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Crotaphytus collaris and C. reticulatus are apparently parapatric in northeastern Coahuila, México. Lizards from the zone of potential contact (actual sympatry not yet discovered) resemble *C. collaris,* but exhibit melanic, subquadrate dorsal spots reminiscent of the markings on *C. reticulatus.* Convergence, polymorphism by mutation, or introgressive hybridization could explain the origin of the black-spotted *Crotaphytus.* The black-spotted populations occur in areas environmentally intermediate between those occupied by *C. collaris* and *C. reticulatus,* or similar to the latter, and they possess some morphological character states which are intermediate between those of the two species. Product-moment correlations do not indicate a causal relationship between the climatic parameters and the morphological characters. Hence, convergence is discounted. Coexistence between the black-spotted lizards and *C. collaris* at some localities, differences in dorsal pattern ontogeny, and the occurrence of one or more localized, melanic-spotted populations of *C. collaris* in the Great Plains region, are taken as evidence for polymorphism. However, additional data do not support this simple explanation. Discriminant Function Analysis yields generally intermediate scores for the Mexican black-spotted *Crotaphytus* with respect to *C. collaris* and *C. reticulatus.* Morphological and ecological evidence of character displacement in the black-spotted lizards imply a history of genetic and competitive interaction with *C. reticulatus.* Most of the black-spotted populations are distributed along the interface between the Chihuahuan and Tamaulipan biotic provinces in habitat which is considered ecologically marginal for *C. collaris* and *C. reticulatus.* Moreover, the geographically annectant black-spotted lizards and *C. reticulatus* share an albumin variant, suggesting introgression. The tentative conclusion is reached that the black-spotted *Crotaphytus* are of hybrid origin. Coefficients of morphological variability and electrophoretic patterns of lactate dehydrogenase indicate these lizards are not F_1 or early backcross hybrids. Post-Wisconsin events leading to hybridization, and a long history of backcrossing with *C. collaris* are postulated.

WHEN natural populations of related species come into contact following a period of geographic or ecologic isolation, some form of interaction usually ensues. The kind and magnitude of interaction depends on the genetic and ecologic similarities of the populations involved. Studies of interaction between natural populations can provide a better understanding of such phenomena as character displacement, convergence and introgressive hybridization. From such studies, biologists can determine the ecological roles of the interacting populations, make inferences concerning past events, and if monitored over a sufficient time span, formulate predictions about the evolutionary fates of the interacting populations.

This study is concerned with the genetic and ecological relationships of natural populations of the collared lizard, *Crotaphytus collaris,* and the reticulate collared lizard, *C. reticulatus,* near a zone of potential contact in northeastern Coahuila, México. *Crotaphytus collaris,* occurring throughout the arid mountains of the Sierra Madre Oriental, is characterized by distinct, black collar marks and a greenish or gray ground color with numerous white spots. *Crotaphytus reticulatus,* endemic to the Lower Rio

Grande Valley, exhibits faint collar marks, a brown ground color with white reticulation and rows of melanic, subquadrate spots. Populations of questionable identity occur along the eastern slopes of the Sierra Madre Oriental, bordering the Rio Grande Valley, as well as in areas to the southwest. These lizards resemble *C. collaris* in color pattern except for the presence of melanic, subquadrate dorsal spots. Convergent evolution, polymorphism, or hybridization could account for the existence of these black-spotted *Crotaphytus*. This paper presents the results of comparative studies on the ecology, morphology and biochemistry of *Crotaphytus collaris* and *C. reticulatus* with the purpose of providing a most probable explanation for the origin of the black-spotted populations in México.

METHODS AND MATERIALS

Statistical methods.—Discriminant Function Analysis (Lawrence and Bossert, 1967) is the multivariate approach used to determine the morphological relationships of the black-spotted *Crotaphytus* to both *C. collaris* and *C. reticulatus*. The program employed variance-covariance mathematics to differentially weight characters relative to their within- and between-group variability. A discriminant multiplier (coefficient) was calculated for each character by the program, the size of the coefficient (regardless of sign) being proportional to the within-group conservatism of the character. The value of each character was multiplied by its respective coefficient; the resulting products were summed for each individual to yield its discriminant score. Scores were then plotted on frequency histograms to compare the test sample (black-spotted *Crotaphytus*) with the two reference samples (*C. reticulatus* and *C. collaris*). The reference samples were selected from areas adjacent to, but outside the zone of geographic contact. The sample of *C. collaris* was taken from the Bolsón de Cuatro Ciénegas, Coahuila, and that of *C. reticulatus* was taken from Webb and Dimmit Counties, Texas. The test sample of black-spotted *Crotaphytus* comprised specimens from two general areas: the Río Sabinas Valley, Coahuila (in the zone of potential contact), and the Río Nazas Valley, Durango (geographically distant from the zone of contact).

Thirteen meristic and eight morphometric characters were used to describe the samples (see below). Students *t*-test was employed in pair-wise comparisons of sample means. Males and females were pooled in samples for meristic characters lacking sexual dimorphism. Morphometric characters, based on males with a snout-vent length of 90 mm or greater, were expressed as ratios of the ear to snout length (ES) which is the most precise linear measurement. No significant difference was found in the proportion of ES to the snout-vent length among the samples. Ratios were transformed to arcsin values. Measurements were taken with dial calipers and recorded to 0.1 mm.

The Dice-Leraas histograms (Figs. 3–4), which depict morphological variation, are based on the following samples: *C. reticulatus* from Webb and Dimmit Counties, Texas (38); *C. collaris* from the vicinity of Cuatro Ciénegas, Coahuila (17); black-spotted *Crotaphytus* from the Río Sabinas Valley (22), and the Río Nazas Valley and vicinity (17), or in some cases both black-spotted samples pooled (26). See material examined section for collection designations.

The meristic and morphometric characters used herein are defined as follows:

Number of frontonasals (FN).—Scales along a straight line immediately anterior to orbits, including outermost pair of canthals.

Number of supraoculars (SO).—Scales covering left orbit along a straight line midway through orbital area and at a right angle to long axis of skull.

Number of parietals (NP).—Scales along a straight line between bony, postorbital protuberances.

Number of suboculars (OC).—Series of distinctly enlarged, elongate, keeled scales surrounding the lower margin of orbit. Taken on left side only.

Number of temporals (NT).—Scales between postorbital protuberance and supralabial row, along a line perpendicular to long axis of skull. Taken on left side only.

Number of lorilabials (NL).—Scales along a line perpendicular to long axis of skull, from supralabial row to anteromost edge of preocular. Taken on left side only.

Minimum number of lorilabial rows (ML).—Minimum number of scale rows between supralabials and suboculars. Taken on left side only.

Number of supralabials (SP).—Scales bordering lip of upper jaw exclusive of rostral;

taken on left side only, ending with last distinctly enlarged scale directly opposite last infralabial.

Number of infralabials (IF).—Scales bordering lip of lower jaw exclusive of mental; taken on left side, terminating with last distinctly enlarged scale at jaw juncture.

Number of postmentals (PM).—Scales forming a posterior border to mental scale, but not including infralabials.

Scales bordering postmentals (SM).—Scales forming a row immediately posterior to postmentals.

Number of femoral pores (FP).—Scales bearing femoral pores, recorded from the left thigh.

Number of fourth toe lamellae (TL).—Scales along ventral surface of toe from its tip to its insertion on sole of foot.

Ear to snout length (ES).—Actual distance from anterior margin of ear opening to extreme tip of snout (caliper touching rostral).

Eye to snout length (SL).—Distance from the anterior edge of orbit (caliper inserted against inner, bony edge) to tip of snout (caliper touching rostral).

Width of snout (DS).—Diameter of snout taken at level of posterior margins of nostrils.

Anterior width of head (HP).—Taken at level of bony prefrontal ridges immediately anterior to orbits.

