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DISTRIBUTION AND GEOGRAPHIC VARIATION OF THE AMEIVAS OF PUERTO RICO AND THE VIRGIN ISLANDS [1]

by

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[1] HERPETOGEOGRAPHY OF PUERTO RICO. III.

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INTRODUCTION

The broad outlines of the taxonomy and distribution of the Antillean ameivas have been sketched by BARBOUR & NOBLE (1915). Two principal ancestral stocks were recognized: (1) One gave rise to the *Ameiva ameiva* group whose center of origin and dispersal was northeastern South America, and which extended westward into Central America and also up the Lesser Antilles to Puerto Rico and Hispaniola.[1] (2) The other gave rise to the *Ameiva undulata* group which originated in and dispersed from Central America, moving into northwestern South America and into the Greater Antilles as far eastward as Hispaniola. In addition to these two main stocks, they postulated still a third origin for a small group of species in the Bahamas – Puerto Rico – St. Croix area (*A. maynardi*, *A. wetmorei* and *A. polops*), but which they allied more closely to the *A. undulata* than to the *A. ameiva* group. A final, somewhat problematic group consists of the South American *Ameiva bifrontata* and its subspecies. They postulated that it either arose from the *Ameiva ameiva* group or from still a fourth stock.

Accordingly to BARBOUR & NOBLE's view, then, the Antilles comprise two main groups which have invaded the area from opposite directions and which overlap on Hispaniola (or from Hispaniola to St. Croix if *Ameiva wetmorei* and *A. polops* are considered allied to the *A. undulata* group – see below).

COCHRAN (1941) in a review of the Hispaniolan forms modified this scheme by (1) considering *A. wetmorei* closely related to

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[1] Since this paper was finished, BASKIN & WILLIAMS (1966) have discussed the movement of South American ameivas up the Lesser Antillean chain. They suggest three separate invasions resulting in three species groups. Our usage of the term "*Ameiva ameiva* group" includes these subgroups.

A. lineolata of Hispaniola, thus allying the former with one of the species Barbour & Noble had definitely placed in the *A. undulata* group, (2) pointing out that *A. polops* is related to *A. taeniura* of Hispaniola rather than to *A. wetmorei* of Puerto Rico, and (3) synonomizing *A. vittipunctata* (considered by Barbour & Noble as belonging to the South American stock) with *A. chrysolaema* (of Central American stock). Clearly, a re-study of the relationships of the Antillean ameivas is in order. This paper deals with those forms existing from Mona Island to Anegada inclusive (Figs. 17 and 24).

In the Puerto Rican area, three described forms belong to Barbour & Noble's South American stock. They are *Ameiva exsul* Cope from Puerto Rico and the Virgin Islands, *Ameiva alboguttata* Boulenger from Mona Island and *Ameiva birdorum* Grant from Diablo Key. In this paper we place the latter in the synonomy of *Ameiva exsul* and also describe a new species, *Ameiva desechensis*, from Desecheo Island. We shall subsequently refer to these forms as the *Ameiva exsul* subgroup.

The *Ameiva undulata* group is represented in the area by three named forms, *A. wetmorei* from Puerto Rico, *A. eleanorae* from Caja de Muertos Island (the latter is placed in the synonomy of the former

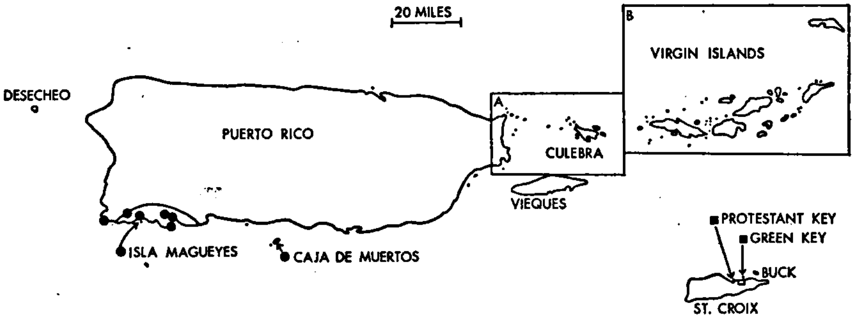

Fig. 17. Map of the Puerto Rico-Virgin Island area showing distribution of *Ameiva wetmorei* (dots) and *Ameiva polops* (squares). Solid symbols represent localities from which specimens have been examined; open symbol represents a literature record (Cope 1862). Line surrounding most of the *A. wetmorei* localities is the 30 inch isohyet. A. indicates the area shown in Fig. 25 and B. that shown in Fig. 26.

in this paper) and *A. polops* from St. Croix. The last is more closely related to a Hispaniolan form than to any on the Puerto Rican island shelf (COCHRAN 1941) and probably represents an independent invasion of the *A. undulata* group eastward.

We are grateful to the following persons and institutions for the privilege of examining specimens: ERNEST E. WILLIAMS of the Museum of Comparative Zoology at Harvard, DORIS COCHRAN of the U. S. National Museum, the late NORMAN HARTWEG of the University of Michigan Museum of Zoology, CHARLES M. BOGERT of the American Museum of Natural History, WILLIAM DUELLMAN of the Museum of Natural History of the University of Kansas and R. F. INGER of the Chicago Natural History Museum. CHARLES WALKER facilitated our work in many ways while we examined specimens at the University of Michigan.

The following people aided our expeditions to St. Croix and surrounding keys: BILL MILLER, GEORGE SEAMAN, JOHN WOODSON and DONNA CRANK of Christiansted, St. Croix, and HERMINIO LUGO LUGO of the University of Puerto Rico. TITO WIRSHING of the Don-Q Rum distillery and Prof. LUIS ESCABÍ of the Catholic University of Puerto Rico provided transportation and lodging on expeditions to Caja de Muertos and Platillo Islands. EUNICE BOARDMAN of Beef Island provided various kinds of aid on our expedition to the British Virgin Islands. The police department of Cabo Rojo, P. R., the Institute of Marine Biology of the University of Puerto Rico at Mayagüez, and the U. S. Coast Guard provided transportation and lodging during various expeditions to Mona and Monito Islands and to southwest Puerto Rico. We are grateful to ALAN BATHAM, REGINALD PENN and the BIGELOW family of the British Virgin Islands for permission to collect on their properties.

FAUSTINO MCKENZIE, RICHARD LEVINS, MANUEL VELEZ and FRANCIS ROLLE assisted in the collection of specimens. SHEILA BLASINI, ISABEL COLORADO, SARA ARMSTRONG, and ANA VASQUEZ performed some of the statistical calculations; AUDRY HEATWOLE and OLGA TORRES helped prepare the manuscript. THOMAS JACKSON did the photography.

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MATERIALS AND METHODS

Various characters used in separating species of *Ameiva* have been the number of longitudinal rows of ventral scales, whether or not the caudal scales are oblique, the placement of the nostril, scutellation pattern of the head and legs, etc. In the Antillean forms these seem to be relatively constant within a species and hence not particularly valuable for an analysis of intraspecific variation. *Ameiva exsul, Ameiva wetmorei,* and *Ameiva polops* can be easily distinguished from each other on the basis of the above kinds of characteristics and no attempt is made here to repeat the previous statements of various authors who have outlined these differences. Rather attention is concentrated on the variation among populations within a particular species, and on comparing very closely related populations, not separable by the above categories of characters, but which have been accorded specific or subspecific rank on the basis of number of femoral pores and/or color pattern. These closely related, previously named forms are: (1) *Ameiva wetmorei – Ameiva eleanorae* and (2) *Ameiva alboguttata – Ameiva exsul – Ameiva birdorum.*

The following CHARACTERS were used:

1. Number of femoral pores: "Number of femoral pores" throughout this paper indicates the sum of the number of pores on the right and left sides. Usually the counts of the two sides did not differ by more than 1 or 2. The femoral pores (more appropriately called glands) do not regenerate. Hence data were discarded for animals in which some of the pores had been obliterated by injuries.

2. Number of scales in 15th tail ring. The caudal scales are arranged in rings. Beginning just behind the cloaca, the scale-rings were counted posteriorly until the 15th one was encountered; the number of scales in this ring was then recorded. These are subsequently referred to as "caudals." Data were discarded for all animals which had lost their tails anterior to this region even if subsequent

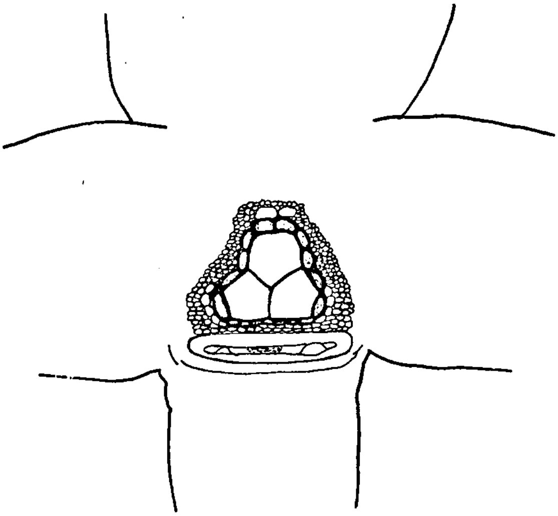

Fig. 18. Scutellation of ventral area anterior to vent in *Ameiva exsul* showing the preanal plates surrounded by preanal scales. The latter are stippled and outlined in heavy lines.

regeneration had occurred; scales of regenerated tails are smaller and greater in number.

3. **Preanal scales**: Antillean ameivas have a series of 3–5 flat enlarged scales just anterior to the cloaca known as preanal plates. Encircling these is a row of smaller scales which we have chosen to call the preanal scales (Fig. 18). The number of these served as one of the characters analyzed.

4. **Transverse rows of ventrals**: The number of longitudinal rows of ventral scales is rather constant within a species of *Ameiva* and has been used as a character for the separation of species. However, the number of transverse rows of scales varies and it was thought that it might be a useful character in analyzing infra-specific variation. The number of rows were counted beginning with the first one behind the prepectoral fold and proceeding posteriorly to the abrupt point where the scales are no longer arranged in rows.

5. **Number of brachials**: The number of brachial scales on the right and left forelimbs were counted and the sum of both sides used in analyzing patterns of variation. Difficulty was sometimes experienced in deciding which scale represented the first brachial.

6. **Ratio of snout length to body length**: Body length was considered the distance from the tip of the snout to the anterior edge of the vent. Snout length was taken from the posterior edge of the nostril to the anterior border of the eye. All measurements were made with Vernier Calipers.

7. **Color pattern**: All species and subspecies either now or previously recognized for the area under consideration, have been collected alive by the authors. Color pattern as well as scutellation has been used in defining species although no form has been recognized solely on the basis of color pattern. Use of color pattern as a taxonomic character in *Ameiva* is complicated by the great ontogenetic changes that take place and also by the wide variability even within the same locality, in some species. For example, BEEBE (1919) collected "perfectly typical specimens" of 4 named subspecies of *Ameiva ameiva* within an area of about 500 yards around a research station in British Guiana. Clearly, care should be exercised in basing diagnoses on coloration.

All animals except small ones classed as juveniles, were sexed by examination of the gonads unless the hemipenes were protruding.

The names of Museums will be abbreviated in the following manner throughout the remainder of the paper: AMNH – American Museum of Natural History; CNHM – Chicago Natural History Museum; KU – Museum of Natural History, University of Kansas; MCZ – Museum of Comparative Zoology; UMMZ – University of Michigan Museum of Zoology; UPRRP – University of Puerto Rico at Río Piedras; USNM – United States National Museum.

The 1,043 specimens which were examined are listed in the chapters concerned.

EFFECT OF SIZE AND SEX ON CHARACTERS USED

Before comparison between populations can be made it is necessary to know whether there is an ontogenetic change or a difference between the sexes in the characters used. Figure 19 shows a plot of the snout length to body length ratio plotted against size for the sample of *Ameiva exsul* from the San Juan area. Figure 20 shows the same type of analysis for *A. wetmorei* from La Parguera, P. R. No ontogenetic change in the ratio is evident in either species. Inasmuch as the scale characters used are fixed during early development (pre-hatching) such an analysis was unnecessary for them.

The same group of lizards was also used for comparing males and females. Using the graphic test of significance of Dice & Leraas (1936), it was found that there was no significant difference between the sexes in any of the characters used for *Ameiva exsul* (Fig. 21). Hence the data for both sexes were grouped for the analysis of geographic variation. The same was true for *A. wetmorei* except for femoral pores which were significantly lower in females (Fig. 22). In subsequent analyses of this character in *A. wetmorei* the sexes are treated separately.

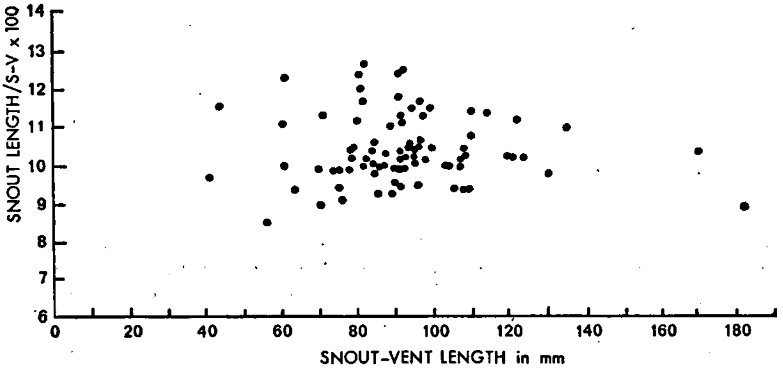

Fig. 19. Relationship of ratio of snout length and body length to size in *Ameiva exsul* from San Juan, P.R.

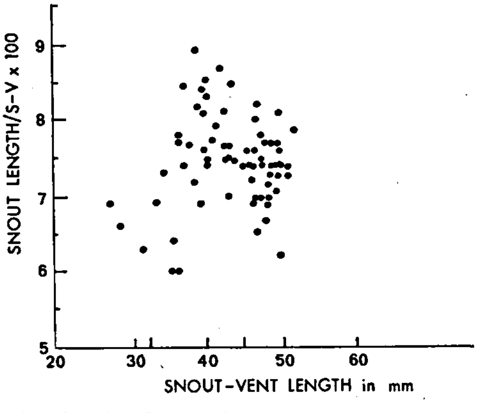

Fig. 20. Relationship of ratio of snout length and body length to size in *Ameiva wetmorei* from La Parguera, P.R.

