REPRODUCTIVE AND FAT CYCLES IN CARIBBEAN ANOLIS LIZARDS

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PAUL LICHT and GEORGE C. GORMAN

(A contribution from the Department of Zoology and the Museum of Vertebrate Zoology
of the University of California, Berkeley, California)

INTRODUCTION

A WEALTH of data has been accumulated over the past few decades on annual reproductive activities in temperate-zone lizards. Sufficient species have been studied to permit broad generalizations regarding variations in reproductive patterns of temperate species (e.g., St. Girons, 1963; Mayhew, 1968; Licht et al., 1969) and considerable progress has been made toward understanding the mechanisms underlying these cycles. However, understanding of saurian reproductive strategies is still limited by a paucity of phenological data for tropical lizards. Although the tropical lizards represent the richest part of the lizard fauna, comparative data for these are insufficient to allow any conclusions regarding the nature of variations in annual reproductivity or the factors that might be responsible for such variations where they exist. The present investigation represents a preliminary attempt to gain such comparative information on these important aspects of the ecology of the widely distributed neotropical lizard genus, *Anolis*.

Anolis is a suitable genus for comparative reproductive studies. There are numerous species (approximately 250) and the systematics of a large proportion of these are well understood. Many are very abundant, hence easily collected. In addition, perhaps more is known about the reproductive cycles of one member of this genus, *A. carolinensis,* both in nature and in the laboratory, than of any other lizard.

Anolis is widely distributed in Mexico, all of Central America, the northern half of South America, on virtually all Caribbean islands, and on the continental United States. The genus is divided into two major groups, α and β (Etheridge, 1960), based upon osteological differences, and each of these groups is divided into species series. We have chosen seven species from various islands in the West Indies for intensive study.

The species and localities included permit numerous comparisons to be made. (1) *Anolis grahami,* a native of Jamaica, has been successfully introduced onto Bermuda to the north. Populations from both localities have been sampled, to allow comparison of the same species under rather different environmental conditions. (2) *Anolis conspersus* is a close relative of *grahami* on an adjacent island. (3) *Anolis lineatopus* is sympatric with *A. grahami* in Kingston, Jamaica; thus sympatric congeners can be compared. (4) *Anolis sagrei* is found on the western half of Jamaica, and is compared with the two preceding species from a different part of that island, as well as with a population of *sagrei* that lives in Florida. (5) *Anolis richardi griseus* and *A. trinitatis* are endemic to the island of St. Vincent.

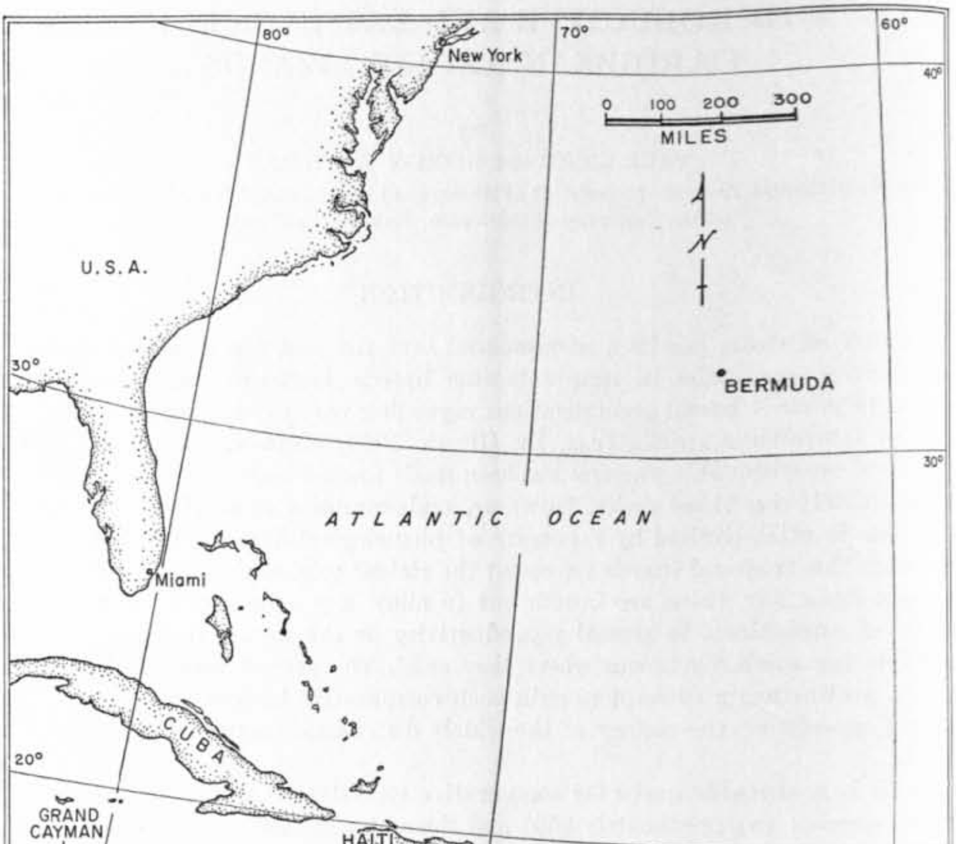

Fig. 1. Map of the Caribbean region showing collecting sites of the areas involved in this study.

Again we can compare sympatric congeners, and can compare these lizards with relatives on more northerly islands that experience greater variation in photoperiod and different rainfall patterns. (6) *Anolis cybotes*, an endemic of Hispaniola, is at the same latitude as Jamaica but experiences different rainfall patterns and thus provides an additional source of comparison. Figure 1 shows the geographical relations among the various habitats included in this study.

The taxonomic breakdown of the species studied is as follows:

GROUP	SERIES	SPECIES
Alpha	*latifrons*	*A. trinitatis, A. richardi*
Alpha	*cristatellus*	*A. cybotes*
Beta	*grahami*	*A. grahami, A. lineatopus, A. conspersus*
Beta	*sagrei*	*A. sagrei*

MATERIALS AND METHODS

COLLECTION, PRESERVATION, AND AUTOPSY OF SPECIMENS

Samples of most species were collected at approximately monthly intervals over a one- to two-year period with the assistance of individuals stationed in the various localities. Jamaican collections of *A. grahami, A. lineatopus,* and *A. sagrei* were supervised by Mr. Ethon Lowe; St. Vincent collections of *A. trinitatis* and *A. richardi* by Mr. Michael DeFreitas; Bermuda collections of *A. grahami* by Mr. David Wingate; Florida collections of *A. sagrei* by Mr. Phil Baker; and Grand Cayman collections of *A. conspersus* by Mr. John Gray, Jr. Freshly collected specimens of *A. cybotes* from Port-au-Prince, Haiti in 1968–1969 were obtained through Georges René; Mr. J. Borno supplied a few collections in 1966. Data for other Hispaniola localities were obtained from collections in the Museum of Comparative Zoology at Harvard University through the courtesy of Dr. E. E. Williams. Dr. J. Wright of the Los Angeles County Museum and Dr. H. Campbell of the Florida State Museum, University of Florida, provided numerous specimens of *A. sagrei* from southern Florida and adjacent islands.

Most specimens were fixed in 10 percent buffered formalin shortly after collection; a few of the *A. cybotes* collected in 1966 were obtained alive about a week after collection, and the *A. sagrei* from Florida were preserved in Bouin's fixative. Museum specimens of *cybotes* and *sagrei* were stored in alcohol and the method of preservation was unknown. Upon receipt in the laboratory, formalin fixed specimens were transferred from 10 percent to 4 percent formalin for at least a day and then rinsed in running tap water for a few hours before autopsy. Each individual was measured (snout-to-vent length) and examined for nutritional and reproductive condition as indicated below. Testis weight was found to vary with the method of fixation: Formalin caused an increase of about 16 percent and Bouin's solution caused a reduction of about 15 percent of fresh weight. Thus, testis weights cannot be compared among all species but weights should be consistent for species obtained from each collector.

FAT STORAGE

The weights of the paired abdominal fat bodies were taken as an index of energy balance; i.e., whether or not fat storage was occurring. Studies on *Anolis caro-*

linensis by Dessauer (1955*a*) have shown that the seasonal variations in fat body size generally reflect changes in total body lipids, the fat bodies accounting for about half of the increase in body lipid with the remainder being divided between the liver and carcass (Licht and Jones, 1967). We initially measured liver weight, but variability due to fixation made these weights too unreliable and this measurement was discontinued. In general, monthly mean hepatic weights tended to vary in parallel with the weights of the abdominal fat bodies. In most samples, we found that the weight of the fat bodies was independent of body size (length) within the range of sizes used (see below). Therefore fat body weight is expressed as an absolute value.

REPRODUCTIVE STATUS OF MALES

The reproductive condition of the males was judged by the weight of the testis and by the histological appearance of the germinal epithelium and accessory sexual structures (epididymis and sexual segment of the kidney). Autopsy procedures were the same as those described in previous studies on *Anolis* in this laboratory (see Licht, 1967*a*). The left testis was weighed to the nearest 0.1 mg. The right testis, epididymis, and kidney were embedded in Paraplast, sectioned at 8μ and stained with Ehrlich's hematoxylin and eosin for histological examination. In all species, the two testes were found to be similar in histological appearance and weight; the few specimens showing gross variation between right and left testis weights were not used. Variations in testis weights between monthly samples are considered statistically significant if the means differed at the 5 percent level using the Mann-Whitney U or Student *t* test. To facilitate visual comparisons among monthly samples we have employed a graphical presentation of data including means, standard errors, and 95 percent confidence limits about the mean ($t_{.05} \cdot \mathrm{SE}$). In most cases nonoverlap between the 95 percent limits and means of two samples indicates a statistically significant difference; for a more detailed discussion of this method see Simpson et al. (1960:351).

The spermatogenic and interstitial cell activity of the testes were assessed qualitatively according to the seven categories previously described for *A. carolinensis* by Licht (1967*a*) (table 1). The renal sex segment was examined qualitatively to assess the degree of development; the hypertrophy of the renal sex segment generally requires a higher level of androgens than does the enlargement of the epididymis (Licht and Pearson, 1969*a*). It is important to emphasize the independence that may exist between testis size and spermatogenic activity. Endocrinological studies in *A. carolinensis* have shown that when gonadotropin levels are relatively low, the testis may be very small but it still shows all stages of spermatogenesis and androgen production (stage 6) while a large testis may be only partly developed from these standpoints (see Licht and Pearson, 1969*a,b*). In general, we assume that a gross decline in average testis weight, especially when accompanied by reduced spermatogenic stages in at least part of the population, indicates a reduction in the rate of sperm production. The significance of variations in testis size are considered more fully in the discussion.

The influence of body size on the indices of testicular activity presented a greater problem than did the size-gonadal relation in females. It was relatively easy to ascertain the size of sexual maturity for males by the appearance of sperm in the testes and epididymis, and above this limit, the spermatogenic staging of each species is independent of body size. However, among sexually mature males, testis weight correlated significantly with body size. In many cases, the slope of the regression of testis weight on body length was close to 0.5, but the value for this regression varied interspecifically and from month to month within each species. The effect of body size on testis weight was greatest when the testes were maximal in size since the testes regressed to approximately the same minimal weight in mature individuals of all sizes. Thus, a simple gonosomatic index (e.g., ratio of testis weight to body length) proved inadequate for correcting for variations related to body size. Rather than attempt a more complex transformation of the data, we chose to minimize the influence of body size on testis weights by limiting analysis to a relatively narrow range of body sizes which included only large adult males. Furthermore, attempts were made to insure that the mean and variance in body size were approximately the same for all monthly samples of each species, so that variations in monthly mean testis weights cannot be accounted for simply by inequalities in the size of the animals in different samples (table 2).

TABLE 1

CLASSIFICATION OF SPERMATOGENIC STAGES IN ADULT MALE ANOLIS[1]

Stage	Histological condition	
	Testis seminiferous tubules	Epididymis[2]
1	Involuted with only resting spermatogonia and Sertoli cells	Atrophic and empty
2	Beginning of spermatogenesis, spermatogonial multiplication and primary spermatocytes	Atrophic and empty
3	Secondary spermatocytes and early spermatids abundant	Atrophic and empty
4	Transforming spermatids with a few spermatozoa	Atrophic and empty
5	Marks the beginning of androgen secretion; spermatozoa becoming more numerous	Hypertrophied but still no sperm
6	All stages of spermatogenesis abundant; spermiation has occurred[3]	Hypertrophied and sperm filled[3]
7	Regression of epithelium; spermatozoa may still be abundant but spermatids and spermatocytes are scarce	Grades from hypertrophic to atrophic

[1] Based on the classification of spermatogenesis proposed for *Anolis carolinensis* by Licht (1967*a*: table 1).

[2] Hypertrophy is indicated by an average epithelial height over 15μ with conspicuous secretory activity in the lumen.

[3] Sexual segment of kidney usually becomes enlarged and secretory (hypertrophied) at this time.

REPRODUCTIVE STATUS OF FEMALES

The genus *Anolis* has a relatively unusual type of egg production among lizards. Only one follicle matures and ovulates at a time in each ovary and there is typically an alternation between the two ovaries. A second ovulation never occurs from an ovary before the previous egg is laid. Consequently, only one egg appears

TABLE 2

SUMMARY OF BODY SIZES OF ANOLIS USED IN REPRODUCTIVE ANALYSES[1]

Source	Species	Length of males (mm)				Lengths of females (mm)			
		Sexual maturity[2]	Minimum used	Maximum observed	Monthly mean[4]	Sexual maturity[3]	Minimum used	Maximum observed	Monthly mean[4]
St. Vincent	*richardi*	63	67	123	93.2 (88–105)	60	63	88	76.0 (72.5–79.7)
	trinitatis	45	55	71	63.3 (61–64.5)	41	43	50	46.1 (43–47.6)
Jamaica	*grahami*	49	55	73	63.9 (62–67)	38	43	51	46.0 (44.3–47.3)
	lineatopus	45	55	71	62.5 (61.5–64.3)	41	43	51	45.7 (43.6–48.3)
	sagrei	35	42	52	46.5 (43–48)	34	35	41	37.9 (35–40)
Haiti	*cybotes*	52	55	73	66.7 (64–68.4)	45	46	56	50.0 (48–52.6)
Grand Cayman	*conspersus*	<50	55	73	63.5 (62–65.5)	38	40	47	41.4 (40–42)
Florida	*sagrei*	44	48	63	55.5 (50–59)	38	39	47	42.0 (40–44)
Bermuda	*grahami*	49	55	75	63.9 (62–66.9)	42	43	50	45.7 (43–48)

[1] Body sizes are presented as snout to vent lengths of preserved specimens.

[2] Smallest male in which testis was at stage 6. These values are not intended as accurate limits since in many cases we did not examine a wide range of small animals.

[3] Smallest female containing an oviducal egg. Not intended as accurately defining lower limits of maturity (see note 2).

[4] Values show average mean and range of means (in parentheses).

at a time in each oviduct and if an oviducal egg is present in each oviduct, one is always older. Only a single egg, presumably the oldest, is laid at a time (i.e., clutch size is one). Some of the details of this pattern of egg production are described by Hamlett (1952) for *Anolis carolinensis* and our data suggest that a similar phenomenon exists for all the species studied here.

Measurements were made of the diameter of the largest follicle in each ovary, and the presence of oviducal eggs was noted. Ovarian follicles of 3 mm or more were typically yolky, and these are considered to be in the process of maturation; ovulation occurs at about 8 mm. Females were placed into four classes:

I. No oviducal eggs, and follicles undeveloped (clear and less than 3 mm in diameter)

II. At least one ovarian follicle developing

III. One oviducal egg

IV. Two oviducal eggs (one in each oviduct)

To facilitate discussion of data, females in class I are designated as "nonreproductive" and those in the other three classes are considered "reproductive."

Females with oviducal eggs are referred to as "ovigerous." We recognize several limitations in the use of such data for judging reproductive rates and these will be considered in more detail in the Discussion.

To facilitate analysis of annual reproductive patterns it was necessary to limit analysis to females known to be reproductively mature. A preliminary determination of the size at sexual maturity for each species was based on the smallest ovigerous female collected. It is recognized that some error might result from using this lower limit for judging sexual maturity, since it is likely that some variation in the exact size at sexual maturity might occur. To minimize such errors only females about 2 mm above this minimal size were used. Also, such errors should be small since the vast majority of the females used were well above this minimal size. Furthermore, care was taken to insure that the distribution of sizes of females in monthly samples was not biased toward large or small individuals (data are summarized in table 2).

Climatological Influences on Reproduction

In a preliminary attempt to evaluate potential environmental influences on reproductive activity, correlations between reproductive activities and various climatic factors were examined. Climatological data were obtained from local meteorological stations for the period during which collections were made. These data may not all be equally reliable. Data for St. Vincent were obtained from the Department of Agriculture in Kingstown, as tabulated by Mr. M. DeFreitas. Jamaican data were supplied by the Meteorological Service at Palisadoes Airport, Kingston. Haitian data were supplied by the Observatoire Meteorologique Seminaire-College St. Martiae in Port-au-Prince. Data for Grand Cayman were provided by the United States Department of Commerce Weather Bureau. Florida data were obtained from the United States Department of Commerce's *Local Climatological Data.* Bermuda data were taken from the Department of Agriculture and Fisheries Botanical Gardens in Paget.

