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CHARACTER DISPLACEMENT AND COEXISTENCE IN TWO POECILIID FISHES OF THE GENUS *Poecilia* (*Mollienesia*) FROM HISPANIOLA[1]

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ABSTRACT: Character displacement in animals, particularly in fishes, is reviewed and the new approach of Grant (1975) is used in this study to demonstrate character displacement in *P. hispaniolana* and *P. dominicensis*, two closely related and partly sympatric species of mollies endemic to Hispaniola. Background information is given on the probable origin, evolution, attainment of present partial sympatry and length of coexistence of the two species, as indicated by their present distribution and the paleogeography of Hispaniola. It is hypothesized that a common ancestor to both species existed on the island prior to the Miocene about 20 million years ago. It is also hypothesized that the ancestral population was split during the Miocene-Pliocene for a period of about 18 million years, that the two species evolved during that time, and that the barrier to their dispersal was eliminated in late Pliocene about two million years ago. It is assumed that during that last period the present distribution and partial sympatry were attained, and that the two species have coexisted twice as long in the localities where character displacement shows greater magnitude. Analyses of meristics, morphometrics, and reproduction are given to demonstrate character displacement in fin ray, scale, and gill-raker number, and in body size and fecundity. Divergent, convergent, and parallel displacement were found to occur as well as a change of reproductive strategy for *P. dominicensis* in sympatry. Causes and effects of displacement in the two species are discussed and later summarized in combination with tentative conclusions.

Brown and Wilson (1956) were the first to name and define the concept now currently known as "character displacement." According to these authors, when two closely related species of animals are partly sympatric they are more divergent and easily distinguished where they occur together than where either occurs alone. In other words, species populations show divergence (displacement) where they they occur together and convergence where they do not. Brown and Wilson considered character displacement to be of potential major significance in animal systematics. Subsequently, Mayr (1963) indicated that the phenomenon of character displacement had been previously described by Darwin as "character divergence" and proposed the term "sympatric character divergence." Brown (1964), however, challenged Mayr's interpretation of Darwin's character divergence and suggested that the term "sympatric character divergence" be rejected.

A breakthrough in the interpretation of character displacement was achieved when Grant (1972) redefined the concept in the light of additional evidence as "... the process by which a morphological state of species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively. The antithesis is character release, which can be defined in the same way except that the word absence is substituted for the word presence. Character displacement and character release can be brought together

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under the general term character shift." Grant pointed out that convergence, as well as divergence, may arise between closely related sympatric species and that, according to Brown and Wilson's (1956) interpretation, character displacement is practically synonymous with divergence. He, therefore, proposed that "character displacement," as used previously, be replaced by "divergent character displacement" and its opposite by "convergent character displacement." Grant also pointed out that displacement can conceivably occur without a convergent or divergent result. This prediction is confirmed for one character in the present study, and I propose the term "parallel character displacement" for cases where displacement shows neither divergence nor convergence.

Character displacement apparently occurs widely in many groups of animals but published examples have been based mostly on ants, beetles, crabs, frogs, and especially birds (see Brown and Wilson, 1956 and Grant, 1972, 1975). Hurlbutt (1968) pointed out that, in soil mites, the geographic distribution and variation of most species are too poorly known to detect cases of character displacement. Schoener (1970) discussed size patterns in West Indian *Anolis* lizards in reference to displacement and convergence. In a symposium recently published in the American Zoologist, character displacement was discussed in Devonian trilobites (Eldredge, 1974), in insects (Walker, 1974), in frogs (Blair, 1974), in lizards (Huey and Pianka, 1974), and in fishes (Nursall, 1974). Also in this symposium, Crozier (1974) discussed niche shape and genetic aspects of character displacement by computer simulation.Reproductive and mating-call character displacement were each shown to occur in chorus frogs by Fouquette (1975), and Waage (1975) discussed the potential for character displacement in two species of damselflies. Fagerstrom (1978) discussed the paleobiologic application of character displacement, and Orr and Maple (1978) proposed character displacement as a possible explanation for absorption time differences between populations of salamander larvae.

Only one illustration based on fishes (Centrarchidae) was discussed by Brown and Wilson (1956) and a search of the literature subsequent to that paper has revealed relatively few additional examples of possible character displacement in fishes. Displacement related to courtship preferences in the poeciliid fish *Gambusia* was discussed by Hubbs and Delco (1962). Richards (1963) indicated the possibility of character displacement in one of two partly sympatric darters of the genus *Etheostoma.* Smith (1966) showed that overlap in number of gill rakers is reduced where two partly sympatric species of *Catostomus* occur together. On the negative side, Thomerson (1966) could not demonstrate character displacement in two partly sympatric species of *Fundulus* because of the unstable nature of their syntopic association. Nursall (1974) reviewed character displacement in fishes and noted that ichthyologists largely have ignored this phenomenon. He discussed the families Coregonidae, Cyprinidae, Catostomidae, Gadidae, Gasterosteidae, Poeciliidae, Cichlidae, Cottidae, Periophthalmidae, and Pomacentridae. Nursall, however, presented evidence suggesting the possibility of character displacement only between two forms of *Gasterosteus aculeatus* and among certain species of *Periophthalmus.* Although not specifically referring to it, Echelle *et al.* (1976) presented biochemical evidence indicating the possible occurrence of character displacement between two species of darters of the genus *Etheostoma.* McEachran and Martin (1977) discussed the possible occurrence of character displacement in two sympatric species of skates. Finally, in a recent publication (Rivas, 1978), I mentioned, but did not demonstrate, the possible occurrence of character displacement in the two species of *Poecilia* which are the subject of this study.

As pointed out by Fagerstrom (1978) uncontested examples of character displacement are rare. To my knowledge, no attempt has been made, as yet, to demonstrate character displacement in fishes according to the approach suggested by Grant (1975). By following Grant's principles and methods, divergent, parallel, and convergent character displacement is herein demonstrated to occur between *Poecilia hispaniolana* Rivas and *P. dominicensis* (Evermann and Clark), two closely related and partly sympatric species of poeciliid fishes endemic to the island of Hispaniola.

In a recent publication (Rivas, 1978), *P. hispaniolana* was described as new, *P. dominicensis* was redescribed, and the taxonomic relationship between the two species was treated in detail. Despite their very close relationship, complete reproductive isolation apparently exists between the two species in sympatry because no hybrids were found, at least among adults.

The possibility of character displacement between *P. hispaniolana* and *P. dominicensis* first became apparent after counts were made on series of specimens from all available samples. In addition to meristic character shift, it was noted that, in sympatry, size increased significantly in both species and that fecundity was greater in *P. dominicensis* but not in *P. hispaniolana.*

METHODS AND MATERIALS

This study is based on 4,686 specimens of *Poecilia hispaniolana* and 741 specimens of *P. dominicensis* for a total of 5,427. Although specimens were obtained in 18 localities, adequate samples were collected only in 16. Also not considered in this study are samples corresponding to recent locality records contributed (*in litt.*; Rivas, 1978) by Franz and Thompson, because they are either too small or composed mostly of immature specimens. To avoid repetition of locality descriptions in the text, tables and figures, each of the 16 localities is assigned a number (Table 1). The two localities omitted and the Franz and Thompson records mentioned above are not numbered but they are shown in Figure 1. Also, to conform with the distribution of steam systems and the allopatric and sympatric distribution of the two species, the numbering sequence begins in the southern drainage with the Rio Yaque del Sur system and continues clockwise around the island. The material from all 18 localities mentioned above, its source, and its disposition were recently described in detail by me (Rivas, 1978). The elevations of collecting localities are expressed in meters and were determined with an aneroid altimeter.

The characters analyzed in this study are limited to those found to show interspecific differences that can be expressed quantitatively. After study and comparison of the two species the number of dorsal, pectoral and branched caudal rays, number of lateral scales, number of gill rakers, fecundity, and body size were found to be the most suitable characters. Secondary sexual and trophic characters also were examined but no quantitatively expressible differences, except the number of gill rakers, were found. There may be other usable subtle characters but these, if they exist, have so far escaped my detection.

All the specimens in each of the 16 samples analyzed were counted and separated into immature and adult in-

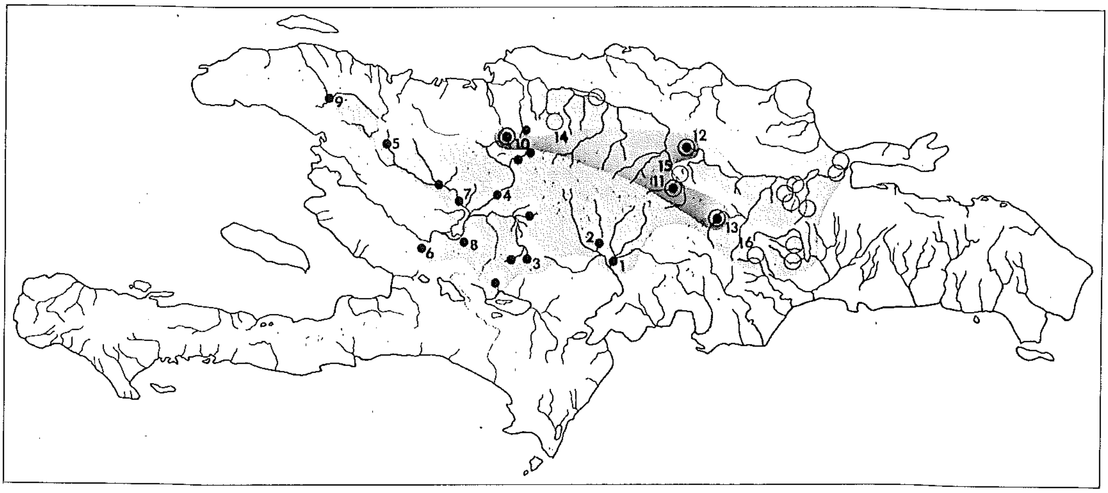

Figure 1. Geographic distribution (light shade) of *Poecilia hispaniolana* (black dots) and *P. dominicensis* (open circles). Black dots inside open circles indicate localities where both species were collected together (syntopic). Approximate area of sympatry is shown in dark shade. See Table 1 for locality descriptions.

dividuals. Adult males were determined as those having a fully developed gonopodium, regardless of body size. Adult females were selected by determining the smallest specimen bearing eggs and all those of the same size and larger were considered adults.

Counts were made in the manner recently described by me (Rivas, 1978). Only adults were used in the analyses of meristic characters and 36 or more specimens were selected from each sample, except when the total number of adults in the sample was less than 36.

Body size is expressed as the standard length measured to the nearest millimeter. All the adult males and females from each sample were used for this character.