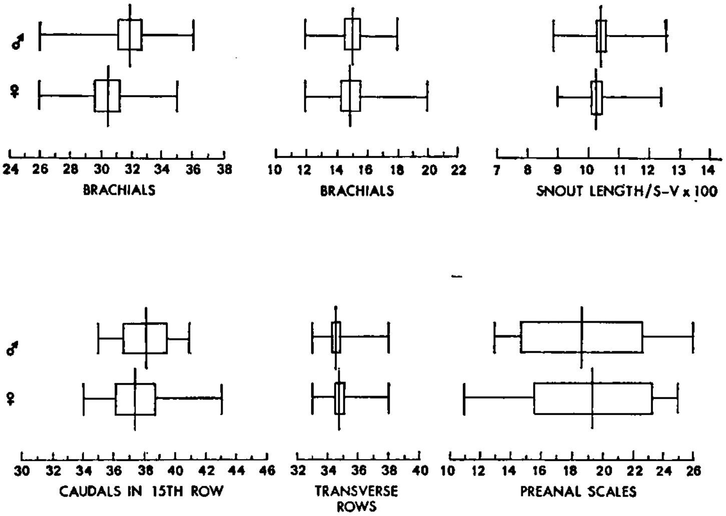

Fig. 21. Comparison of males and females of *Ameiva exsul* from San Juan, P.R., with respect to various characters. Central vertical bar represents the mean, terminal vertical bars represent end points of the range and rectangles represent 2 standard errors on each side of the mean. Failure of these rectangles to overlap indicates significant differences (Dice & Leraas 1936). N = 28 (♀), 48 (♂).

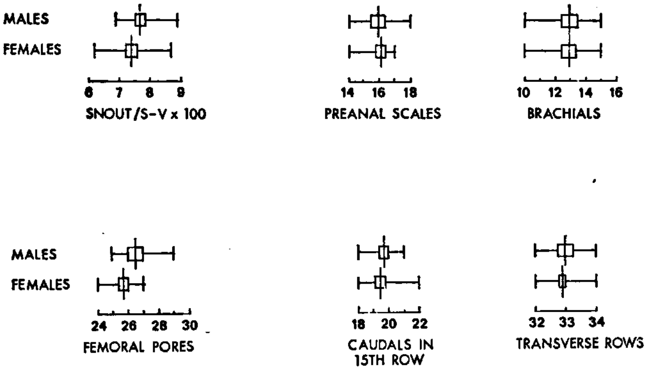

Fig. 22. Comparison of males and females of *Ameiva wetmorei* from La Parguera, P.R., with respect to various characters. N = 37 (♀), 26 (♂). Symbols the same as in Fig. 21.

The similarity in relation of snout length to body length for the two sexes was not expected. Mr. ANGEL MALDONADO, who had been doing experimental work on *Ameiva exsul* can sex them quite accurately (verified by examination of the gonads) by looking at the side of the head. He felt that the males had longer snouts than females, although his subjective determinations apparently are based on some more subtle cue.

Ontogenetic changes in color pattern are discussed later.

EFFECT OF TIME ON SCALE CHARACTERS

Inasmuch as specimens collected over a period of more than half a century were lumped together and used for studying geographic variation, it was necessary to ascertain whether measurable changes had occurred within a locality during that time. To do this, data from specimens collected in the San Juan area prior to 1900 were compared to those from lizards collected in the same region between 1960 and 1966. The results (Fig. 23) indicate no significant differences in most of the characters used, i.e., no observable evolution had occurred. However, there was one exception (caudal scales in 15th row), indicating that at least for some characters, 60 years is sufficient time for measurable changes to occur. Consequently, some of the inter-locality differences in caudal scale number subsequently described, may reflect temporal as well as spatial differences. In all cases where conclusions are

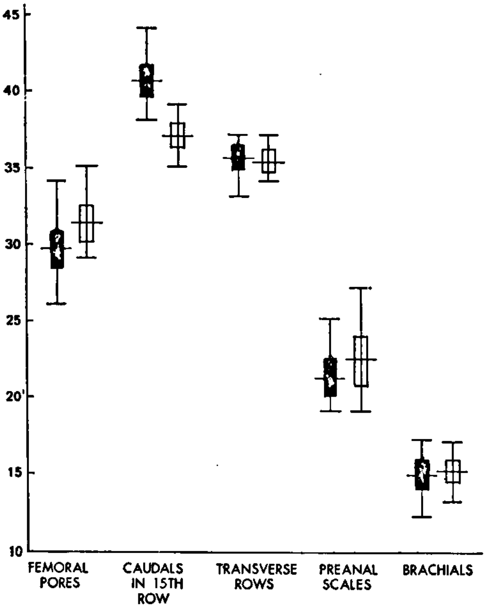

Fig. 23. Comparison of scale characters of a sample of *Ameiva exsul* collected prior to 1900 (solid bar, N = 13) with a sample from the same locality collected between 1960 and 1966 (open bar, N = 10). Symbols as in Fig. 21.

drawn from comparison of this character among localities, the specimens from each place involved were collected at about the same time.

Unfortunately, comparable data are not available for very small islands where more rapid changes might be expected. However, in view of the above results, it is reasonable to assume that for most characters patterns of variation reflect present day inter-island differences, rather than discrepancies in date of collection of the material.

Ameiva ameiva group

Ameiva exsul subgroup

Ameiva exsul Cope 1862

HABITS

STAHL (1883) gives the habitat of *Ameiva exsul* (under the name of *A. plei*) as "arenales y pedregales"; STEJNEGER (1904) lists it as sandy or gravelly soil, and SCHMIDT (1928) says "*Ameiva exsul* distinctly prefers a sandy soil, and is everywhere more abundant on sand." It is true that this species is primarily a beach form and may have been restricted to this habitat in Pre-Colombian times. Now, however, it can also be found in a variety of open areas with low vegetation, such as lawns, vacant lots, roadsides, city parks and plazas, and around human dwellings. It is well adapted to the conditions created by man and can frequently be seen on the sidewalks near vacant lots in the San Juan metropolitan area. On a number of occasions we have seen it wandering about on the floor of an open restaurant on the University of Puerto Rico campus. We have never observed it in heavy forests although it is encountered along roadsides or on lawns which have scattered trees.

When running rapidly, *Ameiva exsul* frequently utilizes a bipedal type of locomotion.

These lizards spend their inactive periods in burrows which they dig. Usually the burrow is beneath a stone, piece of wood or other loose object although sometimes the entrance is beside a plant or less frequently in the open. SCHMIDT (1928) mentions that they made burrows under tramway ties, sidewalks, and under stones or other loose objects. Their main habitat requirements seem to be (a) an open area, (b) soil suitable for digging, and (c) objects lying on the surface of the ground.

Ameiva exsul is strictly diurnal and is usually active in direct sun. According to WOLCOTT (1923) it feeds at mid-day. However, GRANT (1931a) indicates that there are two activity periods, one in late morning and another in early afternoon. He describes it in the following terms: "They never venture out in the cool of the morning. If, when hunting, they suddenly come to a strip of sunlight, they will flatten out, hind legs stretched out, and bask for a few minutes. During the extreme heat of the day they are quiescent, seeking the shady places. As the afternoon cools, they are again active, but retire well before sunset into holes which they themselves excavate under stones or boards, or seek a natural crevice where available." This difference of opinion is probably explained by the observation of DANFORTH (1925) that during the winter *A. exsul* came out only in the middle of the day, but after

April they could be found any time the sun was shining. A bimodal activity pattern is also found in several other teids (Carpenter 1961, Hirth 1963).

As is true of at least some other members of the genus (Beebe 1945) this species feeds by foraging rather than sitting and waiting for prey to approach within reach. The lizards walk along examining small objects and poking into clumps of grass, under leaves, etc., frequently extending their tongue in snake-like fashion as they do so. They are generalized omnivores. Wolcott (1923) examined the stomachs of 15 specimens and found that their food was 78% insects, with smaller proportions of other arthropods, earthworms, and snails. Of especial interest was the fact that non-moving food was also taken; 2 different individuals had each eaten lizard eggs; one had eaten only mushrooms. Schmidt (1920, 1928) examined 20 stomachs and found that 11 contained vegetable material, mostly red-coated seeds. Additional items were insects, crabs, lizards eggs, and the tail of an *Anolis cristatellus*. Thus they may be an important predator on other saurians. They also frequently eat table scraps put out for dogs or cats, and Grant (1931a) has reported them feeding primarily on "refuse and vegetable matter" including onion trimmings and potato peelings. We have observed them on numerous occasions eating cactus fruits, bananas, apples, and crawling into recently discarded spaghetti, ravioli, and meat cans and eating the remaining bits of food. We suspect that one of the reasons Palominitos Island can maintain its surprisingly large population of *Ameiva exsul* is because of the energy entering the system in the form of garbage scattered unceremoniously on the beach by weekly infestations of picnickers. Heatwole *et al.* (1963) reports that *Ameiva exsul* eats monkey-chow put out for monkeys on Cayo Santiago, P. R., and suggests that this has resulted in an increase in population size on part of the island.

Little is known of the reproduction in this species although Noble & Bradley (1933) have published a few observations of its courtship and mating. The tail is apparently necessary for effective mating. Field observation indicates that males which have recently lost heir tails (not yet regenerated) are unsuccessful in attempts to copulate (MacKenzie, personal communication). The pink eggs are

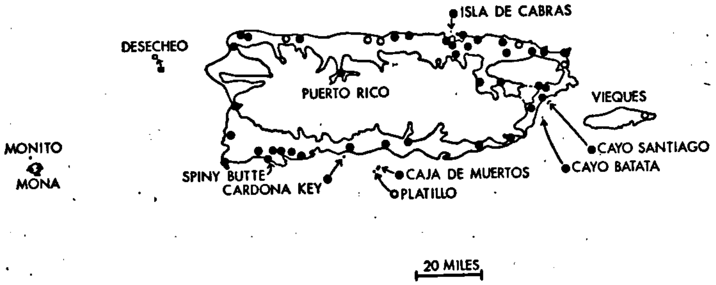

Fig. 24. Map of Vieques and Puerto Rico and the latter's northern, southern and western outlying keys, showing distribution of the *Ameiva exsul* subgroup. Triangles represent *Ameiva alboguttata*, squares represent *Ameiva desechensis* and dots represent *Ameiva exsul*. Open circles indicate sight records of *Ameiva exsul* by the authors except for the one on Vieques which is a literature record (Grant 1932 e).

laid in loose soil several inches below the surface of the ground; they are 20–22 mm × 13–15.5 mm and are found in groups of 4–7 (Wolcott 1923). A hatchling collected on 5 February 1965 and still possessing its yolk-sac scar, measured 36 mm s-v.

Growth seems to occur long after achievement of sexual maturity. Most adults encountered are not 100–120 snout to vent. However, giant individuals are occasionally encountered which are as large as 200 mm s-v. They are presumably very old individuals which have continued to grow throughout their life. We have examined several such specimens, the largest of which was a male from Playa Humacao (MCZ 58775; s-v 201 mm) and have seen others about the same size in the field. SCHMIDT (1920, 1928) lists the maximum size as "much exceeding half a meter" in total length.

DISTRIBUTION OF *Ameiva exsul* ON THE PUERTO RICAN MAINLAND

As is immediately evident from Figure 24, *Ameiva exsul* is restricted to the lower elevations, not having been collected above an altitude of 500 ft, although it has been observed in open areas and along roadsides somewhat higher. WOLCOTT (1923) gives its distribution as "near the coast or in river valleys, but sometimes occurs in hills of no great elevation." It intuitively appears unlikely that altitude *per se* should be a factor limiting the distribution of this species and some factor correlated with altitude appears more plausible. Temperature, rainfall, vegetation, and soil vary throughout the island and all show at least a rough correlation with altitude.

As indicated in the section on habits, *Ameiva exsul* seems to prefer a sandy soil and is most abundant in sandy habitats. Most of the lowland soils tend to be sands or sandy loam whereas the upland ones are more often clay. However, this is not the factor controlling the lizards' distribution, for when the collection sites of *A. exsul* were superimposed on a soil survey map, they fell on such diverse soils as sands, silty loams and clays (ROBERTS 1942). The possibility of this lack of correspondence to soil type being an artifact due to local pockets of sandy soil has been ruled out by our direct observation of this species inhabiting Caguas clay. Geological formations are similarly unimportant as *A. exsul* is found in areas characterized by limestones and other sedimentary rocks, as well as in those with substrate of volcanic origin (MITCHELL 1954).

Nature of vegetation is probably a factor in the distribution of this species inasmuch as it is not found in heavy forest. This is probably because of the reduced light intensity and/or temperature below the level required for their activity period. They are found in the more open scrubby arborescent vegetation in the hotter areas, e.g., on Caja de Muertos island.

Inasmuch as cloudy or rainy, cool weather inhibits the activity of this species, one might suspect that in the cooler areas of the island with heavy rainfall, the activity period may be cut so short that the species cannot find enough food to maintain itself and reproduce.

The distribution of *Ameiva exsul* (shown in Figure 24) is delimited on the inland side by the 76° isotherm for mean annual temperature (PICÓ 1954, p. 116) almost as well as by the 500 ft countour line. In fact the 76° F isotherm appears as a "smoothed out" diagram of the 500 ft contour line. The only *A. exsul* locality to fall in a cooler area is Utuado which occurs between the 74° and 76° F isotherms; many coastal localities were in areas with mean annual temperature *greater* than 76° F.

The pattern of rainfall is complex in Puerto Rico with the greatest amount occurring at the higher altitudes and with (at comparable altitudes and exposures) the eastern end of the island receiving more rain than the western one. Distribution of *Ameiva exsul* although generally in the drier areas, shows no precise correlation with any isohyet (PICÓ 1954, p. 135).