In particular, attention was focused on the three most readily available types of climatological data: photoperiod, rainfall, and temperature. Daily photoperiods (or day lengths) were determined from standard tables of sunrise and sunset for the latitudes corresponding to the various collecting sites (List, 1966). Studies on one lizard (*Anolis carolinensis*) indicate that the additional low levels of illumination during twilight are probably not important for photo-sexual responses (Licht, 1969*a*). Since most anoles sleep in relatively open sites, they are probably exposed to almost the full photoperiod.

RESULTS OF STUDIES ON ST. VINCENT

Geography, Climate, and Species

St. Vincent is a volcanic island of about 150 square miles that lies in the southern portion of the Lesser Antillean chain, at 13° 15′ north latitude and 61° 15′ west longitude. The specimens that we studied were collected on the coast, in and around Kingstown, the capital city. (Most of the lizards were collected in the Botanic Gardens.) Very little seasonal temperature change is evident in Kingstown, but photoperiod and rainfall show distinct seasonal cycles (fig. 2). Day length varies by about 1.5 hours, ranging from 11 hours, 25 minutes to 12 hours, 55 minutes. Average monthly minimum and maximum air temperatures show virtually no seasonal change, and the difference between these two levels (i.e., maximal diurnal variation) is only about 7° to 8° C. Rainfall is variable, with a low of 50 mm per month to a high of 350 mm, but the period of low rainfall (dry season) is very short when compared to the other Caribbean islands studied. In 1968, January and February were relatively dry (around 50 mm), but rainfall

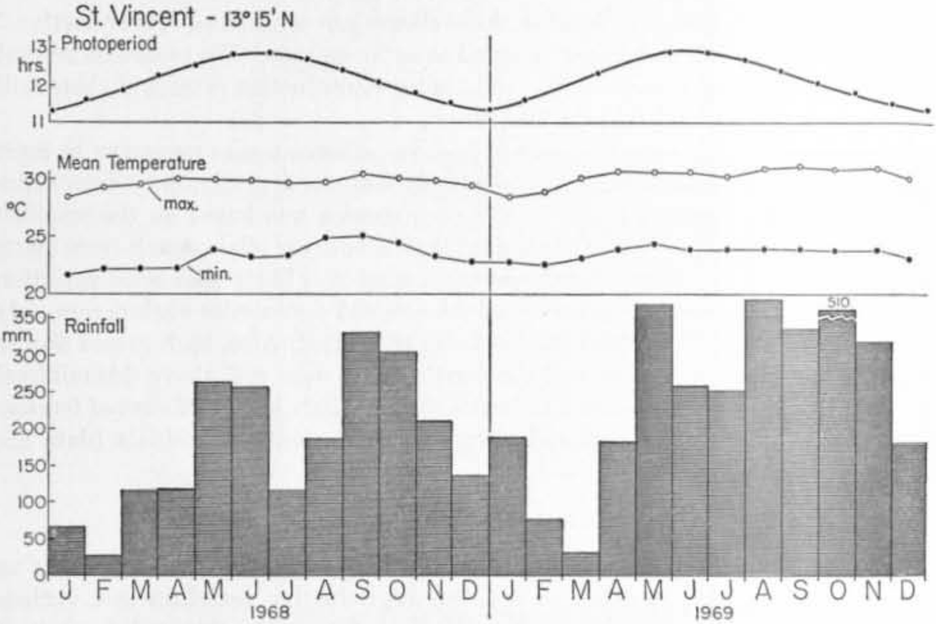

Fig. 2. Climatological data for St. Vincent during the period included in this study. All values represent monthly averages. Photoperiod is between sunrise and sunset.

increased to over 100 mm in March. In 1969, January had high rainfall, but February and March were as dry as January–February, 1968 (fig. 2).

Our study included both of the species of *Anolis* (*A. trinitatis* and *A. richardi*) found on the island. *A. trinitatis* is a sexually dimorphic, moderate size anole (table 2). *A. richardi griseus* is one of the "giant" members of the genus and represents the largest species in our study (table 2); males are almost twice as long as most other species. There is a sexual dimorphism in body size, but even the females of this species are larger than the males of most other species. Aspects of the behavior of these species have been presented by Gorman (1967), and evolutionary relationships by Gorman and Atkins (1968).

REPRODUCTIVE AND FAT CYCLES OF ANOLIS TRINITATIS AND A. RICHARDI GRISEUS

Both sexes of *A. trinitatis* and *A. richardi griseus* in St. Vincent showed some reproductive activity in all months. However, seasonal fluctuations in the level of reproductive activity were evident in *A. trinitatis*, and both species showed relatively large seasonal variations in fat storage.

Anolis trinitatis

(Fig. 3)

Virtually every female *A. trinitatis* collected in the 25 monthly samples had either an enlarging ovarian follicle (class II) or an oviducal egg (classes III and IV); only 8 percent of the 295 adult females collected were nonreproductive. However, no samples were taken in which all females were ovigerous; the proportion of such females ranged from 40 to 85 percent. Furthermore, only 14 of the total adult females (or 7 percent of the 190 ovigerous females) had two oviducal eggs, and these were distributed over eight months. Only slight changes in female reproductive activities were evident. A decline in the frequency of ovigerous females from about 80 percent to 40 percent occurred between January and March in both years. These periods coincide with the relatively brief "dry" season (see fig. 2); however, a similar decline in ovigerous females was also observed in the two relatively large samples from November and December 1969, which are comparatively wet months. Thus, it is not clear that a reduction in egg production is associated with rainfall.

Female *A. trinitatis* did not show a distinct cycle in fat body weight. There was no month in which all females had dissectable fat bodies, and fat bodies were usually completely lacking in all animals. The highest frequency of females with readily dissectable fat bodies occurred in the samples between January and April 1968, and again between January and March 1969; i.e., during the dry months when the frequency of ovigerous females was reduced. However, there was no apparent relation between the presence of oviducal eggs and the size of fat bodies within a given monthly sample.

The testes of the vast majority of the male *A. trinitatis* collected in all months were judged to be reproductively active (stage 6). However, a significant reduction, of ca. 50 percent in testis weight occurred during the wet winter months in both years (fig. 3), suggesting a seasonal cycle in reproductive activity. It is noteworthy in this connection that the November samples of both years were the only ones in which more than one individual was not at stage 6; in 1969, three of the nine animals were at stages 2 to 3. Testes remained small for about three to four months and growth occurred in January or February, when reproductive activity of females was minimal.

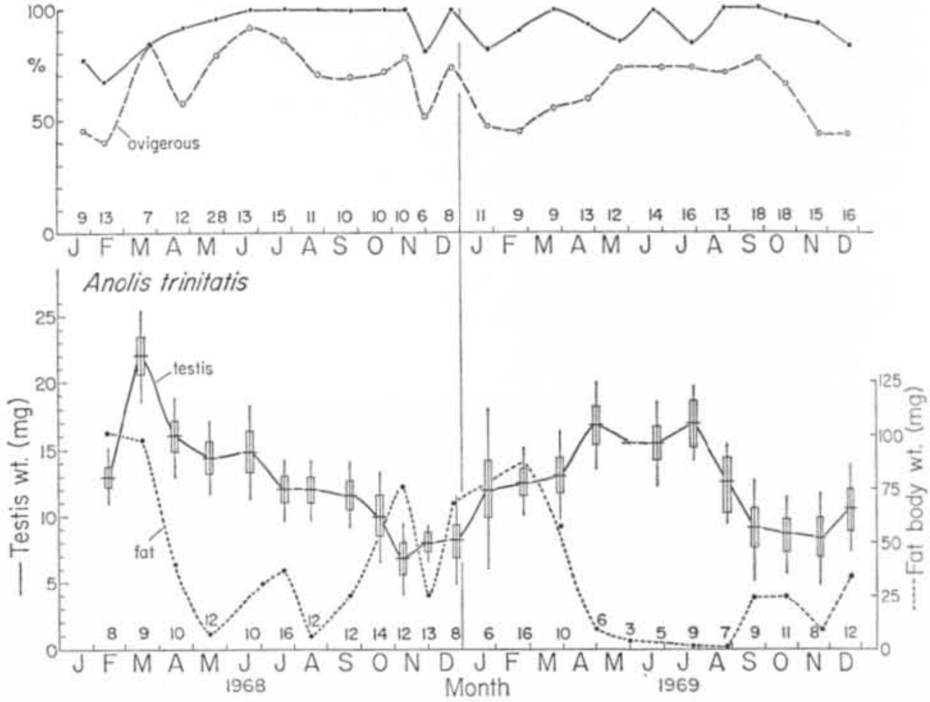

Fig. 3. Reproductive and fat body data for *Anolis trinitatis* on St. Vincent. The numbers of animals in each sample are shown on the abscissas above the months. Average fat body weights are shown by the small dashed curves (● - - - ●) and refer to the values on the ordinate on the right (females lacked fat and no data are given). Data for testis weights (lower graph and left ordinate) include means (horizontal lines), one standard error about the mean (vertical bars), and the 95 percent confidence limits about the mean (vertical lines); the solid curve connects the means.

Reproductive data for females (upper graph): solid line and shaded circles (●——●) show the percentage of each sample which was reproductive (combined values for classes II, III, and IV); and the dashed curve with unshaded circles (o - - - o) shows the percentage of the total sample that was ovigerous (classes III and IV). The two curves or points coincide when all reproductive females were ovigerous.

Usually, at least a few males had dissectable fat bodies in all months, but there was a pronounced increase in fattening during late winter 1968 and 1969, with fat bodies remaining large in all individuals for several months thereafter. In general, the greatest increase in fat body size occurred a few months after the decline in testis weight, and fat bodies decreased again a few months after testis weight had again increased. In general, the males were fattest during the driest months of the year.

Anolis richardi griseus

(Fig. 4)

Virtually all female *A. richardi* collected between August 29, 1968, and December 20, 1969, were judged to be reproductive (classes II to IV); however, considerable monthly variation occurred in the proportion of ovigerous females (fig. 4). Only 7 of the 112 females had two oviducal eggs (class IV). There was a decline in the frequency of ovigerous females between March and April 1969, with a gradual increase in this proportion during the next four months. However, it is difficult to evaluate these changes because monthly samples tended to be relatively small (between 5 and 10) and in the samples when ovigerous females were scarce (e.g., May 2, 1969), all of the females had very large yolky follicles (about 10 mm) that appeared ready to ovulate. Furthermore, since our collection spanned only one year, it is difficult to ascertain whether these changes represent a regular cycle.

Females showed two separate peaks of fattening in the winter of 1968 and at about the same time again in 1969. Most females were reproductive during these periods of increased fat body size.

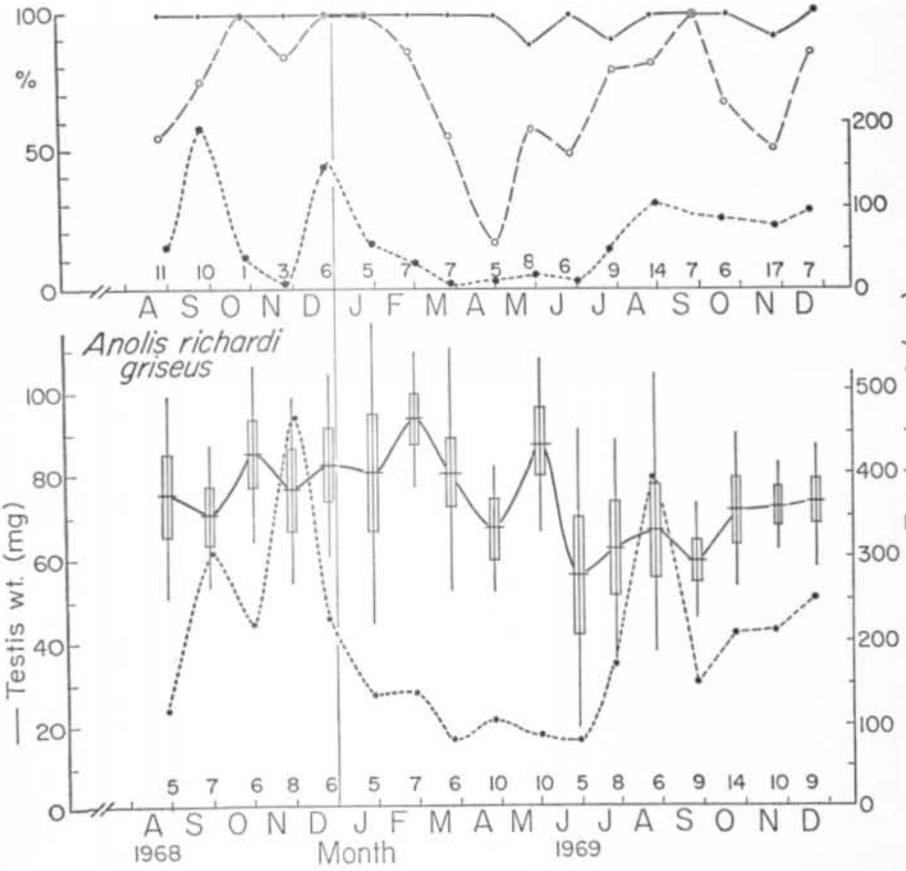

Fig. 4. Reproductive and fat body data for *Anolis richardi griseus* on St. Vincent. Data presented as in figure 3.

Testis weights and histology in *A. richardi* were constant throughout the period of study (fig. 4). Variance tended to be relatively high in all samples and this was probably because of the wide range in body size of adult males (table 2). In 1968, fat body weight rose markedly in September and reached a peak in November with a relatively abrupt decline thereafter. A distinct fattening occurred again in 1969, except that the fat bodies increased in August, about a month earlier. There is no evidence of altered testicular activity or size during these periods of annual fattening.

RESULTS OF STUDIES ON JAMAICA

Geography, Climate, and Species

An island of about 4400 square miles, Jamaica lies approximately 18° north of the equator between 76° to 78° west longitude. The annual fluctuation in day length is about 2 hours, ranging from a maximum of 13 hours, 14 minutes to a minimum of 11 hours, 2 minutes. The average monthly minima (i.e., nocturnal) temperatures vary less than 5° C (from 20° to 24.5° C) with March through August being the warmest period. Monthly maxima are similarly uniform and the diurnal fluctuation is only about 8° C. The distribution of rainfall shows a pronounced seasonality, with a distinct single wet and dry season each year. Rainfall is typically low from December through April, and September and October are the wettest months. Vegetation on the island becomes conspicuously brown during the dry season. Our study spanned parts of three consecutive dry seasons. There are regional differences in rainfall within Jamaica that are important to our study, and distinct variations in rainfall also occurred between the two years of study, as shown in figure 5.

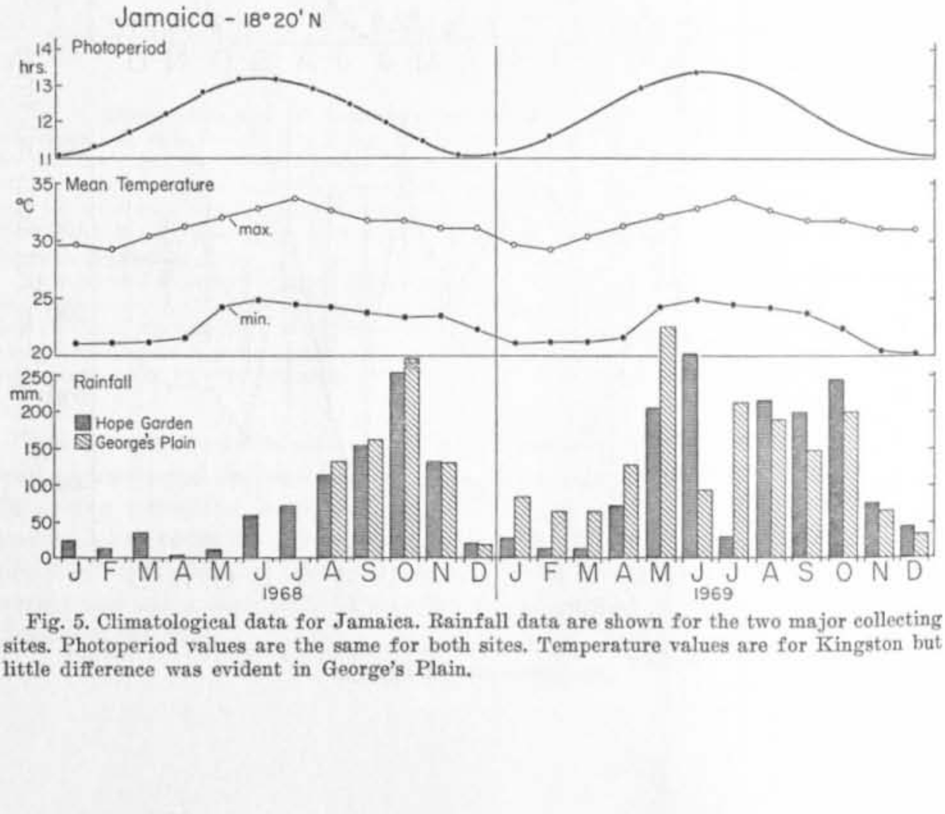

Fig. 5. Climatological data for Jamaica. Rainfall data are shown for the two major collecting sites. Photoperiod values are the same for both sites. Temperature values are for Kingston but little difference was evident in George's Plain.

