, regularly continue to practice their colony activities over the twenty-four-hour period.

The activity of termites in this regard is unknown. Andrews (1911) reported that certain Jamaican termites were active at night. The arhythmicity of oviposition of termite "queens" is apparently substantiated, the queen laying her eggs through the day and night in an unbroken stream. On the other hand, the production of alates and the colonizing flight are periodic. The latter seems to be primarily correlated with the periodicity of rain. Both a field and an experimental analysis of activity of these highly social animals is needed from the point of view of the activity pattern they possess.

There seems to be little doubt that man is arhythmic, or at least the human species has no inherent pattern of activity. In the long polar nights or days the Eskimos have highly irregular periods of activity, and of eating and sleeping (Pearse 1926). The fact that man forms habits easily may give a superficial appearance of periodicity. No uniform type of twenty-four hour variation was found in a study of energy expenditure and performance (Freeman 1935) which again confirms human arhythmicity. In an important experimental study of the activity of human infants, Szymanski (1918b) using recording equipment found that infants were polyphasic, viz. had more than one large activity period and more than one inactive period over the twenty-four hour cycle. Szymanski viewed his findings as demonstrating that the adult human depends upon the sense of vision to a great extent, and hence becomes secondarily a diurnal, monophasic organism. Szymanski (1922) later continued his research on human activity, confirming his earlier view as to the monophasic character of adults. He found in general that the ratio of activity to rest was a fairly constant one, and our common experience of

modern human communities impresses us with the ability of man to adapt his rest and activity periods to the exigencies of his particular occupation and the demands of his diverse avocations. Kleitman (1937) found that during the first year of life, the human infant's range of body temperature was gradually established; during the second year of the child's life, the adult type of body temperature curve becomes definitely fixed. The relation of the body temperature curve to the curve of activity and inactivity is generally close. This lends to human activities a distinct resemblance to the purely endogenous type of activity.

The apparent arhythmicity of such social species is interesting. It suggests that the society, in basing its existence upon mutual cooperation, places in operation a system of demands upon the individuals composing the aggregate. These demands can be satisfied only by ignoring the rhythmic natural sequence of the twenty-four-hour cycle, and consequently a purely physical periodic environment is replaced with a relatively constant social environment. Under the social system some individuals are active regardless of when a sample is taken. If this is true, social life may not flourish save in species with a highly plastic behavior. If the social medium is regarded as a relatively constant influence, then the conclusion emerges that arhythmicity is a correlative of constant environments. Thus such highly social forms as ants, man, possibly termites, and on the other hand log-dwelling passalids (which are definitely semi-social) and cave crayfish resemble each other in the relative constancy of their particular habitats. Apparently the more periodic activity-inactivity cycle of other social Hymenoptera, such as the bees and wasps, is an exception to the view given above and this aspect of the problem has been treated recently in a theoretical paper on community symmetry (Park 1940).

THEORETICAL DISCUSSION OF THE GENERAL PROBLEM

Students of animal distribution have not given sufficient attention to the bearing of activity pattern upon the problems of biogeography. Isolated suggestions have been made, often by investigators whose research interests lay elsewhere; these ideas should be interwoven to present the nocturnal aspect of zoögeography. The view of Clark (1914) has been discussed recently (Park 1938), but it should be noted that Clark held that such typical nocturnals as elephant, hippopotamus, tapir, sloth, various edentates, many lemurs, non-aquatic monotremes, geckos, onychophores and diplopods are found either abundantly or exclusively in the equatorial rain forests; that where there is relatively little imperfection in the geological record, such nocturnals are shown to have a long palaeontological record and that these forms are more archaic than diurnal types. Here is a zoogeographic suggestion that nocturnals are more primitive than diurnals, and are notably present in abundance in the rain forests. This general view is partially expressed

again by Barbour (1926, p. 8) for certain reptiles. The ecological geography of nocturnality will necessarily emphasize the essential difference between nocturnal habits in hot deserts, where they are conditioned by the extremes of the physical environment and such habits in a tropical rain forest, where we may interpret them as due to the competition of a rich fauna. In a stimulating theoretical paper, Kennedy (1928) discussed the geographic, seasonal and twenty-four hour distribution of the insects in relation to their phylogeny. This paper brings forth substantial evidence that primitive insects have lower rates of metabolism than modern insects; that the tropics have a greater energy intensity than boreal regions, the hot and illuminated day a greater energy intensity than the cool and dark night. Thus the primitive forms usually occur in cool, darkened habitats such as deep forests or are nocturnal, or both, while more modern orders tend to be diurnal. The exceptions are naturally numerous, but the general point of view agrees with that of others, namely that modern relics of primitive groups are more apt to be nocturnal, and are often tropical. Rau (1929) after working with saturniid moths and finding certain species with a deeper-seated activity rhythm than other species, concluded that the form with the more deeply seated nocturnal pattern was phylogenetically older than a species with a less deeply seated activity pattern. Although such a criterion of phylogenesis may not prove true for unrelated groups of organisms, it may be admissible for closely related forms within a common group. It again reflects the view that phylogeny and activity patterns, and hence distribution of the activity periods, whether deeply seated or not, may be related. Walls (1934) in a study of the reptilian retina, presents histological evidence over a wide range of material to substantiate his view that many groups of modern reptiles have become nocturnal secondarily. This change in activity pattern, according to Walls, has nearly always been accompanied by a transmutation of all or some of the cones of an ancestral diurnal and pure-cone retina into a nearly or wholly pure-rod retina adjusted for nocturnal vision.

From the separate ideas there emerges the view that nocturnalism is a specialization which arises from an original diurnal stock, and that the existing nocturnal forms are generally more primitive than the modern diurnal groups. This phylogenetic consideration can be tested in the study of animal distribution, but the application must be in the hands of zoogeographers skilled in the details of distribution of special groups of animals. The Matthews theory (1915) of the more modern and consequently more effectively adjusted species at the center of the dispersal area, and the more primitive and less effectively adjusted species at the periphery of the dispersal area, may be combined with this view of primitive nocturnality and modern diurnality. If such a combination proves sound, we should expect to find either the primitive forms at the center of the dispersal area, as nocturnal species to avoid competition; or the primitive stocks distributed peripherally and either

preponderantly nocturnal, or diurnal according to their subsequent history in the new environment. Light would be cast on this precise point by a general review of the habits of the Madagascan lemurs. The Central African and Asiatic lemurs are notably nocturnal forms, thus evidently escaping the main biotic pressure of the rich associated fauna. The Madagascan lemurs, without the competition of the modern carnivores, might be expected to exhibit a higher proportion of diurnal forms.

There are other problems, relating to the evolution of activity pattern. It is obvious that the world environment is rhythmic, which fact can serve as our point of departure for an analysis of biological periodism. We have found that environmental periodism and biological periodism are synchronized, but is this correlation apparent or real? It has been previously and repeatedly held that this is a real correlation, in fact that the environmental rhythmicity has been the cause of biological rhythmicity (Reynolds 1920, Bouvier 1922, Welsh 1938). This assumption is very plausible, but the argument should be critically examined and if possible carried further.

Circumstantially, when we survey the problem ecologically we find that where the environment is rhythmic, the organisms inhabiting the environment are rhythmic in their major activities. Since an organism must adjust to prevailing conditions, migrate or die, we view the extinction of species as a failure to adjust, or move into the relatively few constant habitats. These species have been replaced by more plastic forms, or by others whose adaptations allowed survival.

