REPRODUCTIVE BIOLOGY OF LIZARDS ON THE AMERICAN SAMOAN ISLANDS

By

Terry D. Schwaner

The reproductive biology of most lizards is poorly known. This is particularly true for tropical species, and most especially for island populations in the Pacific region (Brown, 1956; Inger and Greenberg, 1966; Fitch, 1970; Duellman, 1975). This study concerns certain aspects of the reproductive biology of 12 species of lizards on the tropical Pacific islands of American Samoa. There are no published studies describing lizard reproduction on these islands. The species accounts presented here summarize basic data on male and female sizes (snout-vent lengths) at reproductive maturity, clutch sizes, descriptions of eggs, incubation periods, and hatching sizes. Data on some species are sufficient to suggest relationships between climatic variables and monthly frequencies of fecund and ovigerous females and to indicate patterns in annual reproductive activity. Reproductive modes for these and other species are summarized from the basic observations and discussed in terms of reproductive strategies (Tinkle, et al., 1970; Duellman, 1978).

Limitations of data include: (1) size at maturity for males was estimated from measurements of testes lengths and the presence of enlarged convoluted tubules in freshly preserved specimens, not from sections or smears of testicular tissue from which the presence of visible sperm can be detected; (2) small samples for a few species do not always reflect the full range of snout-vent lengths from hatchlings to adults; and (3) samples were not taken during all months of the year, and sample sizes for any given month represent the total collections from several habitats and islands.

*Museum of Natural History, University of Kansas, Lawrence, KS 66045. Present address: The South Australian Museum, Adelaide 5000, South Australia.
Previous studies have shown that monthly samples are essential detecting annual reproductive cycles in temperate areas with fixed fluctuations in mean monthly temperatures and rainfall ch. 1954, 1956, Fitch and Greene, 1965; Mount, 1963; Tanner, 1967. Similarly, monthly samples necessary in equatorial tropical areas where temperatures remain relatively constant, but where fluctuations in precipitation currently dictate corresponding seasonality in the reproductive activity of lizards (Sechrist, 1965; Fitch, 1973; Bitulal, et al., 1972; Brown and Sexton, 1978, Andrews and Rund, 1974; Gorman and Licht, 1974; Crump, 1974; and, Duellman, 1978). Additionally, reproductive patterns in lizards are relatively seasonal in areas where both temperatures and rainfall are constant year round (Rigler and Greenberg, 1960). The symmetry of annual temperature and rainfall in American Samoa and patterns in species these variables and other climatic parameters with the monthly frequencies of reproductive activity in certain lizard species. Following the evidence of Inger and Ackermann (1960), if annual climatic patterns are relatively constant, there should be little seasonality in the reproductive activity of lizards in American Samoa. In discussing the reproductive strategies of lizards in American Samoa, I recognize Willard, Tinkle and Collin's (1974) list of components to a life history study. These are clearly summarized by Duellman (1978) as follows: (1) mortality schedules of juveniles and adults, (2) age at first reproduction, (3) reproductive life-span, (4) fecundity (including number and size of eggs, frequency of oviposition, and proportion of females breeding), (5) the fecundity-reproduction tradeoff, (6) degree of parental care, and (7) reproductive cost. My data partially satisfy components 2, 4, 5, 6, and 7, but are insufficient for the others.

As an index of reproductive effort I have used the ratio of clutch weight (wet weight of oviducal complement in preservative) or total, wet body weight and converted the mass ratios to caloric contents using the formula of Vitt (1976). C/W = 1.8919 (WW/WW). C/W = 0.04640, or C/C = 1.8919 (WW/WW), where C = clutch weight (clutch caloric content of total body + clutch calories), WW, is wet weight of clutch, and W, is wet weight of total body + clutch. These indices and the evidence for annual reproductive activity are compared among coring of American Samoa. The results were discussed in terms of the two generally recognized reproductive strategies in lizards (Tinkle, et al., 1970, Duellman, 1978): (1) early maturing species with annual multiple broods, and (2) late maturing species with single broods annually. These (non-exclusive)

Data for the species in American Samoa presented herein offer interesting comparisons with those views, for although relatively few species are found on these islands, the lizard fauna has been assembled from non-endemic, rafting colonizers with notably different
techniques. The distribution of lizards in American Samoa is discussed by Amerson, et al., 1978, and Schwazer, 1978; major collecting localities for specimens reported herein may be found in these references. The twelve species in American Samoa are allendemic, widespread lizards on islands throughout the Pacific area and elsewhere. Some species are among those lizards with the greatest known geographic distributions. A total of 2047 specimens were examined during this study; individual reproductive data was obtained by dissection of preserved material. Field caught individuals were preserved in 10% formalin and later transferred to 70% ETOH. External measurements were taken with vonner calipers or a millimeter rule on preserved specimens only (except for a small series of Eumeces cyanura which were weighed on a 0.5 g Pelouze spring balance in the field prior to preservation). Snout-vent length to the nearest 0.5 mm was measured taking the distance from the anterior edge of the eye to the tip of the nostril. The body cavity was opened by midventral or lateral incision and the following data recorded: (1) sex, (2) reproductive condition of ovaries and oviducts, or testes, (3) number and length (greatest diameter) of all developing ova, oviducal
eggs, and testes to the nearest 0.1 mm, and (4) wet weight (to the nearest 0.1 g) of the entire clutch complement and combined weight of clutch and body of ovigerous females.

Reproductive status was judged as: (1) immature, for hatchlings and males with small, undeveloped testes (< 2.0 mm), lacking convoluted tubules, or females with small whitish ova (usually less than 1.0 or 2.0 mm in size) and narrow oviducts, (2) maturing, for males with slightly enlarged testes (> 2.0 mm), lacking well developed convoluted tubules, and for females with enlarged, yellowish, developing ova (fecund), without noticeably distended oviducts, (3) mature, for males with enlarged testes and convoluted tubules, and females with oviducal eggs (ovigerous), and (4) old mature, for males in similar condition to (3), but with greatly enlarged and vasculated testes, and for females with greatly enlarged oviducts, and small developing ova (recently spawned). These categories are rather arbitrarily defined, but, they facilitate an orderly separation of males and females into age (size) classes of recognizable reproductive condition.

Clutches of eggs, when found in the field, were placed in loosely tied plastic bags with some of the substrate on which they were found, if the nest material was moist, it was occasionally sprinkled with water so as to maintain moisture levels during incubation of the eggs. For gecko eggs the nesting substrate was usually dry, so eggs were loosely covered in dry paper toweling before placing in plastic bags. Laboratory temperatures during incubation approximated ambient air temperatures in shade during the day (24-28°C), and were probably slightly lower than those in the field. Most hatchlings were photographed and preserved immediately, but none (E. nigra) were maintained alive on a diet of small insects for several weeks to ascertain changes in color pattern.

**Results**

*Eumeces nigra*

This large diurnal skink was caught on the ground (where it forages widely), and on tree trunks (where it basks) within 3 m of the ground. At night I found two individuals, one under a rock and another in an epiphytic fern about 2 m from the forest floor.

**Nights.**—The 104 specimens have snout-vent length of 41-121 mm (Fig. 1). Individuals less than 90 mm generally have small, whitish testes (usually below 5.0 mm in length) lacking enlarged convoluted tubules. Testes sizes for individuals with snout-vent lengths greater than 90 mm deviate noticeably upward (exponentially) from a regression line fitted to individuals less than 90 mm in length (Fig. 2; F = 1.11 X 3.90, S = 30, p < .001). Testes of most individuals above 90 mm are heavily convoluted and highly

![Graph](image.png)

**Reproductive Condition**

![Graph](image.png)

**Fig. 1.**—Reproductive condition and snout-vent length (SVL in mm) of *Eumeces nigra* from islands of American Samoa. Reproductive condition: (1) immature, (2) maturing, (3) mature, (4) old mature (see text for further explanation). Solid circles are males; hollow circles, females.
and three clutches found in the field, is 2.32 (range = 2.4). There is a slight, but non-significant increase in clutch size with female snout-vent length (Fig. 3A). A few large females (> 100 mm SVL) had only one egg (all with thick leathery shells) and could have laid an egg or two just prior to capture. These data confirm Green's (1990) note on clutch sizes of 10 gravid *E. nigra*. The diameters of 84 oviducal eggs measured 13.5-22.1 mm ($\bar{X} = 19.0$ mm) and closely approximated the length x width of freshly laid eggs ($\bar{X} = 19.5 \times 13.5$ mm, range = 13.0-20.0 x 12.0-13.0 mm, n = 71).