The three species of *Anolis* studied from Jamaica (*A. grahami, A. lineatopus,* and *A. sagrei*) were collected in two localities. Kingston, the major site, is the capital city and is on the south coast on the eastern third of the island. The city lies in the rain shadow of the Blue Mountains, and is normally semiarid. When this study began in January 1968, the Kingston area was in the third year of a relatively severe drought, and rainfall had been low for several months. The dry season of 1967–1968 was unusually severe and extended. Rainfall was below normal levels each month from the end of November 1967 through June 1968. Although the rainy season generally commences around mid-April, there was essentially no precipitation until the first week of June 1968 (about six weeks late), and then rain did not occur again until the last few days of June. Thus the dry season lasted about six months. Rainfall dropped abruptly by the last week of November 1968, marking the beginning of the next dry season. The second dry season, in 1968–1969, lasted only four months, being terminated by relatively heavy rainfall (ca. 40 mm) during the first week of April, two months earlier than in 1968. The third dry season (1969–1970) started about a month early; there was very little rain in November 1969. Temperatures also dropped to unusually low levels in late 1969, the mean minima being several degrees below those recorded in earlier years.

The second locality sampled was George's Plain in the flat sugar growing belt near the west-central end of the island. The area is generally wetter than Kingston, and was not so severely affected by the drought. Unfortunately, our study began in July 1968, hence we missed any effects the drought might have had.

Both *A. grahami* and *A. lineatopus* occur throughout the island but our collections were made primarily around Kingston, at the Hope Botanical Gardens and on the campus of the University of the West Indies. Both species are arboreal and may be found perched on trees as well as buildings. *A. lineatopus* tend to occur nearer to the ground and are often active at slightly lower body temperatures, but there is certainly a large overlap in distribution of the two (Rand, 1967*a*,*b*). A few of each of these species were also collected at George's Plain along with the *A. sagrei.* However, these collections were relatively small and less regular, and the major emphasis here will be on the Kingston samples.

Anolis sagrei is restricted to the western half of Jamaica and was collected only in George's Plain. This species is the only nonendemic Jamaican anole. It is found in Cuba, many of the Bahamas, the Cayman Islands, Florida, and several Central American coastal localities, where it may have been introduced. From its pattern of distribution on Jamaica, Underwood and Williams (1959) postulated that it was a relatively recent colonist, possibly originating from Cuba. The Jamaican populations of *sagrei* appears distinctly smaller than those from other localities and it is the smallest species included in our study (table 2).

REPRODUCTIVE AND FAT CYCLES OF ANOLIS GRAHAMI, A. LINEATOPUS, AND A. SAGREI

Anolis grahami

(Fig. 6)

Collecting dates and detailed information on the reproductive condition of female *Anolis grahami* are shown in table 3 and figure 6. Some females were reproductive in every month, but pronounced seasonal fluctuations occurred in the level of reproductive activity, with the peak of egg production occurring during the rainy season. Virtually every female *grahami* from Kingston was reproductive during the annual rainy season (between June and October 1968 and May and November 1969). During these periods, almost every female was ovigerous, and about half of them contained two oviducal eggs. Many of these females also contained additional yolky follicles in the ovary suggesting a high rate of egg production. In contrast, during the three dry seasons included in our study, there was a decline in the proportion of reproductive females; few were ovigerous and only rarely did a female have two eggs in the oviducts.

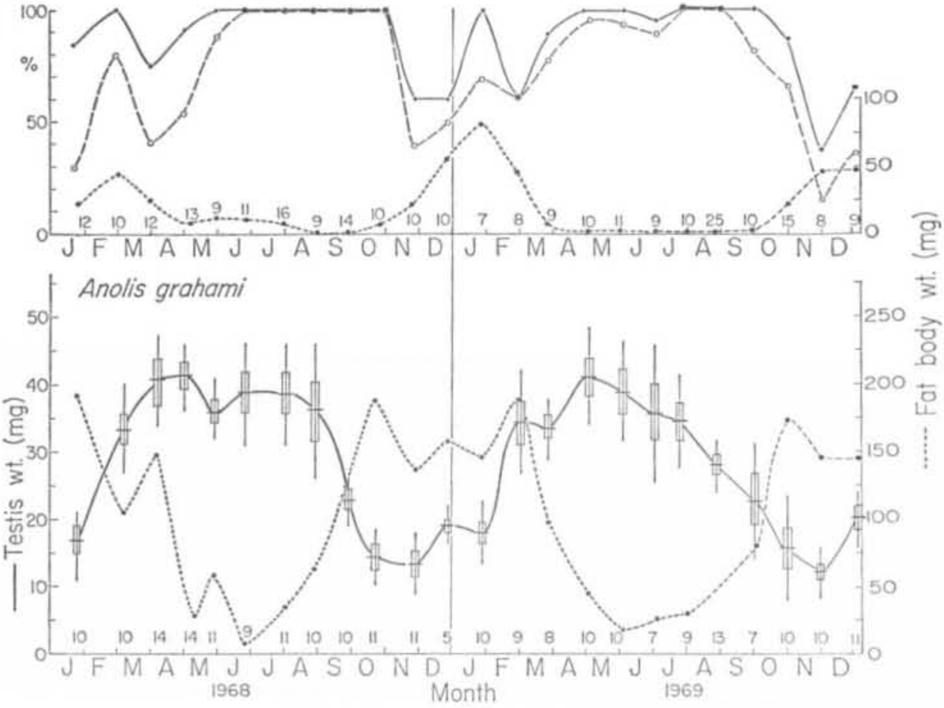

Fig. 6. Reproductive and fat body data for *Anolis grahami* in Kingston, Jamaica. Data presented as in figure 3. Additional details for females are given in table 3.

The close association between low rainfall (the dry season) and reduced reproductive activity among the females is evident from the correlation between the lengths of the period of reduced reproductive activity and the dry seasons. In 1968, when the dry season was unusually long, reproductive activity remained low until the beginning of June, whereas in 1969, all females were ovigerous again by May (table 3). A Chi-square analysis of the distribution of the four reproductive classes in relation to rainfall (tables 4 and 5) indicates that the frequency of nonreproductive females was significantly greater in the dry season of each year, and that reproductive activity was significantly lower in the severe and extended dry season of 1968 than in 1969 (table 5). In general, the reduction in reproductive activity occurred very early in each dry season and high reproductive activity appears to be established almost immediately after the first heavy rains

TABLE 3

Reproductive Activity of Adult Female Anolis grahami and A. lineatopus in Monthly Samples from Kingston, Jamaica*

Collecting date	*A. grahami*					*A. lineatopus*				
	Sample size	Frequency of reproductive classes (%)				Sample size	Frequency of reproductive classes (%)			
		I	II	III	IV		I	II	III	IV
1968										
Jan. 21	12	17	50	33	..	12	16	32	50	..
Mar. 2	10	..	20	80	..	12	32	16	50	..
Apr. 1	12	25	33	33	8	12	58	17	17	8
May 4	13	8	40	54	..	11	70	30	..	..
May 27	9	..	11	77	11	16	70	..	18	12
June 22	11	..	..	55	45	10	..	..	60	40
July 29	16	..	..	63	37	15	..	..	20	80
Aug. 27	9	..	..	45	55	12	..	..	50	50
Sept. 29	14	..	..	93	7	12	..	..	58	42
Oct. 26	10	..	..	80	20	11	..	..	73	27
Nov. 29	10	40	20	40	..	14	14	8	28	50
Dec. 22	10	40	10	50	..	9	..	33	55	11
1969										
Jan. 29	7	..	14	72	14	9	33	..	44	22
Mar. 1	8	40	..	60	..	9	33	11	55	..
Mar. 22	9	11	11	55	23	12	50	8	33	8
May 8	10	..	..	70	30	13	24	38	38	..
June 7	11	..	9	82	9	11	..	..	80	20
July 2	9	11	11	78	..	13	7	7	70	15
July 27	10	..	..	60	40	12	..	8	42	50
Aug. 23	25	4	..	56	36	26	..	..	50	50
Oct. 4	10	..	20	60	20	14	5	..	50	45
Nov. 1	15	13	20	60	7	13	..	15	62	23
Nov. 30	8	44	63	25	12	9	22	33	33	11
1970										
Jan. 8	9	38	31	22	11	11	59	22	18	..

* Reproductive activity is described by the distribution of animals into the four reproductive classes (I–IV).

that mark the wet season (figs. 6 and 9). There was a relatively early drop in the frequency of reproductive females in late 1969 (in early November), which correlates with the early onset of the dry season in this year.

During the rainy season when the frequency of reproductive and ovigerous females was high, fat bodies were lacking in the females. In contrast, there was a marked increase in the frequency and size of fat bodies during the dry season when reproductive activity appeared to be reduced (fig. 6). Even the females that were considered reproductive (classes II and III) had fat bodies at this time and there was no correlation between the size of fat bodies and the presence of eggs. In both years the decrease in fat body size coincided with the increase in reproductive activity.

TABLE 4

RELATION BETWEEN RAINFALL AND THE REPRODUCTIVE STATUS OF FEMALE ANOLIS GRAHAMI AND A. LINEATOPUS IN KINGSTON, JAMAICA

Season[1]	*A. grahami*						*A. lineatopus*					
	Sample size	Frequency of reproductive classes (%)				Fat bd. wt. (mg)	Sample size	Frequency of reproductive classes (%)				Fat bd. wt. (mg)
		I	II	III	IV			I	II	III	IV	
Dry 1968 Jan 21–May 25	56	10	32	54	4	20.2	63	52	20	27	3	35.4
Wet 1968 June 22–Oct. 26	60	..	..	67	33	4.9	60	..	..	49	51	14.1
Dry 1968–69 Nov. 29–Mar. 22	44	27	11	55	7	40.6	53	26	12	43	19	33.1
Wet 1969 May 8–Nov. 2	90	6	9	63	22	4.1	100	6	9	54	31	13.3

[1] Dates show the collection time of the first and last sample included in the season (see table 3 for detailed dates). Seasons were defined by the abrupt changes in rainfall, the dry season including months in which total rainfall was less than 50 mm.

Male *A. grahami* also showed a distinct annual cycle in reproductive activity as judged by the size and appearance of the testis but this cycle was not synchronous with that of the female (fig. 6). In both years of the study, testis weight decreased to about 30 percent of maximal values during the wet winter months when day lengths were decreasing, starting in September or October. They remained small for about 4 to 5 months, increasing relatively rapidly in February, the middle of the dry season. The timing of the regression and recrudescence was similar in both years of study.

Histological examination of the testis revealed that despite the pronounced decline in testis weight, spermatogenesis and androgen secretion continued throughout the year in the majority of the population. In all except the November samples, all testes were at spermatogenic stage 6 and the renal sex segment was hypertrophied. However, when the testes were relatively small, they clearly contained fewer of all cell types, and the sperm were less abundant in the epididymis. In November 1968 when testis weight was minimal, eight of the eleven animals examined still had all stages of spermatogenesis (stage 6) but the remaining three were fully regressed (stage 1); likewise, in November 1969, seven of the ten animals were at stage 6, and three at stage 1. The testes cycle does not show the same relation to wet-dry seasons as was observed in females (fig. 9).

TABLE 5

Chi-Square (χ^2) Values for the Analyses of Reproductive Activity of Adult Female Anolis grahami and A. lineatopus in Relation to Rainfall*

Seasonal comparison	*A. grahami*		*A. lineatopus*	
	χ^2	Probability	χ^2	Probability
Dry 1968 vs. Wet 1968	29.80	$<.001$	97.07	$<.001$
Dry 1969 vs. Wet 1968–1969	15.344	$<.001$	14.13	$<.001$
Dry 1968 vs. Dry 1969	8.88	$.05 > p > .02$	17.41	$<.001$

* Compares distribution of the four reproductive classes within each season (see table 4). The null hypothesis is that reproduction is independent of rainfall.

Males underwent very large seasonal changes in fat deposition, and these fat cycles were inversely correlated with testis weight cycles (fig. 6). When testes were enlarged, fat bodies were absent in virtually all animals. Fat body size rose sharply at the time when testes weight began to decline, and reached a peak when testes were minimal in weight. Fat body weight then declined rapidly as soon as testis recrudescence was complete.

The reproductive cycle of the two sexes are out of phase in several respects: the females tend to remain maximally reproductive several months after the testes have regressed in weight, and the testes increase in size before the females show a return to maximal reproductive activity.

The male *A. grahami* collected at George's Plain showed approximately the same decline in testis weight and increase in fat during the last few months of the year as was observed at Kingston. For example, the mean testis weight of ten animals collected January 6, 1969, was 19.2 mg and fat bodies averaged 123 mg. There was a significant increase in testis weight to 42.4 mg and a decrease in fat to 23 mg by May. These gonad and fat weights are the same as those in the Kingston animals at the same times (see fig. 6).

At least a few females collected at George's Plain each month had eggs, but samples were too small to assess seasonality in reproduction. However, it is noteworthy that all females collected in January and February had dissectable fat bodies, whereas almost none had fat in other months.

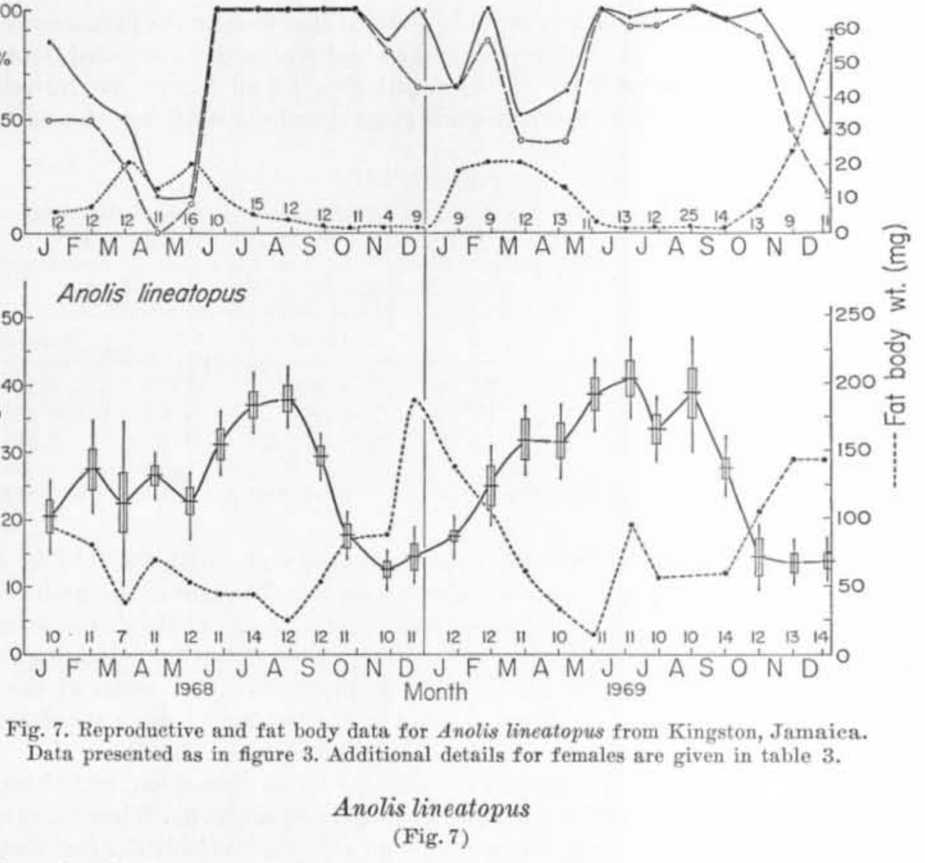

Fig. 7. Reproductive and fat body data for *Anolis lineatopus* from Kingston, Jamaica. Data presented as in figure 3. Additional details for females are given in table 3.

Anolis lineatopus

(Fig. 7)

Reproductive and fat cycles of female *A. lineatopus* around Kingston were generally similar to those described for *A. grahami*, except that the former showed a greater depression of reproductive activity in the extended dry season of 1968 (figs. 7 and 9 and table 3). The frequency of reproductive and ovigerous females fell progressively during the first few months of 1968, reaching a very low level during the last month of the dry season in May. In the two samples collected in May only eight (30 percent) of the twenty-seven females were reproductive. An abrupt increase in reproductive activity to maximal levels occurred during June 1968 at the same time that the *A. grahami* became ovigerous again. In 1969, there was a similar period of reduced reproductive activity (which started with the end of the rainy season in November 1968), but the frequency of reproductive females remained above 50 percent, and maximal reproductive activity was observed by June 7, at least a month earlier than in 1968.

Statistical analysis (Chi-square) of the frequency of the four reproductive classes in relation to the dry and wet season (tables 4 and 5) shows a highly significant reduction in the frequency of reproductive females during the dry season of each year. There was also a highly significant difference between the 1968 and 1969 dry seasons (table 5). Comparison of the females of the two species in Kingston shows that the proportions of the four reproductive classes were the same during the relatively moderate dry season in 1969 ($\chi^2 = 4.03$; $p > 0.20$), but reproductive activity of *A. lineatopus* was significantly lower than in *A. grahami* during the severe dry season of 1968 ($\chi^2 = 22.25$; $p < .001$). The greatly reduced reproductive activity in the severe dry season in 1968 was correlated with the length of the season; for example, reproductive activity of the *A. lineatopus* was very similar during the first few months of the two dry seasons, and the major decline in reproductive activity occurred during the last month of the dry season in 1968 (fig. 7).