In summary it can be stated that the distribution of *Ameiva exsul* on Puerto Rico does not correlate with soil type or with pattern of rainfall, but does correlate with altitude and temperature. The former is believed to be an indirect relation in that temperature and altitude are themselves correlated. The hypothesis is put forward that *A. exsul* is restricted to the lowlands in Puerto Rico because the lower thermal level at higher altitudes shortens their activity period to the extent that they cannot obtain sufficient food to subsist over a long-term period. The final resolution of the problem awaits, of course, a detailed study of habitat selection and activity pattern, tolerance limits, and eccritic limits of this species to various environmental factors. Here we are simply attempting to describe the geographic distribution and its correlation with environmental patterns in the hope it will suggest experimental approaches aimed at the solution of this problem.

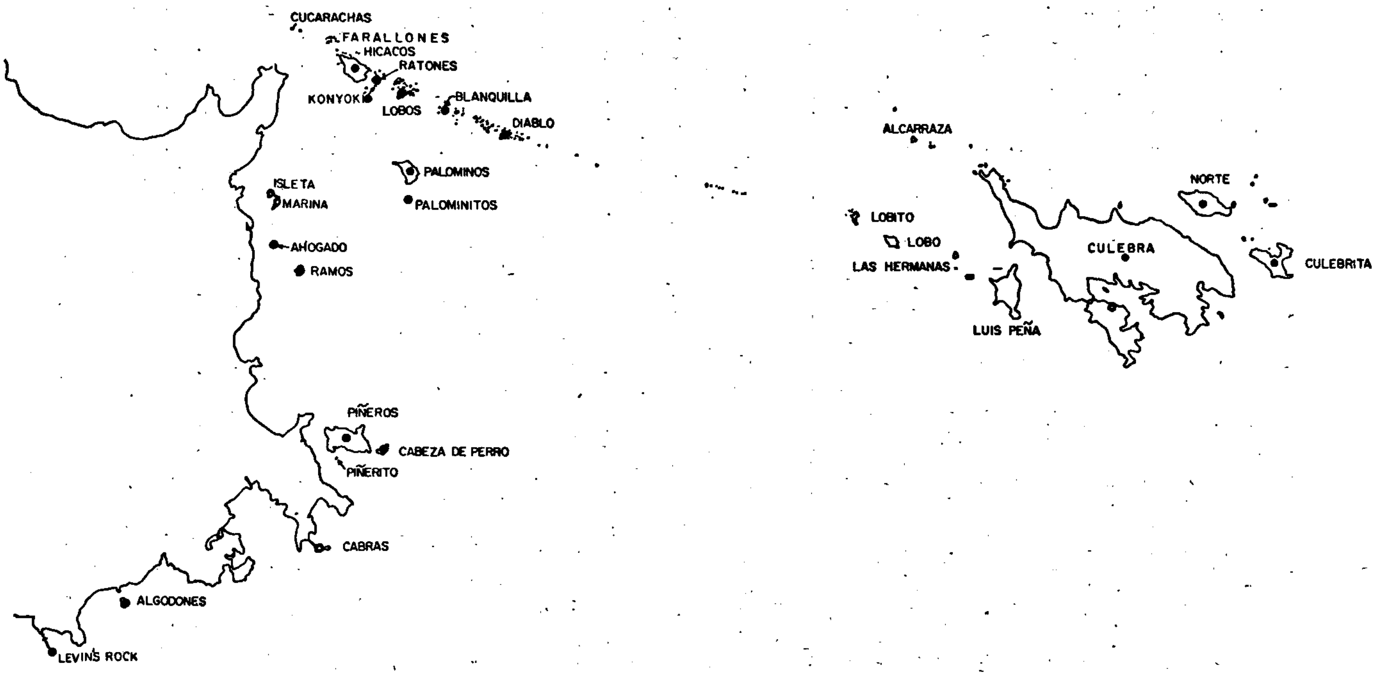

Fig. 25. Map of the northeastern keys of PUERTO RICO showing distribution of *Ameiva exsul* (See Section A of Fig. 17). Dots represent localities from which specimens were examined, circles represent sight records by the authors.

DISTRIBUTION OF *Ameiva exsul* ON OTHER ISLANDS

In the Puerto Rico – Virgin Island area there are several instances of more than one island having the same name, e.g., there is a Buck Island near St. Croix, another near St. Thomas and still another near Tortola. Where such possible sources of confusion exist, the name of the island is followed by that of its nearest large island in parenthesis. As seen in Figures 24, 25 and 26, *Ameiva exsul*

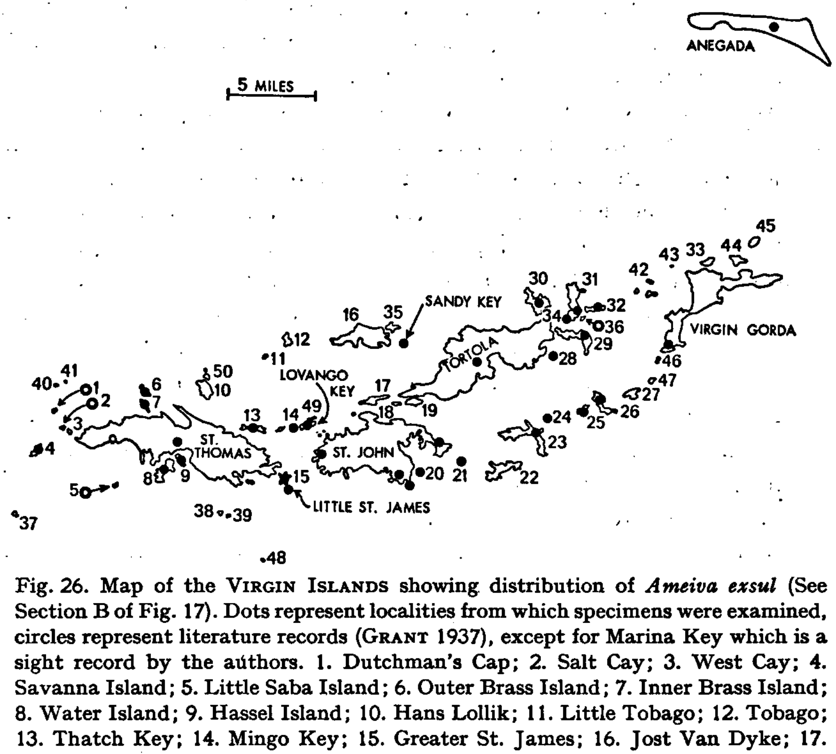

Fig. 26. Map of the VIRGIN ISLANDS showing distribution of *Ameiva exsul* (See Section B of Fig. 17). Dots represent localities from which specimens were examined, circles represent literature records (GRANT 1937), except for Marina Key which is a sight record by the authors. 1. Dutchman's Cap; 2. Salt Cay; 3. West Cay; 4. Savanna Island; 5. Little Saba Island; 6. Outer Brass Island; 7. Inner Brass Island; 8. Water Island; 9. Hassel Island; 10. Hans Lollik; 11. Little Tobago; 12. Tobago; 13. Thatch Key; 14. Mingo Key; 15. Greater St. James; 16. Jost Van Dyke; 17. Great Thatch Island; 18. Little Thatch Island; 19. Frenchman's Key; 20. Leduck Island; 21. Flannigan Island; 22. Norman Island; 23. Peter Island; 24. Dead Man's Chest; 25. Salt Island; 26. Cooper Island; 27. Ginger Island; 28. Buck Island; 29. Beef Island; 30. Guana Island; 31. Great Camanoe; 32. Scrub Island, 33. Mosquito Island; 34. Little Camanoe; 35. Little Jost Van Dyke; 36. Marina Key; 37. Sail Rock; 38. Buck Island; 39. Capella Island; 40. Cockroach Island; 41. Cricket Rock; 42. The Dog Islands (George Dog, West Dog, and Great Dog); 43. Seal Dogs; 44. Prickly Pear Island; 45. Necker Island; 46. Fallen Jerusalem; 47. Round Rock; 48. Frenchman Cap; 49. Congo Key; 50. Little Hans Lollik.

occurs on all of the larger islands from Puerto Rico to Anegada except St. Croix. It was recorded from Desecheo (SCHMIDT 1928) but the Desecheo form is not *A. exsul* and it is described in this paper as a new species. *Ameiva exsul* is lacking on some of the smaller islands within its general range. In some cases this is probably because the island has not been herpetologically explored rather than an actual absence of the species. However, on a number of these islands absence of *Ameiva* is probably real. GRANT (1931b, 1932a, b, 1937) collected on Cockroach Island (St. Thomas), Buck Island (St. Thomas), Dog Island, Congo Key and Luis Peña Key and found no ameivas on any of them.

We have examined a number of the small keys northeast of Puerto Rico and found them to lack ameivas. These are the Cucarachas, the Farallones, and various of the small islands around Diablo Key and Blanquilla Key, and between Culebrita Island and Cayo Norte (Fig. 25). A few of these lacked vegetation, although most had a herbaceous plant cover and some of them, arborescent vegetation. However, with a few exceptions, none had beaches and the shorelines of most consisted of vertical cliffs, under cut several feet at the base by wave action. Off the southwestern coast of Puerto Rico, all keys except one (Spiney Butte) lacked *A. exsul.* Some of these islands were surrounded by mangroves, others had sandy beaches.

All of the small islands containing *Ameiva exsul* have characteristics similar to those of the coastal areas of Puerto Rico, i.e., low altitude, mean annual temperature above 76° F and open, i.e., not heavily forested, areas. Rainfall is scant on most and the substrate is usually either sand or limestone. The larger islands are either similar in their entirety or have coastal areas with these characteristics.

This is also true of St. Croix and its outlying keys and yet *Ameiva exsul* is lacking there. Earlier reports of this species from St. Croix (BARBOUR 1914, BARBOUR & NOBLE 1915, SCHMIDT 1928) have been questioned by a number of authors (BARBOUR 1930, 1937) and were apparently based on confusion with *A. polops* which superficially resembles the juveniles of *A. exsul* (GRANT 1937). Inasmuch as appropriate habitat for *A. exsul* occurs on St. Croix, the lack of this species there is probably due to historical considerations and to present barriers to transport between St. Croix and the other islands (see discussion). Failure to compete successfully with *A. polops* is a further possibility. However, *A. polops* has now been exterminated by the mongoose on the mainland of St. Croix, yet *A. exsul* has not become established there. *A. exsul* itself does not seem to be greatly influenced by the mongoose as evidenced by its abundance on mongoose-infested islands.

BARBOUR (1930, 1937) reports *Ameiva exsul* as occurring on Anguilla. However, UNDERWOOD (1962) lists the Anguilla species as *Ameiva pleeii*. We have not examined any specimens from that island.

Ameiva exsul is occasionally found on islands too small to support permanent populations. For example on Levin's Rock (Fig. 25) which has an area of only 65 m², the total *Ameiva exsul* population consisted of one male, which had obviously reached the island from Puerto Rico (a distance of only about 5 m at low tide). Similarly, one individual reached Cayo Ahogado, a small (3,000 m²) sparsely vegetated sand bar 0.8 km east of Puerto Rico (Fig. 25). This island had been visited frequently over a period of 18 months and no *Ameiva* found there until 23 June 1965, when 2 individuals were present. Just previous to that date, the Fajardo River opposite the key, had flooded, casting adrift much debris. The lizards had disappeared again by 30 July 1965. After similar conditions of flooding on the mainland, one individual was found on Cayo Ahogado on 17 October 1965.

These observations suggest that this species can be dispersed at least short distances via sweepstakes routes, and that it may temporarily inhabit small islands not able to permanently support a population.

VARIATION IN *Ameiva exsul* ON THE PUERTO RICAN MAINLAND

The *Ameiva exsul* on the Puerto Rican mainland do not constitute a single homogeneous population but rather certain characters show geographic patterns of variation. Disregarding for the moment those populations partially isolated in the inland river valleys and focusing on the coastal localities (represented by heavy lines in

Figs. 27 and 28), it is seen that the dominant pattern of variation is an east-west cline along the northern coast. This appears in the number of femoral pores with the northwestern ameivas having a significantly lower number than those from the San Juan area or the northeastern tip of Puerto Rico (Fig. 28). The connecting population in north central Puerto Rico is intermediate in number of femoral pores and does not differ significantly from those either to the west or to the east. Thus the change in number of pores is gradual and the extreme populations at the two ends of the island are connected by intermediate ones. The eastern and southern coastal areas are not significantly different from each other or from those of the eastern end of the cline. The number of caudals in the 15th row of scales around the tail shows the same geographic trend, i.e., a low number of scales in northwestern and north central Puerto Rico becoming significantly higher in the San Juan area and in northeastern Puerto Rico. With respect to this character, the eastern and southern populations are identical to the northeastern populations and all are significantly higher than the

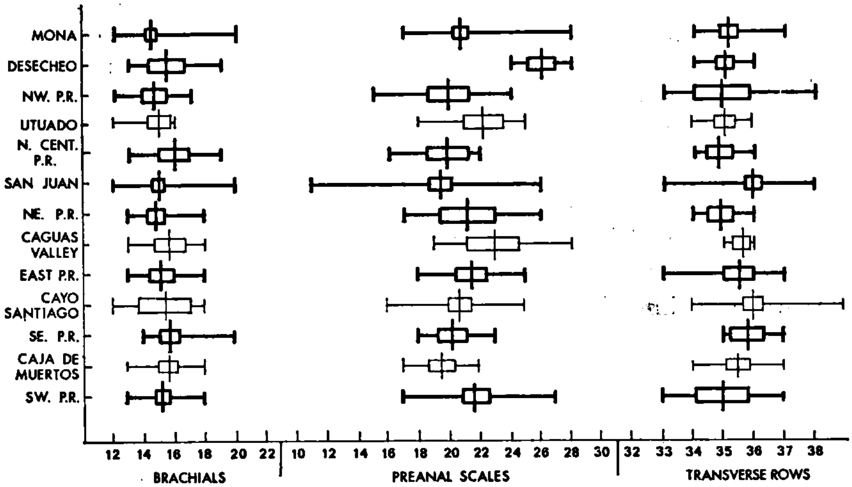

Fig. 27. Variation in numbers of brachials, preanal scales, and transverse rows of ventrals of *Ameiva exsul* from Puerto Rico, Cayo Santiago and Caja de Muertos, *Ameiva alboguttata* from Mona, and *Ameiva desechensis* from Desecheo. Symbols same as in Fig. 21. N varies between 10 and 115 specimens per locality.

northwestern ones. The cline seems to be steepest between the north central populations (Cibuco and Dorado Beach) and San Juan as the northwestern and north central populations do not differ significantly from each other although both are significantly different from San Juan and northeastern Puerto Rico. The latter two areas are not significantly different (Fig. 28).