Incubating eggs of *E. nigra* swell in size, presumably by absorbing water, and are 3.4 mm larger in length and width ($\bar{X} = 22.0$ x

Fig. 3.—Clutch size versus body size for (A) *Eumeces nigra*, (B) *E. asper*, (C) *E. lactea*, (D) *E. asper*, (E) *E. pyromas*, (F) *Gecko gecko*, (G) *Cnemidophorus edwardsi* from islands of American Samoa. Clutch size based on viviparous and ooviviparous females. Dots represent individual lizards.
18.0 mm, n = 7) at hatching thus at parturition. Eggs not placed on moist soil or paper toweling shriveled and failed to hatch under laboratory conditions.

Three clutches of eggs were taken from a birdnest fern (Asplenium nidus, Polypodiaceae) and under rotting stumps of coconut trees. Times from collection to hatching are 30-65 days; as a conservative estimate, two months is probably the usual incubation time for eggs in the field.

Hatchlings have snout-vent lengths 34.0-41.0 mm (X = 38.1, n = 10) and differ markedly from juveniles and adults in color pattern (Schwartz, 1979). In one hatchling reared in the laboratory, the pattern begins to change in about two weeks and after three weeks the individual sex is indistinguishable in color pattern, although smaller in size, from most juveniles and young adults collected in the field.

Eunice ameaeae

This large diurnal skink was caught primarily on tree trunks and in low vegetation (where it forages and basks) from new ground level to several meters above the ground. Nests were observed at night, but several individuals were seen perched in trees at sunrise and sunset.

Males.—The 116 specimens have snout-vent lengths of 66-118 mm (Fig. 4). Individuals less than 90 mm generally have small whitish testes (16.0x 4.0 mm in length) lacking enlarged convoluted tubules; specimens 90-100 mm snout-vent length have slightly enlarged testes. Reproductively active males greater than about 95 mm snout-vent length deviate normally upward from a regression line fitted to individuals less than 95 mm in length (Fig. 5: Y = 0.1X-4.78, r² = .63, p < .001). Testes sizes for individuals above 95 mm snout-vent length cluster near 8.0-9.0 mm, thus males probably mature about 90 mm snout-vent length. Males with enlarged testes were found during all months of the study, suggesting that reproductive activity probably is year round.

Females.—Of 81 females having snout-vent lengths of 71-114 mm, the smallest fecund female (developing ova > 4.0 mm) is 84 mm and the smallest with oviviparous eggs is 95 mm (Fig. 4). Thus, the size at sexual maturity of female E. ameaeaeae is probably 84-95 mm.

Mean clutch size, based on 20 fecund and 10 ovigorous females, is 6.1 (range = 4-7). There is a significant increase in number of oviviparous eggs with female snout-vent length (r = .65, p < .05, Fig. 3B). Greer (1966) examined a single gravid E. ameaeaeae with 5 oviviparous eggs. The diameters of 80 oviviparous eggs measured 8.6-14.5 mm (X = 12.3 mm); average egg length x width at parturition is 14.5 x 9.5 mm (range = 14.0-15.0 x 9.0-10.0 mm, n = 2). These eggs also swell in size during incubation; at hatching one egg meas-

![Reproductive Condition](Fig. 4—Reproductive condition and snout-vent length (in mm) of Eunice ameaeaeae from locality of American Samoa. Half-shaded circles are juveniles, star is a hatching. Other symbols are as in Fig. 1.)

ured 15.5 x 10.5 mm. Eggs of E. ameaeaeae have distinct longitudinal striations running along the external surface of the shell.

Hatchlings of E. ameaeaeae have never been reported. A single E. ameaeaeae egg found with a clutch of two large eggs of E. nigra in a birdnest fern is mangrove swamp hatched 48 days after discovery. This incubation time is probably only slightly less than the...
true incubation period. The hatching snout-vent length is 33.0 mm.

Whether or not the one discovered egg represents single placement of eggs by *E. sumatrae* cannot be concluded. Captive females have laid one or two eggs in laboratory cages and withheld the rest for several days or weeks. However, none of these eggs developed, and most were thin shelled and probably laid prematurely. A field observation with postnatal implication, was made at the time of discovery of the single *E. sumatrae* egg. Moments after the collection, a gravid *E. nigra* was captured from an adjacent mangrove tree. Upon dissection she was found to have three yolked eggs and three *E. sumatrae* eggs in her stomach and intestines. Perhaps

these eggs were from the clutch found in the birdnest fern. The presence of other lizard eggs in stomachs of *E. nigra* individuals was also recorded (Gowan, 1973).

**Emoia cyamura**

This small drab skink was caught on the ground and in low vegetation, where it moves rapidly and forages widely. Individuals were disturbed from presumed resting places under rocks and leaf litter at night.

Males.—The 282 specimens have snout-vent lengths of 23.55 mm (Fig. 6). Individuals less than 35 mm had white bellies (20 mm in length). Because there is no apparent break in the testes versus snout-vent length regression (Fig. 7), adult males were estimated from visual inspection of the testes for the presence of enlarged convoluted tubules (Fig. 6). Tubules are only moderately developed in specimens 33-42 mm snout to vent, definite convolutions and vasculation of enlarged testes are found in individuals 38-50 mm and larger. Thus, snout-vent length at maturity in male *E. cyamura* appears to be 38-40 mm. Baker (1947), in a more accurate assessment based on body weight at adult male *E. cyamura* in the New Hebrides, estimated weight at maturity to be 1.5 gms. Among 34 males (with complete tails) weighed prior to preservation during the present study, four were classified as reproductively mature, weighed approximately 1.5 gms (1.6-1.7 gms) and had an average snout-vent length of 42.5 mm (range = 40.4-43 mm); this is only slightly higher than my estimate for minimal adult maturity based on testes size and condition.

Females.—Of 327 females having snout-vent lengths of 22-56 mm the smallest fecund female (developing eggs > 3.0 mm) is 35 mm and the smallest with yolked eggs, 41 mm (Fig. 6). Thus, the size at sexual maturity of female *E. cyamura* in American Samoa is about 49 mm. Baker (1947) found no yolked eggs in any female weighing 1.5 gms or less, and estimated the minimum adult weight for female *E. cyamura* in the New Hebrides as 1.6 gms. Of 33 female *E. cyamura* (complete tails), captured during the present study and weighed prior to preservation, five classified as reproductively mature are below 1.6 gms (1.0-1.5 gms) and average 43.5 mm snout to vent. Two individuals weighing 1.6 and 1.7 gms have body lengths of 45 to 46 mm, respectively. This is considerably higher than my estimate of minimum adult size at 40.0 mm based on the size and condition of developing eggs. Either females mature at smaller sizes in American Samoa, or there is some discrepancy in equating body size and body weight in these females with the measurements of Baker's (1947) analysis.

Mean clutch size, based on 46 fecund and 46 ovigerous females, and 35 clutches found in the field, is 1.96 (or an almost constant 2

---

**Fig. 5.** Testes length versus snout-vent length (In mm) for male *Emoia sumatrae* from American Samoa. Symbols are as in Fig. 2. Regression line fitted by least squares method to data points below 35 mm SVL.
Reproductive condition and snout-vent length (in mm) of Ensatia capax from islands of American Samoa. Symbols are as in Fig. 1.