We have seen that the periodic environment of temperate regions is characterized by numerous adaptive biological rhythms, such as hibernation and aestivation, close phenological correlation of leafing, fruiting and reproductive cycles of animals, lunar cycles, and periodic activities within the twenty-four hour cycle.

Where the annual seasonal cycle is incompletely defined, organisms do not show such uniform periodism. In the tropical regions (Flattely 1920, Visher 1923, Haviland 1926) there is a conspicuous individuality of breeding, leafing and flowering. In these regions, day and night are relatively constant and there is a marked periodicity of those activities associated with the twenty-four-hour cycle (Park 1938, Park, Barden and Williams 1940).

With reference to this cycle of day and night, we have presented evidence for (1) an exogenous activity pattern, (2) an endogenous activity pattern, and (3) an arrhythmic activity. It should be noted that the first two may be combined in many species as (4) a composite activity pattern, and both of these first two patterns may be phylogenetic stages of development of a deeply-seated pattern of activity. The first type has its character induced by environment, the second type is more deeply seated and is continued for a greater or lesser time depending upon the degree of stability of the pattern, and secondly, the tolerance threshold for adverse conditions.

Here, then, is a consistent view of nature, built upon a frame-work of centripetally arranged and overlapping periodicities. There seems to be a sufficient body of evidence to postulate a causal relationship between environmental and biological rhythms over geological time. If such a causal assumption is made, how has the induction taken place? Our position is that biological rhythms have been selected by the rhythmic environment, operating upon mutations which have a positive adjustment value. Protoplasmic inheritance is not necessarily limited to morphological features. Pincus (1931) mated a strain of dilute brown mice with white mice. Both strains had different relations of frequency of respiratory movements to body temperature. The F_1 hybrids of this cross exhibited the relation of respiration to body temperature of one or the other of the parents, not a blend of the two parental relations. Consequently the hybrids inherited the value of the constant unchanged from one parent. This is the inheritance of a purely physiological character. Mutation pressure might well be maintained in the direction of periodic activities, in an environment which placed a survival value upon such periodic patterns.

Furthermore, a natural laboratory is at hand. So far we have been considering the rhythmic environment, but there are at least three relatively constant environments, namely caves, abyssal communities, and complex societies. Caves and abyssal regions are essentially inorganic, but the social matrix is essentially biological. At the present time the experimental investigation of the sea deeps is not feasible. We are led to believe, however, from data accumulated that they present a vast and relatively constant area (Coker 1938), although certain recent data (Livingstone 1937, Welsh, Chase and Nunnemacher 1937) indicate vertical migrations of certain moderately deep water forms over the twenty-four hour cycle. The problems concerned with the activity patterns of true abyssal species are of theoretical importance, but there are insufficient facts at present to warrant discussion of the question.

Caves, on the other hand, are accessible, and the biology of subterranean forms is attracting increasing attention. From the viewpoint of periodism, cavernicoles are perfect experimental material. Regardless of the manner in which caves have been colonized, existing cave forms mark the end product of a natural experiment, an experiment with the beginning lost in geologic time. The control for this natural experiment is the adjacent, phylogenetically related, epigaeous stocks. The cave environment is a constant habitat, not only as to such obvious influences as darkness, temperature, relative humidity, evaporation rate and air movement, but for such lesser known possible factors as cosmic radiations. The food-supply is meager and may be periodically enriched with vernal foods in some caves; in large caverns, such as Mammoth Cave of Kentucky, many species of animals have existed for thousands of years in a remarkably stable habitat.

Activity of cavernicoles has hardly been touched, with the exception of the cave crayfish. If what we have postulated concerning the origin of

biological rhythms is tenable, any cavernicole which is shown to have an inherent activity pattern will acquire new importance. Demonstration of such a rhythm would attest to the tenacity of the activity pattern after many generations in a constant environment in which a day-night periodism would appear to have little positive survival value. At the present time I do not know of such a demonstration, but the research value of such an attempt is high. The arrhythmic pattern of a cavernicole, when present, may suggest either a loss of periodism, or a lack or insufficiency of pattern in the original stock which presumably entered the subterranean habitat and escaped competition in a populous periodic environment. Colonization of caves has been progressing, in all probability, for a long period of time and at different rates, and is probably continuing at the present time. The examination of activity patterns should offer another tool by means of which cave biology may be advanced. Habit, at least for all save the chance cavernicole, can be eliminated in an activity pattern here, and since the constant environment is normal for the species, inherent patterns if they exist could be readily demonstrated, under constant laboratory conditions.

It seems therefore, that study of nocturnalism and its inter-relations is a comprehensive biological program, the working out of which may further illuminate such problems as organismal periodism, environmental adjustment, vision, protective coloration, sleep, social life, zoogeography, and phylogeny.

At the turn of the century the anatomy of cave animals was being studied; Howard and others were observing the flight of insects at night; Verrill was speculating on the protective value of color patterns at night; the effects of weather upon activity were being observed, and Dubois and Kiesel were studying internal physiological rhythms. Later, the rhythms in protozoan reproduction and their relation to experimental environmental conditions were being investigated by Woodruff and his students. It was some twenty years before Szymanski was to employ recording apparatus in a general study of activity; thirty years before either controlled ecological experiments on activity, or the study of nocturnal parts of communities, or exact experimental demonstration of internal rhythms as a function of definite physiological states. The problem is much more clearly seen now. Certain questions have been answered, new questions have arisen through the progress of research. These new questions must be tested externally by ecologists, internally by physiologists, and the inheritance of innate functions analyzed by geneticists before the full meaning of nocturnalism can be appreciated.

BIBLIOGRAPHY

- Allard, H. A. 1930. The chirping rates of the snowy tree cricket (*Oecanthus niveus*) as affected by external conditions. *Canad. Ent.* **62**: 131-142.
1931. The photoperiodism of the firefly *Photinus pyralis* Linn.; its relation to the evening twilight and other conditions. *Proc. Ent. Soc. Wash.* **33**: 49-58.
1931a. The locomotion of the slug. *Sci. Mo.* **41**: 559-563.
1935. The natural history of the box turtle. *Sci. Mo.* **45**: 325-339.