Fat bodies increased in weight during the period of reduced reproductive activity, but this increase did not occur until the end of January, about two months after the reduction in reproductive activity was first noted; in *A. grahami* the fat bodies were enlarged in late November as soon as reproductive activity began to decline. In both species the fat bodies disappeared at the same time that all of the females became ovigerous again.

Seasonal fluctuations in the testes and fat bodies in male *A. lineatopus* (fig. 7) generally paralleled those observed in *A. grahami*. Maximal testis weights are very similar in the two species, and in *A. lineatopus* the testes also decline to about 30 percent of the maximum from October through January (fig. 9). However, the spermatogenic activity of *A. lineatopus* seemed even less affected than in *A. grahami* in 1968 and 1969, since in the former, all individuals were judged to be at stage 6 in all samples (i.e., even when testis weight was minimal). However, of the fourteen *A. lineatopus* collected January 7, 1970, six were only between stages 1 and 4, whereas all of the *A. grahami* taken at the same time were at stage 6. Several other interspecific differences are evident between the timing of the testes cycles.

In 1968 the testes of *A. lineatopus* did not attain maximal levels as early as in *A. grahami*. The testes grew during February but tended to remain at an intermediate level during the dry season. In 1969 a similar intermediate plateau in weight was evident in the early part of the dry season, but the maximum was attained somewhat earlier (by the end of May). Also in both years, the decline in testis weight in *A. lineatopus* occurred about a month after it was observed in *A. grahami* (fig. 9).

Fat body weight of male *A. lineatopus* also showed a marked annual cycle which was inversely related to testis weight as described for *A. grahami*. However, *A. lineatopus* more frequently had relatively large fat bodies during the period when the testes were enlarged, the increase in fat body size occurred slightly later, and fat bodies tended to decline in weight sooner after the testes began to enlarge. The delayed fat body cycle corresponds partly to the slightly later decline in testis weight in *A. lineatopus*.

Fluctuations in testis and fat body weight were also evident in the few collections made at George's Plain but the testis weight cycle was less distinct and regular than at Kingston. At George's Plain, testis weight decreased significantly, from 40 mg in August and September 1968 to 27 mg in January 1969; fat increased markedly during the same period. However, testis weight did not return to the initial high level later in 1969. It remained at about 29 mg during the summer of 1969 and then declined further to 18.7 mg by the end of October.

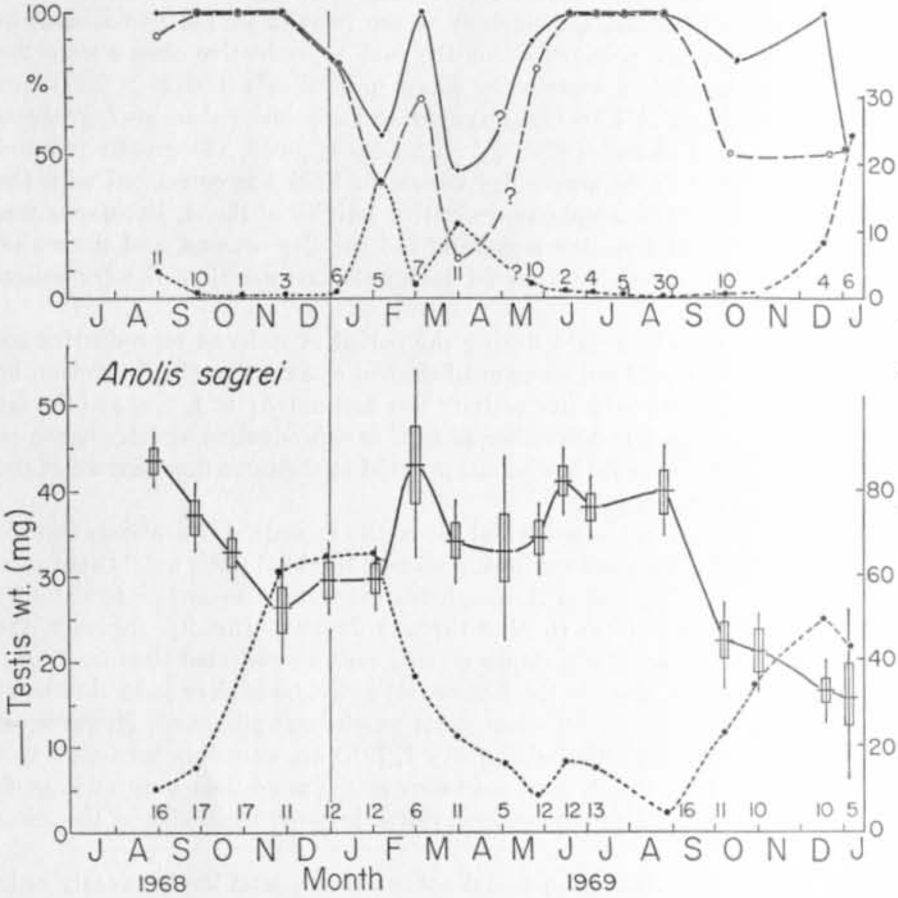

Fig. 8. Reproductive and fat body data for *Anolis sagrei* from George's Plain, Westmoreland, Jamaica. Data presented as in figure 3. Additional details for females are given in table 6.

Anolis sagrei

(Fig. 8)

Data for the *A. sagrei,* especially for females, are less complete than for the other two Jamaican species, but similar seasonal trends are evident in both reproduction and fattening (figs. 8 and 9 and table 6). The frequency of reproductive females is lower during the dry season than during the wet season (table 7). However, the reduction in reproductive activity was not noted until January 1969, almost two months after reproductive activity was observed to decline in the Kingston populations. Fat bodies tended to be large during the dry season when egg production appeared to be lowest, and fat bodies were absent during the rainy season.

TABLE 6

REPRODUCTIVE STATUS OF ADULT FEMALE ANOLIS SAGREI COLLECTED AT GEORGE'S PLAIN, WESTMORELAND, IN JAMAICA

Collecting date	Sample size	Frequency of reproductive classes (%)			
		I	II	III	IV
1968					
Aug. 29	11	..	10	45	45
Sept. 24	10	..	..	90	10
Oct. 15	1	..	..	100	..
Nov. 22	3	..	..	100	..
1969					
Jan. 11	6	17	..	83	..
Feb. 10	5	40	20	20	20
Mar. 1	7	..	30	58	14
Apr. 5	11	55	18	27	..
May 24	10	..	10	80	10
Jun. 15	2	..	50	50	..
July 2	4	..	..	75	25
Aug. 2	5	..	..	60	40
Aug. 25	30	..	..	50	50
Oct. 15	10	20	30	50	..
Dec. 15	4	..	50	50	..
Dec. 30	6	50	..	33	17

TABLE 7

RELATION BETWEEN RAINFALL AND REPRODUCTIVE ACTIVITY IN ADULT FEMALE ANOLIS SAGREI FROM GEORGE'S PLAIN, JAMAICA[1]

Season	Sample size	Frequency of reproductive classes (%)				Fat bd. wt. (mg)
		I	II	III	IV	
Wet 1968 Aug. 29–Nov. 22	25	..	4	72	24	1.8
Dry 1969 Jan. 11–Apr. 5	29	32	18	47	3	8.0
Wet 1969 May 24–Sept. 15	61	..	5	57	34	0.6

[1] See note 2 to table 4 for explanation of seasons.

Although the male *A. sagrei* are much smaller than those of the other two Jamaican species, their testes reach the same absolute size. The testes of *A. sagrei* declined significantly in weight in late autumn at the same time that regression was observed in *A. lineatopus* in Kingston. However, the extent of testis weight regression was somewhat variable in *A. sagrei* (fig. 8). In 1968 testis weight declined by only about 30 percent, which was about half the decline observed in the other two species (fig. 9), whereas in mid-winter, 1969, testes of *A. sagrei* declined to the same extent (about 70 percent) as in the other species (fig. 9). Spermatogenic activity did not cease in either year; all males were at spermatogenic stage 6. Fat bodies increased abruptly in weight as the testes regressed in October, and the fat was lost again as the testes grew in February. Fat bodies grew to about the same size in both years.

Comparison of the testis weight cycle in the three species of Jamaican *Anolis* (fig. 9) shows that despite a slight difference in initiation of regression, all three tend to reach minimal values at about the same time—at the end of the wet season—and in all three, recrudescence begins early in the dry season. Differences between the two sexes of each species and the close association between rainfall and reproductivity in the females of all three species are also shown in figure 9.

RESULTS OF STUDIES ON HISPANIOLA

Geography, Climate, and Species

Hispaniola is a large island (ca. 30,000 square miles) situated at about 18° 30′ north latitude, a few hundred miles east of Jamaica. Politically, it is divided into Haiti (western third) and the Dominican Republic. We obtained samples of *A. cybotes* (the lizard studied) from several localities throughout the island; however, the major focus of our study was on the population in Port-au-Prince, the capital city of Haiti. This city lies in a flat plain surrounded by steep mountains to the north and south. A second relatively large series of *A. cybotes* was available from Île de la Gonave, a small island 40 to 50 miles west of Port-au-Prince. Consideration of the relation between reproductive cycles and climate will be focused on the Port-au-Prince collections since climatological data were most complete for this area.

Photoperiod changes in Haiti are the same as those described for Jamaica. The level and extent of fluctuation in mean monthly minimal and maximal temperatures in Port-au-Prince (fig. 10) are also similar to those in Kingston, Jamaica. The seasonal distribution of rainfall around Port-au-Prince is somewhat more variable than in Jamaica and Haiti does not have as long and regular a dry season. Usually rainfall is relatively low during the mid-winter (November and March), but January and February 1969 were exceptionally wet (fig. 10).

A. cybotes is one of about twenty-two species of *Anolis* on the island of Hispaniola and is widespread throughout the island, as indicated by the samples discussed below. It has a superficial resemblance in form and size to the Jamaican *A. lineatopus* (table 2). Some observations on the natural history of *A. cybotes* are given in Rand (1962).

Several live collections were shipped to the United States during 1966. Because of the delay in killing these, the fat body size was not considered reliable. Collections made during 1968–1969 were preserved in the field. The history of the specimens deposited in the Harvard Museum of Comparative Zoology was not always known, but most were probably fixed with formalin in the field and all were then stored in 70 percent ethanol.

REPRODUCTIVE AND FAT CYCLES OF ANOLIS CYBOTES
(Fig. 11)

Data from all localities establish the existence of a distinct annual cycle in reproductive activity in both sexes of *A. cybotes* in Hispaniola.

In the Port-au-Prince collections (fig. 11) testis weights declined to about 25 per cent of maximal values during November and December in all three years; a high variability in testis weights during September indicates that regression begins at this time. However, despite this marked decline in testis weight, spermatogenic and interstitial cell activities are not uniformly suppressed. All but two of the ten animals collected in November 1968 contained sperm in the testes and epididymis (stage 6) and had enlarged renal sex segments. In December 1966, five of the nine animals were still at stage 6, the other showing regression (stage 7) or some intermediate stages of recrudescence (stages 3 and 4). Similar trends were evident in November and December of 1969.

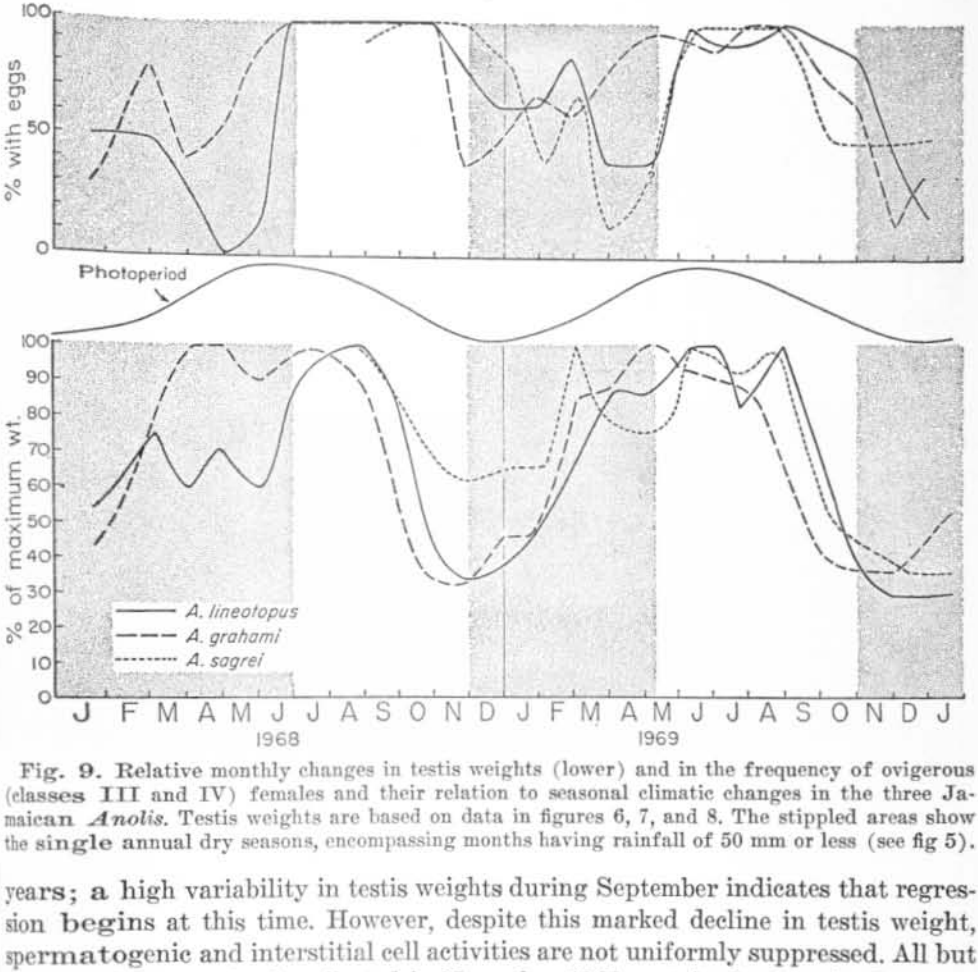

Fig. 9. Relative monthly changes in testis weights (lower) and in the frequency of ovigerous (classes III and IV) females and their relation to seasonal climatic changes in the three Jamaican *Anolis*. Testis weights are based on data in figures 6, 7, and 8. The stippled areas show the single annual dry seasons, encompassing months having rainfall of 50 mm or less (see fig 5).

Recrudescence in testis size was evident by early January and complete by the end of February; all animals were at stage 6 in January and throughout the summer. Dissectable fat bodies were found in most individuals in all months, but a marked fattening occurred in November when the testes were regressing in weight. Fat bodies reached a maximum during January when gonadal recrudescence was beginning.

Collections of females were unfortunately incomplete, but available data suggests a distinct seasonality in egg production (fig. 11 and table 8). In general, the females show a decline in reproductive activity in late winter (November–January) when rainfall tends to be relatively low. Fat bodies were not measured in all samples but it was clear that they were small in size during the summer months and greatly enlarged (weighing about 135 mg) in late winter when reproductive activity is minimal. At this time, fat was present in all females and the size of fat bodies was not correlated with the presence of enlarged follicles or eggs. Fat remained high through March.

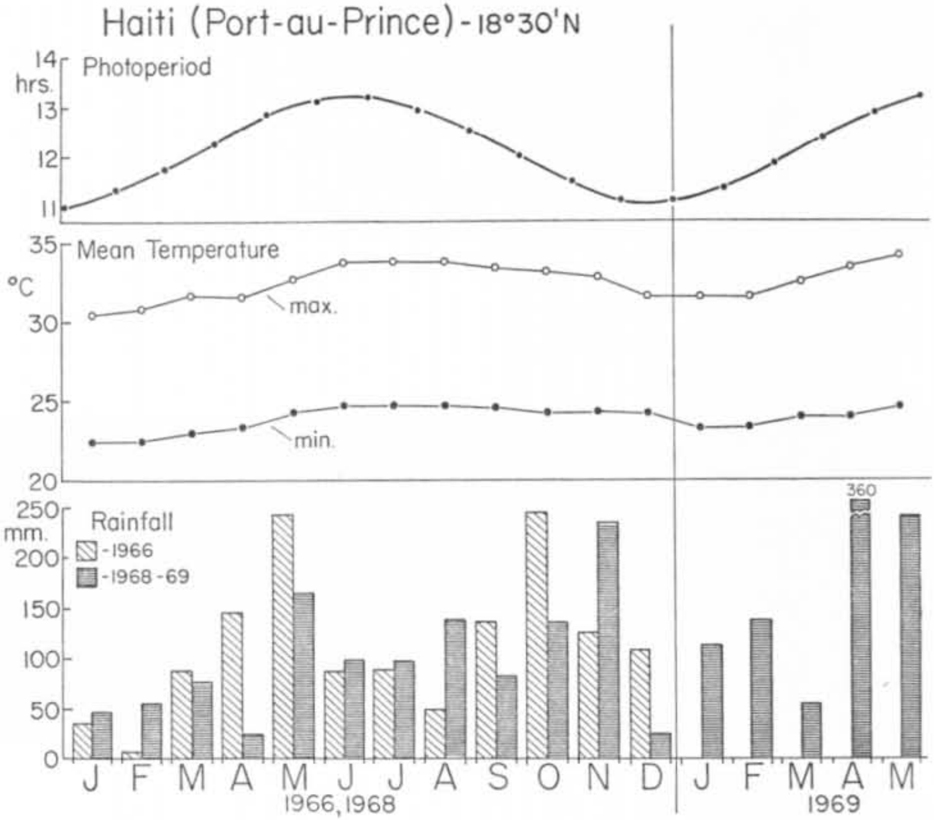

Fig. 10. Climatological data for Port-au-Prince, Haiti, on the island of Hispaniola. Data presented as in figure 2.