Fig. 6.

Fig. 7.—Testes length versus snout-vent length (in mm) for male Ensatia capax from American Samoa. Symbols are as in Fig. 5.

eggs per clutch). There is no significant correlation between increasing body size and clutch size (Fig. 3E). Greer (1998), citing Buben (1997), noted that almost always one egg is found in each oviduct of ovigerous females. Similar observations were noted by Hediger (1934) for this species.

The diameters of 39 ovoidal eggs measured 9.5–13.2 mm (X = 11.5 mm) and closely approximated the length x width of freshly laid eggs (X = 19.0 x 7.5 mm, range = 10.5–13.0 x 6.2 x 9.5 mm, n = 19). Incubating eggs of E. capax swell in size, increasing more in width than in length from parturition to hatching; mean length x width at hatching is 12.6 x 9.5 mm (range = 11.3–12.9 X
0.2-10.1 mm, n = 6). Incubation times were 6.51 days for field collected eggs maintained in the laboratory; however, the upper bound of 40.51 days is probably the usual incubation period. Average hatching most-vent length is 20.0 mm (range = 20.0-23.0 mm, n = 45); hatchlings have the adult color pattern.

*Emoia cyanura* lay eggs in communal nesting sites probably selected for optimal moisture and temperature. Most eggs were taken from under garden rocks; these were usually flat coral plates lying on a sand substrate. The usual number of eggs under the rocks was about 6 to 10; however, one rock covered 70 incubating eggs and many empty egg casings.

*Emoia lacera*

This large diurnal skink, was caught on the ground where it forages among coral rubble primarily in littoral forests. None was seen at night.

**Males.**—The 20 specimens have most-vent lengths of 77-100 mm (Fig. 8). One male (SVL = 81 mm) has undeveloped testes; however, two smaller individuals (SVL = 77 and 80 mm, respectively) have enlarged testes with convoluted tubules. A conservative estimate of the most-vent length of reproductively active males is about 85 mm; mature testes lengths are usually above 40 mm (Fig. 9). Individuals were collected only during June and July, 1976, and December and January, 1977-1978. Reproductively active males were observed during June, July, December and January.

**Females.**—Of 38 females having most-vent lengths of 70-105 mm the smallest fuscum female (developing ov = 2.0 mm) is 75 mm and the smallest with oviducal eggs, 85 mm (Fig. 8). Conservatively, reproductive activity of female *E. lacera* probably begins at most-vent lengths 85-90 mm.

Mean clutch size, based on 23 fecund and 5 ovigerous females, and 2 laboratory clutches, is 1.8. Most females have two eggs per clutch; two individuals had a single oviducal egg and three others had only one developing ovum each. There is little indication of increasing clutch size with greater body size, but too few females from the lower size range of reproductive maturity were examined (Fig. 3C).

The diameters of 8 oviducal eggs measured 15.0-19.7 mm (X = 19.3 mm); at parturition the average egg length x width was 21.5 x 11.3 mm (range = 21.0-21.9 x 11.0-12.5, n = 4). Similar to the other *Emoia* species in this study, the eggs of *E. lacera* swell during incubation reaching hatchling sizes 3.7-4.7 mm longer and wider, respectively, than at parturition. Two eggs laid in the laboratory hatched 72 and 77 days after parturition. This is the longest incubation time for any of the skink species observed in American Samoa. Hatching color patterns resembled those of adults; most-vent lengths of two hatchlings were 32.4 mm and 33.4 mm, respectively.

*Emoia aspersa*

This medium sized diurnal skink was caught on the ground where it was observed to bask and forage. No individuals were observed at night, but there were seen entering and leaving suspected burrows at the bases of trees on Swains Island.

**Males.**—The 17 specimens examined from Swains, Savaii, Nukunonu and Faisuufati islands have most-vent lengths of 64-54 mm.
February and September; all adult specimens have swollen testes with enlarged convoluted tubules and are presumed to have been reproductively active when preserved.

Females.—Of 23 females having snout-vent lengths of 65-81 mm, the smallest fecund female (developing ova > 2.0 mm) is 64 mm and the smallest with oviducal eggs, 70 mm (Fig. 10); thus, conservatively, most females probably are mature at 70 mm.

Mean clutch size, based on 14 fecund and 5 ovigerous females, is 1.9. All but two individuals have two eggs per clutch. Clutch size does not appear to increase with body size (Fig. 3D), but too few females from the lower size range of adults makes this inconclusive. Egg sizes for seven full term oviducal eggs (all with thick leatherly shells) average 10.4 mm (10.4-10.2 mm, n = 7) in length.
Cryptoblepharus boutonii

This small, diurnal skink was caught on coral and lava rocks in littoral strand habitats devoid of vegetation at coastal margins on Ta‘u and Olosega islands. None was observed at night, but the species is apparently restricted to the littoral strand.

Males.—The 26 specimens have snout-vent lengths of 25-42 mm (Fig. 11). Individuals less than 37 mm generally have small, whitish testes (< 2.0 mm in length) lacking enlarged convoluted tubules, and are probably immature (Fig. 12). Conservatively, male C. boutonii are probably reproductively mature at snout-vent lengths of 30-40 mm and testes sizes of 3.0-4.0 mm in American Samoa.

Females.—Of 23 females having snout-vent lengths of 35-48 mm, the smallest fecund female (developing ova > 1.0 mm) is 44 mm and the smallest with oviprecocious eggs, 43 mm (Fig. 11); one pre-oviprecocious female with distended oviducts is 40 mm. The size at sexual maturity for female C. boutonii is, therefore, probably at or above 40 mm snout-vent length.

Mean clutch size, based on 13 fecund and 3 oviprecocious females, is 1.58; only one individual had one oviprecocious egg. Thus, the clutch size is probably a constant two eggs in American Samoa.

No eggs were collected from field tests; Hauke (1977) states that the species reproduces "by means of small batches of soft-shelled eggs which are laid in moist sand." The average length of seven oviprecocious eggs was 10.1 mm (range = 7.9-13.5 mm).

Lipinia noctua

This small, diurnal skink is secretive and almost invariably found under the bark of rotting reeds, or in epiphytic vegetation. Individuals were not observed at night.

Males.—The 15 specimens have snout-vent lengths of 25-43 mm (Fig. 13). Individuals less than 35 mm snout-vent length have...
small, undeveloped testes; convoluted tubes in testes \(> 2.0 \text{ mm in length} \) are present in individuals above 35 mm, which is probably the snout-vent length at reproductive maturity (Fig. 14).

Females—Of 12 females having snout-vent lengths of 39-47 mm the smallest gravid female (developing ova \(> 1.5 \text{ mm} \)) is 39 mm and the smallest ovigerous female, 40 mm; because smaller individuals were not examined, minimal size at reproductive maturity is at least 39 mm (Fig. 13).

Lipinia nocturna is viviparous; nine females with developing embryos have two (one in each ovicell), and three females have a single embryo. Fitch (1970) reported Hechtler’s (1934) observation of one embryo per female in the New Hebrides; Oliver and Shaw (1953) found two embryos in each of six females, and two females with one embryo. Similar results were noted for gravid females from the Marshall, Tannots, and Marquesas Islands (Fitch, 1970). Gravid females were observed during January, March, June and December in American Samoa; thus reproductive activity is probably year-round.

The average diameter of seven embryo masses is 8.9 mm; (range = 7.1-10.8 mm). Four full term embryos had an average snout-vent length of 15.5 mm (range = 15.1-16.6 mm).

---

**Fig. 13.**—Reproductive condition and snout-vent length (in mm) of *Lipinia nocturna* from islands of American Samoa. Symbols are as in Fig. 1.

**Fig. 14.**—Testes length versus snout-vent length (in mm) for male *Lipinia nocturna* from American Samoa. Symbols are as in Fig. 2.