- Allee, W. C.** 1926. Measurement of environmental factors in the tropical rain-forest of Panama. *Ecology* **7**: 273-302.
 1926a. Distribution of animals in a tropical rain-forest with relation to environmental factors. *Ecology* **7**: 445-468.
- Allen, G. M.** 1899. Notes on reptiles and amphibians of Intervale, New Hampshire. *Proc. Boston Soc. Nat. Hist.* **29**: 63-75.
- Andrews, E. A.** 1911. Observations on Termites of Jamaica. *Jour. Anim. Behavior* **1**: 193-228.
- Annandale, N.** 1902. Notes on the habits of Malayan Phasmidae, and of a flowerlike beetle larva. *Proc. Royal Phys. Soc. Edinburgh* **14**: 439-444.
- Bachman, John.** 1837. Some remarks on the genus *Sorex*, with a monograph of the North American species. *Jour. Acad. Nat. Sci. Phila.* **7**: 362-402.
- Balduf, W. V.** 1935. The Bionomics of Entomophagous Coleoptera. 220 pp. New York.
- Barber, H. S.** 1905. Notes on *Phengodes* in the vicinity of Washington, D. C. *Proc. Ent. Soc. Wash.* **7**: 196-197.
- Barbour, Thomas.** 1923 (1926). Reptiles and Amphibians, their habits and adaptations. 125 pp. London.
- Barnes, P. T.** 1919. Fire-flies flashing in unison. *Sci.* **49**: 72.
- Bayliss, W. M.** 1924. Principles of General Physiology. 4th ed. 882 pp. New York.
- Beebe, William.** 1925. Jungle Days. 201 pp. New York.
 1928. Beneath Tropic Seas. 234 pp. New York.
 1932. Mojave. *Atlantic* **150**: 395-403.
- Behney, W. H.** 1936. Nocturnal explorations of the forest deer mouse. *Jour. Mammal.* **17**: 225-230.
- Beling, I.** 1929. Über das Zeitgedächtnis der Bienen. *Zeit. f. vergl. Physiol.* **9**: 259-338.
- Bennitt, Rudolf.** 1932a. Diurnal rhythm in the proximal pigment cells of the Crayfish retina. *Physiol. Zool.* **5**: 65-69.
- Benson, S. B.** 1933. Concealing coloration among some desert rodents of the Southwestern United States. *Col. Univ. Pub. Zool.* **40**: 1-70.
- Blatchley, W. S.** 1910. Coleoptera or beetles, exclusive of the Rhynchophora, known to occur in Indiana. 1386 pp. Indianapolis.
- Bodenheimer, F. S.** 1934. Studies on the ecology of Palestinean Coleoptera, II. *Bull. Soc. Roy. Ent. Egypte* **1-2**: 211-241.
- Boone, Lee.** 1930. Scientific results of the cruise of the yachts "Eagle" and "Ara," 1921-1928, William K. Vanderbilt, Commanding. Crustacea: Stomatopoda and Brachyura. *Bul. Vanderbilt Mar. Mus.* **11**: 222.
- Borell, Adrey E.** 1937. A new method of collecting Bats. *Jour. Mammal.* **18**: 478-480.
- Borradaile, L. A.** 1923. The animal and its environment. 399 pp. London.
- Boulenger, E. G.** 1938. World Natural History. 268 pp. New York.
- Bouvier, E. L.** 1922. The psychic life of insects. (English translation by L. O. Howard.) 377 pp. New York.
- Boycott, A. E.** 1934. The habitats of land Mollusca in Britain. *Jour. Ecology* **22**: 1-38.
- Bremer, H.** 1926. Ueber die tageszeitliche Konstanz im Schlüpftermin der Imagines einiger Insekten und ihre experimentelle Beeinflussbarkeit. *Zeitschr. wiss. Insektenbiol.* **21**: 209-216.
- Brower, A. E.** 1930. An experiment in marking moths and finding them again. *Ent. News* **41**: 10-15; 44-46.
- Brown, Ludvig Gustav.** 1937. Light in its relation to activity and oestrous rhythms in the albino rat. *Jour. Exp. Zool.* **75**: 375-388.
- Brown, Frank A., Jr.** 1937. Responses of the Large-mouth Black Bass to Colors. *Ill. Nat. Hist. Sur.* **21**: Art. 2, pp. 33-35.
- Buck, John Bonner.** 1935. Synchronous flashing of fireflies experimentally induced. *Sci.* **81**: 339-340.
 1937. Studies on the firefly. I. The effect of light and other agents on flashing in *Photinus pyralis*, with special reference of periodicity and diurnal rhythm. *Physiol. Zool.* **10**: 45-58.
 1937a. Studies on the firefly. II. The signal system and color vision in *Photinus pyralis*. *Physiol. Zool.* **10**: 412-419.

- Bugnion, E. and N. Popoff.** 1914. Les yeux des insectes nocturnes. *Arch. d'Anat. Microsc.* **16:** 261-304.
- Bünning, E.** 1932. Ueber die Erblichkeit der Tagesperiodizität bei den Phaseolus-Blättern. *Jahrb. wiss. Bot.* **77:** 283-320.
 1935. Zur Kenntnis der endonomen Tagesrhythmis bei Insekten und bei Pflanzen. *Deut. Bot. Gesell. Ber.* **53:** 594-623.
 1935a. Ueber die endonome Tagesrhythmis bei Insekten und bei Pflanzen. *Forsch. und Fortsch.* **11:** 400-401.
- Carpenter, G. D. H.** 1937. Mimicry, as viewed by Professor Shull. *Sci.* **85:** 346-359.
- Carpenter, J. Richard.** 1935. Fluctuations in Biotic Communities. I. Prairie-Forest ecotone of Central Illinois. *Ecology* **16:** 203-212.
- Chapman, R. N.** 1923. Observations on the life history of *Taphrocerus gracilis* Say. *Cornell Univ. Agri. Expt. Sta. Mem.* **67:** 13 pp.
 1926. Animal ecology with especial reference to insects. Minneapolis.
- Chapman, R. N., C. E. Mickel, J. R. Parker, G. E. Miller, and E. G. Kelley.** 1926. Studies in the ecology of sand dune insects. *Ecology* **7:** 416-427.
- Chu, Hung Pih and T. Sollmann.** 1925. The autonomic rhythm of the turtle heart, as influenced by various conditions. *Jour. Biochem.* **5:** 87-97.
 1925a. The autonomic rhythm of the turtle heart strips as influenced by the regional gradient and various conditions. II. The maximal tempo, the average rate and the index of inhibition. *Amer. Jour. Physiol.* **74:** 464-473.
 1925b. The autonomic rhythm of the turtle heart, as influenced by various conditions. IV. Types of inhibited rhythms and Luciani groups. *Amer. Jour. Physiol.* **74:** 478-488.
- Clark, Austin H.** 1914. Nocturnal Animals. *Jour. Wash. Acad. Sci.* **4:** 139-142.
- Clarke, G. L.** 1938. Seasonal changes in the intensity of submarine illumination off Woods Hole. *Ecology* **19:** 89-106.
- Clarke, G. L. and D. J. Zinn.** 1937. Seasonal production of zooplankton off Woods Hole with special reference to *Calanus finmarchicus*. *Biol. Bul.* **73:** 464-487.
- Clausen, R. G.** 1936. Oxygen consumption in fresh water fishes. *Ecology* **17:** 216-226.
- Clayden, A. W.** 1925. Cloud Studies. 2nd ed. 200 pp. New York.
- Clements, Frederic E.** 1938. Climatic cycles and human populations in the Great Plains. *Sci. Mo.*, September 193-211.
- Cobb, P. W.** 1923. Dark adaptation, with special reference to the problems of night flying. *U. S. Air Serv. Inform. Circ.*, Vol. 5, No. 403, pp. 14-26.
 1923a. A contribution to the study of dark adaptation. *U. S. Air Serv. Inform. Circ.*, Vol. 5, No. 403, pp. 26-29.
- Coker, R. E.** 1938. Life in the Sea. *Sci. Mo.* **46:** 299-322; 416-432.
- Colton, H. S.** 1933. Wood rats and ground squirrels in activity wheels. *Jour. Mamm.* **14:** 309-311.
- Comstock, J. H.** 1924. An Introduction to Entomology. 1044 pp. Ithaca.
- Conklin, E. S.** 1927. Principles of Abnormal Psychology. New York.
- Cook, W. C.** 1930. Some influences upon light trap catches. *Canad. Ent.* **62:** 95-98.
- Craig, Wallace.** 1917. On the ability of animals to keep time with an external rhythm. *Jour. Anim. Behavior* **7:** 444-448.
- Crawford, S. C.** 1934. The habits and characteristics of nocturnal animals. *Quart. Rev. Biol.* **9:** 201-214.
- Crawford, S. C. and E. P. Jones.** 1933. Field Notes on Some Amphibians from British Guiana. *Copeia*, No. **2:** 232-239.
- Cutright, P. R.** 1940. The great naturalists explore South America. New York.
- Davis, D. H. S.** 1933. "Rhythmic Activity in the short-tailed Vole, *Microtus*." *Jour. Anim. Ecol.* **2:** 232-239.
- Davis, J. J.** 1916. A progress report on White Grub investigations. *Jour. Econ. Ent.* **9:** 261-281.
- Demoll, R.** Über die Wanderung des Irispigments im Facettenauge. *Zool. Jahrb. Physiol.* **30:** 159-180.
 1917. Sinnesorgane der Arthropoden. Braunschweig: F. Vieweg & Sohn.