Posterior width of head (HO).—Taken at level of posterolateral corners of orbits at postorbital protuberances.

Greatest width of head (HG).—Taken at level of greatest width just anterior to ear openings.

Cranial depth (CD).—Distance perpendicular to long axis of head, taken immediately posterior to orbits.

Shape of tail in cross section (TD).—Horizontal and vertical diameters expressed as a ratio, and taken at a distance posterior to vent equivalent to one-half snout-vent length.

In addition to the above characters, two characters were taken from skeletal preparations. The number of mental foramina was recorded for each dentary, and the extent of closure of the Meckelian groove (expressed by the number of tooth positions encompassed) anterior to the splenial was determined from 26 *C. reticulatus*, 28 *C. collaris*, and 26 black-spotted *Crotaphytus*.

Biochemical methods.—Electrophoretic comparisons were based upon samples of 14 *C. reticulatus*, 13 *C. collaris* and 14 black-spotted *Crotaphytus*. The lizards were etherized, and blood was drawn from the severed left carotid artery by pipette rinsed in 4% EDTA. Whole blood was centrifuged for 20 min at 1500 rpm to separate cells from plasma. The red cells were washed twice with 0.9% saline and lysed by the addition of a volume of distilled water three times that of the packed cells. Samples were frozen at –20 C until used. Tissue extracts for electrophoresis were prepared from whole body homogenates. The head, tail, hands, feet and skin were removed from each specimen. The body was minced and placed in a motor driven homogenizer. For each gm of tissue, 2 ml of 0.25 M sucrose was added, and then the sample was homogenized for several minutes. One ml of toluene was added to the homogenate which was then shaken vigorously and centrifuged for 30 min at 15000 rpm at 4 C. The resulting supernatant was stored at –20 C until used. Heads, tails and skins were retained as voucher specimens.

Plasma and whole body extracts analyzed for total protein and for esterase activity were subjected to vertical acrylamide gel electrophoresis. The electrophoresis was conducted at 250 to 350 V and 270 to 300 mA for 3 hr, using tris-versene-borate (pH 8.0) or tris-citrate (pH 6.7) buffers. Eight protein systems were subjected to vertical starch gel electrophoresis. Hemolysate samples analyzed for total protein and hemoglobin activity were electrophoresed for 5 hr at 250 to 350 V and 3.25 to 4 mA, using tris-borate buffer at pH 8.5. Whole body extract analyzed for phosphoglucomutase (PGM), lactate dehydrogenase (LDH) and malate dehydrogenase (MDH) activity was subjected to 5 hr runs at 250 V and 12 to 20 mA, using tris-citrate buffer at pH 6.7. Whole body extract analyzed for α glycerophosphate dehydrogenase (α GPDH), indophenol oxidase (IPO) and glutamate oxalate transaminase (GOT) was subjected to 5 hr electrophoresis at 250 V and 12 mA, using tris-versene-borate buffer at pH 8.0. Runs were standardized to compare the relative mobilities of the samples for a given enzyme by including different representative variants from previous runs.

RESULTS AND COMPARISONS

Color pattern variation.—In life, adult males of the Coahuilan (Sierra Madre Oriental)

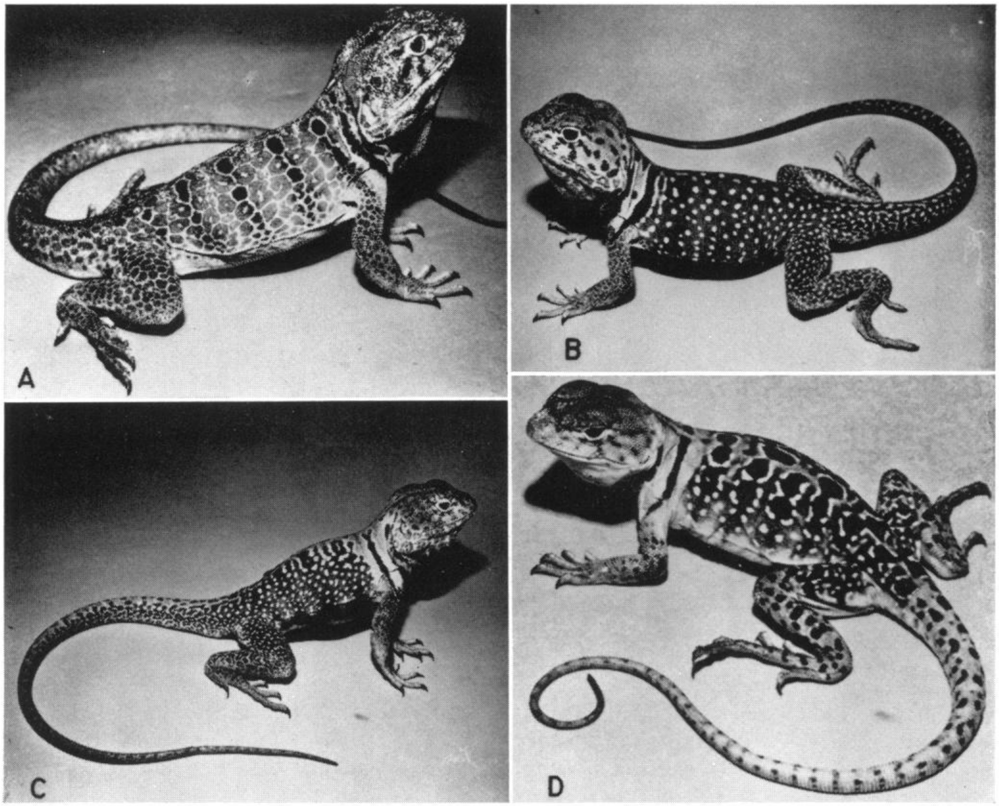

Fig. 1. A. *Crotaphytus reticulatus* (KU 128993, ♂, 115 mm SVL) from 64 km WNW Laredo, Webb Co., Texas. B. *Crotaphytus collaris* (KU 128960, ♂, 101 mm SVL) nr. Cuatro Ciénegas, Coahuila, México. C. Black-spotted *Crotaphytus* (KU 128974, ♂, 108 mm SVL) nr. Don Martín, Coahuila, México. D. Black-spotted *Crotaphytus* (KU 147291, ♀, 80 mm SVL) nr. Múzquiz, Coahuila, México. Photos A–C by Joseph T. Collins.

populations of *Crotaphytus collaris* have a gray-brown to pale gray-green body with faint straw colored crosslines and scattered white dots between them. The hands and feet are usually pale yellow. The head may be chalky gray to beige with chocolate to black spots of variable size scattered over the temporal and occipital areas. Distinct but narrow black collar marks cross a white field on the neck. The two marks are typically broken at the dorsal midline and the anterior collar may be fragmented. The gular area is yellowish green to bluish green centrally, with gray or yellow-orange labial cells separated from one another by white reticulation.

The absence or scarcity of green iridophores is especially characteristic of populations occurring in the arid basins such as Mapimí and Cuatro Ciénegas. Males from populations near Monterrey and Saltillo, however, are brilliant green. Lizards from the vicinity of Mina, Nuevo León, are relatively pale green.