Data for the samples of *A. cybotes* collected at various localities outside of Port-au-Prince in Haiti and in the Dominican Republic are summarized in tables 8 and 9. In general, these data indicate that the testis and ovarian cycles and associated fat body cycles described for the Port-au-Prince populations in 1966–1969 represent relatively regular cycles for the species as a whole throughout the island. However, the amplitude of these cycles may vary from year to year or geographically. Data for Île de la Gonave are particularly valuable for defining the extent of testicular regression that may occur, indicating that at least half of the population may undergo a brief period of nonreproductivity in December. A large series of adult males collected in 1965 showed a significantly greater reduction in testis weight and spermatogenic activity than was observed in Port-au-Prince (the gonads in most of the Îl de la Gonave animals were partially or fully regressed). We do not know the differences in the climate between the Port-au-Prince and Île de la Gonave collecting localities because meteorological data for these areas are incomplete. The females on Île de la Gonave showed slightly more reproductive activity than those in Port-au-Prince (table 8).

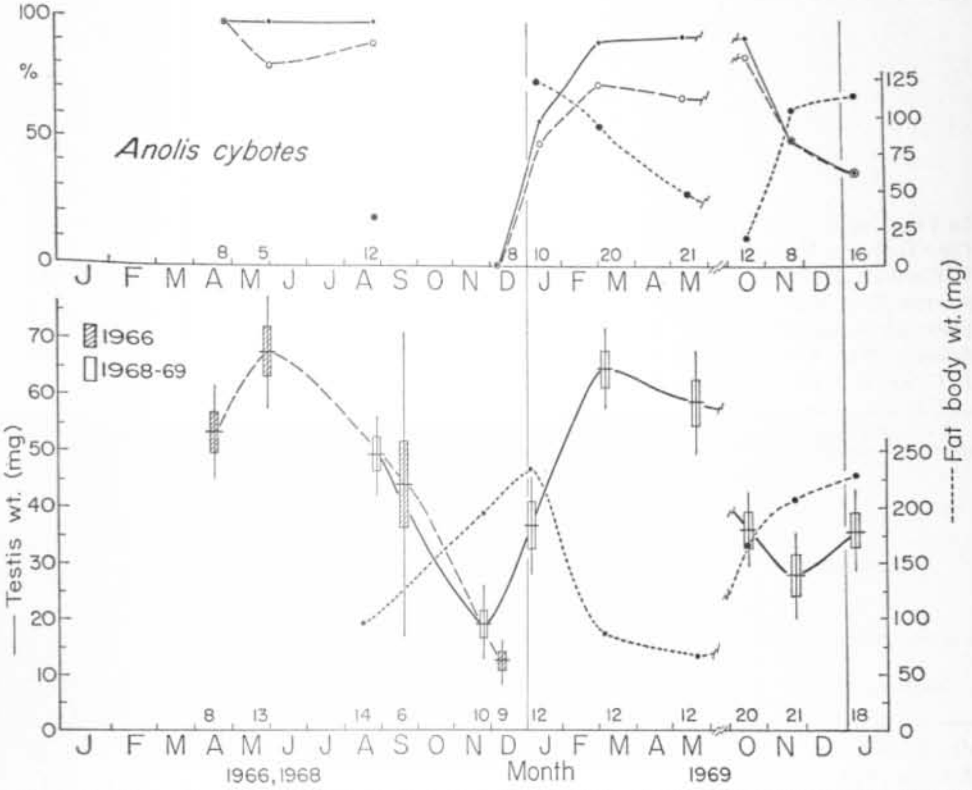

Fig. 11. Reproductive and fat body data for *Anolis cybotes* from Port-au-Prince, Haiti. Data presented as in figure 3. Further details regarding females appears in table 8. The females collected in 1966 can be identified by the dates in which the males were collected; fat body data were not taken from the 1966 samples.

RESULTS OF STUDIES ON GRAND CAYMAN

Geography, Climate, and Species

Grand Cayman is a small low island of about 80 square miles at 19° 20′ north latitude, 82° west longitude. It lies approximately 500 km northwest of Kingston, Jamaica (fig. 1). Climatically, this island differs little from Jamaica. Photoperiod is within a few minutes of that on Jamaica and mean monthly temperatures differ

TABLE 8

REPRODUCTIVE STATUS OF ADULT FEMALE ANOLIS CYBOTES COLLECTED IN HISPANIOLA[1]

Locality	Collecting Date	Sample size	Frequency of reproductive classes (%)			
			I	II	III	IV
Port-au-Prince, Haiti..	April, 1966	8	..	..	100	..
	May 30, 1966	5	..	7	86	7
	Dec. 5, 1966	8	100	..	..	..
	Aug. 23, 1968	12	..	22	75	13
	Jan. 4, 1969	10	40	10	10	40
	Mar. 1, 1969	20	10	15	40	35
	May 19, 1969	21	4	23	46	23
	Oct. 15, 1969	12	8	8	75	8
	Jan. 5, 1970	16	38	..	56	6
La Vega, centr. D.R...	Mar. 30, 1934	13	..	23	55	23
Cape Haitien, N Haiti.	Mar. 2, 1958	8	..	..	..	50
Île Gonave, Haiti......	Apr. 4, 1934	6	..	..	50	50
Samana Bay, NE D.R.	Apr. 6, 1934	15	20	13	60	7
Erov. El Seibo, D.R...	Sept. 5, 1958	7	..	..	60	40
Samana, NE D.R......	Sept. 22, 1969	3	..	..	66	33
Île Gonave, Haiti.....	Dec. 22, 1965	19	42	21	31	5

[1] Data for Port-au-Prince, 1966–1970, are based on collections made in conjunction with the present study. All others are for specimens in the collection of the Harvard Museum of Comparative Zoology.

TABLE 9

REPRODUCTIVE CONDITION OF LARGE ADULT[1] MALE ANOLIS CYBOTES FROM VARIOUS LOCALITIES IN HISPANIOLA

(Based on Harvard Museum of Comparative Zoology collections)

Collecting date[2]	Site	Sample size	Testes		Fat bd. size[5]
			Wt (mg)[3]	Stage[4]	
Mar. 2, 1958.....	La Vega, centr. D.R.	5	41.5 ± 3.9	6	0
Mar. 15, 1961....	Leogone, Haiti	9	45.4 ± 2.8	6	0
Mar. 25, 1959....	Île Gonave, Haiti	2	42.0	6	0
Mar. 30, 1934....	Cape Haitien, N Haiti	10	34.3 ± 2.4	6	0
Mar. 30, 1963....	Prov. El Seibo, E D.R.	6	42.5 ± 2.5	6	0
Apr. 6, 1934......	Samana Bay, NE D.R.	22	35.7 ± 1.5	6	0
Apr. 12, 1934.....	Île Vache, SW Haiti	10	50.4 ± 4.1	6	0
Apr., 1934.......	Île Gonave, Haiti	15	35.3 ± 3.1	6	0
Apr., 1962.......	Saltrou, S Haiti	6	63.4 ± 4.9	6	0
Sept. 1, 1969.....	Cape Haitien, N Haiti	2	52.0	6	+
Sept. 5, 1958.....	Prov. El Seibo, E D.R.	13	31.1 ± 2.1	6	0
Sept. 22, 1969....	Samana, NE D.R.	5	27.0 ± 2.1	6	0–+
Dec. 22, 1965.....	Île Gonave, Haiti	53	7.5 ± 0.8	1–2 (40%) 3–4 (15%) 5–6 (33%) 7 (12%)	all ++

[1] Includes only animals over 54 mm in snout-vent length (see table 2).
[2] Samples are arranged chronologically by month and day.
[3] Mean ± standard error.
[4] See table 1 for details.
[5] Fat body size was judged qualitatively: 0, no fat bodies; +, small fat bodies; ++, conspicuously enlarged fat bodies.

only slightly, being a little cooler. Mean maxima declined gradually from 32° to 28° C between July and December and mean minima declined from 24.5° to 20.5° C in the same period. The distribution of rainfall on Grand Cayman parallels that in Kingston; November through April is considered the dry season, with rainfall usually well under 50 mm. Rainfall varies from 150 to 300 mm in other months, September and October being the wettest. This pattern was observed in 1969; over 240 mm fell in each month between June and October with an abrupt decline to 46 mm in November and 28 mm in December.

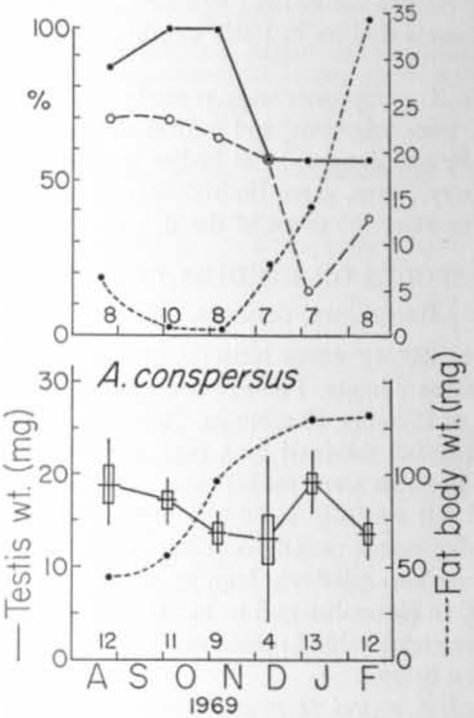

Fig. 12. Reproductive and fat body data for *Anolis conspersus* from Grand Canyon. Data presented as in figure 3. The males collected December 10 were relatively small and fat body data were not included.

There is a single anoline species, *A. conspersus*, on Grand Cayman. This lizard is sexually dimorphic and similar in size to many of the others examined (table 2). It is very closely related to and sometimes placed as a subspecies of *A. grahami;* however, the two differ in karyotype (Gorman, unpublished). Notes on the ecology of *A. conspersus* have been published by Schoener (1967).

Reproductive and Fat Cycles of Anolis conspersus
(Fig. 12)

Although our collections of *A. conspersus* span only the fall and part of the winter of one year (1969), these data are sufficient to demonstrate that this species undergoes a testis and fat body cycle at about the same time as those observed on nearby Hispaniola and Jamaica (fig. 12). A significant decline in testis weight (of about 25 percent) was observed between late August and early November; this decline actually occurred during October. At the same time, fat body size doubled (data for December 10 are not comparable since this included only four small individuals). Since we do not have data on maximal testis weight for this species, we cannot assess the extent to which the testis regress. Histologically, the testes of all individuals were at stage 6 between August and December. The twenty-five percent decline in weight observed was less than in *A. lineatopus* and *grahami* (fig. 9) and *cybotes* (fig. 11). However, since the *A. conspersus* all had relatively well developed fat bodies when the first sample was taken (August 28), it is likely that some decline in testis weight had already occurred by this time.

Most of the female *A. conspersus* were reproductive in September and October, although not all were ovigerous, and half of the animals were nonreproductive in early December and January. Fat bodies were essentially absent in all of samples except January. Thus, these limited data indicate that egg production declines in late winter after the onset of the dry season.

RESULTS OF STUDIES IN FLORIDA

Geography, Climate, and Species

Southern Florida at 25° 47′ north latitude, 80° west longitude, has an essentially subtropical marine climate. Photoperiod changes by about 3 hours, from 10 hours, 35 minutes to 13 hours, 45 minutes. There is typically a long warm summer with abundant rainfall followed by a cool, dry winter. Rainfall in 1968 in Miami (when our collections were made) was relatively high (up to 220 mm) through October and fell abruptly to 30 mm in early November. December was completely dry. The dry season usually continues through the spring. Mean minimum temperatures were also relatively high up through October (ca. 22°–24° C) and then fell to 17° C in November and to 14° C in January. Thus, seasonal temperature changes were comparable to those observed in the northernmost habitat studied, Bermuda (see below).

The anole we studied, *A. sagrei*, from southern Florida was probably introduced from Cuba (Ruibal, 1964). It is larger than the Jamaican *A. sagrei.*

Reproductive and Fat Cycles of Anolis sagrei

Our own collections of *A. sagrei* from Florida were insufficient to describe annual reproductive cycles. However, a compilation of our data from the fall and winter of 1968 with those obtained from museum collections spanning a period of several decades (table 10) clearly demonstrates that this species regularly undergoes a pronounced reduction in reproductive activity with a concomittant increase in fat storage during the winter. Although testis weights may not be comparable for different collections due to variations in fixation, it is clear that testis weight has declined markedly by late October. The testes remain relatively small through November and December and are only partially enlarged by late January. Although late autumn samples of males were sparse, they suggest that testis regression probably begins in September; in our sample of five adults collected September 10, three had almost fully enlarged testes (21–26 mg) while the testes were fully regressed (2.5 and 3.5 mg) in two individuals. Histological examination of testes indicates that spermatogenesis ceases completely in late October (all were stage 1) and only partial spermatogenic recrudescence (to stage 3) was evident in December. Some individuals reach stage 6 by the end of January.

In our 1968 samples, fat bodies were partially enlarged in September (averaging 45 mg) and were twice this size when testes were fully regressed October 29. Qualitative assessment of fat body size in museum specimens indicated similar mid-winter fattening in other years.

TABLE 10

Reproductive Status of Adult Male and Female Anolis sagrei in Southern Florida

Date collected[1]	Males			Females			
	Sample size	Testis wt. (mg)	Spermatogenic stage	Number in each reproductive class			
				I	II	III	IV
Jan. 31, 1959[2]	7	9.9 ± 1.7	2; 3; 4; 6(n = 4)	3	..	..	..
Feb. 19, 1955[3]	4	22.0 ±	6	..	..	..	..
Mar. 5, 1957[2]	2	20, 32	6	2	..	..	..
Mar. 28, 1959[3]	6	31.0 ± 2.6	6	..	..	2	3
Apr. 30, 1949[3]	15	36.5 ± 2.2	6	..	..	1	3
June 3, 1950[3]	11	34.9 ± 2.5	6	..	..	..	1
July 2, 1964[2]	4	25.9 ± 4.3	6	..	..	2	1
July 4, 1965[3]	4	31.2 ± 4.1	6	..	..	1	..
Aug. – –, 1932[3]	3	34.5 ± 4.0	6	..	..	..	..
Sept. 7, 1947[3]	..	..	..	..	..	2	..
Sept. 10, 1968[4]	3	21, 23, 26	6	..	..	2	2
"	2	2.5, 3.5	7	..	..	..	..
Oct. 29, 1968[4]	11	4.4 ± 0.32	1	1	..	..	..
Dec. 12, 1968[4]	12	3.8 ± 0.30	2–3	3	..	..	..

[1] Arranged chronologically in order of month.
[2] From Los Angeles County Museum.
[3] From Florida State Museum.
[4] From this study.

Data for the few females collected (table 10) indicate that egg production ceases completely in mid-winter (by late October) and may not resume again until March. Females tend to be relatively fat during mid-winter and lean during the remainder of the year.

Thus, both sexes of *A. sagrei* in Florida are nonreproductive during the relatively cool dry winter when day lengths are shortest. Complete testis regression probably also occurs at the same time on the nearby Bahamas; two 51 mm males (from the Los Angeles County Museum) collected at Alicetown, Bahamas, on October 26, 1969, had fully regressed gonads weighing under 1 mg. Nine specimens collected in North Bimini in April and June had enlarged testes, averaging 28.5 mg.

In addition to our fresh collections of *A. sagrei* from Miami, we received a few specimens of *A. carolinensis* from that area. One adult male (58 mm) collected September 5, 1968, had a fully regressed testis (5 mg, stage 1) with 20 mg fat bodies. Five relatively small adult males (52–56 mm) collected December 12, had very small testes (2–4 mg) in early stages of recrudescence (stages 2 and 3), and fat bodies were greatly enlarged, averaging 90 mg. Thus, there is probably a distinct testis cycle in this species in Miami that is not unlike that of *A. sagrei.* Two females collected October 29 were nonreproductive, but lacked fat.