- Dennell, Ralph.** 1933. The habits and feeding mechanism of the Amphipod, *Haus-torius arenarius* Slabber. *Jour. Linn. Soc.* **38:** 363-368.
- Douglass, A. E.** 1928. Climatic cycles and Tree Growth; a study of the annual rings of trees in relation to climate and solar activity. *Carnegie Inst., Wash. Publ.* **289**, Vol. II.
- Dubois, R.** 1886. Contribution à l'étude de la production de la lumière par les êtres vivants. Les Elaterides lumineux. *Bull. Soc. Zool. France*, 2 Année.
- Durrant, E. P.** 1935. Influence of the female white rat on bodily activity of the male. *Proc. Am. Physiol. Soc.*, April, p. 37.
- Elton, Charles.** 1927. Animal Ecology. 207 pp. London.
- Elton, Charles, E. B. Ford, and J. R. Baker.** 1931. The health and parasites of a wild mouse population. *Proc. Zool. Soc. London*, 657-721.
- Enders, Robert K.** 1935. Mammalian life histories from Barro Colorado Island, Panama. *Bul. Mus. Comp. Zool. at Harvard Col.*, Vol. 78, No. 4, pp. 385-502.
- Esterly, C. O.** 1917. The occurrence of a rhythm in the geotropism of two species of plankton copepods when certain recurring external conditions are absent. *Univ. Cal. Pub. Zool.* **16:** 393-400.
1919. Reactions of various plankton animals with reference to their diurnal migrations. *Univ. Cal. Pub. Zool.* **19:** 1-83.
- Evans, L. T.** 1936. The development of the cochlea in the gecko (*Gymnodactylus kotschy*), with special reference to the cochlealagena ratio and its bearing on vocality and social behavior. *Anat. Rec.* **64:** 187-201.
- Fabre, J. H.** 1925 (1909). Souvenirs Entomologiques. Vol. X. "Le Ver Luisant," pp. 376-398. Paris.
- Fiebrig, K.** 1912. Schlafende Insekten. Jena. *Zeit f. Naturwiss.* **48:** 315-364.
- Flattely, F. W.** 1920. Rhythms in Nature. *Sci. Prog.* **14:** 418-426.
- Flint, W. P.** 1914. On the capture of living insects by the corn-field ant (*Lasius niger americanus*). *Jour. Econ. Ent.* **7:** 476-478.
- Floersheim, Cecil.** 1906. On some enemies of the diurnal Lepidoptera. *Ent. Rec. and Jour. Var.* **18:** 36-39.
- Folsom, J. W.** 1922. Entomology with special reference to its ecological aspects. Philadelphia.
- Forbes, S. A.** 1907. On the life history, habits, and economic relations of May-beetles. *Ill. Agri. Expt. Sta. Bul. No. 116:* 447-480.
1916. The influence of trees and crops on injury by white-grubs. *Ill. Agri. Expt. Sta. Bul. No. 187:* 261-265.
- Forbes, S. A. and R. E. Richardson.** 1908. The Fishes of Illinois. *Natural History Survey of Illinois*, Vol. III. Ichthyology.
- Franz, V.** 1911. Zur Frage der vertikalen Wanderungen der Planktoniere. *Archiv. f. Hydrobiol. u. Planktonkunde* **7:** 493-499.
1913. Über das Ortsgedächtnis bei den Tieren. *Monatsh. f. Naturw. Unterricht* **6:** 161-178.
- Freeman, G. L.** 1935. Diurnal Variations in Performance and Energy Expenditure. Northwestern Univ. Press.
- Frost, C. A.** 1915. Remarks on collecting at night, with a list of the Coleoptera taken. *Psyche* **22:** 207-211.
- Gamble, F. W. and F. W. Keeble.** 1900. *Hippolyte varians*: a study in color-change. *Quart. Jour. Micros. Sci.* **43:** 589-698.
- Garner, W. W. and H. A. Allard.** 1920. The effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Jour. Agri. Res.* **18:** 553-605.
- Garnett, R. T.** 1920. Notes on the habits of *Promecognathus laevissimus* Dejean. *Ent. News* **31:** 138.
- Gerhardt, Ulrich.** 1933. Zur Kopulation der Limaciden. I. *Zeitschr. Wiss. Biol. Abt. A. Zeitschr. Morph. u. Ökol. Tiere* **27:** 401-450.
1934. Zur Biologie der Kopulation der Limaciden. II. *Zeitschr. Wiss. Biol. Abt. A. Zeitschr. Morph. u. Ökol. Tiere* **28:** 229-258.

- Grabensberger, W.** 1933. Untersuchungen über das Zeitgedächtnis der Ameisen und Termiten. *Zeitschr. vergleich. Physiol.* **20**: 1-54.
 1934. Experimentelle Untersuchungen über das Zeitgedächtnis von Bienen und Wespen nach Verfütterung von Euchinin und Jodthyreoglobulin. *Zeitschr. vergleich. Physiol.* **20**: 338-342.
 1934a. Der Einfluss von Salicylsäure, gelbem Phosphor und weissem Arsenik auf das Zeitgedächtnis der Ameisen. *Zeitschr. vergleich. Physiol.* **20**: 501-510.
- Graenicher, S.** 1911. Bees of Northwestern Wisconsin. Milwaukee: *Bul. Pub. Mus.* **1**: 221-249.
- Gregory, Tappan.** 1936. Mammals of the Chicago Region. *Prog. Activities, Chi. Acad. Sci.* **7**: (Nos. 2 and 3), pp. 13-75.
- Griffin, D. T. and J. H. Welsh.** 1937. Activity rhythms in bats under constant external conditions. *Jour. Mammal.* **18**: 337-342.
- Hamilton, W. J., Jr.** 1937. Activity and home range of the field mouse, *Microtus p. pennsylvanicus* (Ord.). *Ecology* **18**: 255-263.
 1939. Activity of Brewer's Mole (*Parascalops breweri*). *Jour. Mammal.* **20**: 307-310.
- Hatfield, D. M.** 1935. A natural history study of *Microtus californicus*. *Jour. Mammal.* **16**: 261-271.
 1940. Activity and food consumption in *Microtus* and *Peromyscus*. *Jour. Mammal.* **21**: 29-36.
- Haviland, M. D.** 1926. Forest, Steppe and Tundra. Cambridge, Eng.
- Hayward, K. J.** 1930. The night flight of diurnal butterflies. *Ent. News* **41**: 258-261.
- Hemmingsen, Axel M. and Niels B. Krarup.** 1937. Rhythmic diurnal variations in the oestrous phenomena of the rat and their susceptibility to light and dark. *Biol. Meddel.* **13**: 1-61.
- Herrick, Francis Hobart.** 1909. Natural history of the American Lobster. *Bul. Bur. Fish.* **29**: 150-408.
- Hertwig, Richard.** 1912. A Manual of Zoology. (Translated by J. S. Kingsley), New York.
- Hess, W. N.** 1920. Notes on the biology of Lampyridae. *Biol. Bul.* **38**: 39-76.
- Hesse, R.** 1924. Tiergeographie. Jena.
- Higginbotham, A. C.** 1939. Studies on Amphibian Activity, I. Preliminary report on the rhythmic activity of *Bufo a. americanus* Holbrook and *Bufo fowleri* Hinckley. *Ecology* **20**: 58-70.
- Hilden, A. and K. S. Stenbäck.** 1916. Zur Kenntnis der Tagesschwankungen der Körpertemperatur bei den Vögeln. *Skand. Arch. f. Physiol.* **34**: 382-413.
- Hingston, R. W. G.** 1920. A naturalist in Himalaya. 300 pp. London.
- Hintze, A. L.** 1925. The Behavior of the Larvae of *Cotinis nitida* Burmeister. *Ann. Ent. Soc. Amer.* **18**: 31-34.
- Hoagland, Hudson.** 1935. Pacemakers in relation to Aspects of Behavior. *Expt. Biol. Monog. No. 1*. New York.
- Horstmann, Ernst.** 1935. Die tagesperiodischen Pigmentwanderungen im Facettenauge von Nachtschmetterlingen. *Biol. Centralbl.* **55**: 93-97.
- Houghton, C. O.** 1905. Coleoptera at light in Delaware. *Ent. News* **16**: 210-213.
- Howard, L. O.** 1899. Butterflies attracted to light at night. *Proc. Ent. Soc. Wash.* **4**: 333-334.
- Hudson, G. V.** 1891. The habits and life histories of the New Zealand glowworm. *Trans. and Proc. New Zealand Inst.* **23**: 43-47.
- Humboldt von, Alexander.** 1850. Views of Nature. 452 pp. London. (Transl. from the German by Otte and Bohn.)
- Humphreys, W. J.** 1920. Physics of the Air. 665 pp. Philadelphia.
- Huntington, E.** 1914. The climatic factor as illustrated in arid America. *Carnegie Inst. Wash. Publ.* 192, pp. 95-157.
- Imms, A. D.** 1924. A General Textbook of Entomology. New York.
- Isely, F. B.** 1938. Survival value of Acridian protective coloration. *Ecology* **19**: 376-389.