The ground color in *Crotaphytus reticulatus* varies from brown to pale gray with a fine white reticulation covering the back and limbs. A series of black spots is arranged linearly, one large spot on either side of the dorsal midline and two or three additional spots on the flanks producing transverse rows. The cephalic area is brown with at least traces of a pale network. Black collar marks on the neck are present in males, but are usually faint. The central gular area is dark greenish gray with some black invading posteriorly from the collar marks which meet ventrally. The greenish gray gular color is produced by a blending of the black base and greenish blue crown

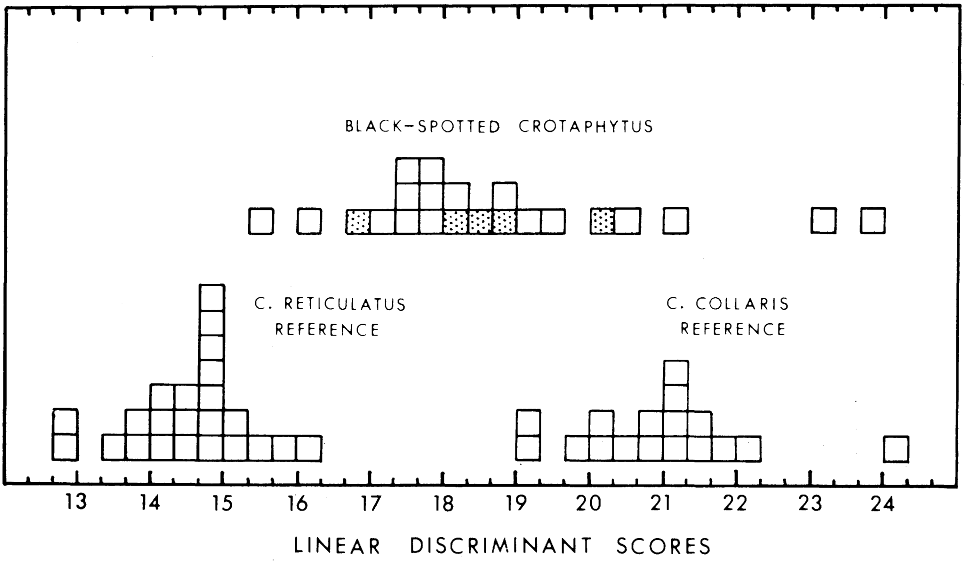

Fig. 2. Histograms of linear discriminant scores for three samples of *Crotaphytus*. Scores are based on seven morphometric and 11 meristic characters describing adult males (≥ 90 mm SVL); each square represents one individual. Sample of black-spotted *Crotaphytus* is composed of lizards from Río Nazas Valley (stippled squares) and Río Sabinas Valley (open squares).

of the individual scales. Laterally, white reticulation separates the rust or yellow-orange labial cells. The chest is golden yellow in breeding males.

Males of the black-spotted *Crotaphytus* are similar in color pattern to males of *C. collaris*. However, green iridophores are usually abundant on the body, and the dorsum is marked conspicuously with melanic, subquadrate spots (Fig. 1). The nature of these melanic markings is highly variable. They may be reduced to a single anterior pair, or a series of several pairs with or without additional spots on the flanks. The spots may fuse partially or entirely in some specimens to produce black crossbands. Two lizards taken by Smith and Taylor (Smith, 1935) 50 km N Matehuala, San Luis Potosí, show this variation. One specimen (FMNH 112452) is typically spotted; the other (FMNH 112451) exhibits black crossbands. White lines may border the black dorsal spots, but none of the specimens examined has the white reticulation that typifies *C. reticulatus*. The gular coloration of the black-spotted *Crotaphytus* is variable. In some individuals it may be green or bluish green as in *C. collaris*, or blue-gray as in *C. reticulatus*. Some gravid females of the black-spotted *Crotaphytus* have a pale pinkish orange gular suffusion. Gravid females of *C. reticulatus* are similarly marked, but females of *C. collaris* apparently lack this color.

The femoral pores are black in males of *C. reticulatus*, but are virtually without pigmentation in *C. collaris*. Most black-spotted *Crotaphytus* and one *C. collaris* show gray pigmentation in the pores, and one specimen (RWA 4031 from 2.2 km N Don Martín, Coahuila) of the black-spotted lizards has a single large black femoral pore in its series.

Juveniles of the three forms have black dorsal spots, but there are ontogenetic differences between the populations. In *C. reticulatus* all or most of the melanic spots are retained throughout life. In the black-spotted *Crotaphytus* some of the dark spots may be lost in adults since mature lizards usually have fewer spots than do the juveniles. In *C. collaris* the spots turn pale brown or disappear at a snout-vent length of 62 to 75 mm.

Morphological analysis.—*Crotaphytus collaris* and *C. reticulatus* are very similar in meristic and morphometric characters. Therefore, Discriminant Function Analysis, a sensitive, multivariate technique, was used in determining the affinities of the black-spotted *Crotaphytus*. Several data sets were

Table 1. Discriminant Multipliers Resulting From a Discriminant Function Analysis Comparing *Crotaphytus collaris* With *C. reticulatus*. See text for explanation.

Character	Discriminant multiplier
Snout diameter (DS)	-26.501
Snout length (SL)	-83.192
Greatest head diameter (HG)	-5.475
Head diameter at orbits (HO)	62.947
Head diameter at prefrontals (HP)	7.924
Cranial depth (CD)	42.143
Tail diameter (TD)	11.466
Frontonasals (FN)	-0.491
Supraoculars (SO)	-0.112
Parietals (NP)	-0.024
Temporals (NT)	-0.368
Lorilabials (NL)	0.647
Minimum lorilabial rows (ML)	-0.130
Supralabials (SP)	0.002
Infralabials (IF)	0.510
Postmentals (PM)	-0.427
Scales bordering postmentals (SM)	0.355
Femoral pores (FP)	0.618

subjected to analysis. Initially, only meristic characters taken from males and females were analyzed. Scores for the black-spotted *Crotaphytus* fell generally between the two reference samples although overlapping more with *C. collaris* than with *C. reticulatus*. However, meristic characters alone did not completely separate the two reference samples. Another run using only morphometric characters from males gave the same results. Separation of the *C. collaris* and *C. reticulatus* reference samples was achieved by combining the meristic and morphometric character sets (Fig. 2). The characters and the discriminant multipliers used in the final analysis are presented in Table 1. Two characters (OC, TL) were not used in the analysis due to missing observations. Note that 13 of the 22 black-spotted *Crotaphytus* are situated between the *C. collaris* and the *C. reticulatus* reference samples. Seven individuals fall within the limits of the *C. collaris* sample and two overlap with *C. reticulatus*. Hybridization is a possible explanation for the generally median position of the black-spotted sample.

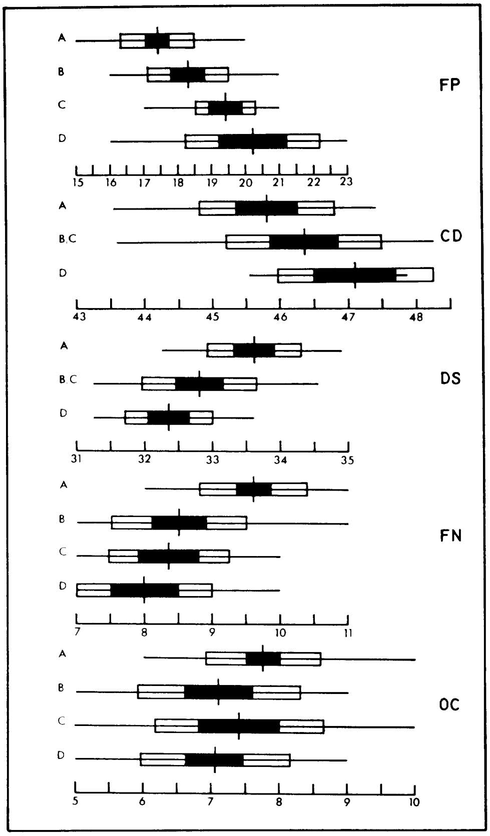

Fig. 3. Dice-Leraas histograms for meristic and morphometric characters showing intermediate states or trends in samples of black-spotted *Crotaphytus*. Samples are *C. reticulatus* from Webb and Dimmit Counties, Texas (A); black-spotted *Crotaphytus* from Río Sabinas Valley, Coahuila (B) and from Río Nazas Valley, Durango, and vicinity (C), and *C. collaris* from nr. Cuatro Ciénegas, Coahuila (D). Range represented by horizontal line, mean by vertical line, standard deviation by open rectangle, and two standard errors of mean by black rectangle. Character abbreviations (given in text) are at right of figures. Sample sizes given in text.