With respect to preanal scales, the northern populations are not significantly different, i.e., there is no northern coastal cline as in the previous two characters. The southern and eastern populations are not significantly different from each other. Except for the southeastern specimens, they have a significantly greater number of preanal scales than the San Juan population. The northeastern population is intermediate between those of the northern and eastern coasts and the character can therefore be considered clinal (Fig. 27).

Variability in the number of longitudinal ventral rows of scales was not great and most of the inter-population differences not

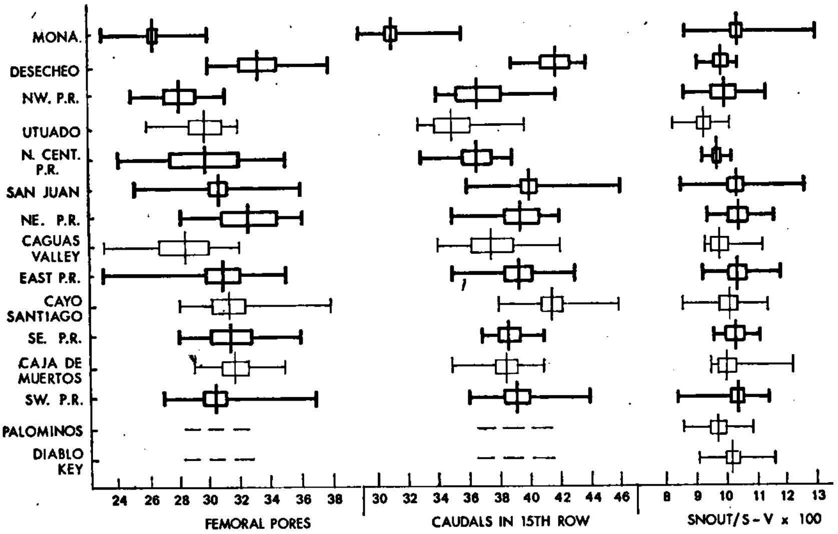

Fig. 28. Variation in numbers of femoral pores, caudals in 15th row, and ratio of snout to body length in *Ameiva exsul* from Puerto Rico, Cayo Santiago and Caja de Muertos, *Ameiva alboguttata* from Mona, and *Ameiva desechensis* from Desecheo. Symbols same as in Fig. 21. N = 10 to 115.

significant. Those of the northern coast are the same except for the San Juan area population which has a significantly larger number of rows than adjacent populations on the northern coast. This may be a reflection of gene-flow from the eastern and southeastern populations through the Caguas Valley, all of which tend to have more transverse rows than the northeastern and north central population (however, differences are significant only for the Caguas Valley).

The two remaining characters which were used were relatively uniform throughout the mainland. There were no significant differences among any of the populations with respect to numbers of brachial scales, although the north central ameivas tended to have a greater number. The north central population had significantly shorter snouts than all of the other populations except for the northwestern ones. None of the other populations were significantly different from each other with respect to this character (Fig. 28).

Populations were studied from two partly isolated valleys. One of these, the Caguas Valley, connects the San Juan area to the eastern coast. From Figure 24 it appears that there is no connection to the east at an altitude below 500 ft. However, this is an artifact due to lack of detail on the contour map. The road between the Caguas Valley and Naguabo (approximately upper dotted line of Fig. 24) follows a narrow valley. Altimeter readings reached a maximum of 250 ft along this route. There is a similar connection containing the road from the Caguas Valley to Humacao (approximately lower dotted line in Fig. 24) with a maximum elevation just at 500 ft.

Because of partial isolation it was thought that the ameivas from this valley might differ somewhat from those of coastal areas. Differences, however, were slight. In comparison to San Juan specimens, those from the Caguas Valley had a significantly lower number of femoral pores and caudal scales, a significantly shorter snout in relation to body length, and greater numbers of preanal scales. The same relation was shown with respect to the eastern populations except that the differences were not so great (although statistically significant) (Figs. 27–28).

As previously mentioned, the number of transverse ventral scale rows in the San Juan area seems to be influenced by gene flow through the Caguas Valley from the eastern populations.

The other area containing a partly isolated population is the valley of the Río Grande de Arecibo and Río Caonillas. It is a dead end, opening only onto the northern coast between the northwestern and north central collection areas (Fig. 24). The specimens studied all came from the town of Utuado. This population did not differ significantly from those of the northwestern and north central areas in any character although differences in number of preanal scales and ratio of snout length to body length were near the borderline of significance. With respect to the cline in number of femoral pores, the Utuado population was intermediate between the northwestern and north central population which is what would be expected for a non-isolated population in that geographic region. Hence, it seems that gene flow into the valley is great enough that little divergence has taken place.

VARIATION IN *Ameiva exsul* ON THE SMALLER ISLANDS

When the characteristics of the ameivas from the principal Virgin Islands are compared with their nearest neighbors on the Puerto Rican mainland (heavy lines on Figs. 29–30) it is seen that the inter-island differences are not great. None of the larger islands are significantly different from any other with respect to the number of preanal scales of their resident ameivas. The same is true of number of transverse rows of ventral scales except that the St. John population has a significantly lower number than all of the other populations except that on Tortola. The number of brachials is the same from Puerto Rico to, and including, St. John; then there is a cline in this character with Virgin Gorda having a significantly greater number than St. John. Tortola is intermediate both geographically and with respect to number of brachials. Number of femoral pores was constant in all of the larger islands except that on St. John the number tended to be lower (significantly so only with respect to Tortola).

There was a marked difference in number of caudals between the western most of the larger Virgin Islands as compared to St. Thomas and Puerto Rico. The populations on St. John, Tortola and Virgin

Gorda all had significantly lower numbers of caudal scales than those on St. Thomas and in eastern Puerto Rico which were practically identical with each other. In this case, this may represent temporal rather than spatial change.

The populations on small keys (thin lines in Figs. 27–30) were usually similar to those on adjacent larger islands although some showed significant variation in one or more characters. For example, there was a significantly higher number of caudals in the Cayo Santiago population than in those of either eastern or southeastern Puerto Rico (Fig. 28). The Caja de Muertos population differs from the southwestern Puerto Rican one (but not from the southeastern one) in having significantly fewer preanal scales (Fig. 27), Palominos specimens had relatively shorter snouts than the nearest Puerto Rico mainland population (Fig. 28). Ameivas on Little St. James had significantly fewer caudals than those on either St. Thomas or St. John between which Little St. James lies. Those from Little St. James had fewer transverse rows of scales than those on St.

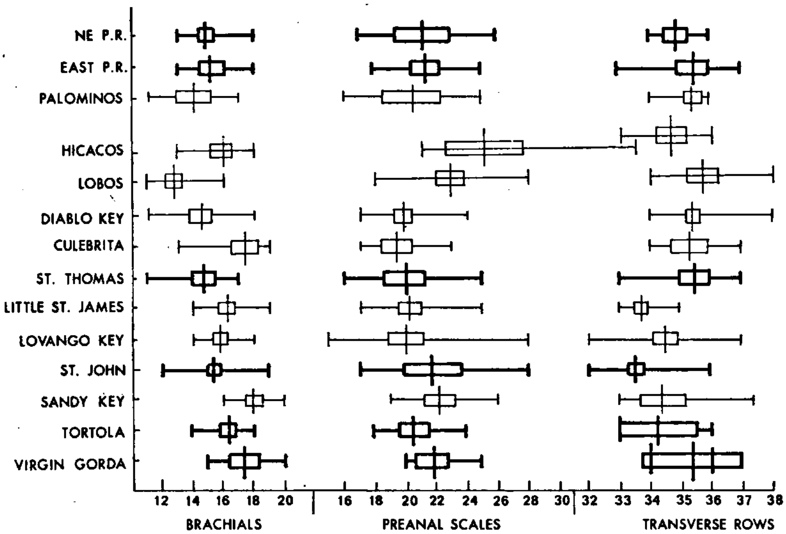

Fig. 29. Variation in numbers of brachials, preanal scales and transverse rows of ventrals in *Ameiva exsul* from the Virgin Islands, various of the northeastern Puerto Rican keys and 2 localities in Puerto Rico. Symbols same as in Fig. 21. N = 10–56 specimens per locality.

Thomas. The population on Lovango key was intermediate between that of St. Thomas and that of St. John and significantly different from both in number of transverse rows of ventrals. It had fewer caudals than the one on St. Thomas. Specimens on Culebrita have a significantly greater number of brachials than those from either St. Thomas or Puerto Rico. We lacked sufficient material from Culebra to make comparisons with Puerto Rico. GRANT (1931b) however, indicates he found no differences between Culebra and Puerto Rican specimens.

In some instances populations on the small keys differ significantly from those of any nearby large island, e.g., Sandy Key and Culebrita in number of brachials and Little St. James in number of caudals. However, in all the other instances where there were significant differences, they occurred between a large island and its eastern small neighbor. Small islands lying west of larger ones tend to have the same characteristics as the larger island even though inter-island distances may be rather great (e.g., Palominos does not differ from St. Thomas in number of femoral pores but does differ

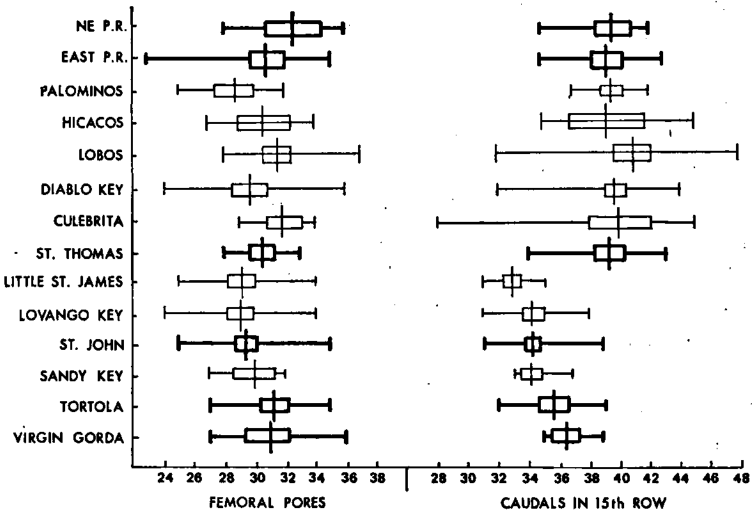

Fig. 30. Variation in numbers of femoral pores and caudals in 15th row in *Ameiva exsul* from the Virgin Islands, various of the northeastern Puerto Rican keys and 2 localities in Puerto Rico. Symbols same as in Fig. 21. N = 10–56 per locality.

from northeast Puerto Rico). This is most clearly seen with respect to Little St. James and Lovango Key, both of which lie about halfway between St. Thomas and St. John. In those characters which differ between St. Thomas and St. John, the smaller two islands resemble the latter more than the former (Figs. 29–30).

Of special interest are the characteristics of the population on Cayo Diablo which GRANT (1932a) described as a separate species, *Ameiva birdorum*, on the basis of color pattern (discussed below) and low femoral pore count. It is obvious from Figures 29 and 30 that the Diablo specimens are not significantly different from those of adjacent islands in number of femoral pores. In those characters (preanals, brachials) in which they do differ from specimens from nearby Lobos and Hicacos, it is the latter 2 islands rather than Cayo Diablo which depart from the more general condition.

COLORATION OF *Ameiva exsul* ON THE PUERTO RICAN MAINLAND

A generalization of the color pattern of *A. exsul* on the Puerto Rican mainland is as follows. Head and back olive brown to olive, becoming olive gray to gray on the tail, scattered black spots on dorsum, particularly posterior part. Sides with a darker ground color containing irregular black markings (sometimes as vertical stripes) interspersed with white dots. The same pattern continues onto the legs and tail. On the side of the tail spots of blue become intermixed with the black and white markings. The white dots on the sides of the body rarely coalesce to form vertical stripes. Sometimes the lower ones fuse to form a white lateral stripe running from axilla to groin. The tip of the snout and lower jaw is pink. Venter whitish to pearl gray with a bluish tinge which becomes much lighter toward the sides and on the underside of the tail and rear legs. The pupil is biloculate, surrounded by an orange-brown iris.

Ontogenetic variation in this pattern occurs. Young animals have a dorsal series of white dots which usually begins at the shoulder. The size and prominence of these spots vary greatly and they tend to be lost with age beginning anteriorally and proceding posteriorly. Even quite large specimens still have them on the base of the tail. The young also have prominent dorsolateral stripes on the body beginning at the supraciliaries. Usually these stripes are bright yellow although cream, buff, or yellowish-green ones are sometimes encountered. Frequently they are bordered on each side by a narrow black line. They begin disappearing early in life but the process is so gradual that it is difficult to indicate a size at which they are completely gone. Furthermore, individuals of the same size may be at quite different stages of loss of stripes (Fig. 31). Occasionally, quite young individuals are found with dim markings. The brightly colored stripes first fade to a pale brown and gradually assume the background color of the dorsum, as does the dark line medial to it. In half grown specimens both the dorsolateral stripes and the dorsal dots are frequently represented by brown areas, slightly paler than the background color. In larger specimens the former location of the dorsolateral stripes is marked by the transition from the background color of the dorsum to the darker coloration of the sides.

Background color is also brighter in the juveniles, sometimes approaching a rusty brown in very small individuals. Later it changes to olive and sometimes gray. The brown remains longest on the head and neck.

The bluish ventral coloration becomes more intense and more widely distributed with age. Very small individuals sometimes have a coppery venter. The throat in larger specimens takes on a pinkish to rose color which increases in intensity with size.