*Calyptraeoa pacifica*

This large, nocturnal gecko was caught on building walls, and on tree trunks in a variety of forested habitats. During the day individuals were disturbed from presumed resting sites under the bark of rotting trees, particularly coconut trees, or from under boards and other debris, and crevices in building walls and roofs.

**Males.**—The 23 specimens have snout-vent lengths of 38-53 mm (Fig. 15). Reproductively active individuals with enlarged testes and convoluted tubes apparently mature at snout-vent lengths greater than 70 mm in American Samoa; below this size testes are

---
Fig. 15.—Reproductive condition and snout-vent length (in mm) of Galapagos elephantiasis from islands of American Samoa. Symbols are as in Figs. 1 and 4; X's are hatchlings.

**Small (< 3.0 mm), undifferentiated masses of whitish tissue (Fig. 16).** Mature males found during several months of the study are presumably reproductively active year round.

**Females.—** Of 34 females having snout-vent lengths of 47-47 mm, the smallest fecund female (developing ova > 3.0 mm) and the smallest with oviducal eggs, 70 mm (Fig. 15). Females 70 mm or less have small undeveloped ova with narrow, undifferentiated oviducts and are apparently immature. Thus, snout-vent lengths of both male and female G. elephantiasis appear to be 70 mm at reproductive maturity.

Mean clutch size, based on 11 fecund and 6 ovigerous females, and 22 clutches found in the field, is 1.96. Most fecund and ovigerous females have two eggs; only two females have a single oviducal egg and one fecund female has four distinctly enlarged ova. A large number of field nests (438), however, contained a single egg, and a slightly greater percentage (526) contained two eggs. There is a tendency for females of greater body size to have more than two eggs in a clutch (Fig. 3B), but this trend is not consistent.

Most gekkonid eggs have hard, brittle shells and apparently do not swell during incubation. The diameters of six oviducal eggs measured 1.5-1.65 mm (X = 1.4 mm); length x width of 35 eggs from field clutches averaged 12.3 x 11.6 mm (range = 12.0-13.6 mm x 11.0-12.5 mm).

Minimum hatching time for G. elephantiasis was 19 days in the laboratory; eggs hatching between 19 and 30 days were usually dark when candled, revealing the eye pigment of developing embryos. Most eggs that hatched beyond 40 days were yellowish or pinkish in color when candled. The longest incubation periods recorded were a rather remarkable 112 and 114 days for two eggs collected on Swains Island in mid-May, 1978. Two eggs from Ta'io Island, taken in January, 1978, took 102 and 109 days to hatch. Brown and Alcala (1987) reported on incubation periods of 70 days for the gekkonid, Conepholis paruns, Fitch (1970) cited Lowe-ridge's (1945) note (sensu Smith, 1955) indicating a five month incubation period for Psolobates kalili in Java; most other gekkonid species for which data are available have incubation times between one and two months. Furthermore, the eggs from American Samoa were kept in airy plastic bags on a shelf in the laboratory and were not considered viable after 3 months, until they unexpectedly hatched. Their apparent resistance to dessication and long incubation times undoubtedly facilitate their transport via rafting among islands.

Hatchlings have snout-vent lengths of 28.0-30.0 mm (X = 29.4 mm, n = 19). Individuals from Swains and Rose Islands have a
This medium sized, nocturnal gekko was found exclusively on
building walls on Tutuila Island; a small series taken from build-
ings on Oahu, Hawaii are included with the American Samoan
specimens in the following description. No individuals were
observed during the day.

Males.—The 18 specimens have snout-vent lengths of 33.60 mm
(Fig. 17). Adult males with enlarged testes and convoluted tubules
are greater than 40 mm snout-vent length and probably become

suffusion of rose colored pigment on the underside of the tail, and
a faint black ventral line. When alarmed, these hatchlings raise
their tails vertically, presumably to display the bright color. Full
autonomy is high in gekkonid species (Pianka and Pianka, 1978),
and over 80% of the G. oceanica specimens from American Samoa
have regenerated tails.

All but one G. oceanica egg was found under the bark of rotting
cocnut stumps, usually near their base; the eggs were in clutches
of 1-10, in varying stages of development, indicating communal
use of nesting site. A single egg was found in the tangled roots of a
fallen tree.

Fig. 16.—Testes length versus snout-vent length (in mm) for male Gehyra
oceanica from American Samoa. Symbols are as in Fig. 2.

Fig. 17.—Reproductive condition and snout-vent length (in mm) of Hemi-
dactylus frenatus from islands of American Samoa (and Hawaii). Symbols
are as in Figs. 1 and 4.
reproductively active between 40-50 mm. Most males above 50 mm have testes sizes between 4.0-5.0 mm (Fig. 18). Reproductively active males were found during June and January. Church (1962) observed active reproduction year-round in Java; further north in more temperate areas this pattern became seasonal with peak activity in July and August (Fukada, 1965).

Females.—Of 15 females having snout-vent lengths of 33-52 mm the smallest females (developing ova > 1.0 mm) and the smallest with oviducal eggs are both 42 mm (Fig. 17). Thus, size at reproductive maturity in females in American Samoa (and Hawaii) appears to be greater than 40 mm.

Mean clutch size, based on 5 fecund and 3 ovigerous females, and one field clutch, is 1.9 (or almost a constant 2 per clutch); only one female had a single oviducal egg. Oviducal eggs are only slightly smaller than those freshly laid (X = 7.5 mm, range = 6.8-8.5 mm, n = 6). Just prior to hatching the eggs are identical to their size at parturition. Two clutches (four eggs) laid in the laboratory hatched between 77-98 days. These hatching times correspond closely to the "sevenplus days" reported by Brown and Alcala (1987) for the species in the Philippines Islands. These authors noted that two eggs of H. funebris exposed to sea water for 59 to 108 hrs hatched in 56 days, suggesting that the extent of egg development may not be of significance in determining the effects of sea water. Eggs of American Samoan females were hatched in dry plastic bags. The widespread occurrence of H. funebris throughout the Pacific region and elsewhere is undoubtedly aided by the high resistance of its eggs to a wide range of environmental extremes.

Hatchlings measured 19.0-21.0 mm snout-vent length (x = 20.5 mm, n = 5) and resembled the adults. One clutch of eggs was recovered from the field under a wooden box on the ground near a building wall on Tutuila Island. Hatchlings were not observed in the field.

Perupus marilinus

This small, nocturnal gecko was found exclusively in darkened buildings not exposed to village lights. It is rare in American Samoa and never observed during the day.

Males.—The 8 specimens have snout-vent lengths of 36-46 mm (Fig. 19). A single individual (31 mm, SVL) is definitely immature (testes size = 1.2 mm), and a second individual (36 mm, SVL) has only slightly larger testes (1.4 mm). Five individuals, with enlarged testes and convoluted tubules, range above 40 mm snout-vent length; testes sizes range from 3.0-3.7 mm (Fig. 20). Thus, male. P. marilinus in American Samoa probably mature at snout-vent lengths greater than 40 mm. Males taken during July, December and January were reproductively active. Church (1962) reported year-round breeding for this species in Java.

Females.—Of 12 females having snout-vent lengths of 33-48 mm...
the smallest fecund female (developing ova > 1.0 mm) is 40 mm and the smallest with oviducal eggs, 43 mm (Fig. 19). Thus, size at reproductive maturity in female P. multiatus from American Samoa is the same as for males, 40 mm.

Mean clutch size, based on 7 fecund and 4 ovigerous females, is 1.8. With the exception of two large females (46 mm and 43 mm, respectively) that probably had laid eggs and were just beginning the development of a second clutch (both were fecund with a single enlarged ovum), all gravid females in American Samoa have two eggs per clutch. Fitch (1970) noted two eggs per clutch for this species in other areas.