When meristic and morphometric characters are examined individually, evidence for competitive, as well as genetic, interaction comes to light. Ten characters are statistically non-significant among the samples, however those characters with large discriminant multipliers did have a limited influence on the scores from the multivariate analysis. The ten characters include measures of head diameter (HG, HO, HP), relative head length and snout length (ES, SL, SP, IF), tail diameter (TD), SO and NL. The black-spotted *Crotaphytus* show intermediate mean values for femoral pores (FP), cranial depth (CD), suboculars (OC), and

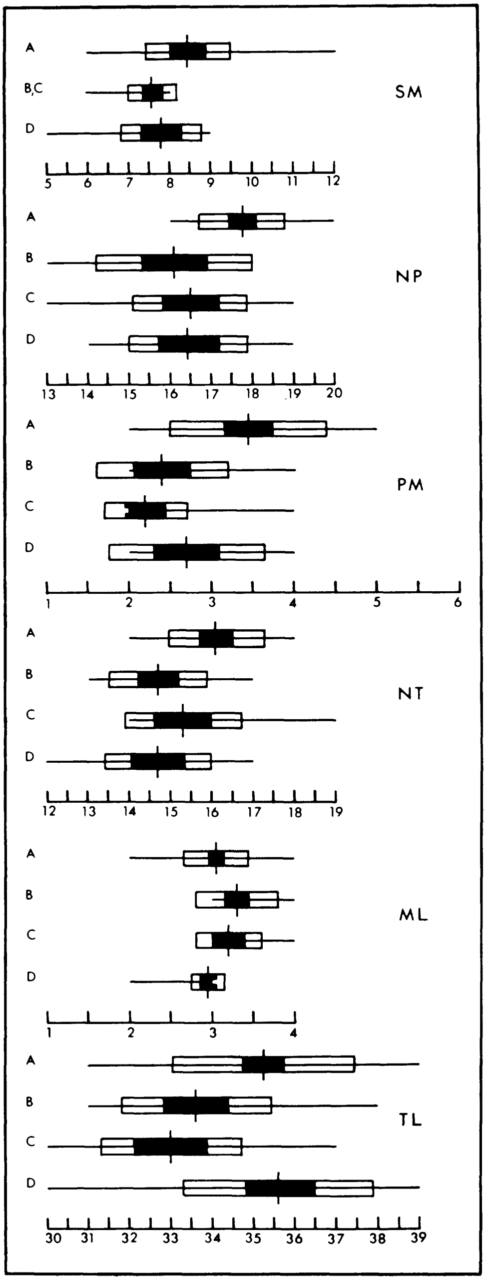

Fig. 4. Dice-Leraas histograms for meristic characters showing trends interpretable as character displacement (except NP, NT) in samples of black-spotted *Crotaphytus*. Explanation as in Figure 3.

trends shown by the frontonasals (FN) and snout diameter (DS) suggest intermediate states (Fig. 3). Evidence for character displacement is presented in Figure 4. The variational patterns shown by the minimum lorilabial scale rows (ML) and number of toe lamellae (TL) are particularly interesting. The sample means for ML and TL show no statistical difference between *C. collaris* and *C. reticulatus* but are significantly displaced in the samples of black-spotted *Crotaphytus*. Also evident, but less convincing, are slight shifts shown by the black-spotted *Crotaphytus* for the characters SM and PM. *C. collaris* and the black-spotted samples appear to have similar mean values for the characters NP and NT. Larger samples than presently at hand could clarify the apparent trends. Character displacement can be considered a fortuitous event or the aftermath of competitive interaction (Brown and Wilson, 1956). I believe the latter applies in this case for there is evidence of habitat partitioning between *C. reticulatus* and the black-spotted *Crotaphytus* (see below). The reduction in number of toe lamellae in the black-spotted lizards probably reflects a shift in substrate preference. The Río Nazas Valley populations of black-spotted *Crotaphytus* also show character displacement. Although *C. reticulatus* apparently does not occur in the Río Nazas area today, the data could suggest past competition between the populations. Little can be said about morphological displacement in *C. reticulatus* from the contact zone because of the absence of an adequate sample. The discriminant score (from meristic data only) of a single female *C. reticulatus* from near Múzquiz, Coahuila, falls near the sample limit of the *C. reticulatus* reference most distant to the *C. collaris* reference.

Evidence for character displacement strengthens the contention that contact has occurred between *C. collaris* and *C. reticulatus*. A considerable period of selection (through competition) would be necessary for character displacement to evolve. Such extended contact between closely related species would greatly increase the probability of chance, interspecific matings. Intermediate character states in the black-spotted *Crotaphytus* suggest hybridization.

Etheridge (1958) indicated that *C. collaris* and *C. reticulatus* differ from each other in the number of mental foramina and extent of closure of the Meckelian groove of the dentary. I examined these characters for evidence of intermediacy, but no significant differences were found among the samples. My counts for mental foramina per dentary are as follows: for 28 *C. collaris*, 3–6 ($\bar{x} = 4.7 \pm 0.26$); for 26 *C. reticulatus*, 3–6 ($\bar{x} = 4.7 \pm 0.36$), and for 26 black-spotted *Crotaphytus*, 4–6 ($\bar{x} = 4.8 \pm 0.26$). Closure of the Meckelian groove (expressed by number of tooth positions encompassed) varies as follows: *C. collaris*, 0–4 ($\bar{x} = 2.0 \pm 0.46$); *C. reticulatus*, 0–3 ($\bar{x} = 1.7 \pm 0.34$), and black-spotted *Crotaphytus*, 0–3 ($\bar{x} = 1.8 \pm 0.40$).

In addition to the above characters, the presence or absence of enlarged postanal scales was recorded from males in the samples. *C. collaris* males usually possess distinctly enlarged scales; males of *C. reticulatus* lack enlarged postanals. All males of the black-spotted *Crotaphytus* show enlarged postanals.

Protein analysis.—Systems that show monomorphism among the samples include MDH, α GPDH, PGM, IPO, GOT (from whole body extract) and total protein (from hemolysates). Polymorphic systems that do not show group-specific differences include esterases (from plasma), hemoglobin (from hemolysates) and total protein (from whole body extract). Esterase patterns from whole body extract are difficult to interpret because of apparently slight differences in mobility and poor resolution.

The albumin component of plasma proteins is polymorphic (Fig. 5), showing homozygous fast (FF), slow (SS), and heterozygous (SF) phenotypes. *Crotaphytus reticulatus* and the black-spotted *Crotaphytus* show all three phenotypes and share the S allele. Among 13 *C. collaris*, all are homozygous for the fast allele except one lizard (SS) taken sympatrically with the black-spotted *Crotaphytus*. Introgressive hybridization could explain the presence of the S allele in *C. reticulatus* and the black-spotted *Crotaphytus*. Unfortunately, a genetic variant shared between two species can be the result of other factors: 1) The polymorphism may have been present in an ancestral species and some of the variants were retained in subsequent lines following divergence. 2) Variants from different species which appear to be identical may actually represent separate mutations. Independent origin is less likely to be a problem in biochemical studies of closely related species than in morphological ones, but it is difficult to rule out. 3) Similar selection pressures on two species where they occur sympatrically may cause the persistence of shared variants which are absent in allopatric populations (Manwell and Baker, 1970).