These changes in color are general trends seen on the Puerto Rican mainland and considerable variation among individuals of the same size is encountered, even within a particular locality (Fig. 31).

COLORATION OF *Ameiva exsul* ON SMALL ISLANDS

On the keys and islands east of Puerto Rico, there is even greater variation than on the mainland. There is a tendency for the dorsolateral stripes to persist longer on some of the islands, particularly from Blanquilla through Culebra. In specimens from the latter, the lateral stripe resulting from a coalescence of lateral spots (mentioned earlier) is frequently prominent. There is also a trend toward larger spots in the populations with persistent dorsolateral stripes. Culebra specimens have the largest dorsal spots of any we have examined. GRANT (1932c) who collected in the Virgin Islands mentions that Guana Island, Peter Island and Anegada "produced large, highly colored specimens, with prominent dorsolateral stripes reminiscent of similar ones on Culebra" although he reports those from Tortola and Buck Island (Tortola) as generally dark, losing their stripes early. Our own field work in the area

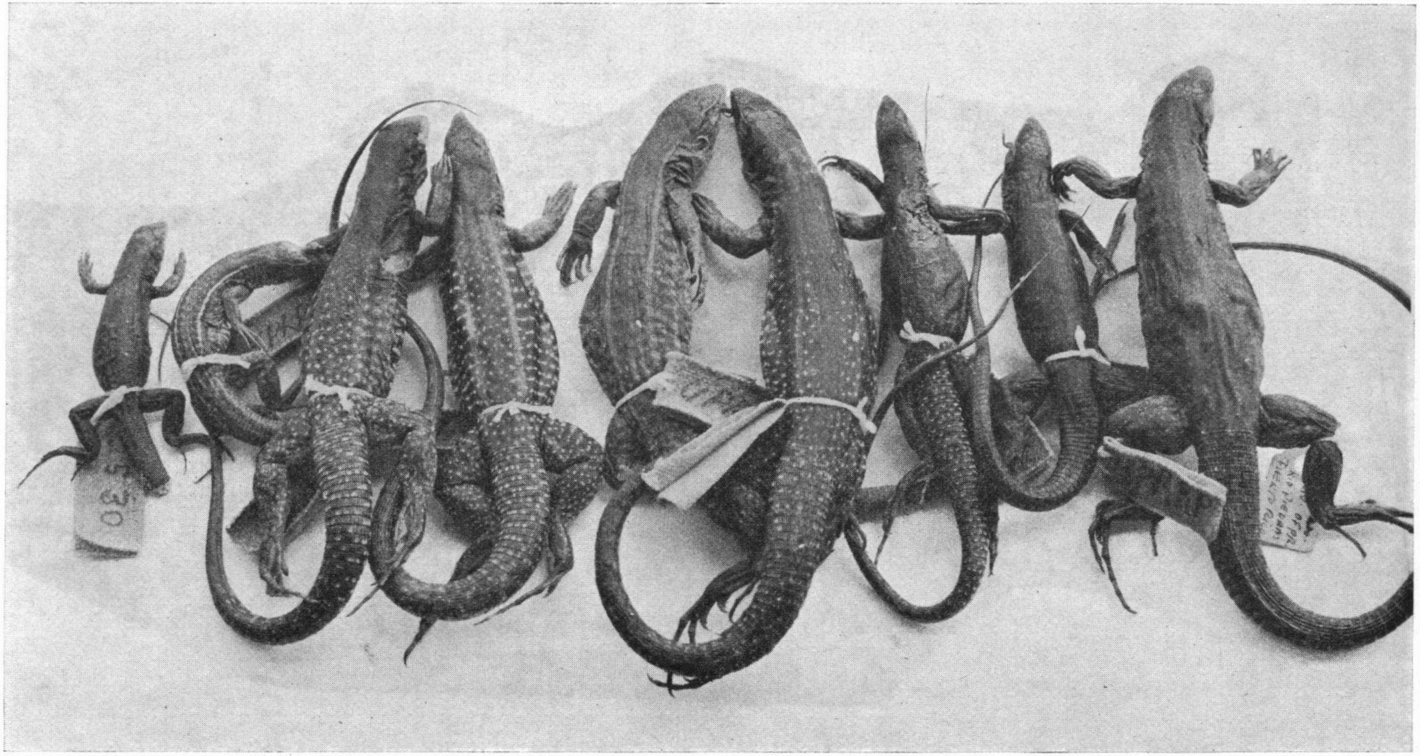

Fig. 31. *Ameiva exsul* from the San Juan, Puerto Rico, area. Note extreme variation. Some juveniles have stripes, others do not; stripes persist in some adults, in others not; amount of spotting is highly variable in all sizes.

has confirmed his observations and added some details. Guana Island, Little Camanoe and Greater Camanoe are all characterized by ameivas with rusty red on the sides of the head and with bright yellow dorsolateral stripes which persist even in large adults. By contrast Scrub Island and Marina Key, slightly east of the above mentioned islands, have ameivas with duller hues on the head and in which the dorsolateral stripes disappear with age. GRANT (1932a) indicates that the background color of individuals from Cayo Diablo is extremely dark. GARMAN (1887) mentioned (under the name of *A. riisii*) that St. Thomas specimens were darker, more olive, and with more conspicuous markings than those from Puerto Rico.

As mentioned previously many of the larger individuals from Puerto Rico and elsewhere have a pinkish to rose colored throat in life (fades in preservative). This is not true of those from Tortola (GRANT 1932c), although we obtained a specimen from nearby Scrub Island with a pink throat. GRANT (1932c) also records an individual from Peter Island with turquoise blue on the sides of the neck and head (usually this color is restricted to the belly, sides and underside of the tail). Most individuals we observed on Peter Island were much as described for Greater Camanoe. However, the larger males had blue heads; the same was true on Scrub Island. GRANT (1932a) lists the chin color of specimens from Cayo Diablo as "purple". However, we have collected live specimens from there and found their chins to be only a slightly deeper shade of rose than those from the Puerto Rican mainland. The difference was not of the magnitude GRANT's usage of the terms "red" (P.R.) and "purple" (Diablo) would suggest.

The islands south of Puerto Rico also have populations slightly different in coloration from those on the main island. GRANT & ROOSEVELT (1932) indicate that the dorsolateral stripe persists longer on Caja de Muertos than on Puerto Rico, whereas on Cardona Key, there was a wide variety of color patterns ranging from nearly unmarked animals to those with extra, white lines below the dorsolateral stripes; none had blue or salmon on the underside.

RELATIONSHIPS OF EASTERN POPULATIONS OF *Ameiva exsul* AND STATUS OF *Ameiva birdorum*

As indicated above, a number of authors have pointed out slight color differences in populations of *Ameiva exsul* among the various islands under consideration, and GRANT (1931a) stated, in reference to *Ameiva exsul*, that "the color and markings vary considerably in individuals but I have been unable to find any correlation between this and their distribution". STEJNEGER (1904) points out that there is extreme variation in coloration on the mainland of Puerto Rico even within one locality. Our observations agree with this and we feel that assigning these various insular populations to separate species or subspecies would not be realistic.

The diagnosis which GRANT (1932a) presents for *Ameiva birdorum* is: "Distinguished from other *Ameivas* [*sic*] of the Puerto Rico region by its black back, blue undersides and low femoral pore count, averaging 13.8" (on one side). BARBOUR (1937) also considered this population a "good, distinct form". However, as mentioned earlier it shares its melanistic tendencies with specimens from other islands, e.g. Tortola and Buck Island (Tortola) as indicated by GRANT himself (1932c). The blue underside is distinctive only in that the Cayo Diablo animals have a slightly more intense blue than other specimens examined alive except for those from Cayo Blanquilla which are equally bright. The low femoral pore count is not a valid distinguishing feature, as discussed in the previous section (see Fig. 30). Other characteristics which were used to distinguish *A. birdorum* from *A. exsul* include (1) persistence, and large size of dorsal dots which, however, is also true of Culebra specimens, (2) absence of a median light band (which is just another way of saying the background color on the back is black), (3) minor details of the black bands, (4) absence of the white line from axilla to groin (also true of most specimens from most localities) and (5) the purple chin (previously discussed and shown not to be distinctive). It is also mentioned in his description that the dorsolateral stripes disappear early, a character also found on Tortola and highly variable on the Puerto Rican mainland and elsewhere, but which is not shared by the Culebra population.

Inasmuch as there is condiderable variation in color pattern within an island as well as from island to island, and most of the characteristics of the Diablo Key population are not unique to it, or to the combined populations of Diablo and Blanquilla keys (e.g. large, persistent spots also occur on Culebra specimens and melanism with early loss of stripes on those from Tortola and nearby Buck), it seems unwarranted to maintain specific status for *Ameiva birdorum* and hence we relegate this name to the synonymy of *Ameiva exsul.*

In summarizing the variation in color pattern of ameivas east of the Puerto Rican mainland, it can be stated that prominent dorsolateral stripes persist longer in individuals from Guana Island, Peter Island, Anegada and Culebra Island and its surrounding keys, than those from other places. Melanism occurs on Tortola and Buck (Tortola), reaching its most extreme condition on Cayo Diablo. Spots are larger than usual in specimens from Culebra, Cayo Diablo and Blanquilla.

It is perhaps true, as BARBOUR (1914) points out in respect to these insular populations of *Ameiva exsul*, that they "represent groups of individuals strongly tending toward the formation of distinct species by isolation". However, because of the great intra-island as well as inter-island variation, observed differences in color or scutellation are true only in a statistical sense for a given character. Furthermore it is evident that each character has its own geographic distribution, relatively independent of the others, and that they occur in various combinations with each other. Despite the insular nature of the range of the species, geographic variation appears "clinal" rather than a series of discretely different populations; sharp gradients in one character do not correspond geographically to those in another one. It is difficult, therefore, to draw sharp boundaries delimiting subspecific categories. Consequently, we consider subspecific recognition for these populations as obscuring rather than clarifying the relationships involved and prefer simply to describe various character gradients and interpret them in terms of relative degree and time of isolation of different populations, and the influence of gene flow among them.

A detailed analysis of characteristics of populations from more of the smaller islands would undoubtedly further complicate the pattern of variation just described. Certain of the small keys differ significantly from any of the other nearby populations in one or more scale characters and by the criteria used by various authors could be considered distinct subspecies, e.g., the population on Sandy Key differs from those of nearby islands in number of brachials. As a result of genetic drift and/or an expression of the founder principle (MAYR 1963) many of the other small islands might be expected to show similar phenomena. However, lack of a sufficient number of specimens from some islands and fear of unduly decimating populations through intensive collecting on some of the smallest ones, has prevented as complete an analysis as might otherwise have been desirable.

PUERTO RICO: AMNH 5786, 5794–97, 12901, 12929–30, 12936–65, 13246, 13265, 13279–81, 13797–802, 13817; CNHM 12450, 12467–68, 38550–51, 130258–76; MCZ 6082–83, 12110, 36468–72, 36478, 36488–505, 36508–19, 36539–43, 57853–55, 58775, 61499; UMMZ 53254, 55825, 73864 (9 individuals), 73878–81, 73887–91 (12), 73894, 78477 (3), 106173–74; USNM 25448–50, 25521, 25581–85, 25608, 25635–38, 25640–41, 25654–59, 25660–70, 25720, 27046, 27146, 27221–22, 58795–96, 86547, 89232–33, 90349–50, 98968; UPRRP 1, 24, 323–332, 1305–10, 1321–24, 1338, 1401–03, 1946, 2458, 2460, 2530–31, 2599, 3448–72, 3606, 3743, 3748, 7 uncataloged.

CAJA DE MUERTOS ISLAND: MCZ 36473–77, 66424–28; UMMZ 73872 (6), Field Series GH 2540–41; UPRRP 2569. — CARDONA KEY: MCZ 36479–83; UMMZ 73867 (4). — CAYO SANTIAGO: MCZ 36484–87; UMMZ 73865 (4); USNM 58794; UPRRP 1815–27, 2542–57. — CAYO BATATA: UPRRP 2095. — HICACOS: MCZ 36522–25; UMMZ 73870 (3); UPRRP 2700–01, 2723–24, 3953. — RATONES ISLAND (near Hicacos): MCZ 36532–33; UMMZ 73862 (2). — KONYOKÍ: UPRRP 3981. — LOBOS ISLAND: MCZ 36526; UMMZ 73863 (2); UPRRP 3543–64. — CAYO BLANQUILLA: MCZ 36534; UPRRP 3518–19. — CAYO DIABLO: UMMZ 73854 (type of *A. birdorum*), 73855 (8), 73895 (12), 73896–98 (16) (last 3 entries paratypes of *A. birdorum*); UPRRP 3506–14. — LEPER ISLAND (Isla Cabras near San Juan): MCZ 36520–21; UMMZ 73866 (2). — SPINY BUTTE: UPRRP 1 uncataloged. — PALOMINOS: MCZ 36527–31; UMMZ 73873 (5). — PALOMINITOS: UPRRP 3603. — RAMOS ISLAND:

UPRRP 3489. — PIÑEROS ISLAND: UMMZ 73882 (2); UPRRP 3784, 3788-89. — CABEZA DE PERRO: MCZ 36467; UMMZ 73883 (2); UPRRP 4020. — ALGODONES KEY: UPRRP 3926. — LEVIN'S ROCK: UPRRP 3939. — CULEBRA ISLAND: USNM 49585; UPRRP 2374–75. — CULEBRITA ISLAND: UMMZ 73892 (3), 80599 (5), 80788 (4). — CAYO NORTE: UPRRP 5067. — ST. THOMAS ISLAND: UMMZ 73877 (13), 80597–98. — ST. JOHN: KU 45465-91, 45529–56; UMMZ 80596. — TORTOLA: UMMZ 73885 (17), 80587 (3). — BEEF ISLAND: UPRRP 4213–16. — VIRGIN GORDA: KU 45446; UMMZ 80595, 80600 (10). — ANEGADA: UMMZ 73874, 80592 (5). — WATER ISLAND: USNM 30696 (type of *A. exsul*). — SAVANNA ISLAND: UMMZ 80601. — OUTER BRASS ISLAND: UMMZ 80602. — INNER BRASS ISLAND: UMMZ 80588. — HASSEL ISLAND: UMMZ 80591. — THATCH KEY: KU 45574. — MINGO KEY: KU 46687. — LOVANGO KEY: KU 45557–73, 45575–88; MCZ 36506–07; UMMZ 73876. — GREATER ST. JAMES: KU 45442–45. — LITTLE ST. JAMES: KU 45447–53, 45492–511. — LEDUCK ISLAND: KU 45454–58. — FLANNIGAN ISLAND: KU 45459–64. — SANDY KEY: KU 45512–22, 45524-28; UPRRP 1 uncataloged. — BUCK ISLAND (Tortola): UMMZ 73868. — GUANA ISLAND: UMMZ 73875. — SCRUB ISLAND: UPRRP 4302. — GREATER CAMANOE ISLAND: UPRRP 4299. — LITTLE CAMANOE ISLAND: UPRRP 4301. — PETER ISLAND: UMMZ 73886 (2), 80594; UPRRP 4241–42, 4262–63. — DEAD MAN'S CHEST: UMMZ 80593. — SALT ISLAND (near Tortola): UMMZ 80590 (2). — COOPER ISLAND: UMMZ 80589.

