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FACTORS INFLUENCING THE DISTRIBUTION OF THE ARUBAN WHIPTAIL LIZARD, CNEMIDOPHORUS ARUBENSIS

by

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Aruba, Netherlands Antilles, is a 175 km^2 xeric island lying off the Caribbean coast of Venezuela. The flat coral and limestone regions of the shore contrast with the rolling hills that rise in the east to elevations of 188 meters. Vegetation types are varied.

The island has excellent maps (LENS 1910, MEUTER 1963), and its natural history has been surveyed and described by various scientists, e.g. MARTIN (1888), BAKER (1924), WESTERMANN (1932), WAGENAAR HUMMELINCK (1940a, 1953), VOOUS (1955, 1957, 1959), STOFFERS (1956), DE BUISONJÉ (1974), while herpetological data have been published by WAGENAAR HUMMELINCK (1940b) and BRONGERSMA (1940, 1948).

Probably the most numerous vertebrate on the island is the endemic blue spotted whiptail lizard, *Cnemidophorus arubensis*. This lizard has been the topic of taxonomic reports by LAMMERÉE (1970) and WAGENAAR HUMMELINCK (1940b) who considered it a subspecies of the mainland form, *C. lemniscatus*. The mainland whiptail was studied briefly by MARCUZZI (1954) and VALDIVIESO & TAMSITT (1963). SEXTON et al. (1964) investigated the influence of environmental structure on *C. lemniscatus* distribution, and later MÜLLER (1971) attempted a general ecological and ethological study. Numerous ecological studies have been completed on North American species of *Cnemidophorus* (e.g. FITCH 1958, HARDY 1962, MCCOY 1965, WALKER 1966).

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Conspicuously lacking in all of these studies are concise data on the factors influencing the local distribution of the whiptails. PIANKA (1970) has contributed the most detailed survey of the effects of habitat on whiptail lizards in his autecological study of *Cnemidophorus tigris*. This report attempts to delimit the major factors that influence the distribution of one species of whiptail, *Cnemidophorus arubensis*.

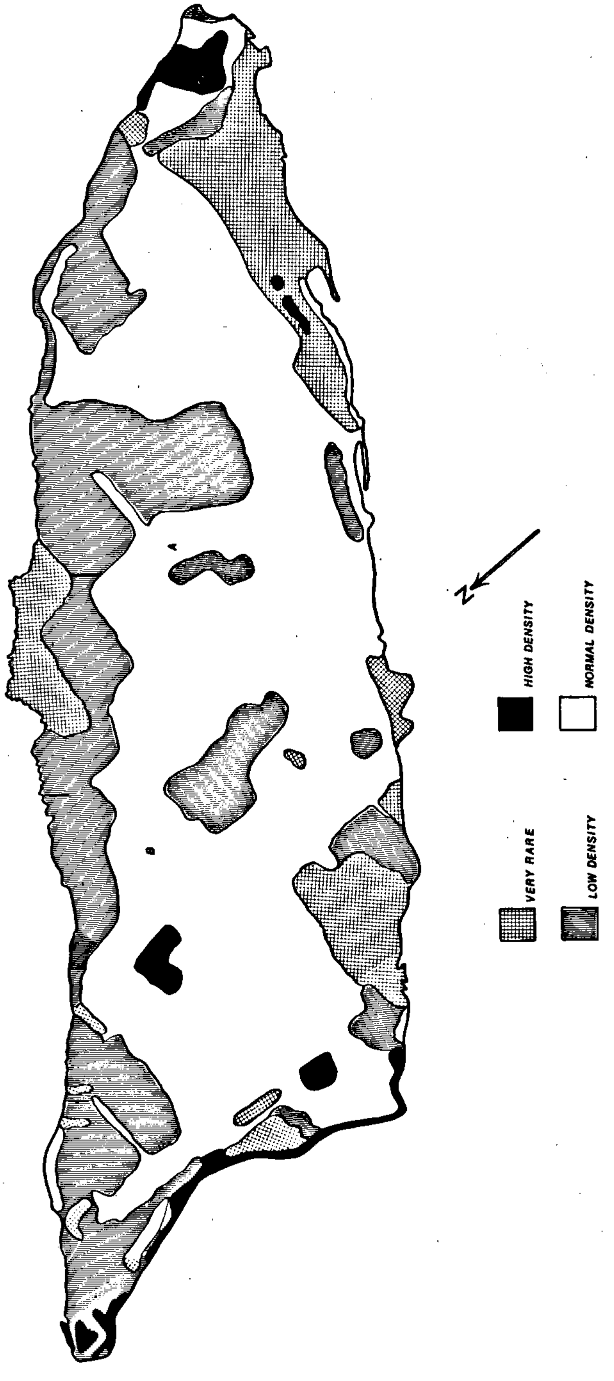
This study reflects the aid and consideration of many individuals. Dr. C. ROBERT SHOOP provided constant material and moral support. He also read the manuscript over many times. Drs. JOHN CRENSHAW and HERNDON DOWLING offered ideas, criticisms, and other aid. The maps were executed by Mrs. LOIS WINN. Dr. LEWIS SMITH and Mr. HAROLD POMEROY aided with the computer analysis. Miss RENE WEYLER served as field assistant, critic, typist, and companion.