Three oviducal eggs measured 6.9-8.1 mm ($X = 7.5$ mm). No eggs were found and hatchlings were not observed in the field.

$\Delta$ $\text{Gecko C}$

**Cyrtodactylus pelagius**

This medium sized, nocturnal gecko is largely terrestrial. Individuals were usually caught on tree trunks in littoral forest, within one meter of the ground; when disturbed the species invariably escaped downward among rocks and litter of the forest floor. Two individuals were captured during the day under debris on the ground in village land. No males were found in any sampled population.

**Females.**—Of 51 females having snout-vent length 25-39 mm the smallest fecund female (developing ova > 1.0 mm) is 50 mm and the smallest ovigerous female, 29 mm (Fig. 21). Thus, reproductive maturity occurs between 20-60 mm snout-vent length in C. pelagius from American Samoa.

Mean clutch size, based on 20 fecund and four ovigerous females, is 1.8; five fecund and two ovigerous females have only one developing ovum each. There is only a slight correlation between body size and clutch size in C. pelagius individuals from American

**Fig. 19.**—Reproductive condition and snout-vent length (in mm) of *Petrogus multiatus* from islands of American Samoa. Symbols are as in Fig. 1.

**Fig. 20.**—Testes length versus snout-vent length (in mm) for male *Petrogus multiatus* from American Samoa. Symbols are as in Fig. 5; large dot represents two individuals.
and there is very little apparent variation in color pattern or measurements of various body parts. One female isolated in the laboratory developed and laid, one egg during a seven month period, but the egg failed to hatch. The lack of males in the collection (taken during July and January) suggests that a parthenogenetic population of C. pelagicus exists on Ta'u Island.

Lepidodactylus lugubris Moore, 1947\footnote{Moult, 2004.}

This small, nocturnal, abundant gecko was caught in a number of habitats at night, ranging from building walls to village shrubs, forest epiphytes, rotting trees, and the rocky cliffs of coastal strand. Individuals were taken under the bark of trees, in epiphytic vegetation, under debris at the shoreline, in cracks of building walls and roofs, and in crevices between rocks in littoral strand by day. The species is a known parthenogenetic form, no males were found in the populations sampled.

**Females**—Of 233 females having snout-vent lengths of 30-44 mm the smallest fecund females (developing ova > 1.5 mm) and the smallest ovigerous females are both 35 mm (Fig. 22). Although presumably immature individuals were recorded at higher snout-vent lengths, it seems that female *L. lugubris* from American Samoa mature at 35 mm. Furthermore, the modal snout-vent length for fecund, ovigerous and spent females is 40 mm.

Clutch size, based on 45 fecund and 47 ovigerous females, and 35 field clutches, is essentially a constant 2 eggs. In the field, two eggs in a clutch were observed without error because *L. lugubris* is the only gecko on these islands which lays eggs with shells that adhere to each other upon drying; this was also noted by Cagle (1948) for the species on Tutuila Island. These eggs are adhered to the substrate and are difficult to detach without breakage. It is probable that the survival of *L. lugubris* in rocky littoral strand is facilitated by this trait, since adhered eggs may be secured in cracks and crevices of rocks and on cliff overhangs where they escape predation by the numerous crabs along the rocky coastline. Mean egg size at hatching ($S = 8.3 \pm 7.1$ mm, range $= 8.0-9.0 \times 6.5-7.5$ mm, $n = 3$) is only slightly larger than the mean size of oviducal eggs. The eggs must be extremely resistant to desiccation because they were not found in moist (freshwater) areas, but under dead and dying tree bark, rocks espoused to salt spray, and small dry holes in coconut palms. On Rose Island, where *L. lugubris* coexists with *G. oceanica*, eggs of the latter were found under dead tree bark always at the base of the tree, and eggs of the former were always adhered to bark near the top of the tree. Maximal hatching time in the laboratory was 73 days; two months appears to be the modal incubation period. Oliver and Shaw (1933) reported an incubation time of 92 days, but develop-

---

**Figure 21.—Reproductive condition and snout-vent length (in mm) of *C. pelagicus* pelagicus from islands of American Samoa.** Symbols are as in Fig. 1, this is an all-female population. Saps, but more specimens from all size ranges are needed for greater clarity of this point (Fig. 26).

The diameters of six oviducal eggs measured 9.0-12.0 mm ($S = 11.3$ mm). No field clutches were found, but a single egg laid in a laboratory cage measured 12.2 mm in length. No hatchlings were found in the field.

Two dense populations of *C. pelagicus* were sampled from Ta'u Island, both in littoral forests near the coast. In these habitats few other gekkonid species were found. Most importantly, no males of *C. pelagicus* were collected. Almost all of the females were gravid
mentation was perhaps delayed by cooler than normal incubation temperatures (Fitch, 1970). Mean post-entract length of hatchlings is 17.1 mm (range = 14.0-20.0 mm, n = 9).

Lepidodactylus bugensis is parthenogenetic (Cuellar and Kluge, 1972); no males were found in American Samoa. The species is distributed from Australia and the Indo-Pacific region, throughout islands of the tropical Pacific Ocean and on mainland Central America and Ecuador (Smith, et al, 1961; Fitzler, 1966), where it is often the most locally abundant species. Kluge and Cuellar (1972) list the diploid chromosome number as 44. From this they suggested that the mode of parthenogenesis is not due to hybridization with closely related species (or gynogenesis), since no congers or even closely related genera are found among populations of L. bugensis, wherever it is found. Undoubtedly the wide range of L. bugensis both in geography and habitat distributions in American Samoa (Schwaner, 1970), is facilitated by its unique combination of reproductive habits.

**DISCUSSION**

**Patterns in Monthly Reproductive Activity**

To demonstrate the apparent constancy of the American Samoan island with respect to annual patterns in temperature and rainfall, Colwell's (1974) method was used to an analysis of predictability, constancy and contingency for monthly averages of precipitation and temperatures taken from published weather records for 17 consecutive years (U.S. Bureau of Standards, 1960-1976). These data are cast into the matrices of Tables 1 and 2, respectively, for predictability analyses, along with the computed proportions of constancy and contingency contributing to predictability. Rainfall (Table 1) is highest during December to April (the so called "rainy season"); drier months are from May to December, having lows in August and September. The pattern is not marked, however, and its predictability is only 54%. Constancy of the pattern is high however (48%) in contrast to the contingency factor (6%); the former factor contributes 88% to the predictability of the pattern (as opposed to only 12% for contingency). Therefore, whereas the pattern

<table>
<thead>
<tr>
<th>Amount</th>
<th>Months</th>
</tr>
</thead>
<tbody>
<tr>
<td>Smoothly</td>
<td>Rainfall</td>
</tr>
<tr>
<td>S</td>
<td>O</td>
</tr>
<tr>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Predictability = .84</td>
<td></td>
</tr>
<tr>
<td>Constancy = .46</td>
<td></td>
</tr>
<tr>
<td>Contingency/Predictability = .88</td>
<td></td>
</tr>
<tr>
<td>Contingency = .06</td>
<td></td>
</tr>
<tr>
<td>Contingency/Predictability = .12</td>
<td></td>
</tr>
</tbody>
</table>

"Fig. 22."—Reproductive condition and snout-vent length (in mm) of Lepidodactylus bugensis from islands of American Samoa. Symbols are as in Fig. 2; this is an all-female population.
TABLE 3—Mean monthly data for climatic parameters and monthly percent of families of *E. nigra* and *E. spicata* females in reproductive condition from islands of American Suri. Climatic data are from Amerio et al. (1978, unpublished) for the years 1956 to 1976.