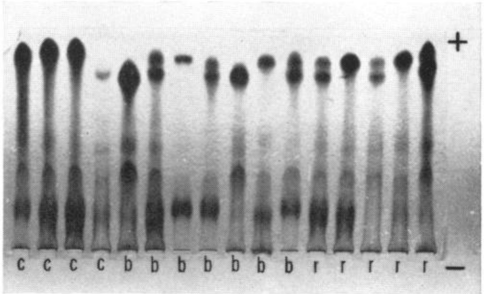

Fig. 5. Electropherogram of plasma proteins of *Crotaphytus collaris* (c), black-spotted *Crotaphytus* (b), and *C. reticulatus* (r). Albumin activity indicated by a single, fast migrating band (homozygous FF), a single, slow migrating band (homozygous SS), or a double band (heterozygous SF). Note that *C. reticulatus*, black-spotted *Crotaphytus*, and a single *C. collaris* taken sympatrically with black-spotted lizards share albumin S allele. Some heterozygotes are heavily stained (presumably due to excess sample) and do not clearly show double band pattern.

Aside from hybridization, a third alternative has probability. According to Dessauer (1970), reptilian albumins are hydrophilic proteins, responsible for at least 50% of the colloid osmotic pressure of the plasma. In lizards and other reptiles living in dry, hot environments, albumins usually occur at high concentrations and exhibit high charge densities. By contrast, reptiles in mesic habitats, such as aquatic turtles, generally have albumins of low charge. *Crotaphytus collaris* from near Cuatro Ciénegas, Coahuila, and other hot, dry localities show the fast migrating (high charge) albumin. A slow migrating (low charge) albumin variant apparently is only present in *Crotaphytus* populations occurring in semi-mesic savanna in the Rio Grande and Río Sabinas valleys (see below).

Lactate dehydrogenase (LDH) is a product of two different genetic loci which may be termed H (heart) and M (muscle). The active enzyme is a tetrameric molecule and the products of the H and M loci can polymerize to form five tetrameric isozymes: H_4, H_3M_1, H_2M_2, H_1M_3, M_4 (Markert, 1964). On gel electrophoresis, the anodally migrating H-

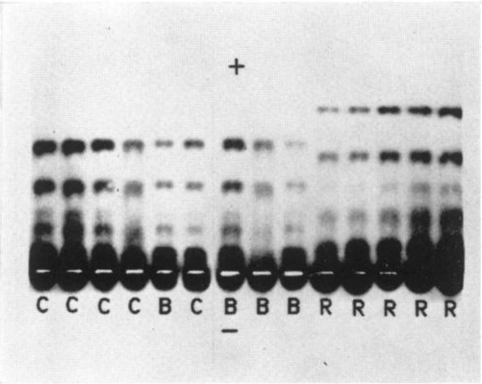

Fig. 6. Electropherogram of lactate dehydrogenase isozymes in *C. collaris* (C), black-spotted *Crotaphytus* (B), and *C. reticulatus* (R) showing a typical 5 band pattern except for presence of a faint satellite band (third from top) migrating in advance of the H_2M_2 isozyme. Starch gel was subjected to a 14 hr run at 250 V and 20 mA. See text for further discussion.

LDH is more rapid in *C. reticulatus* than in *C. collaris*; this accounts for the fast mobilities of the four isozymes containing H subunits (Fig. 6). An F_1 hybrid between two species differing at one LDH locus could express a 15 banded isozyme pattern (Gorman and Shochat, 1972). Note that the black-spotted *Crotaphytus* are identical to *C. collaris* in the LDH pattern. Although multiple isozyme patterns were absent, this does not negate a possible hybrid origin for the black-spotted lizards. Many generations of backcrossing to parental *C. collaris* could eliminate the hybrid pattern if the H allele of *C. reticulatus* was selectively inferior. By contrast, retention of the albumin S allele in the black-spotted populations could be explained by its selective advantage.

Ecological and distributional relationships.—*Crotaphytus reticulatus* is an inhabitant of the Tamaulipan thorn shrub, a vegetative association characterizing the coastal plain lowlands east of the Sierra Madre Oriental. The Tamaulipan biotic province is megathermal (Thornthwaite, 1948) and lacks a well defined dry season (Contreras Arias, 1942). The vegetation is composed of moderately dense stands of catclaw (*Acacia* spp.), mesquite (*Prosopis glandulosa*), paloverde (*Cercidium macrum*), *Mimosa* and *Opuntia*. Grasses such as *Bouteloua hirsuta, B. rigidseta,* and *Hilaria* are interspersed with the shrubs and small trees. *Crotaphytus reticulatus* occurs at elevations of 68–470 m on terrain ranging from relatively fine alluvium to gravelly sandstone and limestone hillocks (Montanucci, 1971).

The interior ranges of the Sierra Madre Oriental and adjacent Chihuahuan desert of north-central Coahuila, occupied by populations of *Crotaphytus collaris,* is a region that typically experiences dry spring seasons (Contreras Arias, 1942). The vegetation is difficult to characterize, but usually consists of low, sparse perennials and annuals. Dominants include creosote bush (*Larrea divaricata*), blackbrush (*Flourensia cernua*) and ocotillo (*Fouquieria splendens*). East of the Sierra Madre Oriental, the desert shrub is limited to the Serranias del Burro and the Rio Grande plain near Ciudad Acuña, Coahuila. Populations of *C. collaris* occur on rocky slopes, gravelly outwash bajadas, or desert flatland. Near Cuatro Ciénegas, Coahuila, these lizards are abundant along bajadas in the *Agave-Larrea* association. Northwest of Mina, Nuevo León, I collected *C. collaris* on flat terrain in the *Opuntia-Fouquieria* association. The elevational range of *C. collaris* in the Sierra Madre Oriental region is from 742 to 1609 m.

Black-spotted *Crotaphytus* inhabit the eastern foothills of the Sierra Madre Oriental, skirting the Rio Grande lowlands. The foothill vegetation is usually a chaparral-like cover composed of *Bovardia, Bumelia, Celtis, Diaspyros, Echeverria, Sophora* and succulents such as *Ferocactus.* Outlying hillocks farther east may support Tamaulipan elements such as *Leucophyllum* and *Mimosa.* Foothill areas peripheral to the Rio Grande Valley are subjected to sporadic rains throughout the year, while the southern regions in San Luis Potosí occupied by black-spotted *Crotaphytus* experience dry winters. Populations occurring in the drainage valleys of the Río Nazas and Río Aguanaval, as well as those occupying the highlands of San Luis Potosí, are apparently disjunct from the populations in the eastern foothills (Fig. 7).

Allopatric populations of *Crotaphytus collaris* and *C. reticulatus* occur on a variety of substrates including rocky slopes and desert flatland with or without extensive rock cover. Presumed ecological displacement has occurred in the Río Sabinas Valley and vicinity where black-spotted *Crotaphytus* and *C.*

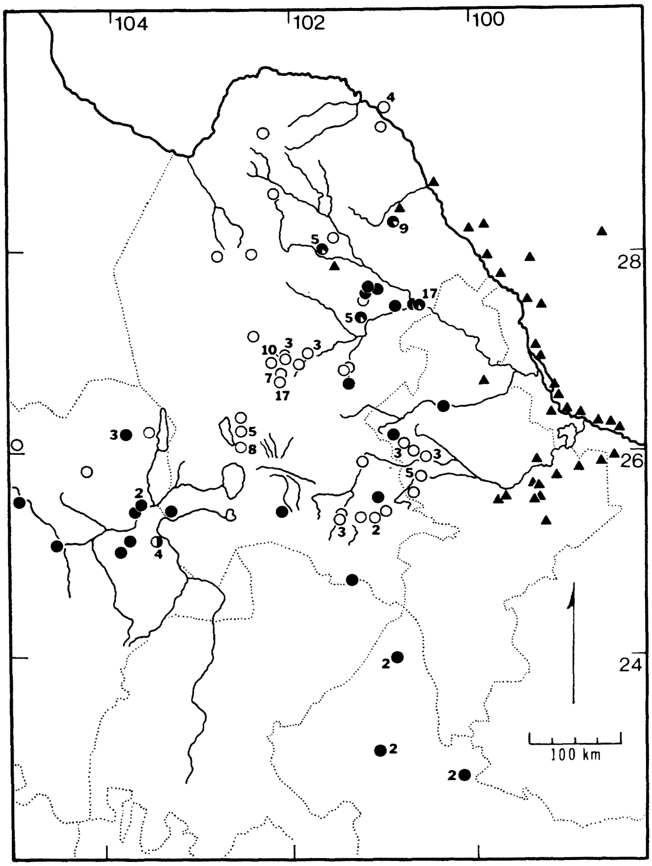

Fig. 7. Distribution of black-spotted *Crotaphytus* (dots), *C. collaris* (circles), and *C. reticulatus* (triangles) in northern México. Bicolored symbols indicate relative abundance of black-spotted *Crotaphytus* and *C. collaris*. Numbers indicate sample size greater than one.