- Jennings, H. S.** 1906. Behavior of the Lower Organisms. 366 pp. New York.
- Johnson, M. S.** 1926. Activity and distribution of certain wild mice in relation to biotic communities. *Jour. Mammal.* **7:** 245-277.
 1939. Effect of continuous light on periodic spontaneous activity of white-footed mice. *Jour. Expt. Zool.* **82:** 315-328.
- Jores, A.** 1937. Die 24-Stunden-Periodik in der Biologie. *Tabulae Biologicae* **14:** 77-109. (Not read by author.)
- Juday, Chancey.** 1904. The diurnal movement of plankton Crustacea. *Trans. Wis. Acad. Sci. Arts and Letters* **14:** 534-568.
 1921. Observations on the Larvae of *Corethra punctipennis* Say. *Biol. Bul.* **40:** 271-286.
- Kahmann, Hermann.** 1930. Untersuchungen über die Linse, die Zonula ciliaris, Refraktion und Akkommodation von Säugetieren. *Zool. Jahrb. Abt. Allg. Zool. u. Physiol. Tiere* **48:** 509-588.
- Kalmus, H.** 1934. Ueber die Natur des Zeitgedächtnisses der Bienen. *Zeitschr. vergleich. Physiol.* **20:** 405-419.
 1935. Periodizität und Autochronie (Ideochronie) als zeitregelnde Eigenschaften der Organismen. *Biol. Gen.* **11:** 93-114.
- Keeble, Frederick.** 1910. Plant-Animals. A study in symbiosis. 163 pp. Cambridge, Eng.
- Kellerman, K. F.** 1926. A review of the discovery of photoperiodism. *Quar. Rev. Biol.* **1:** 87-94.
- Kendeigh, S. C. and S. P. Baldwin.** 1936. The mechanical recording of the nesting activity of birds. *Auk* **47:** 471-480.
- Kennedy, C. H.** 1928. Evolutionary level in relation to geographic seasonal and diurnal distribution of insects. *Ecology* **9:** 367-379.
- Kiesel, A.** 1894. Untersuchungen zur Physiologie des facettirten Auges. *Sitzungsber. kais. Akad. Wiss., Wien* **103:** 97-139.
- Kimball, H. H.** 1924. Variations in solar radiation intensities measured at the surface of the earth. *U. S. Mo. Weather Rev.* **52:** 527-529.
- Klauber, L. M.** 1939. Studies of Reptile Life in the Arid Southwest. Part I. *Bul. Zool. Soc. San Diego, No. 14*, pp. 1-64.
- Kleber, E.** 1935. Hat das Zeitgedächtnis der Bienen biologische Bedeutung? *Zeitschr. vergleich. Physiol.* **22:** 221-262.
- Kleitman, N.** 1923. Studies on the Physiology of Sleep. I. The effect of prolonged sleeplessness of man. *Amer. Jour. Physiol.* **66:** 67-92.
 1925. Studies on the Physiology of Sleep. III. The effect of muscular activity, rest and sleep on the urinary excretion of phosphorus. *Am. Jour. Physiol.* **74:** 225-237.
 1928. Studies on the Physiology of Sleep. V. Some experiments on puppies. *Amer. Jour. Physiol.* **84:** 386-395.
 1929. Sleep. *Physiological Reviews* **9:** 624-665.
 1933. Studies on the Physiology of Sleep. VIII. Diurnal Variation in Performance. *Am. Jour. Physiol.* **104:** 449-456.
 1939. Sleep and wakefulness. 664 pp. Chicago. (Not seen.)
- Kleitman, N. and Camille, N.** 1932. Studies on the Physiology of Sleep. VI. The behavior of decorticated dogs. *Amer. Jour. Physiol.* **100:** 474-480.
- Kleitman, N. and Doktorsky, A.** 1933. Studies on the Physiology of Sleep. VII. The effect of position of the body and of sleep on the rectal temperature of man. *Amer. Jour. Physiol.* **104:** 340-343.
- Kleitman, N., Titelbaum, S. and Hoffman, H.** 1937. The establishment of the diurnal temperature cycle. *Amer. Jour. Physiol.* **119:** 48-54.
- Laird, D. A. and Muller, C. G.** 1930. Sleep—Why we need it and how to get it. New York.
- Laurens, H. and Detwiler, S. R.** 1921. Studies on the retina. The retina of *Alligator mississippiensis* and its photomechanical changes. *Jour. Expt. Zool.* **32:** 207-234.
- LeConte, J. L. and Horn, G. H.** 1883. Classification of the Coleoptera of North America. *Smithsonian Miscl. Coll.*, No. 507: 1-567.