All collections were made by the author with a 30′ x 4′ standard minnow seine of 1/4″ mesh. At each locality, as

Table 1. Description of the 16 localities where adequate samples of *Poecilia hispaniolana* and/or *P. dominicensis* were collected on the Island of Hispaniola (also see text and Fig. 1).

No.	Locality description (D.R.) = Dominican Republic (H) = Haiti	Date
1	Rio Yaque del Sur NW of Villarpando, Prov. Azua (D.R.)	4/21/49
2	Rio Mijo at Sabana Alta, Prov. San Juan (D.R.)	4/21/49
3	Rio Vallejuelo at El Cercado, Prov. San Juan (D.R.)	4/21/49
4	Rio Artibonito at Pedro Santana, Prov. Elias Pina (D.R.)	4/22/49
5	Stream W of St. Michel de l'Atalaye, Dept. Artibonite (H)	4/10/51
6	Riviere La Tombe SW of Mirebalais, Dept. de l'Ouest (H)	4/11/51
7	Riviere Guayamouc at Hinche, Dept. Artibonite (H)	4/10/51
8	Riviere Los Pine N of Lascahobas, Dept. de l'Ouest (H)	4/11/51
9	Riviere Trois Rivieres S of Gros Morne, Dept. de l'Ouest (H)	4/09/51
10	Rio Massacre at Loma de Cabrera, Prov. Dajabon (D.R.)	4/22/49
11	Rio Yaque del Norte at Jarabacoa, Prov. La Vega (D.R.)	4/24/49
12	Rio Camu W of La Vega, Prov. La Vega (D.R.)	4/24/49
13	Rio Yuna at Bonao, Prov. La Vega (D.R.)	4/24/49
14	Rio Tomines at Sabaneta, Prov. Rodriguez (D.R.)	4/23/49
15	Rio Jimenoa NE of Jarabacoa, Prov. La Vega (D.R.)	4/24/49
16	Rio Haina NW of Villa Altagracia, Prov. S. Cristobal (D.R.)	4/24/49

many seine sweeps as necessary were made to fill (snugly) with poeciliid fishes a quart jar containing 10% formalin. Because of time limitations, not more than one hour was spent at each collecting site. At the end of this self-imposed period, collecting was terminated regardless of whether or not the one jar quota had been filled. No attempt was made to obtain more specimens of any one of the species detected and/or discard others; and all specimens, large and small, were preserved. The sampling, therefore, was purposely random at each locality. Furthermore, *Peocilia hispaniolana* and *P. dominicensis* were not recognized as distinct in the field.

Analysis, presentation, and interpretation of the data were conducted according to the approach and methods proposed by Grant (1972, 1975). In the present paper, however, only the approach of comparing sequentially adjacent populations (samples) has been employed. This method is more suitable to the geographic relationships between the two species and, besides, it is not dependent on any irregularity in allopatry.

As a background to the subsequent discussions of character displacement the various subjects concerning distribution, origin, habitat, coexistance, etc. are presented first. Some of these subjects already have been outlined in a previous study (Rivas, 1978) but not in the detail required for the purposes of this paper. Following the background sections, the characters analyzed are each discussed in separate sections followed in turn by a section on discussion and a final section on summary and conclusions.

GEOGRAPHIC DISTRIBUTION, ORIGIN AND EVOLUTION

P. hispaniolana and *P. dominicensis* appear to be confined to the highlands of Hispaniola, excluding the southwest peninsula (Fig. 1). The species are syntopic, that is, they both coexist in the same habitat, in four localities representing a central area of sympatry. *P. hispaniolana* occurs allopatrically westward of the area of sympatry and *P. dominicensis* to the east. It may be inferred, therefore, from their present geographic distribution and close relationship, that the two species evolved allopatrically from the same common ancestor. In the subsequent process of dispersal toward each other, the two species overlapped their ranges and became partly sympatric. This hypothesis is supported by the paleogeography of Hispaniola as recently outlined by Maurrasse (1981) who has kindly provided additional information.

According to Maurrasse (pers. comm.) the present combined range of both species occupies the portion of Hispaniola which was once divided into two islands throughout the Miocene and most of the Pliocene. One of these islands, herein referred to as the northern island, is now represented by the portion of Hispaniola north of the Rio Yaque del Norte — Rio Yuna valleys which form the graben running WNW from Samana Bay to the Bay of Monte Cristi. The other island is now represented by the central highlands and is herein referred to as the central island. In turn, this central island was separated from the rest of Hispaniola, to the SW, by the present graben which runs NW from Ocoa Bay through the Artibonite Valley to the Gulf of Gonave. The two islands were split apart in late Oligocene, remained separated by an arm of the sea for a period of 15 to 20 million years, and were again rejoined not more than two million years ago.

It is possible, therefore, that the common ancestor was extant at least 17 to 22 million years ago, that the original ancestral population was split and evolved into the present two species during a

15 to 20 million-year period, and that the present partial sympatry was attained during the last two million years. The present distributional pattern and the paleogeography described above indicate that *Poecilia hispaniolana* evolved on the central island and *P. dominicensis* on the northern island.

A model summarizing the hypothetical origin, evolution, and attainment of the present geographic distribution of the two species is given in Figure 2. It appears that *P. hispaniolana* and *P. dominicensis* represent an example of vicariant speciation followed by dispersal.

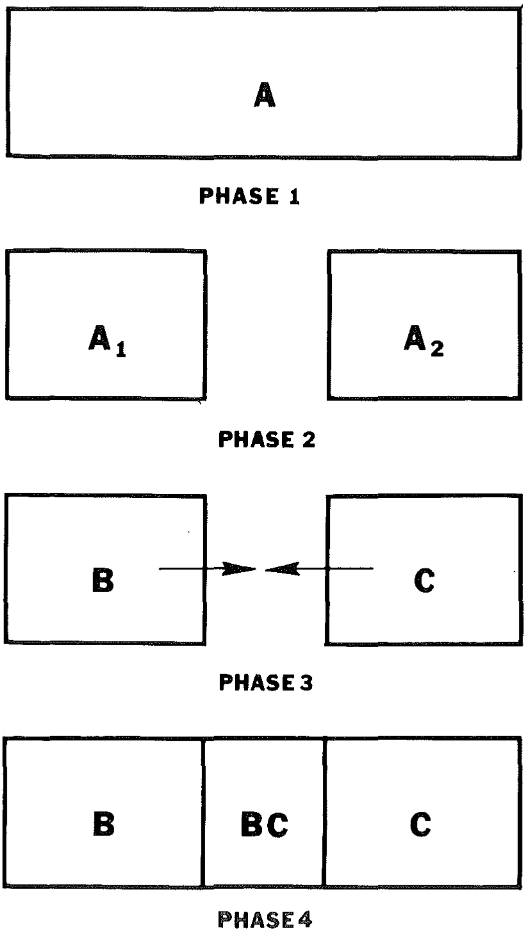

Figure 2. Model of origin, evolution, and geographic distribution of *Poecilia hispaniolana* and *P. dominicensis*. Phase 1. Original range of common ancestor A. Phase 2. Fragmentation of original range giving rise to two allopatric populations A_1 and A_2. Phase 3. Populations A_1 and A_2 each evolves allopatrically into species B (*P. hispaniolana*) and C (*P. dominicensis*). The newly evolved species begin to disperse toward each other's range. Phase 4. The gap is closed, the two ranges overlap, and the two species become partly sympatric.

ALTITUDINAL DISTRIBUTION AND HABITAT

In the area of allopatry the altitudinal range for *P. hispaniolana* is 250 to 732 m with a mean of 464 and, for *P. dominicensis*, 30 to 323 m with a mean of 194. In the area of sympatry the elevation ranges from 91 to 579 with a mean of 328 which is about intermediate between the mean elevations in the areas of allopatry.

As would be expected from their altitudinal distribution, *P. hispaniolana* and *P. dominicensis* differ in their habitat. My field observations show that for *P. hispaniolana*, in its area of allopatry, the water was shallow and clear, the current fast, and the bottom was composed of rock, stones, gravel, and sand (Fig. 3A). For *P. dominicensis*, in its area of allopatry, the water was deeper and slightly turbid, the current sluggish, and the bottom was mostly muddy with some sand (Fig. 3C). In the area of sympatry, where both species were collected together, the habitat was a combination of deep and shallow water, fast and slow current, and muddy and rocky bottom (Fig. 3B).

LENGTH OF COEXISTENCE

It is reasonable to assume that, within the area of sympatry, coexistence of the two species may have lasted longer in localities 11 and 12 than in 10 and 13, as further implied by the model in Figure 4. This model is an expansion of, and complements the model in Figure 2, on the basis of a more detailed sequence of events and a more detailed application of the chronology discussed in the preceding section. The model in Figure 4 also

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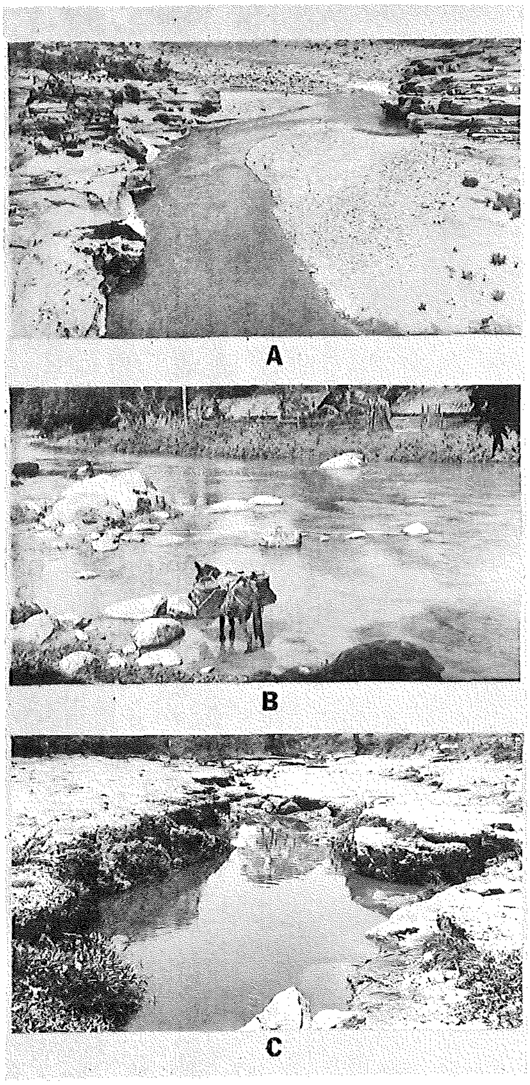