METHODS AND MATERIALS

I reported elsewhere (SCHALL 1973) that the Aruban whiptail does not hybridize with the mainland form under natural conditions. Therefore, throughout this report I refer to this endemic lizard as *Cnemidophorus arubensis*.

The factors classically stated as influencing animal distribution fall into two categories, physical and biological. The physical environmental factors I investigated were: temperature relations; slope; wind; soil texture, reflectivity, color, and depth; habitat structure; insolation; shade; and geographic position in relation to other habitat types. The biological factors studied were structure and kinds of vegetation, predation, intraspecific relations, and interspecific competition. The latter two are reported separately (SCHALL 1973) and are not considered in this report.

To investigate *C. arubensis* distribution I spent five months on Aruba from September 1971 to the end of January 1972. Ecological zones on Aruba are well defined and relatively simple in structure. The size of the island also permits easy access to all zones. The first phase involved visiting every part of the island. Data obtained for more than 500 sites included approximate lizard density, structure of the habitat, kind of vegetation cover, nature of the substrate, and geographic position. Periodically, counts of lizards were made at a site and densities computed to ascertain the precision of my estimates. In general, the estimates were a good representation of true population densities. These data were used to construct maps showing lizard density and the island's physiognomy.


N
VERY RARE
LOW DENSITY
HIGH DENSITY
NORMAL DENSITY

The second phase included the selection of 10 sites representing a wide variety of habitat types. These sites varied from 1000 m² to 10,000 m². The method of selection of these sites is presented elsewhere (SCHALL 1974). At each of these sites I investigated those parameters which I thought influenced the whiptails' distribution.

Lizard densities were obtained by slowly moving through the area, at least three times, and counting all the animals observed. Soil depth and quality, slope, habitat structure, and percentage of ground level insolation in early afternoon were determined. Substrate and air temperatures at 1 cm below and above ground level, respectively, were recorded. These readings were taken in open sun, shade, and in bushes at least 10 times for each condition. Thermal diversity for open area and in bushes was estimated by computing variance of all temperatures taken in those locations.