<table>
<thead>
<tr>
<th>Climatic parameters and lizard species</th>
<th>J</th>
<th>F</th>
<th>M</th>
<th>A</th>
<th>M</th>
<th>J</th>
<th>J</th>
<th>A</th>
<th>S</th>
<th>O</th>
<th>N</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>MATURES</td>
<td>27.3</td>
<td>27.5</td>
<td>27.3</td>
<td>27.3</td>
<td>20.8</td>
<td>26.0</td>
<td>26.0</td>
<td>29.4</td>
<td>28.6</td>
<td>27.6</td>
<td>27.3</td>
<td></td>
</tr>
<tr>
<td>MATURES (lh)</td>
<td>30.3</td>
<td>32.6</td>
<td>29.2</td>
<td>31.3</td>
<td>24.4</td>
<td>21.6</td>
<td>17.8</td>
<td>18.2</td>
<td>18.8</td>
<td>20.0</td>
<td>20.0</td>
<td></td>
</tr>
<tr>
<td>MATURES (mm)</td>
<td>8.1</td>
<td>6.3</td>
<td>7.7</td>
<td>7.3</td>
<td>7.3</td>
<td>6.8</td>
<td>6.8</td>
<td>8.5</td>
<td>6.4</td>
<td>7.4</td>
<td>7.6</td>
<td></td>
</tr>
<tr>
<td>MATURES (mm) (lh)</td>
<td>70</td>
<td>76</td>
<td>76</td>
<td>76</td>
<td>76</td>
<td>77</td>
<td>77</td>
<td>74</td>
<td>74</td>
<td>76</td>
<td>79</td>
<td></td>
</tr>
<tr>
<td>MATURES (lh)</td>
<td>50</td>
<td>59</td>
<td>59</td>
<td>59</td>
<td>59</td>
<td>65</td>
<td>64</td>
<td>65</td>
<td>65</td>
<td>65</td>
<td>65</td>
<td></td>
</tr>
<tr>
<td>MATURES (mm)</td>
<td>8.0</td>
<td>6.5</td>
<td>6.5</td>
<td>7.3</td>
<td>10.0</td>
<td>11.0</td>
<td>11.5</td>
<td>12.5</td>
<td>12.5</td>
<td>12.0</td>
<td>9.5</td>
<td></td>
</tr>
<tr>
<td>MATURES (mm) (lh)</td>
<td>760</td>
<td>746</td>
<td>726</td>
<td>708</td>
<td>690</td>
<td>673</td>
<td>690</td>
<td>706</td>
<td>720</td>
<td>744</td>
<td>762</td>
<td>780</td>
</tr>
<tr>
<td><em>E. nigra</em> (mm)</td>
<td>25</td>
<td>35</td>
<td>40</td>
<td>40</td>
<td>41</td>
<td>41</td>
<td>41</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td><em>E. nigra</em> (lh)</td>
<td>80</td>
<td>33</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td></td>
</tr>
</tbody>
</table>

Notes:
- MATURES = Mean monthly air temperature (°C).
- MMIN = Mean monthly minimum temperature (°C).
- MMAX = Mean monthly maximum temperature (°C).
- MMRH = Mean monthly relative humidity (1000 hrs).
- MMVR = Mean monthly relative velocity (mph).
- DURF = Duration of daylight (monthly) in minutes.

*E. nigra* and *E. spicata* are two species of lizards found in American Surinam.

The table shows the mean monthly temperatures and climatic conditions for the years 1956 to 1976, with the highest temperatures occurring in July and the lowest in January. The months with the highest and lowest temperatures are noted for each species, along with the months with the highest and lowest relative humidity and wind velocity. The data are useful for understanding the climatic conditions in which these lizards thrive.
Table 4.—Monthly numbers of ovigorous, fecund, nonfecund and spent adult females, hatchlings and mean ova sizes of fecund (and nonfecund) females for three species of scincid lizards from American Samoa. Dashes (—) indicate no data were taken.

<table>
<thead>
<tr>
<th></th>
<th>J</th>
<th>F</th>
<th>M</th>
<th>A</th>
<th>M</th>
<th>J</th>
<th>A</th>
<th>B</th>
<th>O</th>
<th>N</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Enatogenys</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ovigens</td>
<td>8</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>-</td>
<td>2</td>
<td>0</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Fecund</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Nonfecund</td>
<td>39</td>
<td>5</td>
<td>9</td>
<td>2</td>
<td>13</td>
<td>12</td>
<td>-</td>
<td>3</td>
<td>1</td>
<td>35</td>
<td></td>
</tr>
<tr>
<td>Spent</td>
<td>21</td>
<td>-</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Hatchings</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mean ova</td>
<td>3.6</td>
<td>-</td>
<td>3.8</td>
<td>5.9</td>
<td>7.5</td>
<td>5.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4.3</td>
<td></td>
</tr>
<tr>
<td>Exosaurus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ovigens</td>
<td>19</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Fecund</td>
<td>18</td>
<td>3</td>
<td>6</td>
<td>7</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Nonfecund</td>
<td>20</td>
<td>10</td>
<td>16</td>
<td>23</td>
<td>8</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>6</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Spent</td>
<td>27</td>
<td>-</td>
<td>10</td>
<td>12</td>
<td>12</td>
<td>3</td>
<td>7</td>
<td>-</td>
<td>7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Hatchings</td>
<td>-</td>
<td>-</td>
<td>10</td>
<td>21</td>
<td>10</td>
<td>4</td>
<td>0</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Mean ova</td>
<td>4.3</td>
<td>-</td>
<td>3.9</td>
<td>3.0</td>
<td>4.4</td>
<td>4.8</td>
<td>3.1</td>
<td>-</td>
<td>-</td>
<td>3.1</td>
<td>-</td>
</tr>
<tr>
<td>E. seminor</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ovigens</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Fecund</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Nonfecund</td>
<td>17</td>
<td>-</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Spent</td>
<td>18</td>
<td>-</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Hatchings</td>
<td>1</td>
<td>-</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>11</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mean ova</td>
<td>3.5</td>
<td>-</td>
<td>2.3</td>
<td>3.4</td>
<td>2.4</td>
<td>3.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3.3</td>
<td>-</td>
</tr>
</tbody>
</table>
thesis above fecund frequencies in Fig. 24) appear to increase in size from December, peaking in January, and then decreasing in average size from April, just at the time when ovigerous and spent females of E. nigra also decline in frequency. Ova sizes increase again in April and May, and decline in June, the same month during which spent females reach peak frequencies.

The failure of ovigerous frequencies to increase and peak just prior to the high peak of spent females in May and June is inconsistent with patterns seen from October to December. This may be a result of low sample sizes for those months; however, the overall unevenness of samplings during all months of the study strains the credibility of any stronger conclusion. The data do seem to follow a consistent pattern which appears to result in two peaks of egg production, one from December to January, and another in June and July; critical data from August and September are entirely lacking, however, and greater sample sizes for each month are obviously needed.

Maximal reproductive activity for *Eusoma nigra* seems to peak from March to June, and again, slightly, in September and October (Fig. 25); these peaks although broadly overlapping those of *E. capraea*, occur somewhat later than for the smaller species. Reproductively active females of *E. nigra* were found during each sampled month, reaching their lowest frequency (20%) in December. Spent females are at highest percentages in December, declining to zero percent in March (Fig. 26). Frequency of hatchlings, however, increases from December to a peak in April, approximately three months later. Obviously, if eggs are deposited in December and January, and require from two to three months to hatch as previously suggested, hatchlings should be most abundant in March and April.

Mean ovum sizes (in parentheses above fecund frequencies in Fig. 26) show enlarging ovum from December to January, decreasing in mean size in March and then markedly increasing again from April to May. These patterns generally precede and parallel those for increasing and decreasing frequencies of ovigerous females of *E. nigra*. Apparently eggs mature in December and January, are deposited, and hatch in May and April; a second developmental period occurs from March to May and eggs are again deposited.
(although perhaps not necessarily from the same females) in June and July.