RESULTS OF STUDIES ON BERMUDA

Geography, Climate, and Species

Bermuda, a small island of about 21 square miles lies at 32° 20′ north latitude, 60° 40′ west longitude. It is about 600 miles due east of Cape Hatteras, North Carolina. Because of warm ocean currents, it supports essentially a warm temperate and subtropical vegetation despite its northern latitude: climatic data for our study period are shown in figure 13. Day length changes by 4 hours, ranging from 10 hours, 22 minutes to 14 hours, 22 minutes. Temperature shows marked seasonal fluctuations with a range of about 9°–10° C in average monthly minima and maxima. Rainfall does not show a distinct annual cycle with discrete wet and dry seasons, although the late winter months (December–February) tend to have heavy winds and rainfall. During the study period, rain exceeded 50 mm in all months and was usually above 75 mm per month, with the number of days of rain

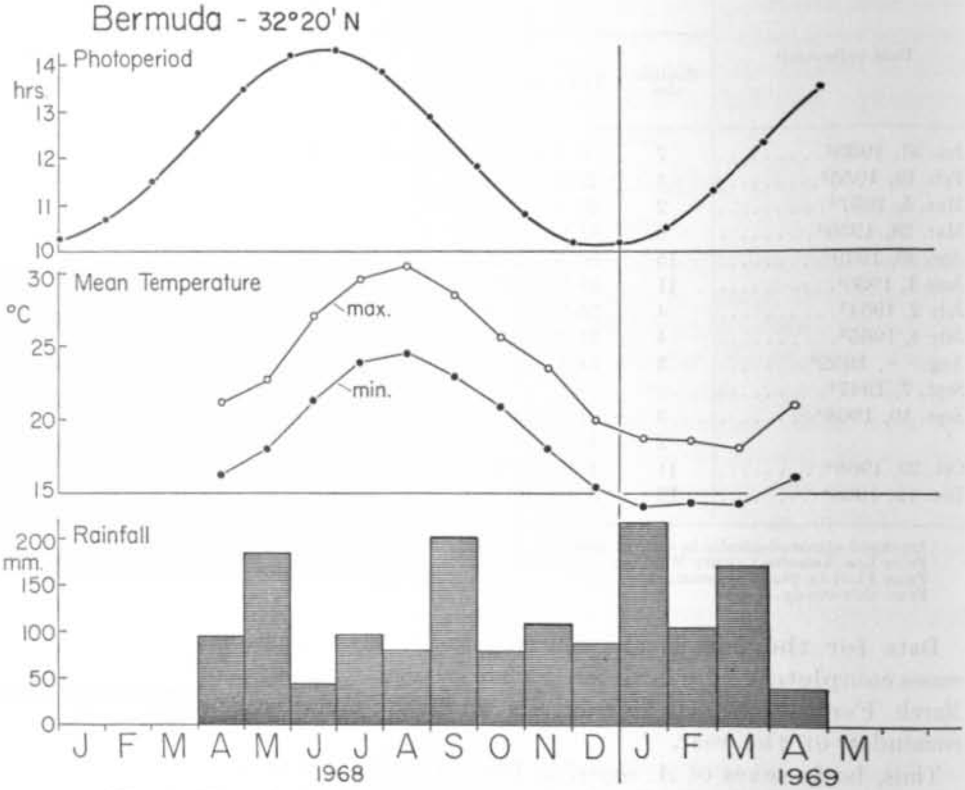

Fig. 13. Climatological data for Bermuda. Data presented as in figure 2.

per month varying from a low of five in June to 17 to 18 in December, January, and February.

In general, temperature and photoperiod changes represent the major aspects of climatic seasonality. A warm summer with relatively high nocturnal temperatures and a cool winter with both cold nights and short days can be recognized: days are often cool enough to curtail lizard activity in the winter.

There are no native anoles on Bermuda, but three species have been successfully (and intentionally) introduced. Wingate (1965) wrote a comprehensive review of the herpetology of Bermuda. *A. grahami*, the species we studied, was the first *Anolis* to be established on the island: 26 males and 45 females were brought in from Kingston, Jamaica, and released in a public garden in September 1906. Within six weeks some were seen one mile distant from the release point. Today they are island wide and abundant. The specimens obtained from Bermuda were identical in size to those collected around Kingston, Jamaica.

According to Wingate (1965), *A. grahami* are primarily arboreal but may be seen on a wide variety of perching sites, including tree trunks, branches, houses, stone walls, fences, tall weeds, and even open ground as much as 25 feet from cover. They remain active all year, although on windy, wet or overcast days they take shelter. During the course of our study, Mr. Wingate (our collector) reported great difficulty in finding animals during late December and January; this was a period of unusually wet weather.

REPRODUCTIVE AND FAT CYCLES OF ANOLIS GRAHAMI

(Fig. 14)

Reproductive activity in both sexes of *A. grahami* on Bermuda was highly seasonal and a distinct nonbreeding season lasting 4 to 5 months can be recognized. Both sexes also underwent marked seasonal changes in fattening with fat body weights being inversely related to reproductive activity (fig. 14 and tables 11 and 12).

Egg production ceased completely in the cool wet winter months and was not resumed until temperatures and day length increased in the spring. This drop in reproductive activity occurred very abruptly, essentially within the last two weeks of October (table 11), at the same time that a sharp increase in fat body size occurred. Recrudescence of the ovary with the appearance of eggs in the oviduct also occurred rapidly in March. Fat bodies began to shrink slightly in February, about a month before the initiation of egg production (fig. 14).

The gonadal cycle in the males was relatively well synchronized with that of the female. An abrupt regression in testis weight occurred in September. Minimal testis weights, averaging only about 10 percent of maximum, were attained by November, at the same time that egg production ceased. At this time there was almost a complete cessation of spermatogenic activity in the population (table 11). The period of spermatogenic arrest was relatively short and some recrudescence was evident by mid-December when day length and temperatures were minimal. In fact, half of the fourteen males collected December 12 already had sperm in the testis and epididymis (stage 6), although the sexual segment of the kidney was still atrophic. Testes grew slowly through March, with a final growth "spurt" in

April that coincided with the increase in temperature; this was the same time when the females become reproductive again. Histologically, spermatogenic recrudescence and androgen secretion appeared complete by early March, in the month before the maximum testis size was attained.

TABLE 11

Reproductive Status of Adult Female Anolis grahami Collected in Bermuda

Collecting date	Sample size	Frequency of reproductive classes (%)			
		I	II	III	IV
1968					
Apr. 20	6	..	..	100	..
May 20	10	..	30	50	20
July 1	11	..	9	91	..
July 29	15	..	13	67	20
Aug. 20	4	..	..	50	50
Sept. 20	14	..	21	14	8
Nov. 1	11	45	36	18	..
Dec. 14	14	100	..	..	..
1969					
Feb. 5	6	100	..	..	..
Mar. 1	22	100	..	..	..
Apr. 1	11	9	18	64	9

TABLE 12

Seasonal Changes in Spermatogenic Activity of Adult Male Anolis grahami in Bermuda During 1968 and 1969

Collection date	Sample size	Number in each spermatogenic stage						
		1	2	3	4	5	6	7
Apr. 20	18	..	..	..	..	2	16	..
May 19–Aug. 20*	74	..	..	..	..	..	74	..
Oct. 12	15	..	..	2	..	..	11	2
Nov. 1	11	8	2	..	..	..	1	..
Dec. 14	14	..	1	3	2	1	7	..
Feb. 5	5	..	..	1	1	1	2	..
Mar. 1	8	..	..	..	..	..	8	..
Apr. 1	10	..	..	..	..	..	10	..
May 1	8	..	..	..	..	..	8	..

* Includes four separate collections during this period.

The seasonal change in fat body weight of males was inversely related to the regression of the testes. Fat weights rose precipitously during September when the major decline in testis weight occurred. Fat bodies remained almost fully enlarged until February and did not disappear until the testis had attained maximal size.

Reproductive cycles in the Bermuda and Jamaica populations of *A. grahami* are compared in figure 15. The timing of testis regression and recrudescence was similar in both, but the Bermuda population underwent a significantly greater regression in weight and spermatogenesis. Also, the testis attained slightly greater weights immediately before regression in Bermuda. Reproductive cycles of the females in the two populations differ in several respects: (1) the Bermuda population shows a more rapid and complete cessation of egg production and (2) ovarian regression in the Bermuda population occurred at least a month earlier than any decline in reproductive activity was evident in Jamaica.

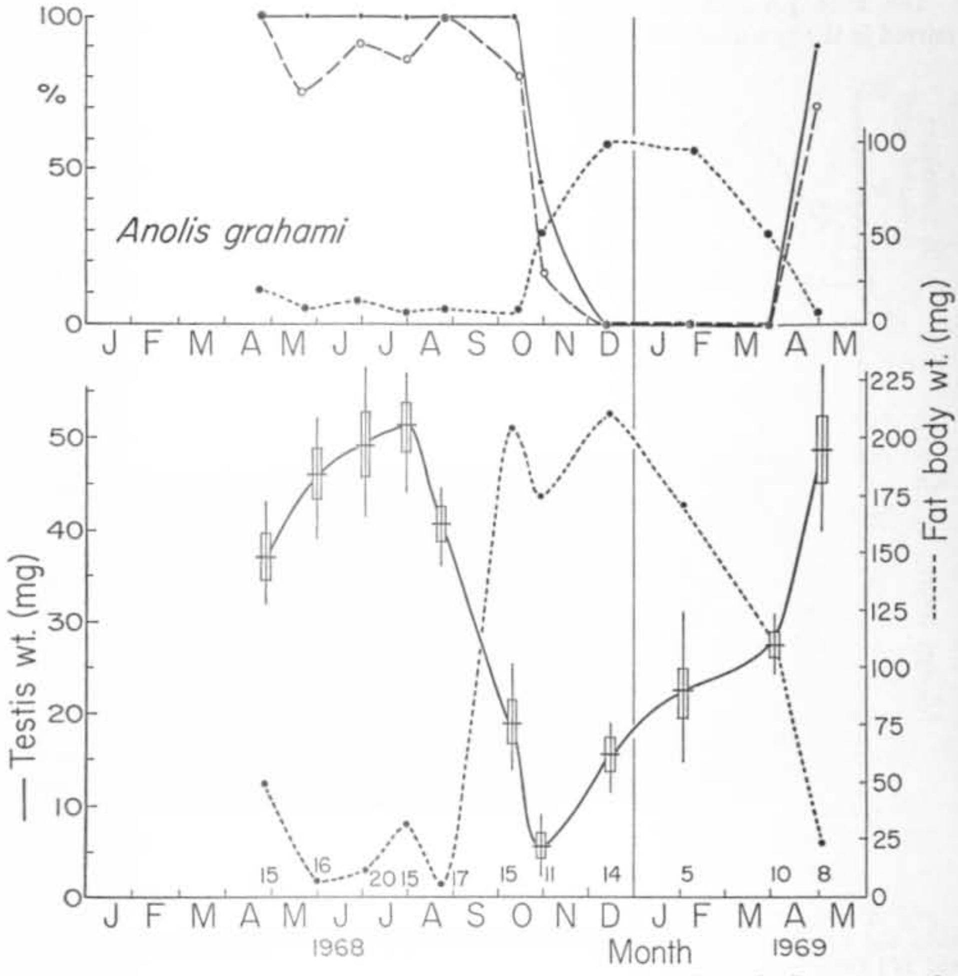

Fig. 14. Reproductive and fat body data for *Anolis grahami* from Bermuda. Data presented as in figure 3. Additional data for females are given in table 10 and for males in table 11.

DISCUSSION

Existence of Reproductive Cycles in Anolis

Our phenological data indicate that some fluctuation in reproductive activity occurs in all of the populations of *Anolis* examined, except perhaps the giant species, *A. richardi*, on St. Vincent. The extent of these fluctuations varies between sexes, between species (even when syntopic), and between different geographical populations of the same species. Before considering the details and possible causes of these differences it is useful to review the general patterns of reproductive activities that we observed in the anoles.

The most pronounced seasonality in reproduction involving both sexes occurred in the two most northern latitude populations, *A. grahami* on Bermuda and *A. sagrei* in Florida. Distinct breeding seasons have also been described for populations of a native temperate anole, *Anolis carolinensis,* in Louisiana (Dessauer, 1955*a;* Fox, 1958; Hamlett, 1952; Licht, 1967*a*), north Florida (Carr, 1940), and south Florida around Miami (King, 1966, and this study). Another introduced anole around Miami, *A. distichus,* also exhibits a distinct breeding season (King, 1966).

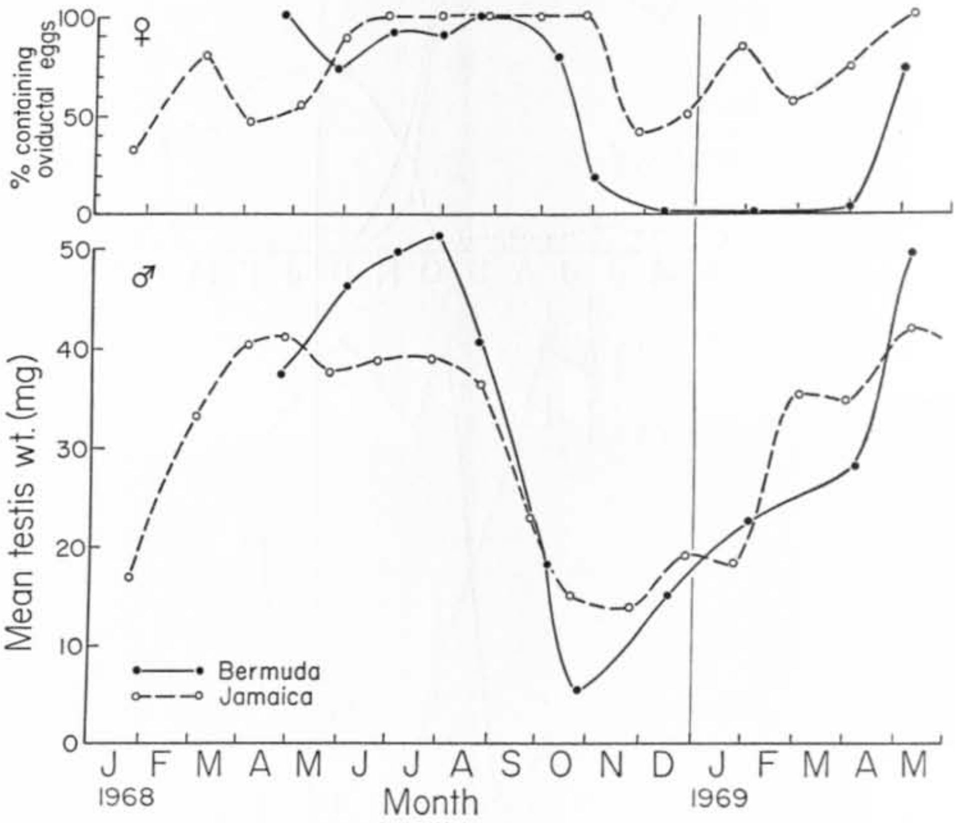

Fig. 15. Comparison of testis weight and female egg-laying cycles for *Anolis grahami* in Bermuda and Kingston, Jamaica. Data for females show the frequency of ovigerous (classes III and IV) females in each sample.

Distinct breeding seasons are the rule for temperate zone lizards, although the exact pattern of breeding activity varies. Several distinct testis cycles can be recognized on the basis of the timing of gonadal regression and recrudescence (St. Girons, 1963; Mayhew, 1968; Licht et al., 1969). Figure 16 summarizes these patterns of testis activity in temperate lizards and compares them with the testis cycles observed in the tropical species of *Anolis.*

In general, all four northern populations of *Anolis* examined (*A. carolinensis,* *A. grahami, A. sagrei,* and *A. distichus*) tend to have longer breeding seasons than most temperate species of lizards (fig. 16), but interspecific differences are also evident among these four *Anolis.* For example, testes remain enlarged in *A. grahami* in Bermuda (32° N) several months after regression is complete in *A. carolinensis* at about the same latitude in the United States (see fig. 14 and

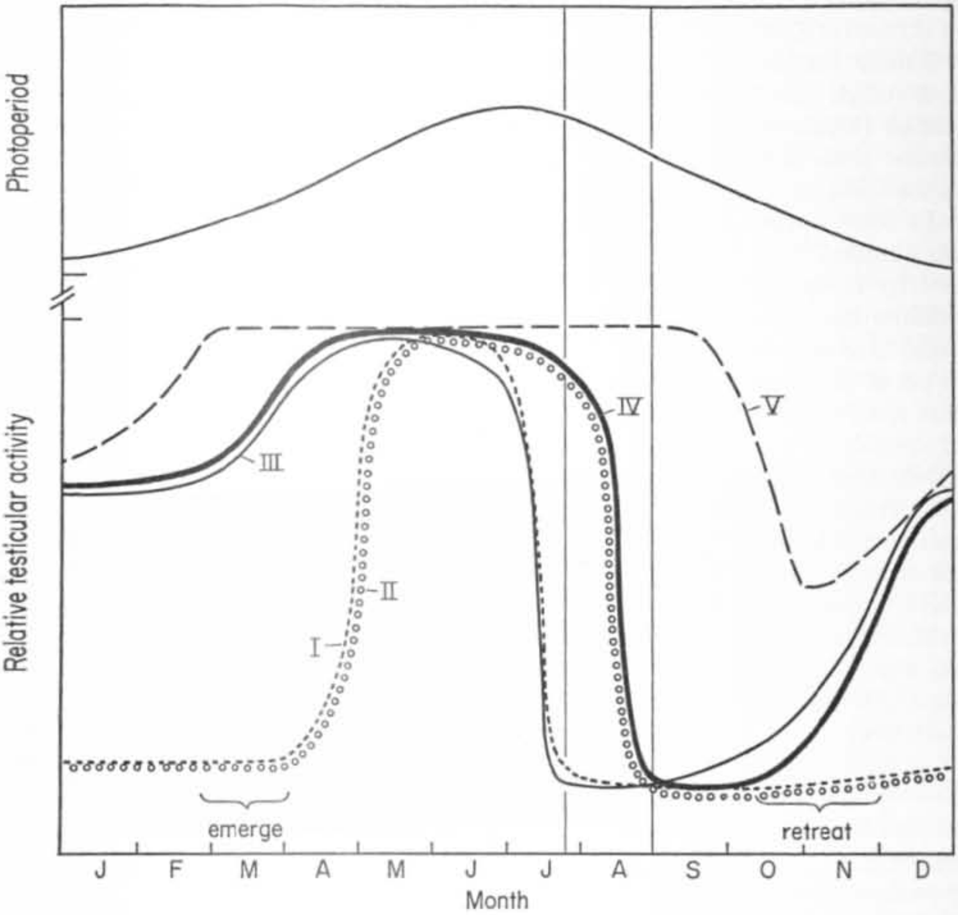

Fig. 16. Schematic representation of the diverse patterns of annual testicular activities in lizards. Patterns I to IV represent temperate-zone species (see further description in Licht et al., 1969). The testis cycle of the most temperate species of *Anolis (A. carolinensis)* is shown by type IV. Type V summarizes the "typical" testis cycle of the Caribbean *Anolis* examined in the present study.