- Lee, Mary and Kleitman, N.** 1923. Studies on the Physiology of Sleep. II. Attempts to demonstrate functional changes in the nervous system during experimental insomnia. *Amer. Jour. Physiol.* **67**: 141-152.
- Lillie, F. R. and Just, E. E.** 1913. Breeding habits of the heteronereis form of *Nereis limbata* at Woods Hole, Mass. *Biol. Bul.* **24**: 147-169.
- Livingstone, Arthur A.** 1937. Ocean Depths and their Denizens. *The Australian Museum Magazine* **6**: 264-266.
- Loeb, J.** 1918. Forced Movements, Tropisms and Animal Conduct. 209 pp. Philadelphia.
- Lutz, Frank E.** 1931. Light as a factor in controlling the start of daily activity of a Wren and Stingless Bees. *Am. Mus. Novitates*, No. 468.
1932. Experiments with Orthoptera concerning diurnal rhythm. *American Museum Novitates*, No. 550, 1-24.
- Mallis, Arnold.** 1938. Army ants in California. *Sci. Mon.* **46**: 220-227.
- Mann, Ida.** 1931. Iris pattern in the Vertebrates. *Trans. Zool. Soc. London* **21**: 355-412.
- Mast, S. O.** 1911. Light and the behavior of organisms. 410 pp. New York.
1912. Behavior of fire-flies (*Photinus pyralis*) with special reference to the problem of orientation. *Jour. Anim. Behavior* **2**: 256-272.
- Matthew, W. D.** 1915. Climate and Evolution. *Am. N. Y. Acad. Sci.* **24**: 171-318.
- Mayer, A. G.** 1908. The Swarming of the Atlantic Palolo. *Carnegie Inst. Publ.* **102**.
- McClure, H. Elliott.** 1938. Insect Aerial Populations. *Ann. Ent. Soc. Amer.* **31**: 504-514.
- McCook, Henry C.** 1877. Mound-making ants of the Alleghenies, their architecture and habits. *Trans. Ent. Soc. Amer.* **6**: 253-296.
- McDermott, F. A.** 1910. A note on the light emission of some American Lampyridae. *Canad. Ent.* **42**: 357-363.
1911. Some further observations on the light-emission of American Lampyridae: the photogenic function as a mating adaptation in the Photinini. *Canad. Ent.* **43**: 399-406.
1912. Observations on the light emission of American Lampyridae. *Canad. Ent.* **44**: 309-311.
1914. Ecologic relation of photogenic function among insects. *Zeit. f. wiss. Insekten Biol.* **10**: 303-307.
1917. Observations on the light-emission of American Lampyridae: the photogenic function as a mating adaptation. *Canad. Ent.* **49**: 53-61.
- Menke, H.** 1911. Periodische Bewegungen und ihr Zusammenhang mit Licht und Stoffwechsel. *Arch. ges. Physiol.* **146**: 37-91.
- Moffat, C. B.** 1905. The duration of flight among Bats. *Irish Nat.* **14**: 97-108.
- Montgomery, T. H.** 1899. Observations on owls, with particular regard to their feeding habits. *Amer. Nat.* **33**: 563-572.
- Mosauer, Walter.** 1936. Temperature relations and activity rhythm of desert reptiles. *Bul. Ecol. Soc. Amer.* **17**, No. 2.
- Necheles, Heinrich.** 1927. Observations on the causes of night activity in some insects. *Chinese Jour. Physiol.* **1**: 143-155.
- Nelson, T. C.** 1921. Report of the Department of Biology. *N. J. Agri. Expt. Sta.*, 31st Ann. Report, pp. 319-349.
- Newcombe, C. L.** 1929. The crayfishes of West Virginia. *Ohio Jour. Sci.* **29**: 267-288.
- Nielsen, Erik Tetens.** 1938. Zur Oekologie der Laubheuschrecken. *Ent. Medd.* **20**: 121-164.
- Noble, G. K.** 1931. Biology of the Amphibia. New York.
- Noble, G. K. and H. T. Bradley.** 1933. The mating behavior of lizards; its bearing on the theory of sexual selection. *Ann. N. Y. Acad. Sci.* **35**: 25-100.
- O'Byrne, Harold.** 1930. The night flight of diurnal butterflies. *Ent. News* **41**: 20.
- Odum, E. P. and S. C. Kendeigh.** 1940. The cardio-vibrometer. *Ecology* **21**: 105-107.
- Oertel, Richard.** 1924. Biologische Studien über *Carabus granulatus* Linn. *Zool. Jahrb. Ab. Systematik, Geog. und Biol.* **48**: 299-366.

- Park, Orlando.** 1930. Seral and seasonal succession of Coleoptera in the Chicago Area, with observations on certain phases of hibernation and aggregation. *Ann. Ent. Soc. Amer.* **23:** 57-80.
1931. The measurement of daylight in the Chicago Area, and its ecological significance. *Ecol. Monog.* **1:** 189-230.
1935. Beetles associated with the mound-building ant *Formica ulkei* Emery. *Psyche* **42:** 216-231.
1935. Studies in Nocturnal Ecology, III. Recording apparatus and further analysis of activity rhythm. *Ecology* **16:** 152-163.
1937. Studies in Nocturnal Ecology, VI. Further analysis of activity in the beetle, *Passalus cornutus*, and description of audio-frequency recording apparatus. *Jour. Anim. Ecol.* **6:** 239-253.
1938. Studies in Nocturnal Ecology, VII. Preliminary observations on Panama Rain Forest Animals. *Ecology* **19:** 208-223.
1940. Concerning community symmetry. *Ecology* (to be published).
- 1940a. Quantitative estimation of rhythmicity. *Ohio Jour. Sci.* (in press).
- Park, Orlando, Albert Barden, and Eliot Williams.** 1940. Studies in Nocturnal Ecology, IX. Further analysis of activity of Panama Rain Forest Animals. *Ecology* **21:** 122-134.
- Park, Orlando, and J. G. Keller.** 1932. Studies in Nocturnal Ecology, II. Preliminary analysis of activity rhythm in nocturnal forest insects. *Ecology* **13:** 335-347.
- Park, Orlando, John A. Lockett, and Dwight J. Myers.** 1931. Studies in nocturnal ecology with special reference to climax forest. *Ecology* **12:** 709-727.
- Park, Orlando, T. W. Roberts, and Stanley Harris.** 1940. Studies in nocturnal ecology, VIII. Preliminary analysis of the activity of the cave crayfish, *Cambarus pellucidus*. *Am. Nat.* (in press).
- Park, Orlando and Sejba, Otto.** 1935. Studies in Nocturnal Ecology, IV. *Megalodacne heros*. *Ecology* **16:** 164-172.
- Park, Orlando and Strohecker, H. F.** 1936. Studies in Nocturnal Ecology, V. An experiment in conducting field classes at night. *Ohio Jour. Sci.* **36:** 46-54.
- Park, Orlando and L. P. Woods.** 1940. A modified Hemmingsen-Krarup mammalian activity recorder. *Proc. Soc. Exp. Biol. and Med.* **43:** 366-370.
- Parker, G. H.** 1932. On certain feeding habits of the sea-urchin, *Arbacia*. *Amer. Nat.* **66:** 95-96.
- Payne, Nellie M.** 1937. Death feigning in *Sitophilus granarius* L., the granary weevil. *Ent. News* **48:** 166-169.
- Pearse, A. S.** 1939. Animal Ecology. 2nd ed. 417 pp. New York.
- Pearson, T. G. et al.** 1936. Birds of America. 289 pp. New York.
- Peckham, G. W. and Peckham, Elizabeth G.** 1898. On the instincts and habits of the Solitary Wasps. *Wis. Geol. and Nat. Hist. Surv. Bul.* **2,** 1-245.
- Pennington, Margaret S.** 1935. Visual Cells of a Nocturnal Animal. *Trans. Ill. State Acad. Sci.* **28:** 259-260.
- Pieron, Henri.** 1913. Le Problème Physiologique du Sommeil. Paris.
- Pike, Nicolas.** 1886. Some notes on the life-history of the common newt. *Amer. Nat.* **20:** 17-25.
- Pincus, Gregory.** 1931. On the temperature characteristics for frequency of breathing movements in inbred strains of mice and in their hybrid offspring. *Jour. Gen. Physiol.* **14:** 421-443.
- Polimanti, O.** 1911. Activité et repos chez les animaux marins. *Bull. Inst. Gen. Psych.* **11:** 125-163.
- Pope, Clifford H.** 1937. Snakes Alive. New York.
- Pulling, H. E.** 1919. Sunlight and its Measurement. *Plant World* **22:** 151-171; 187-204.
- Ratcliffe, Francis.** 1932. Notes on the Fruit Bats (*Pteropus* sp.) of Australia. *Jour. Anim. Ecol.* **1:** 32-58.