Figure 3. Typcial habitats of *Poecilia hispaniolana* and *P. dominicensis* in allopatry and sympatry. A. Rio Yaque del Sur looking northeast from bridge 3 km northwest of Villapando, Province of Azua, Dominican Republic (locality No. 1) where *P. hispaniolana* occurs allopatrically. Elevation 264 m. Water very clear and shallow, current fast, and bottom composed of rock, gravel, and sand. B. Rio Yaque del Norte at Jarabacoa, Province of La Vega, Dominican Republic (locality No. 11) where both species occur syntopically. Elevation 220 m. Water not very clear, riffles alternating with very slow flow, and bottom composed of sand and mud. C. Rio Tomines at Sabaneta, Province of Rodriguez, Dominican Republic (locality No. 14) where *P. dominicensis* occurs allopatrically. Elevation 138 m. Water relatively turbid and deep, current very sluggish, and bottom muddy.

implies that, probably, *P. hispaniolana* had occupied locality 10 long before the arrival there of *P. dominicensis* and, conversely, that the latter had occupied locality 13 long before the arrival there of *P. hispaniolana*. If length of coexistence is a function of the magnitude of character displacement, as it probably is, it may therefore be expected that displacement should manifest itself more strongly in localities 11 and/or 12 and less so, or not at all, in localities 10 and 13, as further confirmed by the following evidence. Subsequent sections of this study show that of 22 cases of character displacement for both species combined, only one (4.5%) reaches its greatest magnitude in locality 10 and four (18,2%) in locality 13. In locality 11, however, greatest magnitude is reached by seven characters (31.8%) and by 10 (45.5%) in locality 12.

Absence of a significant character shift in localities 10 and/or 13 would not necessarily preclude the occurrence of character displacement because *P. dominicensis* and *P. hispaniolana* as suggested by the data could be relatively recent arrivals in these localities. Grant (1975) stated that character displacement is detected by a discontinuity in character states between populations on either side of the allopatry-sympatry boundary, or "zone boundary" (localities 9 and 10 and 13 and 14 in this case). In view of the evidence presented above, however, Grant's statement may not strictly apply in this study.

CHARACTER EVALUATION

Dorsal Rays

Although the number of dorsal rays ranges from 7 to 9 in both species, the mean, in allopatry, is 8.0 in *Poecilia hispaniolana* and 7.9 in *P. dominicensis* (Table 2, Fig. 5). In *P. hispaniolana* there are no significant differences, in allopatry, among the means of the nine locali-

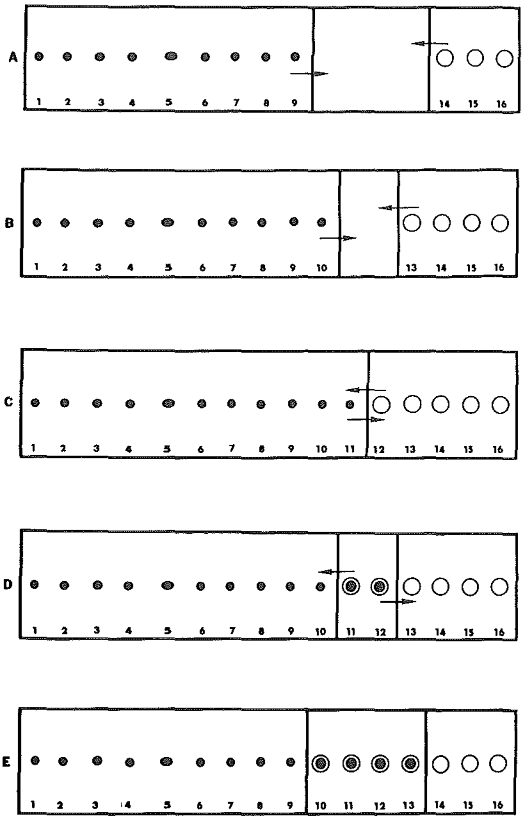

Figure 4. Model of hypothesized duration of coexistence in *Poecilia hispaniolana* (solid dots) and *P. dominicensis* (open circles). A constant rate of dispersal is assumed for both species and the duration of 400,000 years between stages and the total of 2,000,000 years are based on the chronology described in the text. A. Allopatric stage 2,000,000 to 1,600,000 years ago. Both species are dispersing toward each other and the present sympatric localities 10, 11, 12 and 13 are not yet occupied by either. B. Second allopatric stage 1,600,000 to 1,200,000 years ago. Both species continue to disperse toward each other and the gap between their ranges has narrowed. *P. hispaniolana* occupies locality 10 and *P. dominicensis* occupies locality 13. C. Range-contact stage 1,200,000 to 800,000 years ago. Both species continue to disperse toward each other and the gap is closed. *P. hispaniolana* has now reached locality 11 and *P. dominicensis* has reached locality 12. Neither range overlap nor sympatry has yet occurred and the species are now parapatric. D. First sympatric stage 800,000 to 400,000 years ago. Both species continue to disperse in opposite directions and partial sympatry is achieved. *P. hispaniolana* reaches locality 12, *P. dominicensis* reaches locality 11, and coexistence occurs for the first time at these two localities. E. Actual partly sympatric stage 400,000 years ago to present. Both species now coexist in all four localities 10, 11, 12, and 13 but they have coexisted twice as long in localities 11 and 12.

ties. In allopatry, therefore, the number of dorsal rays for *P. hispaniolana* does not show clinal variation and the prediction would be a mean of 8.0 rays in the area of sympatry. This is not so, however, because, as shown in Figure 5, the mean for localities 10 through 13 combined is 8.1 which is significantly higher than the mean of 8.0 for localities 1 through 9 combined. Furthermore, the mean for locality 12 is 8.5 which is very significantly higher than in any of the other localities where *P. hispaniolana* occurs. In allopatry, the number of dorsal rays in *P. dominicensis* shows a trend toward clinal variation and the prediction would be a mean of fewer than 8.0 rays in the area of sympatry. The

Table 2. Comparison of number of dorsal rays among samples of *Poecilia hispaniolana* and *P. dominicensis* in their areas of allopatry and sympatry.

Local. No.	N	Range	X	S.D.	S.E.
			Poecilia hispaniolana		
			ALLOPATRY		
1	35	8 — 9	8.0	0.17	0.03
2	35	8 — 9	8.1	0.28	0.05
3	24	8	8.0	0.00	0.00
4	12	8	8.0	0.00	0.00
5	36	7 — 9	8.0	0.22	0.03
6	36	7 — 9	8.0	0.28	0.04
7	46	7 — 8	7.9	0.33	0.04
8	36	8 — 9	8.0	0.17	0.03
9	24	7 — 9	7.8	0.52	0.10
Totals:	284	7 — 9	8.0	0.28	0.02
			SYMPATRY		
10	36	8 — 9	8.0	0.17	0.03
11	44	8	8.0	0.00	0.00
12	24	8 — 9	8.5	0.50	0.10
13	36	8 — 9	8.1	0.28	0.05
Totals:	140	8 — 9	8.1	0.32	0.03
			Poecilia dominicensis		
			SYMPATRY		
10	28	8 — 9	8.0	0.17	0.03
11	21	7 — 8	8.0	0.20	0.04
12	19	7 — 9	8.0	0.32	0.07
13	33	7 — 8	7.9	0.32	0.05
Totals:	101	7 — 9	8.0	0.28	0.03
			ALLOPATRY		
14	36	7 — 8	7.8	0.41	0.06
15	21	7 — 8	7.9	0.35	0.07
16	47	8 — 9	8.0	0.14	0.02
Totals:	104	7 — 9	7.9	0.33	0.03

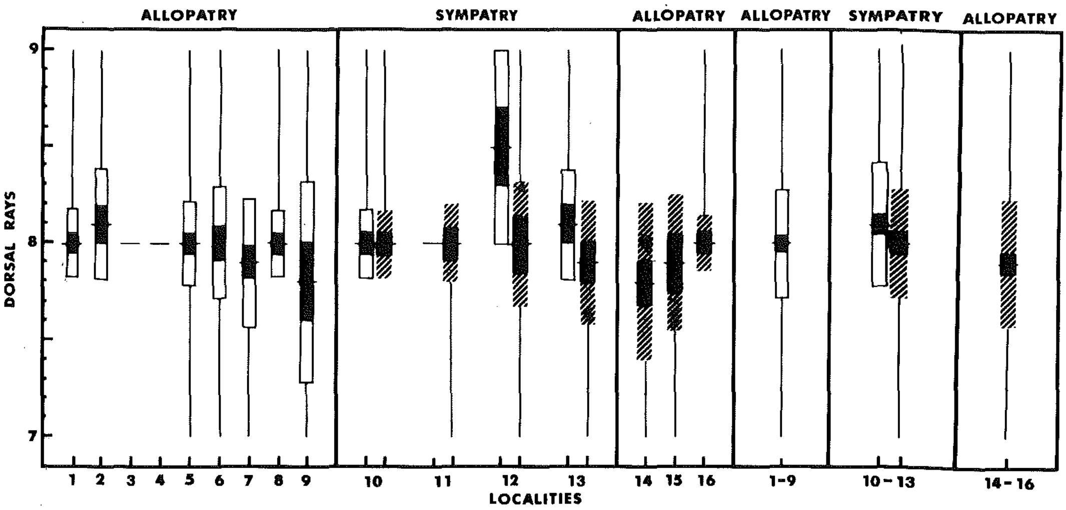

Figure 5. Comparison of number of dorsal rays among samples of *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Because of the character overlap the two species are shown side by side in the area of sympatry. The last three boxes on the right represent the combined samples for each species in the areas of allopatry and sympatry. In each bar diagram the horizontal line indicates the mean, the solid bar represents two standard errors on each side of the mean, and the open vertical bar (dashed in *P. dominicensis*) represents one standard deviation on each side of the mean. The central vertical line represents the total range of the counts. Based on Table 2.

mean in sympatry, however, is 8.0 for localities 10, 11, and 12; it is 7.9 for 13, and 8.0 for all four localities combined.

It may be concluded from the above that shift toward a higher number of dorsal rays appears to have occurred in both species in the area of sympatry. This is particularly true of *P. hispaniolana* in locality 12, in accordance with the already made prediction that character displacement would manifest itself more strongly in localities 11 and/or 12 (see preceding section). Because the shift of 0.1 ray (10%) is the same and in the same direction in both species, there is neither convergence nor divergence and, therefore, parallel character displacement seems to have occurred. This type of character displacement corresponds to category number 12 of Grant (1972).