The temperate species differ in the time when testis regress, when recrudescence commences, and in the rate of recrudescence. For example, recrudescence may occur before or after hibernation (times indicated by "retreat" and "emerge"). Fine vertical lines demarcate the times when most temperate species show a cessation of all spermatogenic activity. Data for temperate species modified from Licht et al. (1969, fig. 1).

Fox, 1958; Licht, 1967*a*). Also, *A. carolinensis* in south Florida undergoes testis regression at least a month earlier than do the *A. sagrei* (table 10) and *A. distichus* (King, 1966) in the same area. The testis cycles of the three introduced species seem to resemble the more southern species or populations more than that of the native *A. carolinensis*.

Similar interspecific comparisons are evident for female *Anolis*. The egg laying cycle of *A. carolinensis* in Louisiana (30° N) and south Florida (25° N) are similar (Dessauer, 1955*a;* King, 1966) and their breeding season is several months shorter than that of the two introduced species in south Florida (*A. sagrei* and *A. distichus*).

In four tropical islands studied (Grand Cayman, Hispaniola, Jamaica, and St. Vincent) there tends to be some seasonal fluctuation in the level of reproductive activity in one or both sexes of each species, but in each, at least one sex usually exhibits some reproductive activity throughout the year. Perhaps the most unusual finding in this regard is the pronounced cycle in testis weight that occurred in six of the seven species examined from these tropical islands, despite the fact that spermatogenesis and androgen production were evident in the vast majority of animals in all months. Furthermore, all of the species that showed such testis weight cycles tended to undergo testis regression at about the same time of year. This occurred in the autumn months at approximately the same time that the more pronounced testis regression was observed in the northern populations. In the females, egg production also fluctuated seasonally but there was more intra- and interspecific variability in the timing of these fluctuations.

The effects of these apparent changes in the amplitude of gonadal activity on the reproductivity of the population are considerably more difficult to evaluate than in the case where there is an obvious cessation of reproduction in both sexes. Such evaluations require consideration of the indices of reproductivity used here.

PROBLEMS IN THE INTERPRETATION OF THE REPRODUCTIVE DATA

Females.—The reproductive indices used in this study are based on the "standing crop" of gametes and such static samples must be used cautiously in estimating reproductive rates or "productivity." Hamlett (1952) estimated that female *A. carolinensis* in New Orleans could lay an egg approximately every ten days throughout the breeding season, but nothing is known about the dynamics of egg production in the tropical anoles studied. Egg production in *Anolis carolinensis* is temperature dependent (Licht, unpublished), and we have observed that captive anoles (especially *A. sagrei* and *lineatopus*) may retain the eggs in the oviduct for long periods (e.g., months). Thus, a high frequency of ovigerous females could result from a rapid rate of ovulation or from a temporary cessation of oviposition.

Our data suggest that if conditions were harsh enough to suppress almost fully reproductive activity in part of the population, even the few that remained reproductive might have a low rate of egg production. This postulate is supported by the comparatively small size of ovarian follicles in ovigerous individuals during periods of low reproductive activity. For example, in Jamaican *A. lineatopus,* in twelve of the months when the frequency of ovigerous females was above 70 percent, ovarian follicles averaged 4.7 mm in these ovigerous females. A significantly smaller average of 3.7 mm ($p < .002$) was found in the ovigerous females of the seven samples during the dry season when the frequency of ovigerous females was below 50 percent. In general, it seems a reasonable working hypothesis that gross changes in the frequency of females with enlarging follicles and/or oviducal eggs do reflect true changes in reproductivity of the population as a whole.

Although the lack of quantitative data on the dynamics of egg production precludes detailed interspecific comparisons of reproductive rates, our data suggest some interesting differences in reproductive "strategies" that may correlate with the stability of the climate. In the St. Vincent species, *A. trinitatis,* in which all females remain reproductive throughout the year, we never observed all females to be ovigerous in any month and two oviducal eggs were rare. Similarly, *A. richardi* rarely had two oviducal eggs. In contrast, in Jamaica where egg production is more cyclic, during the height of the reproductive season all females were ovigerous and half or more had two oviducal eggs at a time. The relative proportions of class III and IV individuals were similarly high during the breeding seasons in other populations showing pronounced seasonal egg-laying cycles; e.g., *A. cybotes* on Hispaniola (table 8), *A. grahami* on Bermuda (table 11), *A. distichus* and *A. carolinensis* in southern Florida (King, 1966), and *A. carolinensis* in Louisiana (Hamlett, 1952; Licht, unpublished). These data suggest the possibility that interspecific differences exist in the maximum rate of egg production and these may be related to the nature of annual reproductive cycles.

Males.—Accurate assessment of "reproductive activity" among males is not possible at present. In addition to considering gamete production, daily activities such as courtship, copulatory behavior, and territorial defense are probably controlled largely by steroid secretion of the testes and are associated with an "activated" reproductive system. It is clear that the marked decline in testis weight reflects a decline in the rate of spermatogenesis; i.e., fewer sperm are present in the testis tubules, the epididymis, and the vas deferens. The size of the accessory sexual structures (renal sex segment and epididymis) remains at least partially enlarged throughout the testis cycle in the majority of the population, indicating that testicular androgens are secreted even when testis size is diminished. Although we know that there is copulation and territorial defense throughout the year in the Lesser Antilles (Gorman, 1967) and Jamaica (Rand, 1967*b*) we have no quantitative information on the frequency or intensity of such activity.

Does a relatively low rate of sperm production reduce male fertility seasonally? We do not know. Reduced fertility combined with reduced frequency of mating could have important consequences on population dynamics. Fox (1963) found special receptacles for sperm storage in *Anolis carolinensis* and suggested that sperm might remain viable for as long as five months. Such an adaptation would afford adult females considerable independence of fluctuations in male reproductivity activity.

FAT CYCLES IN ANOLIS

Temperate zone lizards typically show annual cycles of fattening, with increased fat storage tending to occur in autumn before hibernation. Fattening usually occurs when the gonads are regressing and after sexual activity has been curtailed. The adaptive significance of these fat cycles may vary. In males of many species the fat stores are presumed to be a source of energy during "hibernation" but there is little direct information on this. Hahn and Tinkle (1965) have demonstrated that in females of *Uta* the fat is utilized as an energy source for the production of eggs following hibernation, and Marion (1969) suggested a similar situation for female *Sceloporus undulatus*.

None of the populations that we studied hibernate. All of these anoles are probably able to feed in all months of the year although there may be prolonged periods of inactivity with inclement weather during the winter in Bermuda and Florida. The adaptive significance of fat storage in these tropical lizards is not clear but the possibility must be considered that different factors may operate for different sexes or populations.

Pronounced annual fat cycles were found in all of the populations of *Anolis* examined. With the exception of the giant *A. richardi*, fat bodies tend to be completely reduced in most of the population during part of the year, with a marked increase occurring in a relatively short period. As a rule, this increase in the frequency and average size of fat bodies correlates with the decline in reproductive activity already discussed. For example, where the two sexes of a single species are out of phase reproductively (e.g., Jamaica), they are also out of phase in fattening.

The mechanisms underlying seasonal changes in fat storage have not been elucidated. At least three alternatives exist (not mutually exclusive) to explain increases of fattening: (1) increased food availability; (2) increased appetite (hyperphagia); (3) a change in energy partitioning, i.e., a decrease in energy utilization for various activities could lead to a greater storage of assimilated energy even if caloric intake remained constant or even decreased. Of course, different factors may predominate in different populations.

The question of seasonal changes in food availability is complex for insectivores such as *Anolis*, but seasonal fluctuations in food would be expected in most of the habitats involved. Janzen and Schoener (1968) compared insect faunas from three adjacent areas of increasing moisture during the dry season in Costa Rica. Numerous differences in the size, composition, and abundance of insects were observed in the regions with different amounts of moisture and it was inferred that seasonal changes in rainfall in one area might produce similar effects. Marshall and Hook (1960) working on lizards in Africa, Skutch (1950) working with birds in Costa Rica and Guatemala, and Snow and Snow (1964) working with birds in Trinidad also suggested that insect availability increased sharply after the beginning of the rainy season. However, it is not clear that such seasonal changes in the insects would be required or would account for observed fat cycles in the tropical *Anolis*. In the temperate populations of *Anolis* (*A. carolinensis* and *A. grahami*) and other temperate lizards, fattening occurs in late summer or fall but no attempts have been made to relate this to an increased abundance of insects. It is also noteworthy that the two sexes of a species in the tropics may fatten in different seasons, and males of different species fattened at approximately the same time in habitats with distinct patterns of rainfall (cf. Jamaica and Haiti).

Evidence for a seasonal change in appetite is sparse. Dessauer (1955*b*) and Fox and Dessauer (1957) showed that the appetite of *Anolis carolinensis* varies seasonally, and can be controlled by photoperiod. However, these studies indicated that food consumption would be highest during the warm, long days of the year. This corresponds to a time when the anoles are actually lean (Dessauer, 1955*a*). Since they normally fatten in the fall when temperatures and day length decrease, it is unlikely that fattening is due to hyperphagia. With regard to both appetite and food availability, it is noteworthy that Sexton, Bauman, and Ortleb (manuscript) failed to find any differences between dry and wet seasons in the quantity or type of food found in the stomachs of *Anolis limifrons* in Panama; this species undergoes seasonal fat cycles similar to those observed in the tropical *Anolis* species that we studied (Sexton et al., 1970).

Because of its large size, *A. richardi* probably devotes relatively less energy to reproduction than do other smaller species (e.g., Williams, 1966). Schoener and Gorman (1968) showed that male and female *A. richardi* in Grenada take different sized prey. Thus, the existence of fat cycles and sexual differences in fattening in this species may simply reflect seasonal changes in food availability. However, in all of the other species examined, fat stores showed a strong inverse correlation with apparent reproductive activity, and the most likely explanation for seasonal fattening for these species is a change of energy partitioning involving reproductivity. In the *A. trinitatis* on St. Vincent, there was a relatively long lag between the decline in testis weight and fattening, but a correlation between fat storage and reproductive activity is still evident; in this species, only the males showed a distinct gonad cycle and they were also the only ones to fatten.

The best evidence for the above hypothesis, albeit indirect, is in the study (Gorman et al., 1970) of hybrids between *A. trinitatis* and *A. aeneus* on Trinidad. Collections made in July of 1966 and 1968 showed that the parental species had relatively high testes weights, and virtually all females were reproductive (these were comparable to *A. trinitatis* on St. Vincent). Both sexes lacked dissectable fat bodies. Spermatogenesis occurs in hybrid males, although they are largely sterile because of impaired meiosis (Gorman and Atkins, 1968) and degeneration of spermatids (Gorman et al., 1970). Androgen production appeared normal (sexual accessory structures are developed, and they mate and defend territories). The hybrid males also lacked fat bodies. The hybrid females are also largely sterile—few have eggs—and in contrast to normal animals, almost all hybrid females had relatively large fat bodies. Since the parental species and hybrids all live in the same small area, food should be equally available to all. However, only those individuals (hybrid females) not actively engaged in reproductive activities were fat.

The interpretation of the relationship between fattening and reproductive energy requirements is based upon the premise that the lizard is generally unable to obtain sufficient excess energy to fatten at times when reproductive activity is high. Only in the large species, *A. richardi,* do we find some fat present at all times of the year, with periods of marked increases and decreases in fattening that do not correspond to obvious changes in reproductivity. While there is some danger of circular reasoning, the inverse correlation between fattening and decreased testis weight or female reproductivity lends support to our conclusion that our "static" measurements reflect real changes in reproductivity in the two sexes.

ENVIRONMENTAL CORRELATIONS WITH REPRODUCTIVE AND FAT CYCLES

Final analysis of the nature of the relationship between climate and annual physiological cycles such as those observed in reproduction and fat storage must await careful laboratory experimentation. However, valuable insights into these problems can often be gained from examining correlations between natural cycles and the local climate. Our objective here is to call attention to the various correlations that we observed between reproduction and fattening and to review the literature dealing with such environmental correlates for tropical lizards.

Photoperiod, temperature, and rainfall have frequently been shown to influence vertebrate breeding cycles. Many references to these factors have already been made in the individual species accounts of reproductive and fat cycles, and in some cases very obvious correlations were evident. However, before examining these correlations, it is important to recognize the interdependency of these three factors.

The definition of "wet" and "dry" seasons is dependent on many aspects of the climate besides monthly rainfall values; e.g., the temporal distribution of rain, wind, vapor pressure, and temperature may all contribute to the extent of environmental dessication. Unfortunately, we did not have sufficient direct experience to ascertain the full impact of rainfall cycles on the environment in most cases, and the errors involved in our use of monthly rainfall of 50 mm or less to define the "dry" season is recognized.

Although the standard meteorological data indicate that the tropical habitats have very uniform temperatures, several additional factors must be considered in evaluating the thermal relations of lizards. The ability of lizards to exercise control over body temperature by behavioral means is well established, and indeed, such behavioral thermoregulation has been demonstrated in many anoles including several of the species studied here (Rand, 1967*a,b;* Ruibal, 1961; Schoener and Gorman, 1968; Heatwole et al., 1969; Licht, 1968, 1969*a*). While active during the day, these lizards will probably maintain body temperatures near 28° to 34° C, and body temperatures will cool to near ambient levels at night. Since lizards depend largely on insolation to warm to preferred levels, the duration of daily heating will depend on the photoperiod. Likewise, thermoregulation may be curtailed during periods of heavy rainfall, or when cloud cover is dense. Thus, in the Caribbean, some reduction in average daily body temperature would be expected in the "winter" months since these tend to be wettest. With regard to mean monthly minimal temperatures (which best reflect the level of nocturnal cooling), the possibility must be considered that the rate of cooling after sunset may vary even though average minima are constant. In any case, nocturnal cooling will be most extensive during the winter when nights are longest. Thus, it is difficult to separate fully the effects of photoperiod and rainfall from temperature.

Rainfall.—Strong correlations were evident between the dry season and reduced reproductive activity of females of the three species of *Anolis* on Jamaica, and similar trends were evident in *A. trinitatis* on St. Vincent, *A. cybotes* on Haiti, and *A. conspersus* on Grand Cayman. Rand's (1967*b*) observations of seasonal variation in the appearance of young *A. lineatopus* around Kingston, Jamaica, support the conclusion of seasonality in egg production in this population. Differences among these species may be due partly to differences in the severity of local conditions and in inherent interspecific differences in responses to a given set of conditions. For example, the relatively minor decline in reproductive activity on St. Vincent is consistent with the relatively brief dry season in that habitat. However, comparison of the differential response of the two syntopic species in Jamaica (*A. lineatopus* and *A. grahami*) suggest that *A. lineatopus* is more susceptible to the effects of the dry season. The fact that the timing of reduced reproductive activity in these species varies from year to year depending on yearly variations in rainfall patterns suggests that these tropical species are potentially capable of continuous or constant reproductivity, and that they are responding somewhat "opportunistically" to local climatic conditions.

Recent studies on several other tropical anoline lizards suggest that the dependence of egg production on rainfall is a widespread phenomenon in this group. Demographic studies on *A. limifrons* in Panama showed a seasonal variation in recruitment of young that appeared correlated with rainfall (Sexton et al., 1963; Heatwole and Sexton, 1966), and more detailed phenological data on reproductive activity have lent further support to this hypothesis (Sexton et al., in preparation). Similar reductions in egg laying during dry seasons also occurred in two other species (*A. auratus* and *A. tropidogaster*) in the area. In contrast, Campbell (personal communication) found no obvious seasonal variation in the recruitment of young in two species of anole (*A. lionotus* and *A. poecilopus*) in central Panama; but these two occupy stream-side habitats where the effects of seasonal dry periods would probably be ameliorated.