reticulatus may have contacted each other. Records of *C. reticulatus* from Múzquiz and Nava, Coahuila, indicate that it is restricted to mesquite-catclaw savannas. By contrast, the black-spotted *Crotaphytus* are largely confined to limestone hillocks. This habitat partitioning is similar to that observed between *Crotaphytus insularis* and *C. wislizeni* in the Great Basin and Sonoran deserts. The allopatric populations of *C. collaris* and *C. reticulatus* have a similar mean number of toe lamellae (TL, Fig. 4), but the number is significantly reduced in the black-spotted *Crotaphytus*. This is probably a habitat correlated response, reflecting the shift to a rocky substrate. Similarly, populations of *Holbrookia* occurring on firm or rocky soils have fewer toe lamellae than do arenicolous populations (Axtell, pers. comm.).

Crotaphytus reticulatus is undoubtedly rare or may now be locally exterminated in the Río Sabinas Valley. Recent efforts by me, Ernest Liner (pers. comm.), and others to collect this species have failed. However, I have no reason to doubt the collection of this species from Múzquiz by E. G. Marsh in 1938. Recently, I have taken only black-spotted *Crotaphytus* near Múzquiz in the mesquite-catclaw savanna. Ralph Axtell (pers. comm.) has collected black-spotted *Crotaphytus* near Villa Juárez, Coahuila, on arid flatland far from any continuous rocky terrain. These observations suggest that the structural niche of the black-spotted *Crotaphytus* is broadening to include flatland in the Río Sabinas Valley, thus leading to speculation that the black-spotted populations may be displacing *C. reticulatus*. Climatic change may be an associated factor as geologically recent trends have been toward aridity

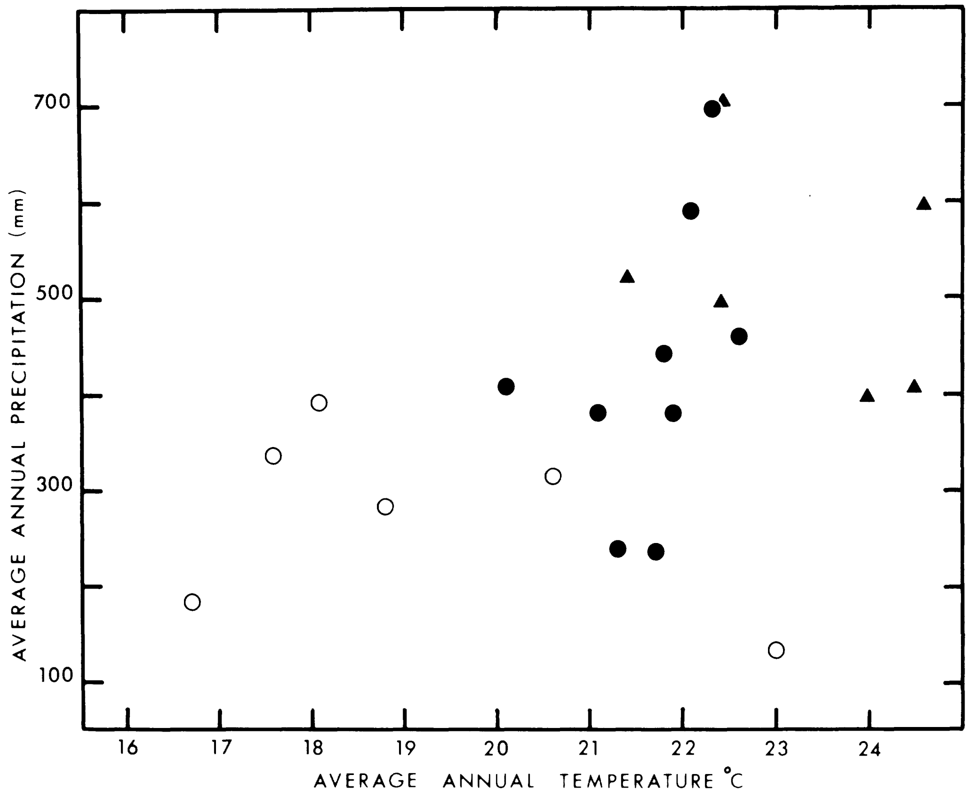

Fig. 8. Scatter plot of precipitation and temperature for localities represented by *C. reticulatus* (triangles), *C. collaris* (circles) and black-spotted *Crotaphytus* (dots). See text for discussion.

(Wells, 1966). Man-influenced changes through lowering of water tables and overgrazing could be accentuating this desiccation. Under these conditions, the Tamaulipan flora could be replaced by sparse, xerophilous Chihuahuan elements, and *Crotaphytus reticulatus* could be driven to extinction by habitat deterioration as well as by competitive pressures from *C. collaris.*

The respective habitats of *Crotaphytus reticulatus* and the black-spotted *Crotaphytus* are similar in having moderate to dense vegetative cover, thus suggesting possible similarities in precipitation, temperature, and other parameters. Climatic data (from Contreras Arias, 1942) reveal that localities occupied by *C. reticulatus* are primarily warm-mesic, whereas those inhabited by *C. collaris* are temperate-xeric (based on annual averages). Localities represented by black-spotted *Crotaphytus* are in general climatically intermediate or similar to the warm-mesic conditions (Fig. 8). The data could suggest that the resemblance between *C. reticulatus* and the black-spotted *Crotaphytus* is a convergence phenomenon attributable to similarities in the selective regimes acting upon the populations.

Discussion and Conclusions

The climatic similarity of areas inhabited by *C. reticulatus* and the black-spotted *Crotaphytus* (whether geographically near or distant) argues for convergence. However, if environmental factors constitute the selective force influencing the intermediate morphology of the black-spotted populations, significant correlations should exist between the climatic parameters and the characters DS, CD, FN and FP. With the exception of DS which alone cannot affect the discriminant scores, the morphological and climatic variables are not correlated (Table 2). Thus, convergence can be ruled out with reasonable certainty.

Polymorphism resulting from mutation rather than introgressing alleles could explain the origin of the black-spotted *Crota-*

TABLE 2. PRODUCT-MOMENT CORRELATION COEFFICIENTS BETWEEN MORPHOLOGICAL CHARACTERS AND CLIMATIC PARAMETERS FOR 14 LOCAL POPULATIONS REPRESENTING 240 *Crotaphytus* (*C. collaris, C. reticulatus, C. insularis*). Tested inter- and intraspecifically, with most significant test presented. Significance levels are 0.05*, 0.01**.