Pectoral Rays

The number of pectoral rays shows a well marked difference between *Poecilia hispaniolana* and *P. dominicensis* throughout the areas of allopatry and sympatry (Table 3, Fig. 6). For this character, variation is greater in *P. hispaniolana* which has 14 to 17 rays, whereas in *P. dominicensis* the range is 13 to 15.

For *P. hispaniolana,* in allopatry, the means of localities 1, 2, and 3 do not differ significantly among themselves but they are higher and significantly different from the means of 4, 5, 6, and 7 which, in turn, of not differ among themselves. The mean of locality 8 does not differ significantly from the means of 1, 2, and 3 and that of 9 does not differ significantly from the means of localities 4, 5, 6 and 7. In allopatric *P. hispaniolana* this character does not show clinal variation, at least for localities 4 through 9, and the prediction would be a mean of 14.9 rays in the area of sympatry. In sympatry, however, the mean for localities 10 through 13 combined is 15.4 which is significantly higher than the mean of 15.0 for the combined allopatric localities 1 through 9. Also, the mean of 15.8 for localities 11 and 12 is very significantly much higher than in any of the other localities where *P. hispaniolana* occurs.

In allopatry, there is no significant

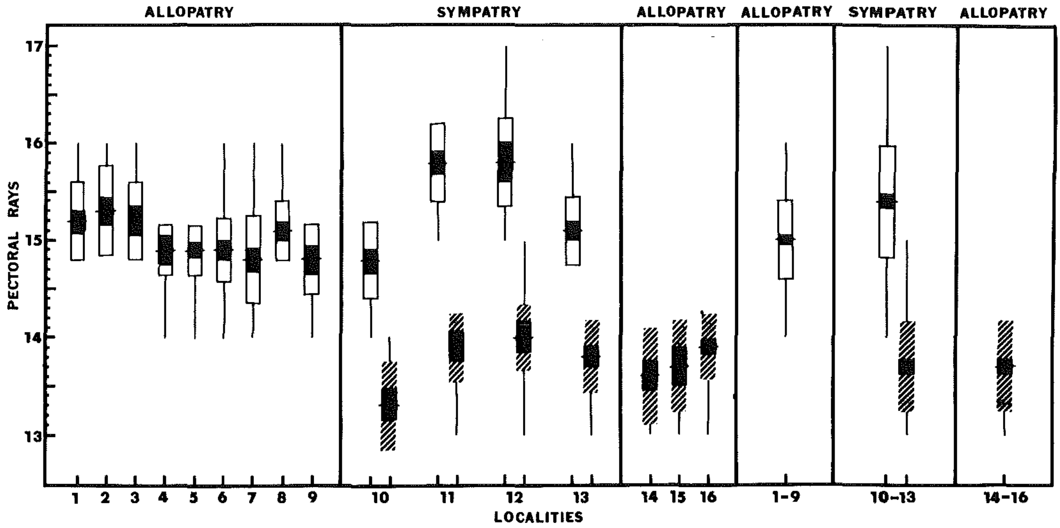

Figure 6. Comparison of number of pectoral rays among samples of *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Rest of legend as in Figure 5. Based on Table 3.

Table 3. Comparison of number of pectoral rays among samples of *Poecilia hispaniola* and *P. dominicensis* in their areas of allopatry and sympatry.

Local. No.	N	Range	X	S.D.	S.E.
		Poecilia hispaniolana			
		ALLOPATRY			
1	35	15 — 16	15.2	0.40	0.06
2	35	15 — 16	15.3	0.47	0.07
3	24	15 — 16	15.2	0.40	0.08
4	12	14 — 15	14.9	0.26	0.07
5	36	14 — 15	14.9	0.26	0.04
6	36	14 — 16	14.9	0.33	0.05
7	46	14 — 16	14.8	0.46	0.06
8	36	15 — 16	15.1	0.30	0.05
9	24	14 — 15	14.8	0.37	0.07
Totals:	284	14 — 16	15.0	0.41	0.02
		SYMPATRY			
10	36	14 — 15	14.8	0.39	0.06
11	44	15 — 16	15.8	0.41	0.06
12	24	15 — 17	15.8	0.47	0.09
13	36	15 — 16	15.1	0.35	0.05
Totals:	140	14 — 17	15.4	0.58	0.04
		Poecilia dominicensis			
		SYMPATRY			
10	28	13 — 14	13.3	0.45	0.08
11	21	13 — 14	13.9	0.34	0.07
12	19	13 — 15	14.0	0.32	0.07
13	33	13 — 14	13.8	0.37	0.06
Totals:	101	13 — 15	13.7	0.47	0.04
		ALLOPATRY			
14	36	13 — 14	13.6	0.49	0.08
15	21	13 — 14	13.7	0.47	0.10
16	47	13 — 14	13.9	0.33	0.04
Totals:	104	13 — 14	13.7	0.45	0.04

difference for *P. dominicensis* in the mean number of pectoral rays between localities 14 and 15 and between localities 15 and 16. There is no clear cut clinal trend, therefore, and the prediction would be a mean of 13.7 in the area of sympatry. Because, in sympatry, the mean is also 13.7 for all the four localities combined, no character shift is apparent for the number of pectoral rays in *P. dominicensis.* In addition, there is no significant difference among the means of localities 11, 12 and 13.

From the above, it may be concluded that a shift toward a higher number of pectoral rays appears to have occurred in *P. hispaniola,* but not in *P. dominicensis,* in the area of sympatry. The much higher means for *P. hispaniolana* in localities 11 and 12 again confirm the prediction that character displacement would manifest itself more strongly in these localities. Character displacement of number of pectoral rays, therefore, has occurred in *P. hispaniolana* in the form of divergence away from *P. dominicensis* whose character state has not changed. This type of character displacement corresponds to category number 8 of Grant (1972).

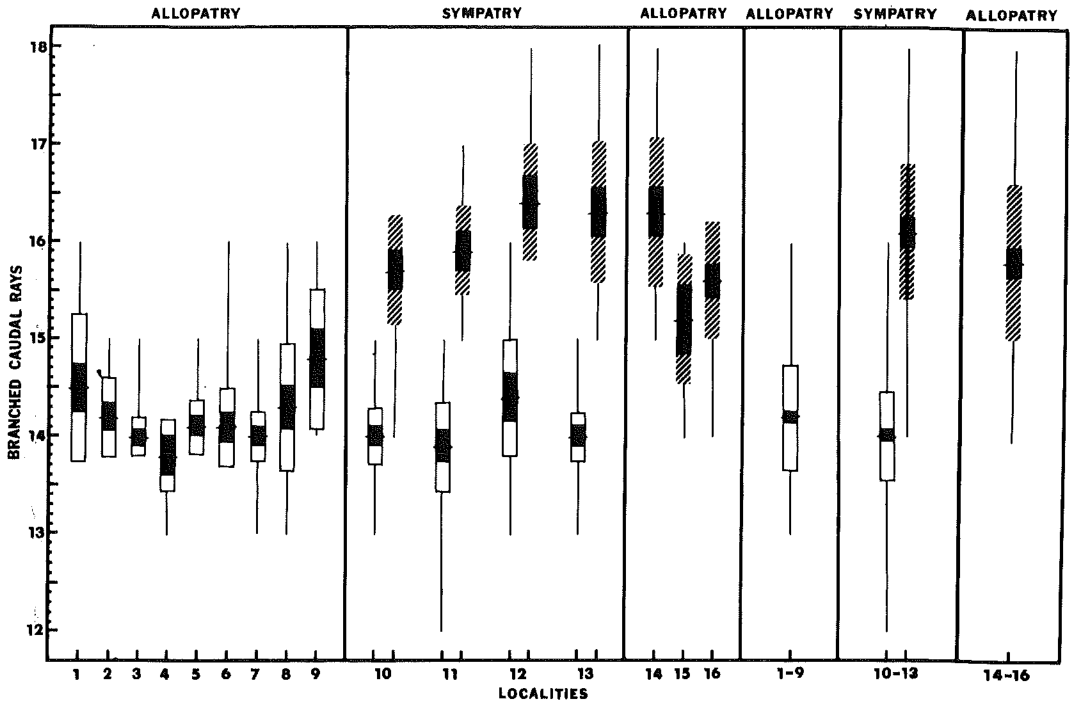

Figure 7. Comparison of number of branched caudal rays among samples of *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Rest of legend as in Figure 5. Based on Table 4.

Branched Caudal Rays

Poecilia hispaniolana and *P. dominicensis* differ very significantly in the number of branched caudal rays in allopatry as well as in sympatry (Table 4, Fig. 7). The range is 12 to 16 in *P. hispaniolana* and 14 to 18 in *P. dominicensis.*

In allopatric *P. hispaniolana*, as shown in Figure 7, the bar diagram is broadly U-shaped and yields a mean of 14.2 for localities 1 through 9 combined. In the area of sympatry, the mean for localities 10 through 13 combined is 14.0, which is significantly lower than the allopatric mean of 14.2. The upward trend shown by localities 7, 8, and 9 predicts, for the area of sympatry, a mean of well above 15.0 for each of the four sympatric populations. The actual means, however, are 14.0, 13.9, 14.4, and 14.0 for localities 10, 11, 12, and 13, respectively. Also, in the area of sympatry, the means of localities 10, 11, and 13 are not significantly different and that of 12 is significantly above, but not too far from the means of the other three. It appears, therefore, that an abrupt, well-marked downward shift in number of branched caudal rays has occurred in *P. hispaniolana* across the allopatry-sympatry zone boundary.

In allopatric *P. dominicensis,* there is no significant difference between the means for localities 15 and 16. The mean of 16.3 is significantly much higher for locality 14 but no trend permitting even a speculative prediction is discernible. Furthermore, there are no significant differences between the mean of locality 14 and those of 13, 12, and 11 across the zone boundary. No marked character shift has occurred, therefore, across the zone boundary. However, the 16.1 mean for sympatry differs significantly from the 15.8 mean for allopatry thereby indicating in *P. dominicensis*, the possibility of a moderate upward shift of branched caudal ray number in the area of sympatry.

Table 4. Comparison of number of branched caudal rays among samples of *Poecilia hispaniolana* and *P. dominicensis* in their areas of allopatry and sympatry.