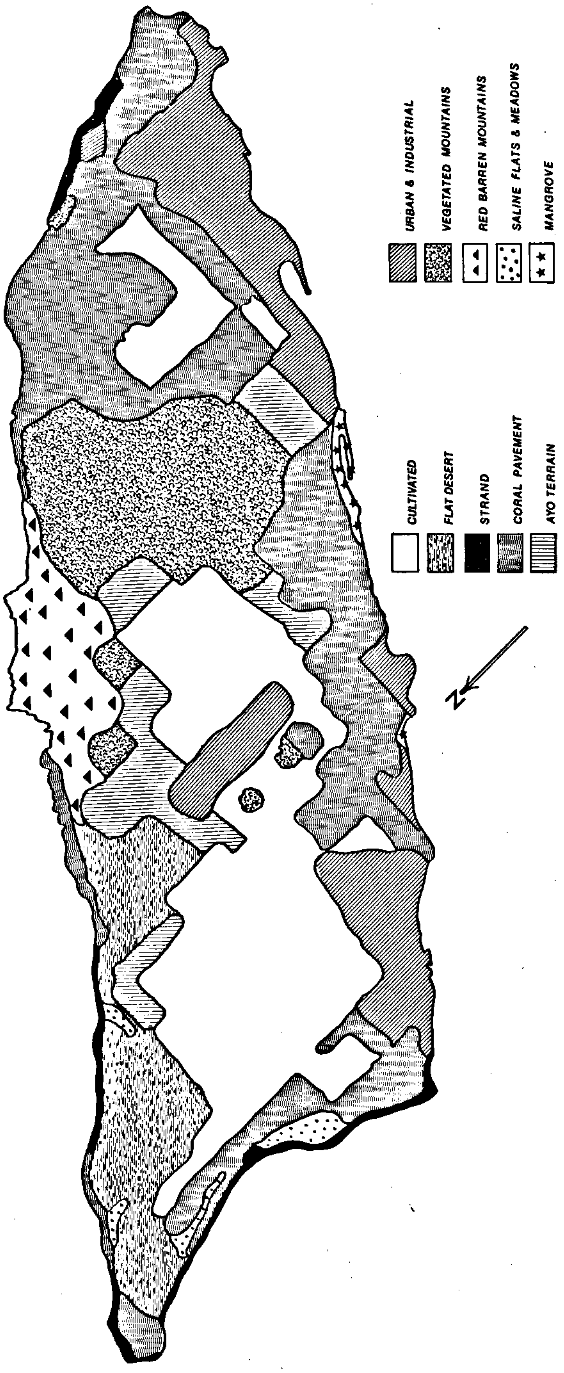
Vegetation presented a variety of possibly important parameters. The percentage of ground covered was carefully computed by measuring all vegetation in the plot. Vegetation structure (height, basal area compared to foliage area), density, diversity of species, and distribution pattern were all recorded. Wind speeds were measured with an Alnor anemometer.

A computer step-wise regression analysis of the data was performed using lizard population density as the dependent variable. This program provided an ordering of the parameters in their importance according to the proportion of variance reduced. If the ultimate cumulative reduction was low, I could assume that important variables had been ignored. For each parameter the regression plot illustrated which state of the parameter is most nearly optimum for high lizard density and the slope provides information on how variably important these states were. The standard error of the regression coefficient reveals if subjective parameter states were properly ordered in the graph from most optimum to least optimum. The program also provided estimates of population densities at each site and compared these with observed field densities. Significant differences between the two indicated the area had a peculiar parameter that I had not entered into the regression.

To determine relationships between environmental variables multiple correlation and partial correlation coefficients were computed.

At each site behavioral observations were made. Burrowing, feeding, and fighting were all recorded. Some animals were staked out to determine behavioral responses to heat stress and to observe if any predators would attack the restrained animals. I collected 166 animals to observe frequency of damaged tails, a potential measure of predator pressure.

Figure 28. Whiptail lizard population density map for ARUBA, Netherlands Antilles. – Very rare = less than 0.3 lizards per 100 m²; low density = 0.4–1.0; normal density = 1.0–6.0; hight density = 7.0–15.0 "A" and "B" are areas of almost "normal" density in marginal habitat. Large areas of "very rare" density in southern part of island are cities of Orangestad and San Nicolas.


URBAN & INDUSTRIAL
VEGETATED MOUNTAINS
RED BARREN MOUNTAINS
SALINE FLATS & MEADOWS
MANGROVE
CULTIVATED
FLAT DESERT
STRAND
CORAL PAVEMENT
AYO TERRAIN
N

RESULTS

Figures 28 and 29 are of the lizard density and habitat physiognomy maps, respectively. On Aruba, whiptails are found in virtually every habitat type. They are present from sea level to the highest point on the island, Mt. Jamanota, at 188 meters. They occur on sand, hard soil, coral shelves, in trees, shrubs, in wet swampy areas, dense shrubs, barren deserts, beaches, and gardens. Very high lizard densities were found in strand areas near the coast and in two agricultural areas. One of these two, the high density area in the area north of Oranjestad, is the site of a now abandoned hydroponics farm. The other is a farm area in the northwestern part of the island. Moderately high densities were in the "cultivated" areas with fence rows and abandoned aloe fields. Lizards are rare in the extremely harsh barren desert area of the north coast, in the wooded steep hills farther south, and in urban areas.