Ameiva alboguttata Boulenger 1896

HABITS

Little is known of the habits of *Ameiva alboguttata*. It is diurnal and forages in much the same way as described for *A. exsul*. At night we have found inactive individuals under limestone boulders. SCHMIDT (1920, 1928) indicates that 20 stomachs yielded mostly vegetable matter (chiefly red-coated seeds) and insects, although land snails and juvenile *Anolis* were also present. *Alsophis* feeds on *A. alboguttata*.

DISTRIBUTION

This species is endemic to Mona Island (Fig. 24) where it is found on the beaches as well as on the limestone cap. The island is hot, dry, and covered with a xeric scrub vegetation which grows up through cracks in the limestone. There is an abundance of limestone boulders as well as crevices in larger rock masses which serve as cover.

The nearby island of Monito which is also a limestone mass covered with xeric scrub has been examined and no *Ameiva* found (ROLLE *et al.* 1964). It is perhaps significant that this island is completely surrounded by cliffs which are undercut at the base by wave action, thereby making repopulation following local extinction difficult, particularly for a non-climbing form like *Ameiva.*

The relatively great distance of Mona from Puerto Rico, the absence of a Pleistocene land connection, and the fact that much of the perimeter is composed of cliffs, probably contributed to genetic isolation of *Ameiva alboguttata*, resulting in divergence from *A. exsul.*

VARIATION IN SCALE CHARACTERS AND COLORATION

Ameiva alboguttata does not differ significantly from *A. exsul* in numbers of brachials, preanal scales, transverse rows of ventrals (Fig. 27) or relative snout length (Fig. 28). However, the number of femoral pores and number of caudals in the 15th row are both significantly lower than for any of the Puerto Rican localities. The coloration of *A. alboguttata* is much less variable from that of *A. exsul*, and differs from the latter in having a gray (rather than olive or brown) background color which does not differ greatly in intensity between the back and sides. The small white dorsal spots begin on the neck rather than the shoulder and persist throughout life. The chin and iris color is the same as in *A. exsul.*

The coloration is uniform enough and sufficiently distinct from that of *Ameiva exsul* that the two species can be distinguished immediately from either live individuals or preserved specimens (Fig. 32), except in the case of rare *A. exsul* which have an exceptionally gray background color and are unusually heavily spotted. In such instances separation can be made on the basis of where the spotting begins anteriorly (neck in *A. alboguttata* and shoulder in *A. exsul*).

There is some ontogenetic variation in *Ameiva alboguttata.* The dorsolateral lines are absent even in some young. Where they are present they are indistinct and disappear early in age. A lateral line running from axilla to groin sometimes occurs in young ones, although it also seems to disappear with age. The largest specimen we have examined was 126.9 mm s-v; the smallest 34.6 mm s-v.

Ameiva alboguttata and *A. exsul* are clearly very closely related. It is perhaps arbitrary whether the former be considered a full species or a subspecies of the latter. We choose to follow previous authors in maintaining it as a distinct species.

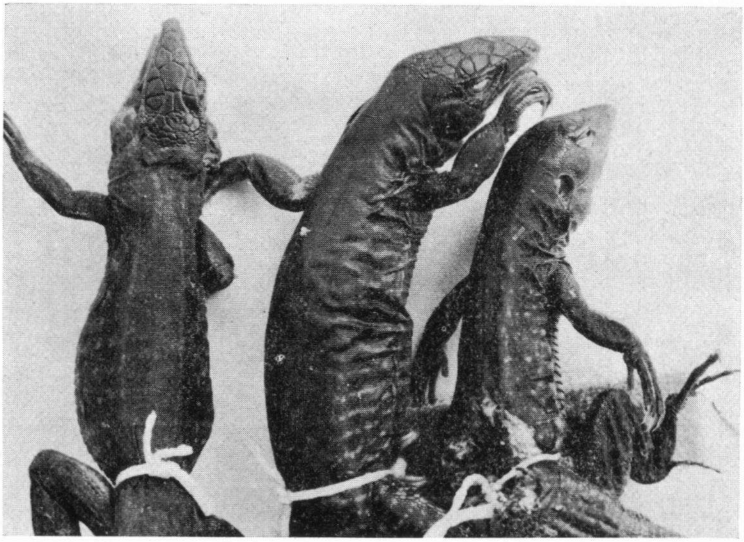

Fig. 32. Species of the *Ameiva exsul* subgroup: left, *A. exsul*; center, *A. desechensis*; right, *A. alboguttata*.

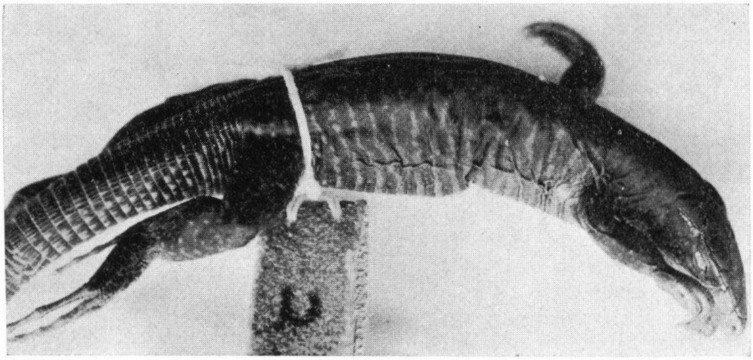

Fig. 33. Side view of holotype of *Ameiva desechensis*. Note absence of dorsolateral stripes and presence of alternating light and dark vertical bars on side.

MONA ISLAND: AMNH 6447–49, 13704–06, 13738–40, 13742–44, 13746–54, 13756–65, 13767–70, 31890, 31894–95, 31899; MCZ 7898; 36351-84; UMMZ 73848–53 (35 inviduals); USNM 29368–72, 29374; UPRRP 3017, 3056, 3069.

Ameiva desechensis sp. nov.

Holotype: UPRRP 235 (subsequently donated to MCZ). Adult female collected by H. Heatwole, DESECHEO Island, P.R., 28 March 1961. Paratypes: UPRRP 230–234, 236–238 (Fig. 32–33).

Diagnosis: A species of *Ameiva* with 10 longitudinal rows of ventral plates, 32 or more femoral pores (sum of those on both sides), 41 or more caudals and 25 or more preanal scales in 95% of the individuals; no dorsolateral stripes at any stage of the life history; dorsal spots inconspicuous and mostly on the tail, seldom extending further anterior than the sacral region; spots and black markings on sides coalesced into a series of alternating black and bluish-white vertical bars.

Range: Known only from Desecheo Island, Puerto Rico.

Description of Holotype: Dorsum nearly uniformly gray, slightly lighter on head and dorsal surface of tail; snout pink; iris orange-brown; sides with a pattern of alternating black and bluish-white vertical stripes which fade out in dorsolateral region; scattered small white spots on dorsal part of tail; becoming larger and more pronounced on sides of tail; venter bluish gray; front and rear legs dark gray dorsally, white with a gray wash beneath, the latter with small bluish white spots above; 10 longitudinal and 35 transverse rows of ventrals; 3 preanal plates; 26 preanal scales; 32 femoral pores; 15 brachials; 41 caudals in the 15th row; upper labials 6 + 6; lower labials 7 + 7; supraoculars 4 + 5; supraciliaries 6 + 7; nostrils in suture between nasals; dorsal scales small and granular except on tail where they are platelike and keeled; ventral plates rectangular and smooth except on posterior 2/3 of tail where they have weak keels; scales of throat small and granular except for an area of about 10 scales in the center of the throat and 4 rows between the gular and prepectoral skin folds; these latter scales larger and almost plate-like; snout vent length 90 mm.

VARIATION AMONG PARATYPES

Other specimens collected at the same time and place as the type were similar in most aspects of the color pattern. In the smaller specimens, the black and white vertical markings tended to extend across the dorsum and connect with their counterparts of the opposite side to form a transversely striped pattern. These dorsal markings were less distinct than on the sides, however, and were lacking entirely in larger specimens. No individuals showed a trace of dorsolateral stripes, even a very young specimen only 43.1 mm snout to vent. Coloration seems to be much more uniform in *Ameiva desechensis* than in *A. exsul*, its nearest living relative. Both *A. desechensis* and *A. alboguttata* differ in the same direction from *A. exsul* in their reduction of the dorsolateral line and in the grayness of background color.

The latter is perhaps attributable to the fact that both *A. alboguttata* and *A. desechensis* live on islands consisting principally of gray limestone, whereas many of the Puerto Rican populations occur in areas of brown sand. The "grayness" of the ameivas has parallels in other groups found on Puerto Rico and the two western islands, e.g., *Anolis*, and hence may be convergent responses to selective pressures common to both Mona and Desecheo (as well as to some of the eastern keys). It is possible that degree of dorsolateral striping may have quite different fitness values on different islands and that the extreme inter-island variability in this character as well as in grayness can be related to inter-island differences in substrate color.

The variability of scale characteristics and body proportions can be seen from Figures 27 and 28. *Ameiva desechensis* differs significantly from all mainland populations of *A. exsul* in number of preanal scales. Number of femoral pores is also significantly higher than in any Puerto Rican locality except northeastern Puerto Rico. Numbers of transverse rows and brachials and ratio of snout length to body length is the same as in *A. exsul* and *A. alboguttata*.

RELATIONSHIPS OF THE AMEIVAS OF MONA, DESECHEO AND PUERTO RICO

Examination of Figures 27 and 28 reveals that where *Ameiva alboguttata* and *A. desechensis* differ from *A. exsul,* they diverge in opposite directions. Thus *A. alboguttata* has a lower number of femoral pores than *A. exsul,* whereas *A. desechensis* has a higher number. In addition, *A. desechensis* has a higher number of preanal scales than *A. exsul*; the latter and *A. alboguttata* do not differ in this character. The same trend applies to certain aspects of coloration; *A. alboguttata* shows greater dorsal spotting than *A. exsul,* whereas dorsal spotting is much reduced in *A. desechensis* (Fig. 32). However, it seems that *A. exsul* is close to the ancestral type from which *A. alboguttata* and *A. desechensis* separately diverged, or was perhaps itself the ancestor of these two species. At any rate *A. desechensis* cannot be considered an intermediate between *A. exsul* and *A. alboguttata* – but rather has diverged from *A. exsul* in different ways than has *A. alboguttata.* Both seem to be more closely related to *A. exsul* than they are to each other.

DESECHEO ISLAND: USNM 59760–61; UPRRP 235 (type, donated to MCZ), 230–234, 236–38 (last two entries paratypes).

Ameiva undulata group

Ameiva wetmorei Stejneger 1913

HABITS

Ameiva wetmorei inhabits open, xeric scrub. It is diurnal and forages on the ground in the same way as do other ameivas. It spends its nocturnal inactive period in burrows under rocks. The bright metallic blue tail is frequently lost by autotomy, after which it writhes violently on the ground thereby distracting attention from its owner.

DISTRIBUTION

This species has a very restricted distribution, being found only in southwestern Puerto Rico and on Caja de Muertos island and Magueyes Island (Fig. 17).

The geological formations, soil and vegetation types found in these areas have a wider occurrence in Puerto Rico than does

Ameiva wetmorei, and they thus can probably be excluded as possible factors restricting the lizards' geographic range. Temperatures are similar all along the southern and extreme eastern coasts with the annual mean temperature exceeding 78° F. (Picó 1954). *A. wetmorei* could probably not inhabit the cooler areas at high elevations as GRANT (1931a) mentions that individuals are almost torpid at 75° F. However, the zone of high temperatures extends further east along the southern coast than does the range of *A. wetmorei*. Hence, temperature does not seem to be the factor confining it within the small area it occupies.

The most striking feature of southwestern Puerto Rico is its aridity and it is the only part of the island with a mean annual rainfall of less than 30 inches. In fact the 30 inch isohyet encloses all of the recorded mainland localities of this species except the one on the peninsula of Cabo Rojo (Fig. 17). Rainfall progressively increases from the coast toward the interior mountains and also from west to east until mean annual values of over 200 inches are recorded from some of the eastern peaks (Picó 1954). Although rain data are lacking for Caja de Muertos, it is a relatively hot, dry island, similar in appearance to southwestern Puerto Rico. Other members of the species group also inhabit dry areas. For example *Ameiva maynardi* occurs on Great Inagua and *A. lineolata*, a species which COCHRAN (1941) indicates as a close relative of *A. wetmorei*, is restricted to Beata Island and the arid Cul-de Sac of Hispaniola.

VARIATION

The range of *Ameiva wetmorei* was earlier considered to be southwest Puerto Rico and Caja de Muertos Island (SCHMIDT 1928, and Fig. 17). However, GRANT & ROOSEVELT (1932) set apart the population on Caja de Muertos as a separate subspecies, *A. wetmorei eleanorae*, on the basis of several minor color pattern differences. Later, GRANT (1932d) raised the Caja de Muertos form to a full species, *A. eleanorae*, when he discovered that it had fewer femoral pores than mainland populations. BARBOUR (1937) considered *A. eleanorae* as a "rather ill-defined form". We compared specimens from both areas and have re-evaluated the status of the Caja de Muertos population.