Local. No.	N	Range	X	S.D.	S.E.
		Poecilia hispaniolana			
		ALLOPATRY			
1	35	14 — 16	14.5	0.74	0.13
2	35	14 — 15	14.2	0.40	0.07
3	24	14 — 15	14.0	0.20	0.04
4	12	13 — 14	13.8	0.37	0.11
5	36	14 — 15	14.1	0.28	0.05
6	36	14 — 16	14.1	0.39	0.07
7	46	13 — 15	14.0	0.26	0.04
8	36	13 — 16	14.3	0.65	0.11
9	24	14 — 16	14.8	0.72	0.15
Totals:	284	13 — 16	14.2	0.54	0.03
		SYMPATRY			
10	36	13 — 15	14.0	0.28	0.05
11	44	12 — 15	13.9	0.46	0.07
12	24	13 — 16	14.4	0.60	0.12
13	36	13 — 15	14.0	0.24	0.04
Totals:	140	12 — 16	14.0	0.45	0.03
		Poecilia dominicensis			
		SYMPATRY			
10	28	14 — 16	15.7	0.54	0.10
11	21	15 — 17	15.9	0.46	0.10
12	18	16 — 18	16.4	0.60	0.14
13	33	15 — 18	16.3	0.72	0.12
Totals:	100	14 — 18	16.1	0.69	0.07
		ALLOPATRY			
13	36	15 — 18	16.3	0.77	0.12
15	14	14 — 16	15.2	0.67	0.17
16	47	14 — 16	15.6	0.61	0.08
Totals:	97	14 — 18	15.8	0.79	0.08

It may be concluded from the above that a shift toward a lower number of branched caudal rays has occurred in *P. hispaniolana* and a shift toward a higher number has occurred in *P. dominicensis* in the area of sympatry. The prediciton, however, that character displacement would manifest itself more strongly in localities 11 and/or 12 is not confirmed by this character. Character displacement of number of branched caudal rays, therefore, probably has occurred in both species in the form of divergence away from each other. This type of character displacement corresponds to category number of 2 of Grant (1972).

Lateral scales

There is a significant difference in the number of lateral scales between *Poecilia hispaniolana* and *P. dominicensis* throughout their entire geographic distribution. The range is 27 to 30 for *P. hispaniolana* and 26 to 29 for *P. dominicensis* (Table 5, Fig. 8).

In allopatric *P. hispaniolana* this character does not show clinal variation and the prediction would be a mean of 28.1 scales in the area of sympatry. In sympatry, however, the mean for localities 10 through 13 combined is 28.3 which is significantly higher than the mean of 28.1 for the combined allopatric localities 1 through 9. Also, in the area of

Table 5. Comparison of number of lateral scales among samples of *Poecilia hispaniolana* and *P. dominicensis* in their areas of allopatry and sympatry.

Local. No.	N	Range	X	S.D.	S.E.
		Poecilia hispaniolana			
		ALLOPATRY			
1	35	27 — 29	28.0	0.50	0.08
2	35	27 — 29	28.1	0.67	0.11
3	24	28 — 29	28.2	0.41	0.08
4	12	28 — 29	28.2	0.35	0.10
5	36	27 — 30	28.1	0.63	0.11
6	36	27 — 29	27.8	0.62	0.10
7	46	27 — 29	28.0	0.51	0.08
8	36	27 — 29	28.0	0.29	0.05
9	24	27 — 30	28.3	0.61	0.12
Totals:	284	27 — 30	28.1	0.55	0.03
		SYMPATRY			
10	36	27 — 29	28.0	0.50	0.08
11	44	27 — 30	28.4	0.61	0.09
12	24	28 — 30	28.5	0.64	0.13
13	36	27 — 29	28.4	0.54	0.09
Totals:	140	27 — 30	28.3	0.60	0.05
		Poecilia dominicensis			
		SYMPATRY			
10	28	26 — 28	27.0	0.32	0.06
11	21	26 — 28	27.0	0.37	0.08
12	19	27 — 28	27.1	0.22	0.05
13	33	26 — 28	27.2	0.44	0.07
Totals:	101	26 — 28	27.1	0.36	0.03
		ALLOPATRY			
14	36	26 — 29	27.3	0.61	0.10
15	21	26 — 28	27.1	0.42	0.09
16	47	27 — 28	27.3	0.46	0.07
Totals:	104	26 — 29	27.3	0.52	0.05

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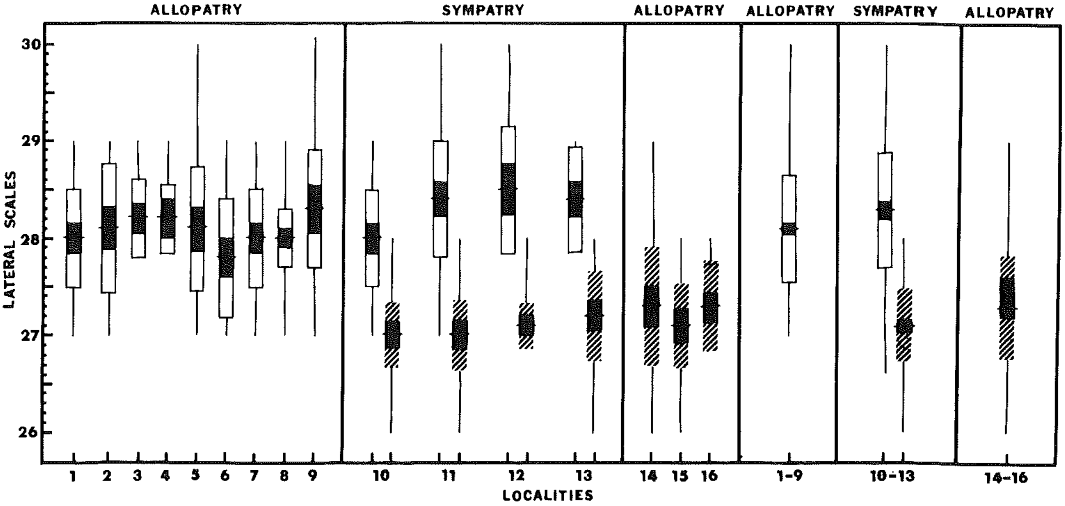

Figure 8. Comparison of number of lateral scales among samples of *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Rest of legend as in Figure 5. Based on Table 5.

sympatry, the means for localities 11, 12, and 13, are significantly higher than the means for localities 1, 6, 7, and 8 which represent 44 percent of the allopatric area. Furthermore, although not significantly so, the mean of 28.5 for sympatric locality 12 is higher than in any of the other localities throughout the geographic range of *P. hispaniolana*.

In allopatry, there is no significant difference for *P. dominicensis* in the mean number of lateral scales among localities 14, 15, and 16. There is no clinal variation, therefore, and the prediction would be a mean of 27.3 in the area of sympatry. In sympatry, however, the mean of 27.1 for localities 10 through 13 combined is significantly lower than the mean of 27.3 for the combined allopatric localities 14, 15, and 16.

It appears from the above that, in the area of sympatry, there are indications of a shift toward a higher number of lateral scales in *P. hispaniola* and a shift toward a lower number in *P. dominicensis*. The prediction, however, that the shift would be more obvious in localities 11 and/or 12 is not confirmed by this character. There is indication, therefore, but not absolute proof, that character displacement of number of lateral line scales may have occurred in both species, in the form of divergence away from each other. This type of character displacement corresponds to category number 2 of Grant (1972).

Meristic character index

In order to reduce or eliminate overlap between the two species and at the same time, summarize the trend of all meristic characters combined, I developed a character index similar to that described by Hubbs and Whitlock (1929). This index represents a composite of the differential meristic features between *Poecilia hispaniolana* and *P. dominicensis* and is hereafter referred to as the "meristic character index" (Table 6, Fig. 9). As pointed out by Hubbs (1936) a character index combines into one figure the measurable characteristics of a population. In this manner, the variation of each single character is smoothed out in the combination and each character is given equal weight. In this study, the count which is low in one species (*P. dominicensis*) is subtracted from the combined counts which are high in the other (*P. hispaniolana*). For each speci-

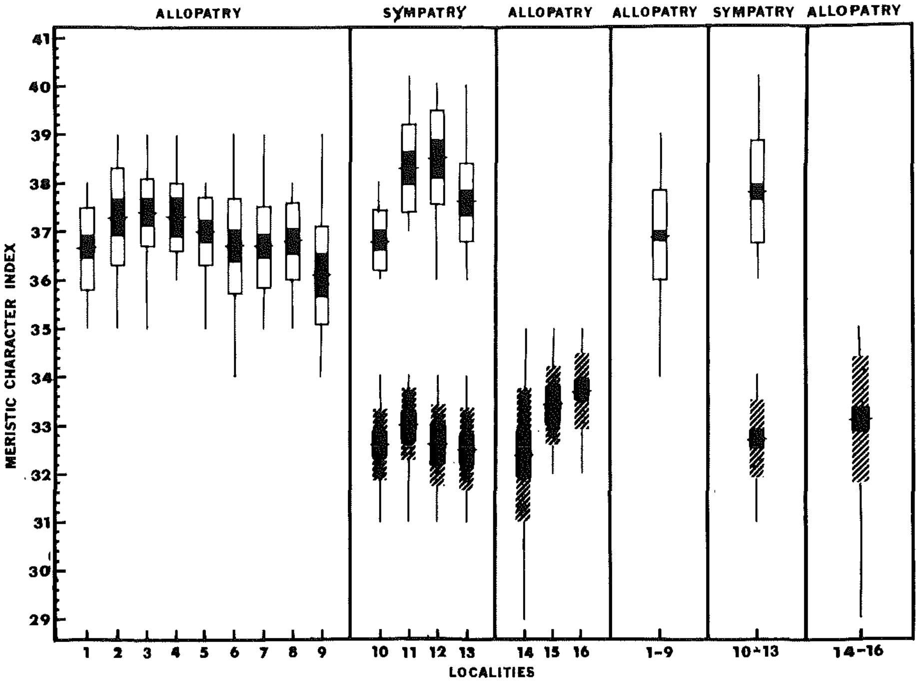

Figure 9. Comparison of meristic character index (sum of dorsal rays, pectoral rays, and lateral scales minus branched caudal rays) among samples of *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Rest of legend as in Figure 5 except that the two species are shown along the same axis in the area of sympatry because of the absence of overlap. Based on Table 6.

men, therefore, the meristic character index is the result of subtracting the number of branched caudal rays from the sum of the number of dorsal rays, pectoral rays, and lateral scales. This method is mathematically sound because both species are treated according to the same formula. The number of gill rakers, because it is a trophic character and the only character showing convergence, is discussed separately is the next session.