Several unusual distribution patterns are apparent from the map. Roads traversing optimal areas may result in densely populated thin strips extending into an adjacent marginal zone. Such areas appear on Figure 28 as "fingers" of higher density in poorer areas. Also, several areas have much higher densities than might be predicted considering habitat features. Two of these areas are designated "A" and "B" on Figure 28. Area "A", a sparsely vegetated desert region, has higher densities than other similar regions nearby.

Data from the 10 extensively studied sites are presented in Table 15. Sites 4 and 5 are located in the two areas with surprisingly high lizard density. Both have a higher actual density than that predicted by the regression analysis (Table 16).

Figure 29. Physiognomy of ARUBA, Netherlands Antilles. – Ayo terrain = vegetated rolling habitat with huge diorite boulders. These areas have been cultivated for hundreds of years. Fence rows of cactus, shrubs, and stones are common. – Red barren mountains = steep hills, scanty vegetation. Trade winds blow strongly from the sea. Red color results from wearing of limestone into a "karren" habitat. – Coral pavement = flat fossil coral plates.

TABLE 15

ENVIRONMENTAL DATA ON THE SITES CHOSEN FOR STUDY IN ARUBA

SITE NUMBER	1	2	3	4
LIZARD DENSITY PER 100 m^2	7.1	2.3	0.4	0.96
HABITAT TYPE	Dry strand	Wet strand	Desert	Desert
SOIL	Coral sand	Coral sand	Diorite, stony	Diorite, stony
SLOPE	0	0	30	70
% VEGETATION COVER	80	50	25	20
NO. OF VEGETATION SPECIES	3	5	6	5
TYPES OF VEGETATION	*Coccoloba*	*Croton, Cordia*	*Croton,* grasses	*Euphorbia*
RATIO OF BASAL AREA TO FOLIAGE AREA OF VEGETATION	Great	Small	Medium	Medium
VEGETATION STRUCTURE	Complex	Simple evenly spaced	Grass with small shrubs	Small patches
WIND IN M PER SEC. AT 6 CM ABOVE GROUND	0–2	2–3	3–5	3–5
% INSOLATION AT GROUND LEVEL	40	80	99	99
EVAPORATION PER 24 HR IN MM	9	11	18	19

TABLE 16

OBSERVED AND PREDICTED POPULATION DENSITIES OF WHIPTAIL LIZARDS AT 10 SITES ON ARUBA

See text.

	Observed	Predicted
1—	7.1	7.07
2—	2.3	2.30
3—	0.4	0.39
4—	0.96	0.39
5—	0.74	0.24
6—	0.21	0.24
7—	1.10	1.09
8—	5.5	5.5
9—	0.05	0.04
10—	2.4	2.39

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5	6	7	8	9	10
0.74	0.21	1.1	5.5	0.05	2.4
Forrested hills	Forrested hills	Old field	Aloe field	Desert hills	Salt meadow
Diabase, stony	Diabase, stony	Lime, sand, and loam	Lime, sand	Diabase, stony	Wet coral sand
15°	15°	0	0	12.5°	0
50	45	80	70	3	80
11	10	9	8	6	2
Acacia, Cereus, *Prosopis*	*Acacia*, *Pisonia*, Cacti	*Mimosa*, *Acacia*	*Aloe*, *Acacia*	Cactus	*Ruppia*
Medium	Small	Great	Great	Small	—
Complex	Complex	Complex	Complex	Small patches	Simple
0–4	0–4	0	0–3	4+	4+
25	25	30	50	99	20
3	5	16	20	20	0

TABLE 17

RESULTS OF REGRESSION ANALYSIS PERFORMED ON DATA FROM 100 SELECTED SITES AND 10 EXTENSIVELY STUDIED SITES ON ARUBA

See text.