Three localities were represented by sufficient specimens for comparison to be made. These were La Parguera and Ensenada, P. R., and Caja de Muertos.

There was a west-east difference in a number of characters. The snout was relatively longer in the eastern specimens than those from the west (Fig. 34). Although the Caja de Muertos specimens were significantly different from those from La Parguera, the Ensenada population was intermediate and not significantly different from either of the other two. The same was true for number of brachials, with the population on Caja de Muertos having the highest number, that from La Parguera the lowest, and that from Ensenada being intermediate. The two end localities were significantly different. Grant's observation that the Caja de Muertos form had a lower number of femoral pores than the mainland form was verified by the present study (Fig. 34). However, there were also differences between mainland populations in this character, the number gradually decreasing from west to east with Caja de Muertos simply being the extreme eastern population.

There were no differences among populations of the various localities in number of caudals in the 15th row. Number of transverse

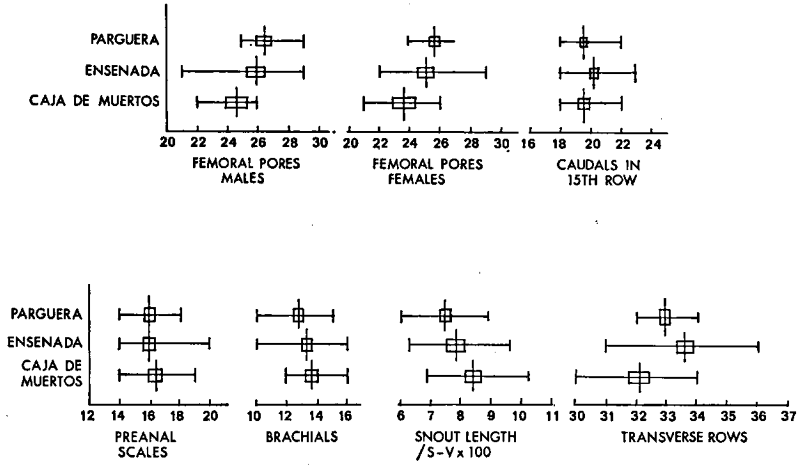

Fig. 34. Variation in scale counts and in ratio of snout length to body length in *Ameiva wetmorei*. Symbols as in Fig. 21. N = 35–69 per locality.

rows varied widely between localities, all of which were significantly different from each other, although there was no orderly geographic sequence.

Both forms are very similar in coloration. The background color is black with a series of longitudinal lines (Fig. 35) which are white, cream or pinkish. One is located middorsally and extends from the tip of the snout onto the tail where it widens and becomes blue, eventually being lost in the general blue color of the tail. At the base of the tail the stripe has a central black line which is somewhat more conspicuous in the Caja de Muertos specimens. In these the white line tends to be wider although there is a great amount of overlap among populations. Lateral to the middorsal stripe is a pair of white

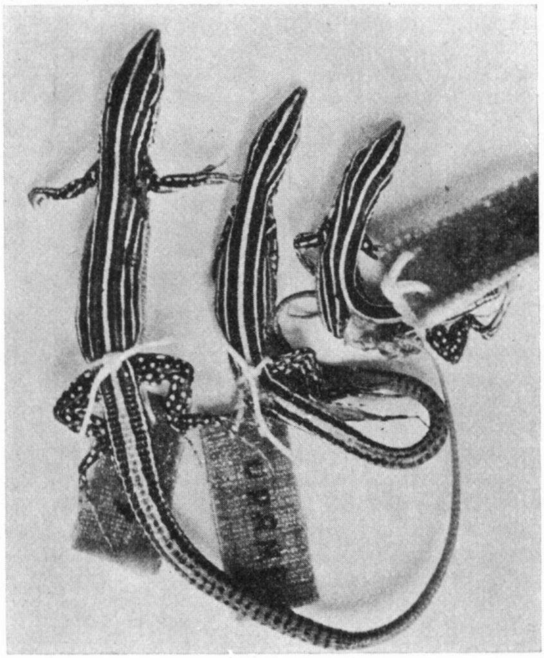

Fig. 35. *Ameiva wetmorei*. Left, specimen from southwest Puerto Rico showing typical persistence of supraocular stripe on mid-body; center, specimen from southwestern Puerto Rico which has coloration similar to that typically found on Caja de Muertos, i.e., supraocular stripe disappears on body; right, specimen from Caja de Muertos.

stripes (supraocular lines) beginning between the nostril and eye, passing across the supraciliaries and extending onto the tail. In the Caja de Muertos population, this stripe fades out and is lost on the neck, not reappearing again until the base of the tail. In most of the southwestern Puerto Rican individuals, this line is not completely lost but only fades out to a rather inconspicuous gray or brown. This difference was considered by GRANT & ROOSEVELT (1932) as diagnostic of the two forms. However, some of the mainland individuals also lose the supraocular stripe in the midbody region and they cannot be distinguished from Caja de Muertos ones (Fig. 35) on the basis of this or other color characters (e.g., UPRRP 2116 and 2289 from Tamarindo, P. R.). Also FOWLER (1918) presents a painting of an *Ameiva wetmorei* from Ensenada, P. R., which lacks the supraocular stripe at midbody. According to GRANT & ROOSEVELT (1932) some Caja de Muertos individuals have a faint remnant of this stripe at midbody, thus resembling the Puerto Rican form.

Lateral to the supraocular stripes is a pair of stripes (subocular lines) beginning just anterior to the eye and passing beneath it, over the dorsal border of the tympanum and extending to about mid-tail. Finally, there is a line extending from the supralabials, below the tympanum, and along the sides of the groin. As GRANT & ROOSEVELT (1932) point out this tends to be more conspicuous in individuals from Caja de Muertos.

In both forms the dorsal surfaces of the legs are black with conspicuous white spots, sometimes coalescing into short bands. The underside of the venter is salmon to coppery (blue in preservative). In life, the posterior part of the tail is metallic green or metallic blue with broken, circular black bands surrounding the tail on the posterior part of each scale ring. In preservative the tail is always blue.

In view of the fact that the Caja de Muertos population simply reflects the extreme eastern end of gradual west-east character gradients, and is not sharply set off from mainland ones on the basis of either scutellation or coloration, we feel it does not warrant specific status. We also feel that the relationships are most clearly expressed by a description of the geographic trends in the characters involved, and that even subspecific status overemphasizes the distinctiveness of the Caja de Muertos population. Consequently, we place *Ameiva eleanorae* in the synonymy of *Ameiva wetmorei.*

PUERTO RICO: AMNH 13803–09, 13818, 13820–22, 13824–27, 13829–36, 13859; CNHM 12387–90, 12447–49; MCZ 36431-66 (69 specimens); UMMZ 73856 (21), 73859–60 (45); UPRRP 1293, 1867–69, 2116, 2289.

MAGUEYES ISLAND: USNM 86548.

CAJA DE MUERTOS ISLAND: AMNH 32946–48; MCZ 36419–30 (paratypes of *A. eleanorae*), 66429; UMMZ 73857–58 (17 individuals, paratypes of *A. eleanorae*); USNM 120785–86 (paratypes of *A. eleanorae*); UPRRP 321, 2589.

Ameiva polops Cope 1862

DISTRIBUTION

This species was originally found on St. Croix (COPE 1862). It was not subsequently found on that island for a number of years and was believed to be extinct (BARBOUR 1937). However, it was rediscovered on two small keys, Green Key and Protestant Key (Fig. 17) north of St. Croix by GRANT (1937) where it is still holding out (SEAMAN 1961 and personal observation).

It is not found on Buck Island near St. Croix, and the two previously mentioned keys seem to constitute the entire range of the species.

Although the mongoose has probably served as a scape-goat and received an undue share of blame for extinction of West Indian reptiles, its reputation is probably deserved in the case of *Ameiva polops*. The mongoose was introduced into St. Croix from Jamaica in 1884 (SEAMAN 1961) and local inhabitants say it is on Buck (St. Croix). It is not on the two keys where *A. polops* occurs. Protestant Key has a hotel which does a lively business and most of the island's vegetation has been modified. The fact that *A. polops* has been able to maintain itself under these conditions would seem to indicate that man has probably not been directly responsible for extinction of the St. Croix populations.[1]

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[1] Since this paper was written, BASKIN & WILLIAMS (1966) have discussed in detail the effect of the mongoose on *A. polops*. Their conclusions do not differ greatly from those presented above. They quote Mr. G. A. SEAMAN as indicating no *Ameiva polops* on St. Croix. However, recently Mr. SEAMAN (personal communication) tells he has discovered a small population there. It is not known whether this is a relict population which had been previously overlooked or whether it represents a re-invasion.

COLORATION

The following description of coloration was made from a live animal immediately after capturing it on Green Key, St. Croix, Virgin Islands, on 17 April 1963 (see also Fig. 36 and a figure presented by GRANT 1937): the chin, throat, chest, side of snout and underside of arms are deep pinkish-red; there is a slight tinge of pink beneath the tail and on the underside of the legs. The venter is a light pearl gray. The pupil is shaped like a figure-eight, surrounded by a light gray-brown iris. The legs are gray-brown with cream colored spots; the rear one has a narrow white line bordered by black on the outer edge of the femoral region. The top of the head is uniform brown; the dorsal pattern consists of a series of longitudinal stripes. There is a middorsal one of light brown followed laterally on each side by a series of other bands in the following order: a wide dark brown or almost black one, a narrow brown one, another black one, a white one, and finally bordering the ventral scales on each side, a dark brown one mottled with white. The narrow, dorsolateral brown line extends forward to the posterior corner of the eye, passing over the top of the tympanum where it becomes confluent with a circle of the same color surrounding the tympanum. The tail contains alternate rings of blue and black. The blue rings are about 2 scale rows wide, the black ones are narrow and result from the dark edges of two adjacent scale rings.

Variation of color among living individuals consists of differences in the prominence and color of these stripes. For example, the narrow stripe surrounding the tympanum is sometimes nearly white and sometimes fades out near mid-body; at other times the stripe next to it laterally is light and the two appear almost as a single, wide, brown stripe.

One adult male had a rather bright blue color on the lateral part of the venter, covering about one third of the total area of the venter on each side. Traces of this same pattern could also be detected in preserved specimens.

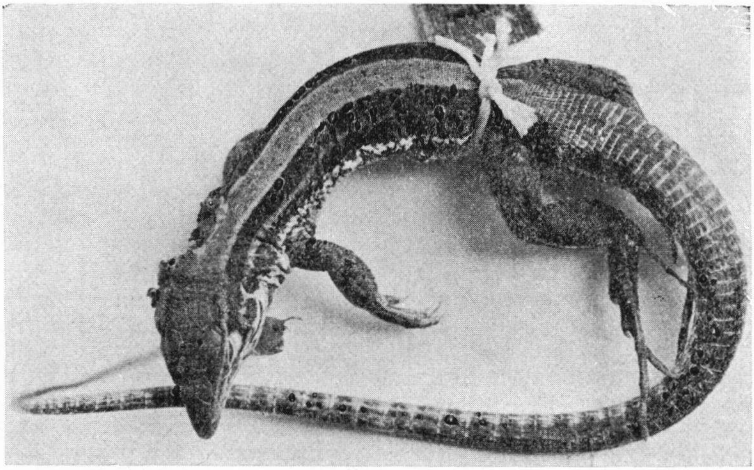

Fig. 36. *Ameiva polops.*

HABITS

Like most ameivas this species is diurnal. On both Green and Protestant Keys it could be seen foraging actively among dead leaves on the ground, frequently extending its tongue, as though supplementing vision by smell in detecting food. This is further suggested by the fact that various individuals came to a piece of waxed paper which had contained a ham sandwich and repeatedly attempted to eat it even though there were no insects or other visible food on it. They were also observed eating ants from the ground. GRANT (1937) reports that stomachs of *Ameiva polops* contained amphipods of the type found in beach debris.

VARIATION

Comparison of the Green and Protestant populations of *Ameiva polops* reveals no significant differences between them in any of the characters studied, with the exception of number of preanal scales. Individuals from Green Key had a significantly higher number of preanal scales than did those from Protestant Key. The ranges did not even overlap (Fig. 37). Thus it appears that some divergence between these populations has taken place. It is probably a reflection of the smallness of both populations and recent lack of gene flow from the mainland of St. Croix. The smallness of these keys reduces the probability of gene flow between them via flotsam transport of individuals.

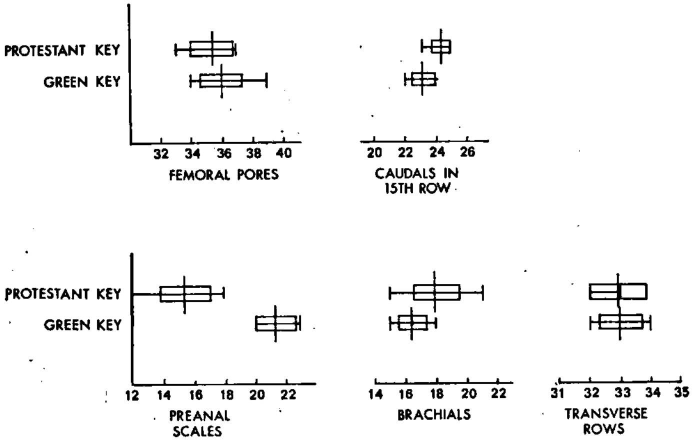

Fig. 37. Variation in scale counts in *Ameiva polops*. Symbols as in Fig. 21. N = 6 (Green Key). N = 7 (Protestant Key).

Green Key: UMMZ 88236 (3 specimens); UPRRP 3677–79.
Protestant Key: UMMZ 80603–04 (6); UPRRP 3675.