As shown in Table 6 and Figure 9 not only the overlap is eliminated in sympatry but a wide gap results. In allopatry, the overlap is much reduced and variation is smoothed out throughout the range of both species. The meristic character index shows a greater difference between the two species than any of the characters taken singly. The meristic character index also shows that, in both species, variation is much reduced in the area of sympatry. In sympatry, variation is reduced by 20 percent in *P. hispaniolana* and by 50 percent in *P. dominicensis.*

For *P. hispaniolana*, in allopatry, the index means of localities 3 through 9 show a downward trend suggesting clinal variation. This trend predicts a mean of 36, or less, in the area of sympatry. In sympatry, however, the mean for localities 10 through 13 combined is 37.8 which is significantly higher than the predicted mean and the 36.9 mean for all combined localities in allopatry. Also the 38.3 and 38.5 means for localities 11 and 12, respectively, are significantly higher than those for all other localities where *P. hispaniolana* occurs. An abrupt upward shift across the zone boundary is shown by locality 10, as compared with adjacent locality 9 and with the trend shown by localities 3 through 9.

In allopatry, for *P. dominicensis*, the index means of localities 14, 15, and 16 show a downward trend suggesting clinal

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Table 6. Comparison of meristic character index (sum of dorsal rays, pectoral rays, and lateral scales minue branched caudal rays) among samples of *Poecilia hispaniolana* and *P. dominicensis* in their areas of allopatry and sympatry.

Local. No.	N	Range	X	S.D.	S.E.
		Poecilia hispaniolana			
		ALLOPATRY			
1	35	35 — 38	36.7	0.81	0.13
2	35	35 — 39	37.3	1.03	0.17
3	24	36 — 39	37.4	0.69	0.14
4	12	36 — 39	37.3	0.72	0.20
5	36	35 — 38	37.0	0.69	0.11
6	36	34 — 39	36.7	0.97	0.16
7	46	35 — 39	36.7	0.84	0.12
8	36	35 — 38	36.8	0.81	0.13
9	24	34 — 39	36.1	1.13	0.23
Totals:	284	34 — 39	36.9	0.93	0.05
		SYMPATRY			
10	36	36 — 38	36.8	0.62	0.10
11	44	37 — 41	38.3	0.92	0.13
12	24	36 — 40	38.5	0.95	0.19
13	36	36 — 40	37.6	0.82	0.13
Totals:	140	36 — 41	37.8	1.06	0.08
		Poecilia dominicensis			
		SYMPATRY			
10	28	31 — 34	32.6	0.71	0.13
11	21	31 — 34	33.0	0.75	0.16
12	18	31 — 34	32.6	0.82	0.19
13	33	31 — 34	32.5	0.85	0.14
Totals:	100	31 — 34	32.7	0.81	0.08
		ALLOPATRY			
14	36	29 — 35	32.4	1.36	0.22
15	14	32 — 35	33.4	0.81	0.21
16	47	32 — 35	33.7	0.75	0.10
Totals:	97	29 — 35	33.1	1.27	0.12

variation and predicting means of less than 32 in sympatry. In the latter area, however, there is no significant difference among the means of localities 10 through 13, all of which are well above 32 with a combined mean of 32.7. No abrupt shift occurs across the zone boundary, but the 33.1 mean for the combined allopatric localities is significantly higher than the 32.7 mean for the combined sympatric localities.

In none of the four meristic characters analyzed was convergence found to occur in sympatry. Dorsal rays show parallel shift and pectoral rays show divergence of *P. hispaniolana* away from *P. dominicensis.* Branched caudal rays and lateral line scales, however, each show divergence from each other for both species. As would be expected, therefore, and as shown by the meristic character index, the four characters combined indicate displacement in both species, in the form of divergence away from each other. The upward shift in sympatry, however, is much more evident in *P. hispaniolana* than is the downward shift in *P. dominicensis.* There also is the abrupt upward shift across the zone boundary in *P. hispaniolana* but not in *P. dominicensis.* In addition, the significantly higher means for *P. hispaniolana* in localities 11 and 12, confirm the prediction that character displacement would manifest itself more strongly in these two localities. This, however, is not confirmed for *P. dominicensis.* The type of character displacement shown by the meristic character index does not correspond to any of the categories of Grant (1972), but it is close to his category number 2.

Gill rakers

Despite the broad overlap, *Poecilia hispaniolana* and *P. dominicensis* differ significantly in the number of gill rakers in allopatry (Table 7, Fig. 10) where the range is 17 to 21 for the former and 18 to 22 for the latter. The mean for *P. hispaniolana* in allopatry is 18.9 and for *P. dominicensis* 19.9. As shown by the bar diagram in Figure 10, there is no significant difference among the means of localities 3 through 9 and 14 through 16. No clinal trend, therefore, is evident for either species in allopatry.

In sympatry, there is no significant difference between the means for both species in each of localities 10 through 13. Convergence, therefore, is indicated as clearly shown by the last three boxes on the right of the bar diagram. There is no significant difference among the means for *P. dominicensis* in sympatry and allopatry nor between sympatry and allopatry. In *P. hispaniolana*, however, the mean for locality 11 is significantly higher than the other three means in sympatry and the means of most of the localities in allopatry.

It may be concluded from the above that a shift toward a higher number of gill rakers has occurred in *P. hispaniolana* in sympatric localities 11 and 12. In these same localities, a trend toward fewer gill rakers is shown by *P. dominicensis*. This tends to confirm once again the prediction that character displacement, whether convergent or divergent, would manifest itself more strongly in localities 11 and/or 12. Character displacement in number of gill rakers, therefore, appears to have occurred, at least in *P. hispaniolana*, in the form of convergence toward *P. dominicensis*. This type of character displacement corresponds to category number 7 of Grant (1972).

Table 7. Comparison of number of gill rakers among samples of *Poecilia hispaniolana* and *P. dominicensis* in their areas of allopatry and sympatry.

Local. No.	N	Range	X	S.D.	S.E.
		Poecilia hispaniolana			
		ALLOPATRY			
1	35	18 — 21	19.1	0.76	0.13
2	35	18 — 21	19.6	0.93	0.16
3	24	17 — 20	18.5	0.91	0.19
4	12	18 — 20	19.1	0.86	0.25
5	36	17 — 21	18.7	0.94	0.16
6	36	17 — 21	18.8	0.95	0.16
7	46	17 — 21	18.5	1.01	0.15
8	36	17 — 20	18.9	0.92	0.15
9	26	17 — 21	18.7	0.98	0.19
Totals:	286	17 — 21	18.9	0.99	0.06
		SYMPATRY			
10	36	17 — 21	18.9	1.02	0.17
11	44	18 — 23	20.1	0.97	0.15
12	24	17 — 21	19.5	1.00	0.20
13	33	17 — 21	18.9	0.99	0.17
Totals:	137	17 — 23	19.4	1.13	0.10
		Poecilia dominicensis			
		SYMPATRY			
10	28	17 — 22	19.3	0.96	0.18
11	21	18 — 22	19.9	0.83	0.18
12	19	18 — 21	19.6	0.98	0.22
13	33	17 — 21	19.5	1.02	0.18
Totals:	101	17 — 22	19.5	0.88	0.09
		ALLOPATRY			
14	36	18 — 21	19.9	0.73	0.12
15	10	18 — 21	19.5	0.81	0.26
16	47	18 — 22	19.9	0.92	0.13
Totals:	93	18 — 22	19.9	0.85	0.09

Body Size

Poecilia hispaniolana and *P. dominicensis* differ significantly in body size, as expressed by the SL, the former being the larger of the two (Table 8, Fig. 11). On the average, however, both species are significantly larger in sympatry than they are in allopatry, especially the females.

For males of *P. hispaniolana*, the bar diagram in Figure 11 does not show character shift in sympatry, except that the mean for locality 12 is significantly higher than those of 10 and 11 and those of allopatric localities 1, 2, 5, 6, 7, and 9. Also, the mean for the combined localities in sympatry is not significantly different from the mean for the combined localities in allopatry. For females, the bar diagram shows a trend similar to that for males but, in sympatry, the means of localities 11, 12, and 13 (75% of sympatry) are significantly higher than those of 3 through 8 (67% of allopatry). Although there is no abrupt upward shift across the zone boundary between populations 9 and 10, the conditions just described are indicative of an upward shift of character state in sympatry.

For males of *P. dominicensis* the bar diagram does not show significant differences among the means of the four localities in sympatry. In turn, the means of localities 14 and 16 in allopatry are not significantly different from the means of localities 10, 11, and 13 in sympatry. The mean of locality 15 in allopatry, however, is significantly much lower than those of all the other localities in allopatry and sympatry and the mean of 12 in sympatry

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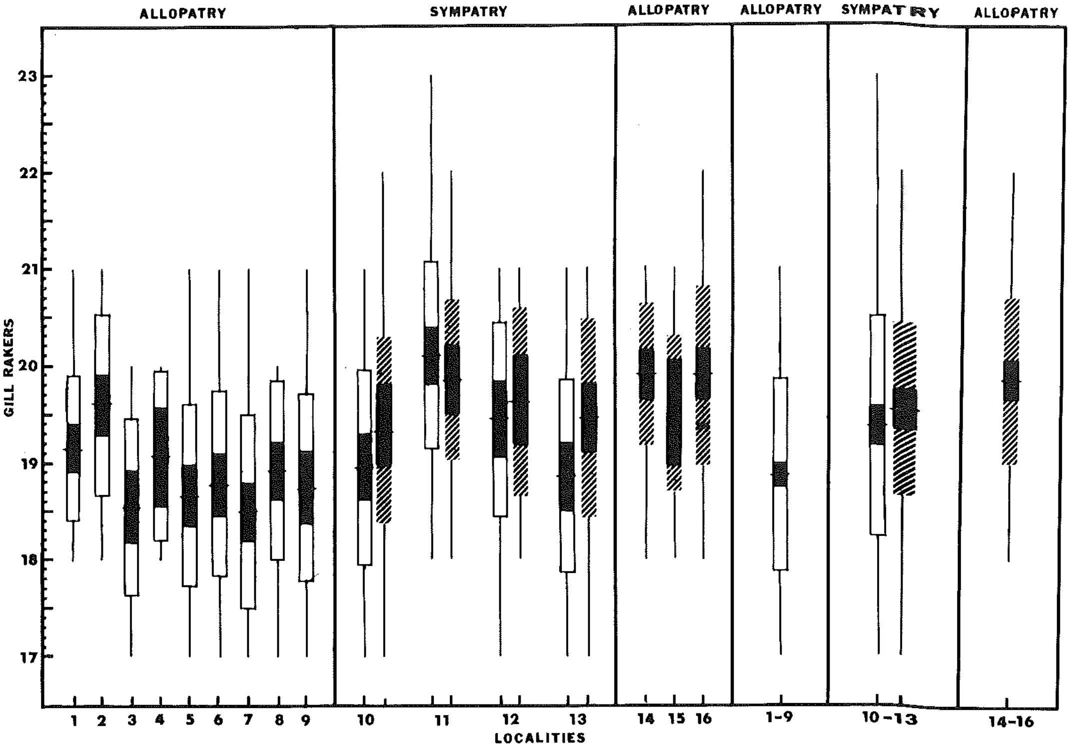

Figure 10. Comparison of number of gill rakers among samples of *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Rest of legend as in Figure 5. Based on Table 7.

is significantly higher than those of 14 and 16. Because of this, the mean of the combined localities in sympatry is significantly higher, although barely so, than that of the combined localities in allopatry. In spite of this, however, character shift in sympatry does not seem to have occurred in males of *P. dominicensis*. As to the females, the bar diagram shows an upward shift in sympatry. Not only are the means in sympatry higher than those in allopatry but also an abrupt upward shift has occurred across the zone boundary between localities 13 and 14. Furthermore, the means of localities 11 and 12 are both significantly higher than those of 10 and 13.