VARIABLE	CUMULATIVE PROPORTION OF VARIENCE REDUCED	CORRELATION COEFFICIENT
Soil	.225	.466
Wind	.340	.571
Slope	.361	.584
Vegetation structure	.374	.590
Soil	.688	.802
Wind	.722	.834
Slope	.831	.854
Interface between vegetation and open	.854	.841
Percentage ground covered by vegetation	.907	.868
Thermal structure	.914	.811
Insolation	.998	.992

PREDATION

Voous (1957) reported that 14% of Aruba's land birds eat whiptails. These include a *Buteo*, two *Falco*, and a small burrowing owl, *Speotyto cunicularia*. I spent many hours watching these predatory birds. Although the birds would often fly low and skim the ground I never saw a lizard taken despite the large numbers of whiptails present in most areas. The density of most predatory birds is low.

One species implicated in predation on whiptails by Voous, a large mockingbird (*Mimus*), is common. Staked animals I quietly watched from a blind were ignored by the mockingbirds. I never saw a mockingbird chase a whiptail.

A rear-fanged snake, *Leptodeira bakeri*, is common on the island and may take juvenile *C. arubensis*. My field observations and examination of six collected snakes suggest that *Anolis* is the most common food for this arboreal serpent.

Of the 94 male lizards collected, 17% had broken or regenerated tails and only 1% of the 72 females had similar damage (95% C.I. = 10–26; 0–8 respectively). I observed nothing to suggest that males are more active or more visible to predators than females. The great difference in the data between the two sexes implies that the damaged tails were a result, not of predation, but probably of intraspecific interactions between males.

THERMAL STRESSES

Animals staked in sunlight at site 1 were able to maintain sublethal body temperatures for at least three hours by behavioral means. In sequence, this procedure involved lifting the forepart of the body off the ground and burying the forelegs into the sand. Sand temperatures in early afternoon of December 10, 1971, were 39°C on the surface; 36°C at 1 mm under surface and 34°C at 5 mm. The lizard would then position its body parallel with the direction of the sunlight and begin to pant. As the stress became extreme, the whiptail extended its cloaca and finally rolled on its back exposing the white belly. The lizards recovered if then released.

FOOD

As detailed elsewhere (SCHALL 1973) *C. arubensis* appears to be an opportunistic herbivore, and plants were available even in the harshest environments. The vegetated, steep hills in the eastern part of Aruba are only sparsely populated by whiptails yet produce large quantities of favored food (berries, new leaves, etc.).

A protein bait (Tuna fish) would often attract large numbers of *C. arubensis*. In other areas the bait was ignored. Attitude toward the bait was independent of lizard density.

Competition for food with other species is probably minor except possibly with the diverse ant community which scavenges effectively.

COMPUTER ANALYSIS

The step-wise regression computed using data from 100 sites selected randomly from the initial survey had only 0.375 of the variance reduced, indicating some important parameters had not been recorded. The computation using data from the ten intensively studied sites resulted in a reduction of 0.998. Probably, all of the important parameters had been recorded at these sites. Table 17 presents some of these results.

The parameters in order of importance were:

Soil quality. Sand and soft loam were optimal. The regression slope is rather steep indicating non-soft ground substrates were marginal. Soil depth did not seem important.

Wind. Any area with a strong wind (4–5 m per sec) at 1 cm above ground was hostile for whiptails. Vegetated areas realized a marked reduction in wind speed below the height of the bushes. Ground level wind velocity in densely populated areas was 0–0.5 m per sec.

Slope. Flat or slightly sloping terrain supported dense lizard populations. Steep slopes of 30° of more had low densities.

Structure of vegetation. Vegetation optimal for high lizard densities was in small, evenly spaced clumps or in fence rows. Agricultural lands provided thin, long rows of vegetation and had some of the highest densities of whiptails. A large proportion of the bush perimeter in this kind of vegetation structure contacted open area. Very high or rather low percentages of cover could be optimal, provided a large interface between shrubs and open areas existed. Very dense vegetation, grassy cover, or bare soil were inadequate habitat for whiptails.

Bushes with a high basal (stem) area compared to foliage area provided more nearly optimal conditions than bushes with small basal diameters. Generally, bushes with small basal areas were arranged individually and provided no thick shelter for the lizards unless they climbed into the foliage.

Thermal structure. Temperatures in the shrubs varied less than temperatures in the open. If all substrate temperatures taken are lumped for each site, those areas with considerable vegetation had a higher variance than unvegetated areas. Thus, thermal diversity was lower in the barren desert (site 6) and the salt meadow (site 10). Thermal diversity in open areas was higher at sites where vegetation was evenly spaced. Shadows being cast, wind eddies, humidity, and roots resulted in higher variance of temperatures in the open at these sites.