Data for *A. pulchellus* in Puerto Rico (Heatwole, personal communication) show that the frequency of ovigerous females and the mean size of ovarian follicles are lowest during the dry season, in January. On St. Croix, a relatively dry area in the Virgin Islands, the frequency of ovigerous females reaches a peak in the wettest months (Ruibal, personal communication). In all of these cases, where data are sufficient, year to year variations in the timing of reproductive changes are evident, and these are correlated with variations in the onset of the dry and wet seasons as we observed in Jamaica. *A. nebulosus* on the west coast of Mexico (about 21°N) shows a cessation of male territorial behavior and aggressiveness between October and December, with a return in such behavior starting in January, and females also appear nonreproductive between September and May (Jenssen, 1970). Jenssen stressed that the breeding season coincides with the rainy season, but it should also be pointed out that the cessation of breeding also coincides with the decline in photoperiod and the winter months are relatively cold.

Fitch (1970) has compiled scattered data for several other anoles not mentioned above. In most cases, data are insufficient to construct breeding seasons but in at least two, *A. humilis* and *A. tropidolepis* in Costa Rica, egg laying seems to occur in all months (testis activity was not examined). Climatic conditions were not given for these species.

Seasonal changes in rainfall have also been implicated in the seasonality of reproductive activities in several other groups of lizards in both the Old and New

World Tropics. Perhaps the best documented case is that of *Agama agama* on the equator in east Africa (Marshall and Hook, 1960). The males did not show a distinct seasonality in reproduction (although testis weights and fat bodies were not measured quantitatively), but the females were reproductive only after heavy rains. Analysis of stomach contents suggested that insect food increased markedly at this time, and it was suggested that egg production depended on this protein-rich diet. A similar phenomenon was observed in populations of this species in Ghana at ca. 5° N, except that there was also some suggestion of a testis cycle here (Chapman and Chapman, 1964). In Liberia (7° 05′ N), this *Agama* breeds in all months but egg production and testis weights peak in the late dry and early wet season (Daniel, 1960). A similar correlation of peak breeding activity with the wet season was observed in *Agama cyanogaster* and also a skink, *Mabuya striata*, in Tanganyika at 8° S (Robertson, Chapman, and Chapman, 1965). Preliminary evidence for a variety of other species in Tanganyika suggested a similar relation between egg production and rainfall (Robertson, Chapman, and Chapman, 1962). Wilhoft (1963, 1965) suggested that varying rainfall might account for seasonal variations in egg production in the skinks *Leiolopisma rhomboidalis* and *L. fuscum* in Australia at 17° 30′ S, although photoperiod could not be ruled out. In the Neotropics, *Iguana iguana* appear seasonal but lay their eggs primarily during the dry season (Rand, 1968). Mayhew (1966) found a correlation between rainfall and reproductive activity in both sexes of the lizard *Uma notata* in the deserts of southern California.

In contrast to the above studies, egg laying tends to be relatively constant in tropical and equatorial populations where rainfall is constant. Inger and Greenberg (1966) concluded that at least four species (including two geckos and two agamids) had relatively constant egg production in Borneo (1° 37′ N) and suggested that the same lack of a breeding season probably characterized six other species in the area. In Java, where there is some seasonality in rainfall but where a distinct dry season was lacking, Church (1962) found little seasonality in reproductive activities of three species of gekkonids (representing three genera).

The physiological bases for the observed relationships between reproduction and rainfall are obscure. It is not known whether the reduction or cessation of egg production in the dry season results from a direct physiological stress on the female or whether saurian reproduction is adaptively timed to avoid producing eggs in a season that might be suboptimal for the survival of eggs or young. In *Agama agama* (Marshall and Hook, 1960) and *Uma notata* (Mayhew, 1966), the effects of rainfall on reproduction appeared related to changes in food supply, especially insect abundance. While such an effect cannot be ruled out for the *Anolis*, it seems unlikely. The invariable fattening that occurred in *Anolis* during the dry season (when egg production was minimal) suggests that the food supply was not severely depressed at this time, and there is no evidence for a shift toward herbivory as in *Agama agama* that would account for this fattening.

Sexton et al. (1970) also found that the fat reserves of female *A. limifrons* in Panama were highest during the dry season when egg production was relatively low. As mentioned earlier, Sexton, Bauman, and Ortleb (manuscript) found no seasonality in stomach contents indicating that the same general type and quantity of prey were taken in wet and dry seasons.

The relatively rapid decline in the proportion of reproductive females that occurred among the Jamaican anoles at the beginning of the dry season (before appreciable environmental drying was likely to have occurred) raises the possibility that the females might be able to "anticipate" or at least "recognize" the advent of the dry season. On the other hand, the magnitude of the decline in egg production (including enlargement of follicles and ovulation) appears to be associated with the severity and duration of the dry season; in Jamaica, egg production ceased only at the end of an usually prolonged dry season. These observations suggest that the dry conditions may be acting as a direct physiological stress on the female independent of whether conditions are suitable for the eggs or hatchlings.

Reproductive activity in the males of the tropical species clearly does not show the same dependence on rainfall that is evident in their females, and rainfall is not clearly implicated in the reproductive cycles of either sex in the northern latitudes. Even though there is some overlap between reduced testis activity and the dry season in the Caribbean (e.g., fig. 9), it seems unlikely that seasonal variations in rainfall can account for testis cycles. The timing of testis regression and recrudescence are relatively regular and do not correlate with year to year variations in the onset of the dry season. The regression in testis weight in the three Jamaican species (fig. 9), *A. trinitatis* on St. Vincent, *A. conspersus* on Grand Cayman, and *A. cybotes* in Hispaniola, coincides with the middle of the wet season. The same timing for testis regression is observed in *A. grahami* on Bermuda and *A. carolinensis* in New Orleans (Licht, 1967*a*) and Miami (King, 1966) even though rainfall patterns are very different from the Caribbean Islands. Studies of several anoline lizards from Panama at about 9° N latitude showed a similar decline in testis weight and activity in mid-winter but the exact timing of regression was not determined (Sexton et al., in preparation).

In Bermuda, egg production in *A. grahami* tended to cease during the wettest time of year. The same phenomenon is observed for *A. carolinensis* in Louisiana (Dessauer, 1955*a*). Thus, the adverse dry season effect evident in the Caribbean is absent in these. Although the relationship between rainfall and egg production is especially difficult to evaluate for species in intermediate latitudes, such as southern Florida, there is no clear dry season effect. Both *A. carolinensis* and *A. distichus* in the Miami area are completely nonreproductive during the early part of the dry season (starting in November); however, both species tend to become reproductive again by February or March, in the middle of the dry season (King, 1966). Thus, the nonreproductive season also coincides with the period when day lengths are shortest and average temperatures are relatively low. Our limited data for *A. sagrei* around Miami (table 10) suggest a similar phenomenon. Furthermore, the *A. carolinensis* in Miami (King, 1966) probably cease egg production in September, several months before the onset of the dry cool season.

Photoperiod—The general timing of the testis cycle, the repeatability from year to year, and the relatively uniform timing of testis regression among the various species suggest that photoperiod (or some closely associated factor) may be important for regulating male reproductive activity. Specifically, the timing of testicular regression suggests that short or decreasing day lengths may be important. However, there is little evidence to indicate that increasing day lengths are important for subsequent testicular recrudescence. It is also possible that photoperiod may be an important proximate factor for the regulation of female reproductivity in the northern populations; notably, *A. grahami* in Bermuda and *A. carolinensis* in the southern United States.

There is considerable experimental evidence for photoperiodism in at least the males of one anole, *A. carolinensis* (Fox and Dessauer, 1958; Licht, 1966, 1967*a*,*b*, 1969*a*,*b*). These experiments have demonstrated that short day lengths (below 13 hours) can induce testicular regression in at least some seasons, and it seems likely that such photoperiodism is responsible for the natural regression of the testis in this species (Licht, 1970 and unpublished data). Further, it is also well established that testicular recrudescence in late winter and spring are essentially independent of day length; and, in fact, *A. carolinensis* is not photosensitive at this time (Licht, 1967*a*,*b*, 1970). Preliminary experiments (unpublished) with several of the Caribbean *Anolis (A. grahami, A. lineatopus, A. sagrei, A. cybotes,* and *A. trinitatis)* have revealed conspicuous interspecific variations in photoperiodic responsiveness.

Details of the field data suggest that there are interspecific differences among the factors that cause testicular regression, even though testis cycles among various species may appear relatively synchronized. For example, in both years of study, the *A. grahami* in Jamaica underwent testis regression about a month earlier than the sympatric *A. lineatopus* and *A. sagrei.* Experimental studies with *A. carolinensis* from Louisiana demonstrated that complete testis regression (with cessation of spermatogenesis) can be induced within 4 to 6 weeks after June by day lengths of about 13 hours or less over a wide range of temperatures (Licht, 1967*a*,*b*, 1969*b* and unpublished data). Thus, this species would be expected to show complete testicular regression by mid-September at any latitude between St. Vincent and Bermuda; this is about two months earlier than maximal testis regression occurs in the species living in these areas. Thus, if the five species of *Anolis* studied here are photosensitive, they must differ in the threshold for regression (critical day length) and also in the amplitude of the response, since testes do not regress completely in most of the southern species.

The difference in extent of spermatogenic regression between *A. cybotes* on Hispaniola and the four species studied at about the same latitude on Jamaica and Grand Cayman may also reflect interspecific differences in photosensitivity. It is difficult to account for the more complete regression on Hispaniola by either temperature or photoperiod since the islands are very similar in these respects during December (c.f. figs. 5 and 10).

The relative importance of photoperiodic influences on the reproductivity of the female anoles is more difficult to evaluate because of a sparsity of experimental data. Preliminary experiments (Licht, unpublished) suggest that long day lengths may accelerate but are not required for recrudescence of the gonads in female *A. carolinensis* in the spring; information on autumnal regression is lacking. The reduction in egg laying in the Caribbean species occurs during the season of declining or minimal photoperiod. While a photoperiodic effect cannot be ruled out, the strong correlation with rainfall already discussed suggests that photoperiod is not an important proximate factor in these females. Since the cessation of egg laying in the Bermuda *A. grahami* coincides with decreasing day lengths with no obvious correlation to rainfall, there is a greater possibility of photoperiodic effects in this population. However, there is no evidence for photoperiodism in the "parental" population of female *A. grahami* on Jamaica where the day length is reduced to 11 hours, 3 minutes during December. In Bermuda, egg production ceases completely in mid-October when day lengths are about 11 hours, 18 minutes and does not commence again until April when day lengths are above 12.5 hours. Hence, on the basis of this rather simplistic consideration of photoperiod, it seems unlikely that egg laying in Bermuda is controlled by photoperiod alone (this discussion does not take into account the possibility that the "effective" day length to which the lizards are exposed differs from this standard value, or that the Bermuda population may have evolved increased photosensitivity in the approximately sixty years it has been on the island).

Baker (1947) concluded that photoperiod, and particularly decreasing day lengths, had important effects on reproduction of both sexes in the lizards he studied in the New Hebrides at 15° S, and Charnier (1965) made a similar suggestion for the male *Agama agama* in Dakar at 15° north latitude. In the latter study, pronounced temperature fluctuations with a prolonged, cold dry winter prohibit the elimination of temperature and rainfall as possible factors underlying testis regression. In Liberia (7° 05′ N) testes in *Agama agama* were minimal in size in the winter months. Although Daniel (1960) suggested that this was related to rainfall, the possibility of a photoperiodic effect could not be ruled out. It is also noteworthy in this regard that there is considerable controversy concerning the importance of day length as a proximate cue for the regulation of avian breeding cycles in the tropics (Snow and Snow, 1964; Lofts and Murton, 1968).

Temperature.—There is a wealth of data regarding the effects of temperature on the reproductive physiology of reptiles. In evaluating the correlation between reproductive cycles and temperature, the possibility must be considered that temperature changes are being used as proximate cues for timing reproduction or that these thermal changes are acting as a direct stress on the individual, perhaps directly on the reproductive tissues (Cowles and Burleson, 1945; Licht, 1965; Licht and Basu, 1967).

Marked effects on reproductive activities in male *Anolis* (especially with regard to photoperiod responses) have been demonstrated to occur with a change of only a few hours in the daily heating pattern (Licht, 1969*b*). Consequently, even relatively small seasonal changes in temperature must be taken into account in attempts to explain seasonal changes in reproductivity. In particular, it is possible that thermal effects may act directly on the reproductive processes of the individual or, as suggested by experiments with *A. carolinensis*, thermal conditions may be extremely important for the lizard's response to other factors, especially photoperiod.

It seems likely that temperature effects may underly the difference in testis regression observed between the Jamaican and Bermuda populations of *A. grahami* (fig. 15) and possibly the Jamaican and Florida populations of *A. sagrei.* The considerably lower temperatures that occur during the winter in the north might be responsible for the more complete suppression of spermatogenesis and androgen production that occurs there.

In the case of the female there is good evidence that egg production in some northern habitats is directly suppressed by low temperatures since there is no evidence of photoperiodism in the females of this species in Jamaica. Such temperature effects for *A. grahami* are indicated by the correlation between the egg-laying season and falling and rising temperatures. A similar phenomenon is suggested for the *A. carolinensis* and *A. distichus* in southern Florida (King, 1966) and for *A. carolinensis* in Louisiana (Dessauer, 1955*a*).

CONCLUSIONS REGARDING THE ENVIRONMENTAL INFLUENCES ON REPRODUCTION

The data obtained for the various populations of *Anolis* studied here suggest that several different factors must be considered in determining the mechanisms regulating reproductive cycles: (1) The reproductive biology of the two sexes of a single species may be responsive to different climatic factors. This seems most striking in the southern latitudes where reproductivity of females correlates primarily with rainfall whereas in males the correlation is with either photoperiod or temperature. (2) Different climatic factors may be the major proximate mechanisms for regulating reproduction in different habitats. These local differences apply to interspecific and intraspecific populations. For example, rainfall is probably very important in the tropical areas and temperature is important in the more northern areas. (3) In addition to local climatic differences, interspecific variations in reproductive patterns may be due partly to inherent species differences in the responsiveness or sensitivity to rainfall, temperature, and photoperiodic changes, but such variations do not correlate with taxonomic groupings.

SUMMARY

A comparative study of annual reproductive and fat cycles was undertaken in seven species of lizards of the large tropical genus *Anolis*. Samples of each species (from nine localities) were made monthly over a period of one to two years. Studies were centered in the Caribbean on islands where most of the species examined were endemic. These included: *A. richardi griseus* and *A. trinitatis* on St. Vincent; *A. sagrei, A. lineatopus,* and *A. grahami* on Jamaica; *A. cybotes* on Hispaniola; and *A. conspersus* on Grand Cayman. Introduced populations of *A. sagrei* in southern Florida and *A. grahami* on Bermuda were also examined. These localities range from about 13° to 32° north latitudes, and encompass a diversity of climates. Attempts were made to correlate seasonal variations in reproductivity and fattening with climatic changes, with special reference to photoperiod, temperature, and rainfall.

In general, reproductive activity was most constant in the two species in the southernmost habitat, St. Vincent, where the climate was most moderate and stable. In all of the other Caribbean populations, both sexes showed some seasonal fluctuations in reproductivity, but some reproductive activity was evident in almost all months. The males (including *A. trinitatis* on St. Vincent) underwent a distinct annual cycle in testis weight suggesting a reduction in the rate of sperm formation, although spermatogenesis and androgen production rarely ceased completely. The females showed a marked seasonal reduction in the rate of egg production in all habitats, except St. Vincent. The two introduced species in the north (in Florida and Bermuda) showed the most pronounced reproductive cycles with a complete cessation of spermatogenesis and egg production for several months in mid-winter. However, the reproductive seasons of these two species were longer than most temperate-zone lizards and longer than the native temperate anole, *A. carolinensis*. Reproductive cycles of the two sexes of each species are not synchronized.

There was a pronounced inverse correlation between fat storage and apparent reproductive activity. Both sexes showed a conspicuous increase in the size of abdominal fat bodies when gonadal activity was reduced. Some seasonal fattening was evident in both sexes of all species examined. It is suggested that increased fattening reflects the decreased expenditure of energy for reproduction (e.g., gamete formation, development of associated reproductive structures and sociosexual behavior) rather than being due to seasonal changes in appetite or food availability. The "giant" *A. richardi* may represent an exceptional case.

The timing of testis cycles was generally similar in all species, from south to north, with minimal weights occurring in "winter" months (usually between October and January). Within each species the timing of cycles was regular from year to year, but significant interspecific differences (of a month or more) were evident in the precise timing of testis regression, suggesting inherent differences in the physiological responsiveness to environmental factors among the species. The testis cycle does not appear to be controlled by rainfall (i.e., wet and dry

seasons). Testis activity may be controlled by photoperiod, temperature or some interaction between the two; the more pronounced regression observed in the north may be related to the much colder winters.

There is a strong correlation between female reproductivity (e.g., egg production) and rainfall in the Caribbean. Egg production tends to decline with the advent of the dry season and increases abruptly with the beginning of the rainy season. The extent of the decline in egg production correlates with the severity (e.g., duration) of the dry season. These correlations were particularly striking in Jamaican species. Egg production in the northernmost population (*A. grahami* on Bermuda) appears independent of rainfall and may be dependent on temperature. Most of the females are probably potentially continuous breeders with seasonal cycles resulting from local climatic stresses.

A review of the literature on reproductive activity among tropical lizards suggests that the dependence of females on rainfall may be widespread. Information on the cyclical activity of males detailed in this investigation has not been presented previously.

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