It may be concluded from the above that a shift toward larger size has occurred in sympatry in the females of both species, but not in the males. There is the possibility, however, that a similar, but very slight shift, may also have occurred in the males. The shift toward larger size in *P. dominicensis* is significantly more pronounced in localities 11 and 12, thus confirming once again the prediction that character displacement would manifest itself more strongly in localities 11 and/or 12. There is, however, no confirmation of the prediction for *P. hispaniolana*. The shift in both species is in the same direction but not of the same magnitude, because the mean shift is 4.4 mm in *P. hispaniolana* and 5.0 mm in *P. dominicensis*. There is, therefore, a significant difference of 12% between the two means. It appears that size displacement has occurred in a form that could be termed "divergent parallel character displacement" corresponding to category number 4 of Grant (1972).

Fecundity Factor

During the course of measuring and counting, it was observed that adult fe-

Table 8. Comparison of mean standard length among samples of male and female *Poecilia hispaniolana* and *P. dominicensis* in their areas of allopatry and sympatry.

	MALES					FEMALES				
Local. No.	N	Range	X	S.D.	S.E.	N.	Range	X	S.D.	S.E.
Poecilia hispaniolana										
ALLOPATRY										
1	29	23 — 35	28.2	2.6	0.49	46	33 — 47	38.6	3.0	0.45
2	73	21 — 36	27.0	3.3	0.39	52	29 — 51	38.5	6.2	0.86
3	33	23 — 44	29.6	4.6	0.80	27	33 — 47	37.5	3.7	0.71
4	9	22 — 34	27.0	4.4	1.46	16	30 — 48	35.9	4.7	1.18
5	32	23 — 31	26.2	2.0	0.36	100	30 — 43	34.2	2.7	0.27
6	20	21 — 27	24.2	1.6	0.36	39	28 — 42	33.3	3.4	0.54
7	51	21 — 32	24.9	2.3	0.32	56	29 — 41	33.5	3.0	0.40
8	28	24 — 33	28.5	2.9	0.55	118	29 — 46	35.7	4.0	0.34
9	52	25 — 35	28.1	2.3	0.32	63	35 — 51	39.6	4.6	0.58
Totals:	327	21 — 44	27.1	3.3	0.18	517	28 — 51	36.1	4.5	0.20
SYMPATRY										
10	61	22 — 32	26.8	2.5	0.32	96	32 — 51	38.6	4.4	0.45
11	23	24 — 33	28.2	2.7	0.56	44	31 — 53	40.4	6.1	0.91
12	23	27 — 36	30.0	2.4	0.50	53	34 — 58	41.0	6.1	0.84
13	27	26 — 32	28.7	1.9	0.37	93	34 — 58	42.3	5.3	0.55
Totals:	134	22 — 36	28.0	2.7	0.23	286	31 — 58	40.5	5.5	0.33
Poecilia dominicensis										
SYMPATRY										
10	8	22 — 25	23.9	1.1	0.37	25	26 — 42	33.6	4.3	0.86
11	11	21 — 26	23.7	1.6	0.47	21	31 — 46	36.5	3.7	0.80
12	10	23 — 27	24.9	1.4	0.44	21	33 — 52	38.9	4.6	1.00
13	21	22 — 26	23.8	1.2	0.27	33	27 — 47	33.6	5.0	0.88
Totals:	50	21 — 27	24.0	1.4	0.19	100	26 — 52	35.3	5.0	0.50
ALLOPATRY										
14	42	22 — 25	23.1	0.9	0.14	51	25 — 39	30.4	3.4	0.47
15	2	20 — 21	20.5	0.5	0.35	11	22 — 30	25.9	2.7	0.80
16	13	21 — 26	23.4	1.2	0.34	59	25 — 43	31.1	4.4	0.57
Totals:	57	20 — 26	23.1	1.1	0.14	121	22 — 43	30.3	4.1	0.37

males of *Poecilia dominicensis* were more noticeably and more frequently "pregnant" than those of *P. hispaniolana.* A difference in fecundity between the two species was, therefore, suspected.

Females of both species have about the same body proportions and eviscerated specimens of *P. hispaniolana* have about the same weight as those of *P. dominicensis* of equal size. Fecundity, therefore, may be expressed quantitatively by using the condition factor (K) formula: $K = 10^5 \times W/L^3$ where W is the weight in grams and L is the standard length in millimeters. The condition factor is normally used to determine body fitness and the gonads and other viscera are removed before weighing the fish. In this case, however, the females were not eviscerated. It follows, therefore, that the greater weight at size yielding a higher factor is the weight added by the production of eggs and/or embryos. Because the factor reflects degree of fecundity rather than body fitness it is hereafter referred to as the fecundity factor.

To avoid misinterpretations resulting from possible ontogenetic variation of the fecundity factor, it was determined whether or not such variation occurred. It was found that this character is isometric at a size of 30 mm SL or larger. For the analysis, therefore, a graded series of 10 specimens ranging from about 32 to 50 mm SL was selected at random from each of the samples, except the one corresponding to locality 15 where adult females measured only 22 to 30 mm SL.

As shown in Table 9 and Figure 12, *Poecilia hispaniolana* and *P. dominicensis* differ significantly in the fecundity factor, the latter being the more fecund of the two. This is further confirmed by examination of the ovaries of two females of each species selected at random from each sample. Eggs and embryos are of the same size in both species, but in *P. dominicensis*, the number of ovarian units (eggs and/or embryos) ranges from 15 to 135 with a mean of 52. In *P. hispaniolana,* however, the number of ovarian units ranges from 11 to 111 with a mean of 37. *P. dominicensis,* therefore, is nearly 30 percent more fecund than *P. hispaniolana*.

No clinal trend is shown for either species in allopatry because there is no significant difference among localities 4 through 9 and between 14 and 16. In *P. hispaniolana* there is no significant difference between allopatry and sympatry but in *P. dominicensis* the difference between allopatry and sympatry may be interpreted as virtually significant. Furthermore, the difference between the means of each species is much greater in sympatry than in allopatry.

It may be concluded from Figure 12 that, in sympatry, a shift toward even higher fecundity has occurred in *P. dominicensis* but not in *P. hispaniolana*. This type of displacement corresponds to category number 10 of Grant (1972). Because there is no significant difference among the means for *P. dominicensis* in sympatry, the prediction that character displacement would be more pronounced in localities 11 and/or 12 is not confirmed in this case.

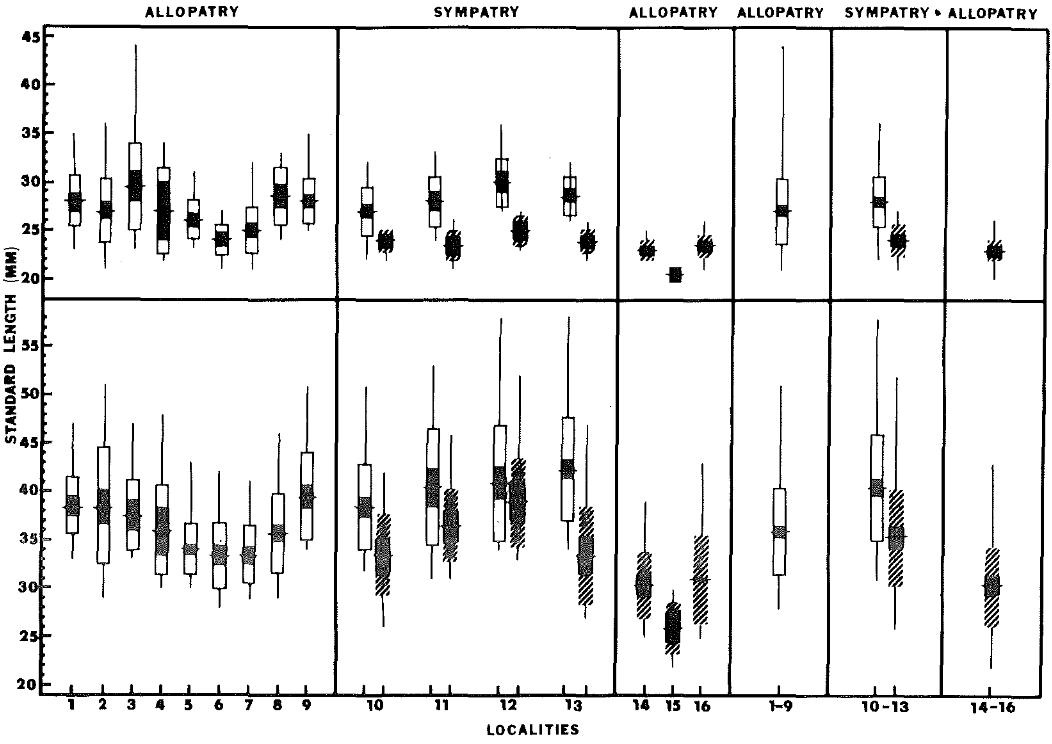

Figure 11. Comparison of mean standard length among samples of male (upper) and female (lower) *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Rest of legend as in Figure 5. Based on Table 8.

DISCUSSION

Character displacement between *Poecilia hispaniolana* and *P. dominicensis* probably has resulted from selection pressure acting upon the two species competing in sympatry. In addition, the magnitude of displacement appears to be a function of length of coexistence in this same habitat, as shown by sympatric localities 11 and/or 12.

At this point, it may be mentioned that no other species of poeciliid occurs in locality 10, but *Curtipenis elegans* (Trewavas) occurs in localities 11 and *Limia zonata* (Nichols) in locality 12. Both of these species occur in locality 13. There are no indications, however, that *P. hispaniolana* and *P. dominicensis*, compete with the latter pair. Also, it is possible that the patterns of displacement shown in this study are the result of competitive interaction between *P. hispaniolana* and *P. dominicensis* and not the result of competition between either member of that pair and *C. elegans* and/or *L. zonata*.