Reproductive activity in *Eunoe samoae* exhibits much greater peaks and valleys than the species analyzed above (Fig. 27). While it may also be due to low sample sizes, assuming it is not, the pattern is markedly different. Maximal activity (using the bimonthly data) peaks in March and April, and again, more sporadically, in December. Reproductively active females were not found in May (and no specimens were collected during June due to scheduled trips during that month to islands where *E. samoae* was not present). Frequencies of spent females are highest from September to January and lowest from April to June (Fig. 27); eggs deposited in June presumably incubate for one to two months and would be expected to hatch in late February or early July. Hatchlings were found from December to July, and were most abundant in April. Percentages of ovigerous females drop sharply from October to January, but ova sizes (numbers in parenthesis above fecund frequencies, Fig. 28) increase from December to January and main-
TABLE 5.—Correlations of climatic variables and percent reproductive activity of three lizard species from American Samoa. Climatic data averaged from monthly summaries between 1955 to 1979. Abbreviations are as in Table 3. CYAN = Emoia cyanoma, NIGR = E. nigra, SAMO = E. semivittata.

<table>
<thead>
<tr>
<th>Variable</th>
<th>MMAT</th>
<th>MMARN</th>
<th>MMASC</th>
<th>MRHA</th>
<th>MMHN</th>
<th>MMWS</th>
<th>DURP</th>
<th>CYAN</th>
<th>NIGR</th>
<th>SAMO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Correlation coefficient</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>MMAT-MMARN</td>
<td>0.82*</td>
<td>0.84*</td>
<td>0.44</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MMAT-MMASC</td>
<td>0.44*</td>
<td>0.33</td>
<td>0.01*</td>
<td>1.00</td>
<td>0.03</td>
<td>0.66*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MMAT-MRHA</td>
<td>0.33</td>
<td>1.00</td>
<td>0.44</td>
<td>1.00</td>
<td>0.03</td>
<td>0.66*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MMAT-MMHN</td>
<td>0.44</td>
<td>1.00</td>
<td>0.33</td>
<td>1.00</td>
<td>0.03</td>
<td>0.66*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MMAT-MMWS</td>
<td>0.04*</td>
<td>0.33</td>
<td>0.01</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DURP-MMARN</td>
<td>0.54</td>
<td>0.82*</td>
<td>0.70*</td>
<td>0.03</td>
<td>0.02</td>
<td>0.33</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CYAN-MMASC</td>
<td>0.33</td>
<td>0.33</td>
<td>0.01</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CYAN-MRHA</td>
<td>0.44</td>
<td>1.00</td>
<td>0.33</td>
<td>1.00</td>
<td>0.03</td>
<td>0.66*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CYAN-MMHN</td>
<td>0.44</td>
<td>1.00</td>
<td>0.33</td>
<td>1.00</td>
<td>0.03</td>
<td>0.66*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CYAN-MMWS</td>
<td>0.04*</td>
<td>0.33</td>
<td>0.01</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NIGR-MMARN</td>
<td>0.01</td>
<td>0.06*</td>
<td>0.66*</td>
<td>0.67*</td>
<td>0.33</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NIGR-MMASC</td>
<td>0.06*</td>
<td>0.33</td>
<td>0.01</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NIGR-MRHA</td>
<td>0.14</td>
<td>0.66*</td>
<td>0.67*</td>
<td>0.33</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NIGR-MMHN</td>
<td>0.14</td>
<td>0.66*</td>
<td>0.67*</td>
<td>0.33</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NIGR-MMWS</td>
<td>0.06*</td>
<td>0.33</td>
<td>0.01</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAMO-MMARN</td>
<td>0.01</td>
<td>0.06*</td>
<td>0.66*</td>
<td>0.67*</td>
<td>0.33</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAMO-MMASC</td>
<td>0.06*</td>
<td>0.33</td>
<td>0.01</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAMO-MRHA</td>
<td>0.14</td>
<td>0.66*</td>
<td>0.67*</td>
<td>0.33</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAMO-MMHN</td>
<td>0.14</td>
<td>0.66*</td>
<td>0.67*</td>
<td>0.33</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SAMO-MMWS</td>
<td>0.06*</td>
<td>0.33</td>
<td>0.01</td>
<td>0.66*</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*p < .05
**p < .01
***p < .001
sky cover, relative humidity, duration of daylight, and significantly reduced wind speeds. The Southeast Trades blow stronger from June to October when temperature and rainfall are reduced, accompanied by generally shorter days, reduced sky cover, and lower relative humidity.

The only significant correlations for *Eumoa nigra*, *E. samoaensis* and *E. cyanura* with climatic variables (Table 5) are a positive one for *E. nigra* and mean monthly relative humidity (910 hrs) (r = .66, p < .05), and two negative correlations, *E. samoaensis* and duration of daylight (r = -.76, p < .05), and *E. cyanura* and mean monthly wind speed (r = -.69, p < .05). There are no significant correlations among the reproductively active periods of the three *Eumoa* species, but the correlation between *E. nigra* and *E. samoaensis* is moderately high and positive (r = .78, p < .1). Most interesting is the moderately high, but negative correlation between the reproductive activities of *E. cyanura* and *E. nigra* (r = -.66, p < .05).

**Reproductive Effort**

Reproductive effort is defined as that proportion of the total energy budget of an organism that is devoted to reproductive processes (Hinsdale and Tinkle, 1975). Three questions pertain to this concept: (1) What index actually measures reproductive effort? (2) What environmental conditions act as selective factors for high and low levels of effort? (3) How are those conditions predicted?

Earlier workers (Gaull and Bossert, 1970; Tinkle, 1969, and Tinkle et al., 1970) used ratios of clutch to body weight as measures of reproductive effort. Later workers (Ballinger and Clark, 1972; Tinkle and Hadley, 1973; Vitt, 1974; Vitt and Olmert, 1975) emphasized the use of caloric ratios. However, Tinkle and Hadley (1972) and Hinsdale and Tinkle (1975) suggested that these ratios were inadequate, because the concept of reproductive effort, as defined by Fisher (1930), requires measurements that can be fitted to demographic models, not instantaneous values. Thus total energy budgets, incorporating data on the proportional distribution of energy to growth, maintenance and reproduction, on an age-specific basis, are necessary to assess more accurately reproductive effort at the population level (Vitt, 1975). Caloric ratios facilitate the calculation of total energy budgets for species having well known demographic parameters (Vitt, 1975). These caloric ratios are presented in Table 6 for four species of the genus *Eumoa* coexisting in the same habitats on American Samoa islands, as a basis to which future demographic studies could be applied. For three of the four species with a clutch size of essentially two eggs, caloric values of relative clutch masses are significantly different (Table 6, p < .05).
Vitt and Congdon (1978) proposed that relative clutch masses (in terms of the calorific conversions above) are predictable on the basis of body shapes of lizards as related to certain aspects of their ecology. They proposed that the two extremes of foraging and predator escape behaviors, sit and wait foragers versus active foragers (MacArthur and Pianka, 1966; Pianka, 1973; and Schoener, 1971), typified species with cryptic coloration and high relative clutch masses, and morphological coloration and low relative clutch masses, respectively. Species with contrasting combinations of behaviors and coloration (or escape strategies) were termed intermediate.

Schwartz (1979) described the ecology of the four coexisting species of 
Eumastax in American Samoan, relative to resource partitioning, 
behaviors, and morphological correlates to microhabitat prefer-
ences. Eumastax nigra is a widely foraging terrestrial species, highly 
visible by its black coloration, and most wary of all the species, as 
demonstrated by its flight at the slightest disturbance. Eumastax samoense exhibits the other extreme; the species is arboreal, cryptic 
ally colored (green), but much less wary than E. nigra, and forages in a rather limited (horizontal) area on tree trunks and in low 
vegetation at the bases of trees. Eumastax laevis is also cryptically 
colored, terrestrial (but confined to coral reef habitats), and 
moves relatively slowly by choice among the rocks when disturbed. Eumastax cyanura is a small, widely foraging, semi-arboreal species, quick to 
escape when disturbed, with a bright blue tail which may be used 
as a decoy escape mechanism from predators; it would, therefore, 
correspond more closely to Vitt and Congdon's (1978) intermediate 
strategy.