Climatic Parameters	Characters			
	DS	CD	FN	FP
Jan. Temp.	-0.247	0.169	0.331	0.443
Jul. Temp.	-0.221	0.123	0.223	0.224
Ann. Ppt.	0.658*	-0.212	-0.425	-0.149
Jun. Ppt.	0.754**	-0.043	-0.466	-0.193
Jul. Ppt.	0.819**	-0.384	-0.451	-0.329
Aug. Ppt.	0.730**	-0.448	-0.427	-0.303

TABLE 3. COEFFICIENTS OF VARIABILITY (CV) FOR MORPHOMETRIC AND MERISTIC CHARACTERS FROM THREE POPULATIONS OF *Crotaphytus*: A. *C. reticulatus*, B. BLACK-SPOTTED *Crotaphytus*, AND C. *C. collaris*.

Character	CV values for samples		
	A.	B.	C.
Snout diameter (DS)	4.4	3.4	4.3
Snout length (SL)	2.0	3.4	3.4
Greatest head diameter (HG)	2.8	2.7	3.2
Head diameter at orbits (HO)	2.5	3.0	3.1
Head diameter at prefrontals (HP)	2.3	3.1	3.8
Cranial depth (CD)	3.3	3.6	4.0
Tail diameter (TD)	7.7	6.4	7.7
Frontonasals (FN)	8.5	10.5	12.8
Supraoculars (SO)	8.7	7.9	10.4
Parietals (NP)	6.0	8.8	8.6
Suboculars (OC)	10.8	16.7	15.7
Temporals (NT)	7.2	9.1	9.0
Lorilabials (NL)	9.6	9.6	10.6
Minimum lorilabial rows (ML)	12.9	14.4	8.0
Supralabials (SP)	6.5	6.2	7.3
Infralabials (IF)	8.2	7.6	10.1
Postmentals (PM)	28.0	31.2	35.4
Scales bordering postmentals (SM)	13.6	8.2	12.6
Femoral pores (FP)	6.3	7.2	10.2
Toe lamellae (TL)	6.1	6.1	6.5

phytus. At least one localized population of *C. collaris* in Kansas exhibits melanic spotting. As previously mentioned, juvenile *Crotaphytus* possess melanic spots which subsequently fade in adult *C. collaris*, but are retained (at least partially) in adult black-spotted *Crotaphytus* and adult *C. reticulatus*. Retention of juvenile characteristics, in essence neoteny, is occasionally related to control gene polymorphism (Manwell and Baker, 1970). Although this is the simplest explanation, it is not supported by most of the data.

The multivariate Discriminant Function Analysis shows that the Mexican black-spotted *Crotaphytus* (Río Sabinas and Río Nazas samples) are generally intermediate between *C. collaris* and *C. reticulatus*, thus suggesting a hybrid origin. Furthermore, morphological and ecological evidence of character displacement implies contact and interaction between the two species. Extended periods of contact, necessary for the evolution of character displacement, would greatly enhance the chances of interspecific matings, especially involving closely related species. Gel electrophoresis suggests that the black-spotted *Crotaphytus* and *C. reticulatus* share the albumin S allele, possibly the result of introgressive hybridization. Even if the slow albumin variant were associated with high environmental moisture, the allele could have been contributed by *C. reticulatus*, probably one of the most mesic-adapted species of *Crotaphytus*. Introgression could have provided fitness to those populations of *C. collaris* invading semi-mesic habitat. The sample of black-spotted lizards is inadequate to determine whether positive heterosis exists at the albumin locus. However, these lizards are relatively more abundant than typical *C. collaris*, and greatly outnumber *C. reticulatus* in semi-mesic areas near the zone of contact (Fig. 7). This observation suggests high fitness in the black-spotted lizards. Finally, the black-spotted populations show an ecological and geographic pattern that is consistent with "weed" species, i.e. occurring in areas that are ecologically marginal for the parental species (a possible interpretation of Fig. 8). The majority of the black-spotted populations, with the exception of those in the Río Nazas area (see historical interpretation below), occur along the transition zone between the Chihuahuan and Tamaulipan biotic provinces.

Postulating a hybrid origin for the Mexican black-spotted *Crotaphytus* seems most reasonable considering the available data. However, several lines of evidence indicate that these populations are not F_1 or early backcross hybrids. The LDH patterns of the black-spotted lizards are identical to those of *C. collaris*, attributable to numerous generations of backcrossing with this parental genotype. Moreover, the black-spotted populations do not show the characteristics typical of an active hybrid swarm. A broad range of character state combinations and high character variability are absent (Table 3).

Foregoing discussions have alluded to a long history of interaction between *C. collaris* and *C. reticulatus*. Migrations during the Pleistocene may have contributed to present-day distribution patterns of *Crotaphytus* and may explain the occurrence of black-spotted lizards in the Río Nazas region and highlands of San Luis Potosí. Conant (1963) reviewed evidence for pluvial Pleistocene connections between the Río Nazas-Aguanaval and Rio Grande river systems. The biotic assemblages of the two river systems share several species of fishes, a turtle (*Pseudemys scripta*) and a snake (*Natrix erythrogaster*). Arellano (1951) described the Torreón basin as having a northern and an eastern outlet both of which may have served as dispersal corridors for terrestrial and aquatic organisms. The present distribution pattern of black-spotted *Crotaphytus* suggests that the eastern corridor may have effected geologically recent dispersals of mesic or semi-mesic adapted assemblages.

Two similar historical interpretations of hybridization between *C. collaris* and *C. reticulatus* are possible. *Crotaphytus reticulatus* may have had a widespread distribution encompassing the Río Nazas Valley and regions to the south during the warm, mesic Climatic Optimum (4000–9000 BP; post-Wisconsin dates taken from Jones, 1964). This seems reasonable in light of geologic and biogeographic evidence for biotic dispersal between the Río Grande and Río Nazas drainage valleys. However, convincing evidence such as peripheral isolates is lacking. With the onset of the dry Xerothermic Period (2500–4000 BP), xeric-adapted populations of *C. collaris* may have migrated southward and eastward. *C. reticulatus* concomitantly may have retreated, leaving low-density, relict populations in locally favorable areas along the periphery of its former range. These low-density populations, perhaps prone to hybridization due to scarcity of conspecific mates, could have hybridized with the relatively numerous, invading *C. collaris*. Eventually the relict populations may have been genetically consumed (swamped out of existence), leaving scattered populations of hybrid origin in their place. The eastward advance of *C. collaris* may have halted along the edge of the Río Grande Valley as the lizards encountered unsuitable, mesic savannas occupied by high-density populations of *C. reticulatus*.

On the other hand, contact hybridization may have occurred along the eastern slopes of the Sierra Madre Oriental, with hybrid populations subsequently spreading southward and westward through semi-mesic habitat. Unidirectional introgression is explained by the presence of semi-mesic habitat suitable for the hybrid genotype only toward the west (because of topography, mesic to xeric transition exists toward the west). Considerable backcrossing may have occurred between the hybrids and *C. collaris*, with eventual displacement of the xeric-adapted *C. collaris* genotype from the semi-mesic areas.

I believe the first interpretation is more plausible than the second. It attributes character displacement and intermediate character states shown by the Río Nazas Valley populations of black-spotted *Crotaphytus* to the former presence of *C. reticulatus*. Moreover, it explains the intermingled distribution patterns of *C. collaris* and the black-spotted lizards.

Problems.—Location of an active zone of hybridization between *C. collaris* and *C. reticulatus* would provide more convincing evidence for the hybrid origin of the black-spotted *Crotaphytus* in México. Detection of F_1 and early backcross hybrids would be possible through electrophoretic analysis of lactate dehydrogenase activity. As stated by Manwell and Baker (1970), for conclusive proof of introgressive hybridization it is necessary, but often difficult, to demonstrate the existence of F_1 hybrids and their backcrossing into one or both parental species. The present relationships of *C. collaris* and *C. reticulatus* suggest a long prior history of interaction. If differences have evolved which successfully effect premating isolation between the two species, production of F_1 hybrids may have ceased. If so, much of what has been written here could remain forever controversial.