As already indicated, the habitat in sympatry is a mixture of each species' typical habitat in allopatry. In sympatry, therefore, a certain degree of ecological segregation must be assumed, or the species would not be able to coexist. Ashmole (1968) pointed out that ecological segregation can be interpreted as the result of character displacement among species that were able to coexist long

Table 9. Comparison of fecundity factor among samples of adult female *Poecilia hispaniolana* and *P. dominicensis* in their areas of allopatry and sympatry.

Local. No.	N	Range	X	S.D.	S.E.
		Poecilia hispaniolana			
		ALLOPATRY			
1	10	22.8 — 26.5	25.0	1.21	0.38
2	10	22.1 — 29.5	27.0	2.13	0.67
3	10	20.6 — 28.2	24.3	2.35	0.74
4	10	22.1 — 29.0	26.4	1.90	0.60
5	10	24.4 — 30.1	27.7	1.83	0.58
6	10	21.9 — 29.0	26.5	2.50	0.79
7	10	24.1 — 29.7	27.2	1.94	0.61
8	10	23.4 — 28.5	26.3	1.52	0.48
9	10	24.7 — 28.7	26.6	1.21	0.38
Totals:	90	20.6 — 30.1	26.2	2.15	0.23
		SYMPATRY			
10	10	25.1 — 30.1	28.2	1.54	0.49
11	10	22.1 — 27.5	25.2	1.81	0.57
12	10	24.6 — 31.2	27.6	1.91	0.61
13	10	23.0 — 28.1	25.9	1.37	0.43
Totals:	40	22.1 — 31.2	26.7	2.02	0.32
		Poecilia dominicensis			
		SYMPATRY			
10	10	27.2 — 35.7	29.2	2.32	0.73
11	10	26.9 — 33.8	30.1	1.92	0.61
12	10	28.2 — 34.7	31.4	1.90	0.60
13	10	26.7 — 34.0	30.7	2.06	0.65
Totals:	40	26.7 — 35.7	30.1	2.22	0.35
		ALLOPATRY			
14	10	22.5 — 31.1	27.9	2.76	0.87
15	Not included because females are too small (see text)				
16	10	24.3 — 32.7	28.9	2.57	0.81
Totals:	20	22.5 — 32.7	28.3	2.70	0.60

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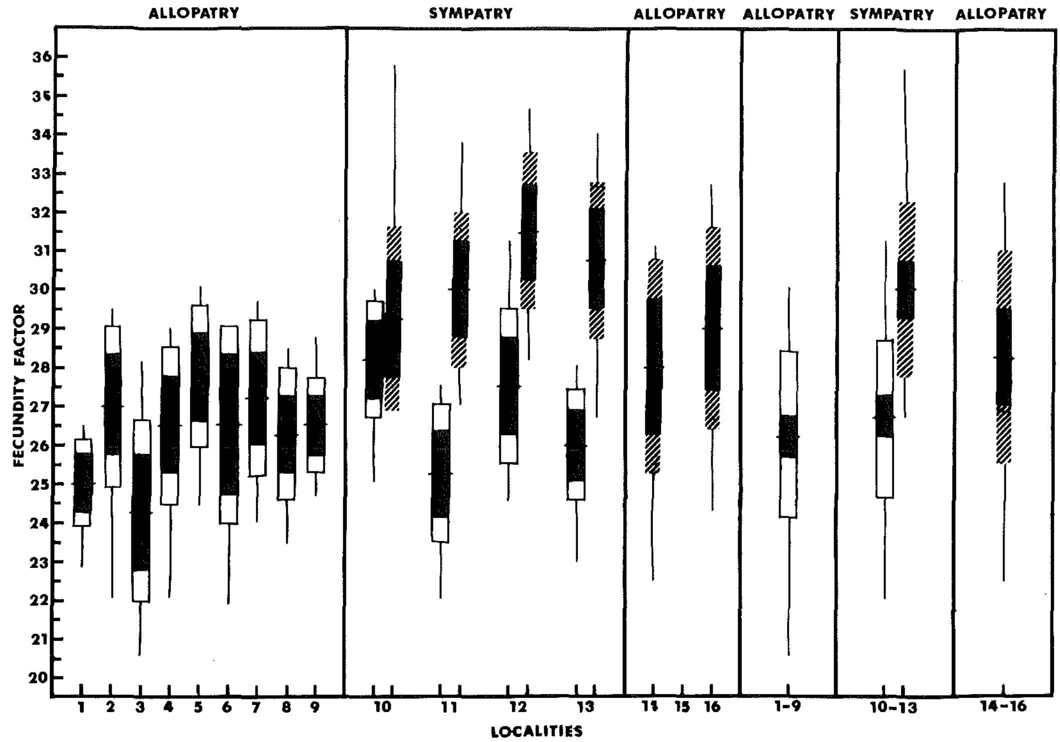

Figure 12. Comparison of fecundity factor among samples of *Poecilia hispaniolana* (1-13, not dashed) and *P. dominicensis* (10-16, dashed) in their areas of allopatry and sympatry. Rest of legend as in Figure 5. Based on Table 9.

enough for it to occur. However, because there is evidence of competition between *P. hispaniolana* and *P. dominicensis* (see below) total ecological segregation probably does not exist. Ashmole also indicated that character displacement provides strong evidence that selection normally favors evolutionary divergence among similar species. An attempt is made in this section to interpret the various types of displacement that have occurred between *P. hispaniolana* and *P. dominicensis*, in conjunction with the nature and interaction of the characters involved.

The divergent meristic character displacement shown by this study (Fig. 9) can hardly be interpreted at first as the direct result of selection because the significant, but minor shift of meristic characters is, in turn, difficult to accept as adaptive. In other words, it does not seem likely that these small meristic differences are adaptations to physical or biological environmental features, nor can they be readily correlated with any other character also showing displacment. It could be argued, however, that, as compared to *P. dominicensis*, the more numerous pectoral rays and lateral scales, fewer branched caudal rays, and nearly truncate caudal fin in *P. hispaniolana* suggest adaptation to its lotic habitat. Also, that, as compared to *P. hispaniolana*, the fewer pectoral rays and lateral scales, more numerous branched caudal rays and nearly rounded caudal fin in *P. dominicensis* suggest adaptation to its lentic habitat. Perhaps, meristic character displacement could also be tentatively interpreted as the indirect result of genetic changes brought about by selection in sympatry. By the same token, reduced meristic variability in sympatry may have resulted in part from competition and may reflect a general decrease in genetic variability incidental to strong selection.

Relative size, shape, and arrangement of teeth are qualitative features not amenable to quantitative expression and, furthermore, these trophic characters are virtually identical in both species (Rivas, 1978). The number of gill rakers is the only trophic character that could be analyzed quantitatively in this study, and as already discussed, and as shown in Figure 10, this character shows total convergence in sympatry where the number of gill rakers is the same in both species. Convergence in sympatry and divergence in allopatry suggest that both species may be exploiting the same gill raker-related type of food where they coexist but not where they do not.

Size increase of both species in sympatry (Fig. 11) and the increase, also in sympatry, of fecundity in *P. dominicensis*, but not in *P. hispaniolana* (Fig. 12) appear to be interrelated and to indicate a change of reproductive strategy in *P. dominicensis*. As pointed out by Huey and Pianka (1974), for animals like fish, where brood size is a function of body size, displacement in size might also involve changes in reproductive tactics. Size increase in the adults of *P. dominicensis*, and especially the fecundity increase in the females, could be interpreted as the reaction by that species to produce more offspring in order to offset population density competition with *P. hispaniolana* which is about six times more abundant. On the other hand, parallel increase in size, but no increase in fecundity in *P. hispaniolana*, could be interpreted as a response to size increase by *P. dominicensis* in order to maintain size-differential equilibrium and, thereby, reduce competition. This is in agreement with Huxley (1942) who was among the first to recognize the importance of difference in body size in reducing competition between closely related sympatric species. On the other hand, the type of size displacement in *P. hispaniolana* and *P. dominicensis* is in disagreement with the findings by Schoener (1970) for size displacement ascribable to food competition in *Anolis* lizards. This is probably because in *P. hispaniolana* and *P. dominicensis* parallel size increase in sympatry does not seem to be related to competition for food. In conjunction with size equilibrium, maintaining in sympatry the same sex ratio as in allopatry may also be important in reducing competition. In both, allopatry and sympatry, the same sex ratio, very close to 1:1, is maintained by the two species.

SUMMARY AND CONCLUSIONS

Evidence presented in this study supports the possibility that meristic and reproductive character displacement have occurred in *Poecilia hispaniolana* or in *P. dominicensis* and that the magnitude of displacement is a function of length of coexistence. Also, that character displacement, in this case, probably has resulted from the interaction of geographic, ecologic, and genetic factors.

Meristic displacement could be explained as the direct effects of selection induced by competition, in the presence of partial ecologic segregation, and resulting in increased adaptation to the proper niche. An alternative interpretation would be that meristic displacement is the indirect result of genetic changes caused, in other characters, by selection.

Reproductive character displacement, on the other hand, appears to have resulted from the interaction of several characters, as reflected by the displacement of size and fecundity. The effect of this interaction indicates a change of reproductive strategy in *P. dominicensis* as a species-survival reactive mechanism in competition with *P. hispaniolana* which

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appears to be the dominant species. Because of this, therefore, it would appear that the two species have been able to stably coexist in sympatry, especially in localities 11 and/or 12, for a long, but undetermined period of time of not more than two million years, according to geologists (Maurrasse, 1981).

Ayala (1972) studied competition between species of fruitflies (*Drosophila*) and came to the conclusion that two closely related species can stably coexist. The following remarks, summarized from his paper, seem applicable to *P. hispaniolana* and *P. dominicensis* in sympatry. "Natural selection is the main directional process by which populations become adapted to their environments and it may lead toward ecological differentiation of competing species. When two species compete for a sufficiently long time, character displacement is likely to occur. With character displacement, the stability of the system is promoted. The more ecologically different the two species become, the less likely it is that one will be excluded from the environment because it has been outcompeted by the other."

It is difficult to predict whether or not stable coexistence will persist but the evidence presented in this study suggests that, in the end, the two species, through competition, may attain full ecological segregation and may even further differ in morphology and behavior. If so, it is possible that they may each become in sympatry specifically distinct from their respective populations in allopatry. On the other hand, it is also possible that *P. hispaniolana* could eliminate *P. dominicensis* from some, or all of the localities where they coexist.

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