- Rau, Phil.** 1932. Rhythmic periodicity and synchronous flashing in the firefly, *Photinus pyralis*, with notes on *Photuris pennsylvanicus*. *Ecology* **13**: 7-12.
 1935. Jungle Bees and Wasps of Barro Colorado Island, Panama. Kirkwood, Missouri.
 1938. Additional observations on the sleep of Insects. *Ann. Ent. Soc. Amer.* **31**: 540-557.
- Rau, P. and N. Rau.** 1916. The sleep of insects: an ecological study. *Ann. Ent. Soc. Amer.* **9**: 227-274.
 1929. The sex attraction and rhythmic periodicity in giant saturniid moths. *Trans. Acad. Sci. St. Louis* **26**: 81-221.
- Reed, C. I. and N. Kleitman.** 1925. Studies on the Physiology of Sleep, IV. The effect of sleep on respiration. *Amer. Jour. Physiol.* **75**: 600-608.
- Regan, Charles Tate.** 1937. Natural History. New York.
- Reynolds, W. E.** 1920. The Cycles and Super-cycles of Nature. *Science Progress* **15**: 250-264.
- Richter, C. P.** 1922. Behavioristic study of the activity of the rat. *Comp. Psychol. Monog.* **1** (No. 2).
 1927. Animal behavior and internal drives. *Quar. Rev. Biol.* **2**: 307-343.
- Richter, C. P. and G. H. Wang.** 1926. New apparatus for measuring the spontaneous motility of animals. *Jour. of Lab. and Clin. Med.* **12**: 289-292.
- Riley, C. V., A. S. Packard, Jr., and Cyrus Thomas.** 1878. First Annual Report of the U. S. Ent. Comm. for 1877 on the Rocky Mountain Locust.
- Rivas, Damaso.** 1920. Human Parasitology. 715 pp. Philadelphia.
- Roberts, T. W.** 1936. Preliminary analysis of activity of the crayfish, *Cambarus virilis*. *Bul. Ecol. Soc. Amer.* **17**: 27.
- Robertson, A. G.** 1939. The nocturnal activity of crane-flies. *Jour. Animal Ecol.* **8**: 300-322.
- Rockwood, L. P.** 1925. On night flying and attraction to light in Acrididae and the relation of meteorological conditions thereto. *Pan-Pacific Ent.* **2**: 36-38.
- Rogers, J. Speed.** 1933. The Ecological distribution of the Crane-flies of Northern Florida. *Ecol. Monog.* **3**: 1-75.
- Roosevelt, Theodore.** 1910. African Game Trails. 583 pp. New York.
- Rowan, W.** 1926. On photoperiodism, reproductive periodicity, and annual migration of birds and certain fishes. *Proc. Boston Soc. Nat. Hist.* **38**: 147-189.
- Sanders, J. G. and S. B. Fracker.** 1916. Lachnostenra records for Wisconsin. *Jour. Econ. Ent.* **9**: 253-261.
- Schick, R.** 1932. Photoperiodismus. *Der Züchter* **4**: 122-135.
- Schleip, W.** 1910. Der Farbenwechsel von *Dixippus morosus*. *Zool. Jahrb.* **30**: 45-132.
- Schmidt, K. P.** 1934. Homes and Habits of Wild Animals. 64 pp. Chicago.
- Schmidt, P.** 1919. Smithsonian Report (1917) : 501-505.
- Schneirla, T. C.** 1938. A theory of army-ant behavior based upon the analysis of activities in a representative species. *Jour. Comp. Psychol.* **25**: 51-90.
- Schour, Isaac and M. M. Hoffman.** 1935. Experimental demonstration of daily apposition of 16-micra of enamel and dentin in growing mammalian teeth. *Jour. Dental Res.* **15** (3 and 4).
 1935. Demonstration of 16-micra rhythm in normal stratification of enamel and dentin in man and other mammals. *Jour. Dental Res.* **15** (3 and 4).
- Schour, Isaac and S. R. Steadman.** 1935. The growth pattern and daily rhythm of the incisor of the rat. *Anat. Rec.* **63**: 325-333.
- Schwarz, E. A.** 1893. (Discussion), *Proc. Ent. Soc. Wash.* **3**: 78.
- Scott, Hugh.** 1932. Swarming of a Harpaline beetle. *Ent. Mo. Mag.* **68**: 13-14.
- Scott, J. W.** 1909. Some Egg-Laying Habits of *Amphitrite ornata* Verrill. *Biol. Bul.* **17**: 27-340.
- Seeman, Ernest.** 1928. The Working Hours of Ants. *Psyche* **35**: 114-118.
- Seton, E. T.** 1909. Life-histories of Northern Animals. New York.
- Sharp, David.** 1918. Insecta. Cambridge Natural History. Vol. 6. New York.

- Shelford, V. E.** 1913. Animal communities in temperate America, as illustrated in the Chicago region. *Geog. Soc. Chicago Bul.* **5**.
1914. Modification of behavior of land animals by contact with air of high evaporating power. *Jour. Anim. Behavior* **4**: 31-49.
1914. The importance of measure of evaporation in economic studies of insects. *Jour. Econ. Ent.* **7**: 229-233.
1918. Chapter II ("Conditions of Existence") H. B. Ward and G. C. Whipple, Fresh-Water Biology. New York.
- Sherman, A. R.** 1929. Summer outings of bats during fourteen seasons. *Jour. Mammal.* **10**: 319-326.
- Shull, A. F.** 1907. Habits of the short-tailed shrew, *Blarina brevicauda* (Say). *Amer. Nat.* **41**: 495-522.
1936. Evolution. 312 pp. New York.
1937. The needs of the mimicry theory. *Sci.* **85**: 496-498.
- Simpson, S. and J. J. Galbraith.** 1905. An investigation into the diurnal variation of the body temperature of nocturnal and other birds, and a few mammals. *Jour. Physiol.* **33**: 225-238.
- Slome, D. and L. T. Hogben.** 1929. The time factor in the chromatic responses of *Xenopus laevis*. *Trans. Roy. Soc. South Africa* **17**: 141-150.
- Slonaker, J. R.** 1908. Description of an apparatus for recording the activity of small mammals. *Anat. Rec.* **2**: No. 3.
1912. The normal activity of the albino rat from birth to natural death, its rate of growth and the duration of life. *Jour. Anim. Behavior* **2**: 20-42.
- Snell, G. D. et al.** 1940. The relation of mating, ovulation and the oestrus smear in the house mouse to time of day. *Anat. Rec.* **76**: No. 1.
- Spencer, D. A.** 1939. Electrical recording of the activities of small mammals. *Jour. Mammal.* **20**: 479-485.
- Spencer, Warren P.** 1929. An Ichthyometer. *Sci.* **70**: 557-558.
1939. Diurnal activity rhythms in fresh-water fishes. *Ohio Jour. Sci.* **39**: 119-133.
- Stanley, W. S.** 1932. Observations on the flight of Noctuid Moths. *Ann. Ent. Soc. Amer.* **25**: 366-368.
- Stephenson, J.** 1930. The Oligochaeta. 978 pp. Oxford.
- Stewart, C. C.** 1898. Variations in daily activity, with description of recording methods. *Am. Jour. Physiol.* **1**: 40-56.
- Stier, T. J. B.** 1933. Diurnal changes in activities and geotropism in *Thyone briareus*. *Biol. Bul.* **64(3)**: 326-332.
- Stülpken, K. and H. Brüll.** 1938. Vom Nestleben der Nachtschwalbe (*Caprimulgus e. europaeus*). *Jour. f. Ornith.* **86**: 59-73.
- Sumner, F. B.** 1934. Does "protective coloration" protect? Results of some experiments with fishes and birds. *Proc. Nat. Acad. Sci.* **20**: 559-564.
1935. Evidence for the protective value of changeable coloration in fishes. *Amer. Nat.* **49**: 245-266.
- 1935a. Studies of protective color change, III. Experiments with fishes both as predators and prey. *Proc. Nat. Acad. Sci.* **21**: 345-353.
- Szymanski, J. S.** 1914. Eine Methode zur Untersuchung der Ruhe- und Aktivitätsperioden bei Tieren. *Arch. ges. Physiol.* **158**: 343-385.
1918. Abhandlungen zum Aufbau der Lehre von den Handlungen der Tiere. *Pflüger's Archiv für die ges. Physiol. des Menschen u. der Tiere* **170**: 1-244.
- 1918a. Die Verteilung der Ruhe- und Aktivitätsperioden bei weissen Ratten und Tanzmäusen. *Pflüger's Arch.* **171**: 324-347.
- 1918b. Versuche über Aktivität und Ruhe bei Säuglingen. *Pflüger's Arch.* **172**: 424-429.
- 1918c. Die Verteilung von Ruhe- und Aktivitätsperioden bei einigen Tierarten. *Pflüger's Arch.* **172**: 430-448.
1922. Aktivität und Ruhe bei Menschen. *Zeitschr. f. angewandte Psychol.* **20**: 192-222.
- Thomson, J. A.** 1911. The Biology of the Seasons. 384 pp. New York.