Key to the Ameivas of Puerto Rico and the Virgin Islands

1a. Eight longitudinal rows of ventral scales . . *Ameiva wetmorei*
1b. Ten (occasionally twelve) longitudinal rows of ventral scales . 2
2a. Dorsal scales of tail arranged in oblique rows . *Ameiva polops*
2b. Dorsal scales of tail arranged in straight rows 3
3a. Dorsal spots prominent and beginning on neck . . . . *Ameiva alboguttata*
3b. Dorsal spots not prominent or if so, beginning on shoulder . . 4
4a. Dorsolateral stripes absent; sides with alternating vertical light and dark bands . . . . *Ameiva desechensis*
4b. Dorsolateral stripes present, or if absent, then sides with irregular marks and spots, not arranged as alternating bands . . . . *Ameiva exsul*

DISCUSSION

The historical events leading to the observed distribution of organisms among islands of the Puerto Rican shelf may have been (1) fragmentation of a once larger land-mass into a series of islands, each containing a population which then differentiated, or (2) dispersal by improbable means, such as transportation by flotsam, into an already dissected archipelago. In either case, divergence of insular populations would be expected, the degree of which would depend on length of time of isolation and/or frequency with which interisland transport of animals occurred. These two categories of events are not mutually exclusive and the distribution and speciation of *Ameiva* on the Puerto Rican shelf probably reflects a combination of the two.

According to Heatwole & MacKenzie (in prep.), Mona, Monito, Desecheo, and St. Croix have been separated from Puerto Rico longer than any of the other islands on the shelf, i.e., they were separated even at maximum sea-level lowering of the Pleistocene. Mitchell (1954) placed separation sometime near the end of the Pliocene. By contrast, Culebra, St. Thomas, St. John, Tortola, Virgin Gorda and Anegada were all connected with each other and with Puerto Rico as late as about 9,000 years ago and Vieques and Caja de Muertos lost their connections with Puerto Rico sometime in the last 8,000 years (HEATWOLE & MACKENZIE MS). Thus, divergence of *A. alboguttata* and *A. desechensis* from the *A. exsul*-like stock may reflect the long period during which Mona and Desecheo have been isolated from Puerto Rico, and/or the relatively great inter-island distances involved (hence less opportunity for successful rafting of individuals between islands).

The lack of speciation in the *Ameiva exsul* group on Puerto Rico and the Virgin Islands is probably a reflection of the short time islands have been isolated. However, we believe that gene flow via sweepstakes dispersal of individuals is an important factor influencing distribution, degree of divergence and pattern of intraspecific variation. The lines of evidence are the following:

(1) Waif dispersal does occur at least over short distances as evidenced by the sudden appearance of individuals on Cayo Ahogado and the presence of one male on Levin's Rock.

(2) The form of small islands influences whether or not ameivas are present. Many small keys with gradually sloping edges have ameivas, whereas similar sized ones at comparable distances from large islands, but which have vertical sides, undercut at the base (e.g. Monito and various of the northeastern keys) lack ameivas even though what appears to be favorable habitat occurs on top. It is presumed that inasmuch as random extinction is more likely on small islands (small populations) and the subsequent re-colonization difficult due to its geomorphology and the poor climbing ability of ameivas, such islands remain devoid of these lizards most of the time.

(3) Patterns of geographic variation in some characters show gradual changes in almost clinal fashion over a series of islands, suggesting influence of the various populations upon each other. More importantly, when relatively sharp character gradients do occur between populations on different islands, these breaks occur at different places rather than coinciding geographically, i.e., the various characters show independent patterns of variation, a condition suggesting considerable gene flow among islands rather than discrete gene pools.

(4) Characteristics of populations on various islands conform to the pattern expected on the basis of wind and water currents. In the Puerto Rico-Virgin Island area, winds are from the east a great proportion of the time and the ocean current runs from east to west (KAYE 1959). Thus, most flotsam transport would be east to west. Small islands contain few individuals and would therefore contribute few waifs to be dispersed to a larger western neighbor, where the effect of such animals would, in any event, be minimal because of the large resident population. Conversely, a large island, with a higher number of individuals available for transport and a greater perimeter from which they would be set adrift, might contribute a significant number of individuals to a small island to its west. Such animals, inasmuch as they would contribute to a small gene pool would have a relatively greater effect than in the reverse situation. This effect is observed in that populations of *Ameiva exsul* on small islands nearby, and to the east of, larger ones tended to be divergent from those of the larger one (e.g. caudal scales on Cayo Santiago). Small islands between two larger ones that differ share the characteristics of the large island to the east rather than the one to the west (e.g. Little St. James and Lovango Key between St. Thomas and St. John). Finally, where there was a group of small islands only, each one tended to have slightly different populations, the direction of divergence seeming not to bear any correlation to characteristics of neighboring islands (e.g. Hicacos, Lobos, Diablo).

It should be pointed out that a special consideration applies to flotsam transport from Puerto Rico west to Mona and Desecheo. The ocean current after passing the southwestern tip of Puerto Rico swings north through the Mona channel (KAYE 1959). Thus, the opportunity for flotsam to reach the western islands is much reduced and any which would arrive there would most likely have its origin in southwest Puero Rico rather than other (closer) localities. In the past the configuration of southwest Puerto Rico was such that it would have deflected the current toward the western islands (HEATWOLE & MACKENZIE). Hence, if the original colonizers reached Mona and Desecheo via flotsam after these islands were isolated, they probably diverged after sea levels rose and the pattern of currents in the Mona channel changed.

(5) A supplementary consideration, though not direct evidence, is that the ecology and habits of *Ameiva exsul* are such as to make their being cast adrift highly probable. LEVINS & HEATWOLE (1963) have pointed out that the probability of a species reaching an island by the sweepstakes method depends on its population density in already occupied areas from which it might be transported, its habits (likelihood of being found in debris which could be washed out to sea), the time required for the trip (in turn depending upon strength and direction of wind and water currents), and tolerances to environmental factors encountered in transit (salt water or spray, high temperature, desiccation, etc.). Not all of these factors can at present be evaluated for *Ameiva exsul*. However, it should be noted that their habitat includes beach areas where they occur in dense populations. Thus, in close proximity to the sea, there are large numbers available for transport. Also, any individuals successfully reaching a new island will immediately encounter a favorable habitat and will not need to journey inland before finding suitable conditions.

Ameiva exsul spends its inactive periods in burrows in the soil, beneath stones and in or under logs or other debris, a habit which would increase their likelihood of being cast adrift. Thus, the population densities and habits of *Ameiva exsul* are such as would favor waif dispersal and subsequent establishment upon reaching an island. These same factors also favor gene flow between islands and re-colonization of an island following local extinction.

Tolerance limits are not known. However, the fact that the usual habitat is relatively hot and dry and in many instances subjected to salt spray, would suggest that tolerances to temperature, desiccation and salinity might be high.

The history of the genus *Ameiva* in the Puerto Rican area can be summarized in the following way:

(1) The first group in the area was probably the ancestral stock of *A. polops*. Present day distribution of members of the group probably represent relicts of a formerly more widespread group.

(2) Following, or perhaps contributing to, the decline of this group, two additional groups of the genus reached the Puerto Rican

area. One of these consisted of the eastward penetration of another member of the *A. undulata* group, *Ameiva wetmorei*. The *A. ameiva* group reached as far as Santo Domingo by "island-hopping" up the Lesser Antillean chain from South America.[1] On what was probably at that time a continuous land mass containing Puerto Rico and all of the Virgin Islands except St. Croix, this stock was represented by an *exsul*-like form which then diverged into *A. exsul* on Puerto Rico, *A. alboguttata* on Mona and *A. desechensis* on Desecheo. Whether this ancestral form reached Mona and Desecheo before or after these islands became separated is problematical. Geographic patterns of variation within *A. exsul* are now probably influenced by gene flow via flotsam transport of individuals from island to island.

LITERATURE

BARBOUR, T., 1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. *Mem. Mus. Comp. Zoöl. Harvard 44*: 209–360.

BARBOUR, T., 1930. Some faunistic changes in the Lesser Antilles. *Proc. New England Zool. Club 11*: 73–83.

BARBOUR, T., 1937. Third list of Antillean reptiles and amphibians. *Bull. Mus. Comp. Zoöl. 82*: 77–166.

BARBOUR, T. & NOBLE, G. K., 1915. A revision of the lizards of the genus Ameiva. *Bull. Mus. Comp. Zoöl. 59*: 417–479.

BASKIN, J. N. & WILLIAMS, E. E., 1966. The Lesser Antillean Ameiva (Sauria, Teiidae). Re-evaluation, zoogeography and the effects of predation. *Studies Fauna Curaçao and other Carib. Isls. 23*: 144–176.

BEEBE, W., 1919. Lizards of the genus Ameiva in Bartica District. Notes on their color and pattern variation. *Zoologica 2*: 235–238.

BEEBE, W., 1945. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 3. Teiidae, Amphisbaenidae and Scincidae. *Zoologica 30*: 7–32.

CARPENTER, C. C., 1961. Temperature relationships of two Oklahoma lizards. *Proc. Okla. Acad. Sci. 41*: 72–77.

COCHRAN, D. M., 1941. The herpetology of Hispaniola. *Bull. U. S. Nat. Mus. 177*: 1–397.

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[1] See BASKIN & WILLIAMS (1966) for a more detailed discussion of this dispersal.

COPE, E. D., 1862. Synopsis of the species of Holcosus and Ameiva, with diagnoses of new West Indian and South American Colubridae. *Proc. Acad. Nat. Sci. Phila. 1862*: 60–82.

DANFORTH, S. T., 1925. Porto Rican herpetological notes. *Copeia 147*: 76–79.

DICE, L. R. & LERAAS, H. J., 1936. A graphic method for comparing several sets of measurements. *Contrib. Lab. Vert. Genetics Univ. Mich. 3:* 1–3.

FOWLER, H. W., 1918. Some amphibians and reptiles from Porto Rico and the Virgin Islands. *Publ. Carnegie Inst. Wash. 252*: 1–15.

GARMAN, S., 1887. On West Indian Teiidae in the Museum of Comparative Zoology. *Bull. Essex Inst. 19*: 1–24.

GRANT, C., 1931a. Notes on the ameivas of Puerto Rico. *Copeia 1931*: 62.

GRANT, C., 1931b. A revised list of the herpetological fauna of Culebra Island. *J. Dept. Agric. P. R. 15*: 215.

GRANT, C., 1932a. The large ameivas of the Puerto Rico region and one new species. *J. Dept. Agric. P. R. 16*: 157–160.

GRANT, C., 1932b. The herpetology of St. John and adjacent keys, U.S. Virgin Islands. *J. Dept. Agric. P. R. 16*: 331–334.

GRANT, C., 1932c. Herpetology of Tortola; notes on Anegada and Virgin Gorda, British Virgin Islands. *J. Dept. Agric. P. R. 16*: 339–346.

GRANT, C., 1932d. Herpetological notes from the Puerto Rico area. *J. Dept. Agric. P. R. 16*: 161–165.

GRANT, C., 1932e. The herpetology of Vieques Island. *J. Dept. Agric. P. R. 16*: 37–39.

GRANT, C., 1937. Herpetological notes with new species from the American and British Virgin Islands, 1936. *J. Agric. Univ. P. R. 21*: 503–522.

GRANT, C. & ROOSEVELT, C., 1932. The herpetology of Caja de Muertos Island and Cardona Key, Porto Rico. *J. Dept. Agric. P. R. 16*: 47–49.

HEATWOLE, H. & SADE, D. S. & HILDRETH, R., 1963. Herpetogeography of Puerto Rico. I. Herpetofauna of Cayo Santiago and Cayo Batata. *Carib. J. Sci. 3*: 1–5.

HEATWOLE, H. & MACKENZIE, F., Herpetogeography of Puerto Rico. IV. (in preparation).

HIRTH, H. F., 1963. The ecology of two lizards on a tropical beach. *Ecol. Monographs 33*: 83–112.

KAYE, C., 1959. Shoreline features and Quaternary shoreline changes Puerto Rico. *Geol. Surv. Professional Pap. 317-B*: 49–140. U. S. Govt. Print. Off., Wash., D. C.

LEVINS, R. & HEATWOLE, H., 1963. On the distribution of organisms on islands. *Carib. J. Sci. 3*: 173–177.

MAYR, E., 1963. *Animal Species and Evolution*. Harvard Univ. Press, Cambridge, Mass. 797 pp.

MITCHELL, R. C., 1954. *A survey of the geology of Porto Rico*. Agric. Exp. Sta. Univ. P. R. Techn. Pap. *13*, 167 pp.

NOBLE, G. K. & BRADLEY, H. T., 1933. The mating behavior of lizards; its bearing on the theory of sexual selection. *Ann. N. Y. Acad. Sci. 35*: 25–100.

PICÓ, R., 1954. *Geografía de Puerto Rico.* Editorial Universitaria, Río Piedras, P. R., 243 pp.

ROBERTS, R. C., 1942. *Soil Survey of Puerto Rico.* U. S. Dep. Agr. Bur. Plant Industry, Wash., 503 pp., maps.

ROLLE, F. J. & HEATWOLE, H. & LEVINS, R. & TORRES, F., 1964. Faunal notes on Monito Island, Puerto Rico. *Carib. J. Sci. 4*: 321–322.

SCHMIDT, K. P., 1920. Contribution to the herpetology of Porto Rico. *Ann. N. Y. Acad. Sci. 28*: 167–200.

SCHMIDT, K. P., 1928. *Amphibians and land reptiles of Porto Rico, with a list of those reported from the Virgin Islands.* Scient. Surv. P. R. & Virg. Isl. *10*, 160 pp.

SEAMAN, G. A., 1961. *Mammals, reptiles & amphibians of the Virgin Islands.* Brodhurst's Printery, Christiansted, St. Croix, 10 pp.

STAHL, A., 1883. *Fauna de Puerto-Rico. Clasificación sistemática de los animales que corresponden á esta fauna y catálogo del gabinete zoológico.* Imprenta del Boletin Mercantil, San Juan, 249 pp.

STEJNEGER, L., 1904. The herpetology of Porto Rico. *Report U. S. Nat. Mus. 1902*: 553–724.

UNDERWOOD, G., 1962. *Reptiles of the eastern Caribbean.* Carib. Affairs (n.s.) 1, 192 pp.

WOLCOTT, G. N., 1923. The food of the Porto Rican lizards. *J. Dept. Agric. P. R. 7*: 5–37.