Areas similar in structure have similar average temperatures (sites 1 and 2; 3 and 4; 5 and 6; 7 and 8). However, there seemed to be no optimal average environmental temperature. Although correlation between lizard density and lumped temperature variance is weak ($r = 0.152$), areas with diverse mosaic of temperatures seemed to be optimal for higher whiptail densities.

Insolation at ground level. Aruba has extremely clear skies most of the year and sunlight is intense almost every day. Areas with only 30% of the soil receiving ground level insolation had high densities of whiptails provided vegetation structure was optimally arranged. The upper level of insolation is reached when shelter areas do not provide relief from the heat.

DISCUSSION

For purposes of this study, I consider optimum environment as a zone containing a breeding population at relatively high density.

Each of the computed regression curves had a high standard error. This emphasizes the difficulty in defining parameters. However, the very high cumulative reduction of variance in the step-wise regression suggests that all important parameters were measured. I believe my results are at least good approximations of those factors affecting distribution of the lizards.

Based on the maps and the statistical analysis a typical optimal zone for whiptails may be defined as sandy or soft soil in flat terrain, with plentiful vegetation arranged so that there is a high vegetation-open area interface, diverse temperature profile, and weak ground level wind. Examples are sandy cultivated areas with long, thin cactus and bushy fence rows or sandy strand areas with *Cordia* thicket and sea grape (*Coccoloba uvifera*) patches.

Predation probably does not affect the distribution to a measurable degree. RAND (1954) reported that the insular whiptails on Ruatan experienced little predatory pressure. The lack of obvious predators, except *Ameiva,* does not rule out the possibility of severe predator pressure on newly hatched juveniles. The *Ameiva* and mockingbirds may eat young whiptails during hatching periods.

Interspecific competition appears minor. The fairly abundant *Ameiva* on Aruba apparently has little effect on *C. arubensis* (SCHALL 1973). Ants may be effective competitors with *C. arubensis* for available protein resources.

The Aruban whiptails are able to maintain sublethal temperatures in very hot habitats. CASE (1972) found that *Sauromalus* was able to keep body temperatures below lethal upper limits at high ambient temperatures. The climatically related problem for *C. arubensis* is to maintain an optimal temperature. Areas with high thermal variance provided an opportunity for whiptails to maintain a temperature optimal for normal activity.

Availability of food is, of course, important to any species. However, the distribution of *C. arubensis* does not seem fundamentally food limited. Other factors surmount food in determining the optimality of a site. Some areas, as the steep wooded hills, with a large production of favored food may have lower densities of lizards than the sparsely vegetated desert areas with low food production.

BUSTARD (1971) stated that gekkos in Australia may not be limited by food as much as by the availability of home sites. Whiptails on Aruba generally forage in open areas and return to the shrubs to cool. In addition, nighttime burrows are dug only along the perimeter of bushes. Shrubs with a large open area-shrub margin enable the lizards to be always near the shelter and coolness of vegetation. Thus whiptails seem to utilize only the margins of vegetation as living sites.

The two most important factors influencing the distribution of *C. arubensis* are soil and plant structure. Soft, loamy, or sandy soil provides excellent material for digging burrows used as nighttime retreats. Plants, when properly arranged, break the speed of the tradewinds, fracture and soften the soil, increase soil depth with falling leaves, provide a diverse temperature profile, provide hiding places, and perches for staying cool or for watching an area.

Thus, habitat structure and its effect on availability of home sites appears the critical limiting factor for the Aruban whiptail.

Unusually high densities in areas I judged as marginal were all located near more densely populated zones. In some cases, roads provided an opportunity for elements of an optimal habitat such as thin strips of vegetation, soft soil, and flat terrain to invade marginal areas. Other such areas (such as areas "A" and "B" on map) were located near a very large area of optimal zone. The optimal habitat may act as a source area to constantly replenish the meager densities in the less favorable areas. All animal populations are constantly fluctuating as the environment changes in time. In marginal areas, the density may fall to near zero. Such places closest to optimal source areas would benefit from rapid repopulation and might eventually have higer population densites than marginal zones far away from optimal areas.

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