Males of *C. collaris* and *C. reticulatus* exhibit interspecific aggression (unpublished data), but it is not known how receptive females act toward heterospecific males. Choice experiments are needed to determine what components of the phenotype function in species recognition. Courtship behavior, releasers, olfactory cues, are likely to diverge in parapatric or allopatric populations of related species, but characters conferring fitness to the physical rigors of the environment could converge, depending on the time span and intensity of selection. This is because similarity in species recognition characters, whether due to convergence or hybridization, might result in frequent mismating leading to energy and gametic wastage even if genetically closed populations were involved. Hence melanic spotting is not likely to serve as a recognition releaser in adjacent populations of *C. collaris* and *C. reticulatus.* Perhaps the spots have a cryptic function or aid in solar absorption while the lizards forage in dense vegetation. Possibly the spotting has pleiotropic implications, due to genetic linkage to an adaptive set of characters. The gular pattern may not be of discriminatory significance owing to high intrapopulational variability in *C. collaris.* Chest coloration (yellow in male *C. reticulatus,* green to greenish blue in male *C. collaris*) and male body color (brown in *C. reticulatus,* greenish in *C. collaris*) may function as recognition characters. Interestingly, green iridophores are relatively abundant in males of *C. collaris* populations adjacent to *C. reticulatus.* Furthermore, other parapatric associations of *Crotaphytus* involve brown-green species pairs. Axtell (1972) described a narrow zone of hybridization between pale brown *C. insularis bicinctores* and green *C. collaris* in western Arizona, and a potential zone of contact in Sonora would involve a buff-colored morph of *C. collaris* and the blue-green *C. dickersonae.* Body color differences in these parapatric populations could be a manifestation of character displacement.

SPECIMENS EXAMINED

Only a partial listing of the 240 adult lizards used in the correlation analysis (Table 2) is provided below. The remainder are extralimital and do not pertain directly to this study, but additional listings are available upon request.

Crotaphytus collaris (Total 105)

TEXAS: *Val Verde Co*: Amistad Dam (KU 126925); Devils River, nr Hwy 90 (KU 126926–29), 1 mi W on Hwy 90 (KU 126924). MÉXICO: *Coahuila*: Allende, 2 km WSW (KU 147280, 147284); Cuatro Ciénegas (FMNH 47235, CM 48334), 1–3 km E (CM 48134–35, CM 48233, KU 128971–72), 7.5 km E (KU 147258–59), 22–26 km E (CM 42941, UIMNH 43225), 1.6 km N, 21.6 km E (KU 39901), 6–8 km N (CM 42938–40), 3.3 km W (CM 48277), 15 km W (BCB 10160), 14.3 km SW (CM 42936), 80 km SW (CM 42942), 24–30 km SSW (KU 128966, 128978, 128961, 128960, 128956, 128959, 128965, 128969, 128962, 128957, 128970), 31–33 km SSW (KU 128958, 128967, 128963, 128964), 6.8 km S (KU 80293), 12–20 km S (KU 147285–288, EAL 2638), 24.8 km S (KU 147289–90), 5 km S, 15 km E (KU 39902); Don Martín Dam, 0.8 km N (RWA 4105), S end (KU 128976, 128985); Sabinas, 33.3 km S (BCB 10159); General Cepeda, 17.5 km N (KU 147296), 12.8 km N (KU 147260), 8.6 km N (KU 147261), 5 km N (KU 147262); La Gacha (KU 38342); Las Delicias, 15.5 km N (KU 143565); Monclova, 10 km S (TNHC 33199); Sierra de la Gloria, E Monclova (FMNH 47234); Motacorona, nr jct hwy 57 and Progreso rd (KU 147301); Múzquiz, 25 km NW (KU 147295); Ocampo, 88.3 km N (KU 38079), 83.3 km N, 33.3 km W (KU 39899); Piedra Blanca, 1.6 km E (KU 28094); Saltillo, 6.6 km N (UIMNH 20334), 6.6–10 km W (FMNH 112457), 23.3 km W on hwy 40 (KU 147263); San Miguel, 50 km N (AMNH 77317); San Pedro de las Colonias, 70 km N (KU 143561–63), 53.6 km N (KU 143564), 70.5 km NE (EAL 2656(2)), 46–53 km NE (EAL 2425, 2514(2), 2426, 2516(2)); Sierra San Marcos, 4 km E on Santa Tecla rd (CM 51151), 3.3 km S (CM 51161); Ciudad Acuña (FMNH 47231). *Durango*: La Campana, 6.6 km N (MSU 2770); Mapimí, 40.6 km W (EAL 2520); Mimbrera, S Río Florido (AMNH 71370); Torreón, 43.3 km S (BCB 3142, 3144). *Nuevo León*: Mina, 18–25 km NW on hwy 53 (EAL 2607, KU 147265, 147303), 13.8 km NW on hwy 53 (KU 147302), 2–3 km NW on hwy 53 (KU 147264, 147304–05); Monterrey, 40.2 km SW (UMMZ 119034); Villa de Garcia, 3.3 km N (EAL 2479(2)), 5.6 km SE (TNHC 33198), 4–7 km S (CM 42943, UNM 8927).

Black-spotted *Crotaphytus* (Total 65)

MÉXICO: *Coahuila*: Allende (FMNH 47233), 2 km WSW (KU 147279, 147281–83); Arroyo Palo Blanco, 3.3 km SE (RWA 3904); Don Martín, 1--2 km N (KU 39900, RWA 4031, 4039, 4321); Don Martín Dam, S end (KU 128973–75, 128977–84, 128986–88), 10 km W (RWA 4034); El Sauz, 13.3 km NE (BCB 10158); La Cruz, 3.3 km E, ca. Monclova, 21.6 km S (BCB 10161); Motacorona, nr jct hwy 57 and Progreso rd (KU 147299–300); Múzquiz, 20–34 km NW (EAL 3138(3), KU 147291–4); Parras, 4 km NE (UMMZ 112928); Progreso rd, 2.8 km S jct on hwy 57 (KU 147297–98); Pueblo Nuevo, ca. 15 km S Sabinas (FMNH 47232); Sabinas, 20 km S (RWA 1795); Torreón, 16.6 km E, 10 km S (AMNH 77280); Villa Juárez, 18.3 km S (RWA 4123). *Durango*: Bermejillo, 47.4 km NW (EAL 3192); Conejos, 5 km E (MSU 729–31); El Palmito, 3.3 km S nr Río de Ramos (MSU 2771); Lerdo, 5 km SW along Río Nazas (AMNH 67452, KU 33787), 18.3 km SW near Río Nazas (AMNH 67451); Pedriceña, 10 km NE (FMNH 112453), 4.2 km S (MSU 8922); Rodeo, 3.3 km S (AMNH 96593); Torreón, 43.3 km S (BCB 3143, 3145). *Nuevo León*: Mina, 43.3 km NW on hwy 53 (RWA 4118); Villaldama, 10.3 km E (RWA 4004). *San Luis Potosí*:

Matehuala, 50 km N (FMNH 112451–52); Presa de Guadalupe (LSUMZ 336, 2556); San Luis Potosí, 110 km N (UIMNH 20335, FMNH 112456). *Zacatecas-Coahuila*: Saltillo, 90 km SW on hwy 54 (KU 143566).

Crotaphytus reticulatus (Total 40)

TEXAS: *Maverick Co*: Eagle Pass, 1.6 km E on Manges Ranch (KU 147266–278, 147257). See Montanucci (1971) for additional records.

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(Note added in proof: The albumin S allele appears to be localized to the potential contact zone between *C. collaris* and *C. reticulatus*. Electrophoretic examination of 19 additional *C. collaris* recently collected in Sonora and southern Arizona revealed an absence of that variant.)

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