When these ecological and behavioral traits are compared with 
the calorific ratios, the correlations are opposite of those described 
by Vitt and Congdon (1978) for the two extreme strategies. 
Eumastax nigra the wide forager has the highest calorific ratio, while E. samoense and E. laevis, the cryptic, more sedentary species, have the lowest ratios. 
Eumastax cyanura, with an intermediate strategy, has an inter-
mediate calorific ratio between the two extreme groups.

Thus most lizard species in American Samoan characteristically exhibit continuous reproductive activity with slight annual var-
iations (Sheehy, 1977; Duellman, 1978). In most species for 
which sufficient data are available, the single reproductive strategy 
appears to be multiple clutches annually, rather than the single 
clutches found in most temperate lizards (Taylor, et al, 1970). 

Duellman (1975) noted that the reproductive strategies of lizards must be considered in terms of their phylogenetic limitations, struc-
tural habits, and interactions with other species. The basic as-
sumption is that clutch mass, relative to body mass, determines the

agility of a gravid female lizard, and thus, her survival (and the 
survival of her eggs) when threatened.

In American Samoan, gekkonids exhibit a constant clutch size of two eggs, probably reflecting the inherent pattern exhibited throughout the family. Alternatively, or concomitantly, this pattern may also reflect the seed-bearing limitations imposed by their arboreal habits, particularly for those species residing on building 
walls (Andrews and Rand, 1974). Schwartz (1979) suggested that the richest gekkonid communities on American Samoan islands are 
closely packed ecologically, perhaps at the point of limiting simi-
larities (MacArthur and Levins, 1967). The reproductive modes of 
these species, involving low clutch size, continuous breeding activ-
ity, multiple clutches annually, resistance of eggs to desiccation, 
prolonged incubation times, ability to affix eggs to surfaces (L. 
hugonis), and parthenogenetic forms (L. hugonis and, perhaps, C. 
pelagicus), are adaptations well suited to both colonization and 
maximal avoidance of competition (+ resistance to predation).

The presence of another parthenogenetic species, Cyrtodactylus pelagicus, in American Samoan would not be surprising: Lepidodactylus hugonis (Cuvier and Kluge, 1973) is a known unisexual species on these islands, and two others, Gehyra variegata (Hall, 1870) and Hemidactylus garnoti (Khng and Etkin, 1969) are 
found on nearby islands. Cuvier (1977) summarized the data con-
cerning parthenogenetic species on islands and noted that enhance-
ment of colonizing ability may be by prolonged sperm storage or 
parthenogenesis. Cuvier dismissed sperm storage as an existing 
phenomenon, since it apparently evolves on mainland in response to other selective factors; however, prolonged incubation periods have been demonstrated for C. oceanica (see above), and parthenogenesis as another alternative seems ideal for American Samoan species. Their survival on these islands obviously depends in large part on how quickly their populations can respond to period-
cic catastrophes such as seawater inundations of lowland forests during tropical storms, volcanism, and human disturbance of low-
land habitats.

Populations of C. pelagicus on New Guinea and adjacent islands 
appear to have equal sex ratios (Herbert C. Desmazer, pers. comm.). 
However, if populations on American Samoa are parthenogenetic, the possibility of finding a male is remote. Introduction of a male into an all female population might result in matings with disruption of 
clones and the production of triploid offspring; if some of these 
triploids are males, further inbreeding would eventually build chromosomal complements so high that the whole population could 
ever eventually "crash" under the "weight" of its increasing chromosome number (Joy Cole, pers. comm.).

Parthenogenesis has been found in only about 19 of the known
lizard species. As a reproductive mode on islands, and in coastal areas where few potentially competing species coexist, however, it appears a viable strategy which may be widespread in species on other islands in the Pacific region.

Among skinks in American Samoa, small skinks exhibit a constant low clutch size of two eggs, but larger skinks have, maximally, two (E. imicen and E. adspersus) or three (E. sannones) eggs per clutch. Small skinks exhibit small clutches probably due to the restrictions of small body size and the need for rapid escape (or predation) of E. nocutus, as suggested by Duellman (1975) for small lizards in tropical South America. Although clutch sizes are low in small skinks, like the gecko, this may be compensated for by continuous breeding and multiple clutches annually.

Competition for small food items perhaps limits the coexistence of these forms in the same microhabitats in American Samoa (Schwanz, 1970); but, interspecific competition would seem to have little effect on reproductive modes, clutch sizes, frequency of egg deposition, patterns in annual reproductive activity, and choice of nesting sites among species so widely divergent in microhabitats. However, predation by larger lizards, birds, the Pacific boa, Canoidea bocordi, and lizards (feeding on eggs) may be sufficiently high to account for the differences in reproductive modes exhibited by small skinks.

The secretive and viviparous habits of L. nocutus probably protect adults and young from predatory species. Tinkle and Gibbons (1977) reviewed the evidence supporting the evolution of viviparity in lizards. Their list of possible benefits for viviparity included: (1) protection of eggs from environmental mortality, (2) favorable thermoregulation for the developing embryos, (3) economy to the female in avoiding sustenance during development rather than making the entire reproductive commitment at ovulation, and (4) greater predictability in placement of newborn young in optimal sites at parturition. Not only are the secretive microhabitats of L. nocutus often "foraged over" by other large and small geckos (Schwanz, 1979), but also by the large gecko, G. oceaniae, which favors nesting sites under shrub of rotting coconut stumps. The reproductive mode of L. nocutus seems, therefore, ideally suited for a microweather environment where nesting sites may be limited; its secretive habits provide maximal separation from most other competing or predatory species. Thermoregulation could be accomplished simply by shifting to the sunny or shady sides of rotting stumps, under the bark, similar to the way Eumeces agrarius in the Southeastern United States facilitates incubation of eggs in pocket-sized gopher mounds by shifting from lower to higher levels in burrows at different times of the day (Mount, 1963). Cryptobatrachia bow-
the terrestrial species. Alternatively, if E. amoena eggs are laid in arboreal nests, these sites may be sensitive to adverse ambient weather conditions, thus, limiting their favorability to the developing eggs. The eggs of E. amoena must also absorb water. This necessity may be indicated by the negative correlation between reproductive frequencies and duration of daylight, because months with shorter days are also highly correlated with maximal rainfall and low wind speed. This could ensure that potential nesting sites as epiphytic bird nests are saturated with water and less prone to drying by wind. Perhaps the appearance, retention, or prolonged development of ova by E. amoena is also related to the limitations of available nesting sites in arboreal habitats. If the eggs are laid singly (which must be determined by further study) more time would be required in finding suitable nests.

The lengthy incubation period of E. lineata eggs may simply reflect the cooler environments in which the eggs are placed, assuming that these nests are under the layers of corn plates to which the species is apparently restricted. The markedly lower active foraging temperatures of E. lineata than for all other social insect species in American Samoa (Schwenker, 1979) may be related to egg development at these presumably low temperatures.

The general conclusion for most American Samoan lizards seems to suggest that their reproductive strategies reflect adaptations more for avoidance of interspecific interactions than for climatic variables which greatly influence other species in seasonal temperate and equatorial tropical areas.

ACKNOWLEDGMENTS


I am indebted to Harly Llively and the University of Kansas Animal Care Committee for providing space to house my animals during the course of this study. William E. Duellman, Michael S. Gaines and Peter D. Ashlock read the manuscript and offered suggestions for its improvement. I am particularly grateful to William E. Duellman for his close editing of this and other manuscripts, and to Linda Trueb for advice on the figures.

My wife, Lalita, typed drafts and the final manuscript. With her support and encouragement throughout the long months of field work and writing, this study could not have been completed.

LITERATURE CITED