- Treadwell, A. L.** 1915. Internal Factors Producing the Swarming of the Atlantic Palolo. *Sci.* **41:** 438.
- Turner, Clarence L.** 1915. Breeding habits of *Centrophilus latens*, the Camel Cricket. *Bull. Wis. Nat. Hist. Soc.* **13:** 32-41.
1926. The Crayfishes of Ohio. *Ohio Biol. Surv. Bul.* **13**, Vol. 3.
- Van Cleave, H. J.** 1931. Some of the biological effects of drought. *Sci. Mo.* **39:** 301-307.
- Vanderplank, F. L.** 1934. The effect of infra-red waves on owls (*Strix aluco*). *Proc. Zool. Soc.*, London, Part III, pp. 505-507.
- Verrill, A. E.** 1897. Nocturnal protective coloration of Mammals, Birds, Fishes, Insects, etc. *Amer. Nat.* **31:** 99-103.
- Visher, S. S.** 1923. Tropical Climates from an Ecological Viewpoint. *Ecology* **4:** 1-10.
- Walls, Gordon L.** 1931. The occurrence of colored lenses in the eyes of snakes and squirrels, and their probable significance. *Copeia*, No. **3:** 125-127.
1934. The Reptilian Retina. *Am. Jour. Ophthalmology* **17:** 892-915.
1934a. The Significance of the Reptilian "Spectacle." *Am. Jour. Ophthalmology* **17:** 1045-1047.
1938. "It's done with mirrors." *Chicago Nat.* **1:** 103-110.
- Walls, G. L. and H. D. Judd.** 1933. The intra-ocular colour-filters of Vertebrates. *Brit. Jour. Ophthalmol.* **17:** 641-675; 705-725.
- Walton, W. R.** 1928. Earthworms as pests and otherwise. *U. S. Dept. Agri. Farmers' Bul.*, No. 1569, 1-14 pp.
- Wanless, Harold R.** 1938. Geological Records of a Rhythmic Nature. *Trans. Ill. Acad. Sci.* **31:** 7-14.
- Ward, H. B. and G. C. Whipple.** 1918. Fresh Water Biology. New York.
- Warren, D. C. and H. M. Scott.** 1936. Influence of Light on Ovulation in the Fowl. *Jour. Expt. Zool.* **74:** 37.
- Warren, E. R.** 1910. The mammals of Colorado. New York, 1-300.
- Watson, J. R.** 1916. Life history of *Anticarsia gemmatalis*. *Jour. Econ. Ent.* **9:** 521-528.
- Welch, Paul S.** 1935. Limnology. New York.
- Welsh, J. H.** 1930. Diurnal rhythm of the distal pigment cells in the eyes of certain crustaceans. *Proc. Nat. Acad. Sci.* **16:** 386-395.
1930a. The mechanics of migration of the distal pigment cells in the eyes of *Palaeomonetes*. *Jour. Expt. Zool.* **56:** 459-494.
1932. The nature and movement of the reflecting pigment in the eyes of Crustaceans. *Jour. Expt. Zool.* **62:** 173-183.
1935. Further evidence of a diurnal rhythm in the movement of pigment cells in eyes of Crustaceans. *Biol. Bul.* **68:** 247-253.
1936. Diurnal movements of the eye pigments of *Anchistiooides*. *Biol. Bul.* **70:** 217-227.
1938. Diurnal Rhythms. *Quart. Rev. Biol.* **13:** 123-139.
- Welsh, J. H., F. A. Chase, and R. F. Nunnemacher.** 1937. The diurnal migration of deep-water animals. *Biol. Bul.* **73:** 185-196.
- Welsh, J. H. and C. M. Osborn.** 1937. Diurnal changes in the retina of the catfish, *Ameiurus nebulosus*. *Jour. Comp. Neurol.* **66:** 349-359.
- Werner, F.** 1911. Über die Schlafstellungen der Fische. *Biol. Cent.* **31:** 41-44.
- Wetmore, Alexander.** 1921. A study of the body temperature of birds. *Smithsonian Miscel. Coll.* **72:** 1-52.
- Wheeler, J. F. G. and F. A. Brown.** 1936. The periodic swarming of *Anchistiooides antiguensis* (Schmitt). *Jour. Linn. Soc.* **39:** 413-429.
- Wheeler, W. M.** 1930. Demons of the Dust.
- Willey, A.** 1904. Crows and Flying Foxes at Barberyn. *Spolia Zeylan* **2:** 50-51.
- Williams, C. B. and P. S. Milne.** A mechanical insect trap. *Bul. Ent. Res.* **26:** 543-551.
- Williams, F. X.** 1917. Life history of North American Lampyridae. *Jour. New York Ent. Soc.* **25:** 11-33.

- Wolf, E.** 1930. Die Aktivität der japanischen Tanzmaus und ihre rhythmische Verteilung. *Zeit. f. vergl. Physiol.* **11**: 321-344.
- Woollard, H. H.** 1927. The differentiation of the retina in Primates. *Proc. Zool. Soc. London* **1**: 1-17.
- Young, J. Z.** 1935. The photoreceptors of lampreys. II. The functions of the pineal complex. *Jour. Expt. Biol.* **12**: 254-270.
- Zolk, K.** 1932. Poldnälkjate rannakud ja seda majustavad tegurid. *Mitt. Versuch. angewan. Entom. Univ. Tartu.* **20**: 3-12.