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POLYMORPHISM IN MEXICAN BROWN JAYS

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The systematic relationship of the Brown Jay *(Psilorhinus morio)* and the White-tipped Brown Jay *(P. mexicanus)* has been a topic for speculation by ornithologists visiting eastern México and those concerned with classification of the Corvidae (Amadon, 1944: 8). They have been carried as separate species in the literature by nearly all writers and are listed as such in the recent Mexican check-list (Miller, *et al.*, 1957), but from time to time in recent years the suggestion has been made that they are color phases or morphs of a single species.

Hellmayr (1934: 15) seems to have been the first to question the status of these jays and to suggest that "the so-called *P. mexicanus* . . . [is] a mutant of *P. morio* rather than a distinct taxonomic unit." More recently Sutton (1951: 233) and Amadon and Eckelberry (1955: 76) expressed belief that the two jays are color phases, and Eisenmann (1955: 74, and 1957: 256) also questioned their status. The principal recent advocates of the view that the two jays are specifically distinct are Wetmore (1943) and Lowery and Dalquest (1951).

The present study is based primarily on data obtained in eastern México in June and July, 1957. Early in this study it became apparent that discontinuous polymorphism, presumably genetic, was involved, and that the morphologically distinct types (Plate 14) which have been considered separate species are in fact color phases of a single species. Both types were found in the same brood, were constantly associated, and showed no differences in habitat selection or behavior.

Attention was then focused on the important problem of geographic variation in morph-frequency, with a view to mapping ratio-clines of the two morphs in Veracruz, Oaxaca, Tabasco, and Chiapas. Fifteen major study areas were visited from Tamaulipas south and east to Campeche, and censuses were made at over 25 localities. A total of 182 specimens of *Psilorhinus* was collected and prepared as study

skins or skeletons; these have been deposited in the Museum of Vertebrate Zoology, Berkeley, California. Additional specimens were obtained on loan from museums. Some preliminary observations and collections of Mexican Brown Jays were made by the author in 1952, 1953, and 1954, and a hybrid between *Psilorhinus* and the Magpie Jay, *Calocitta,* from east-central Chiapas was studied by Pitelka, Selander, and Alvarez del Toro (1956).

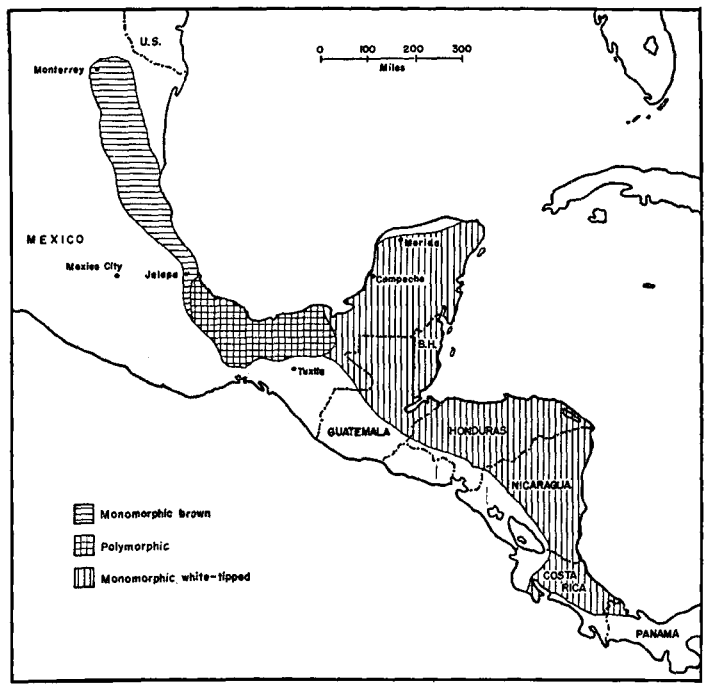
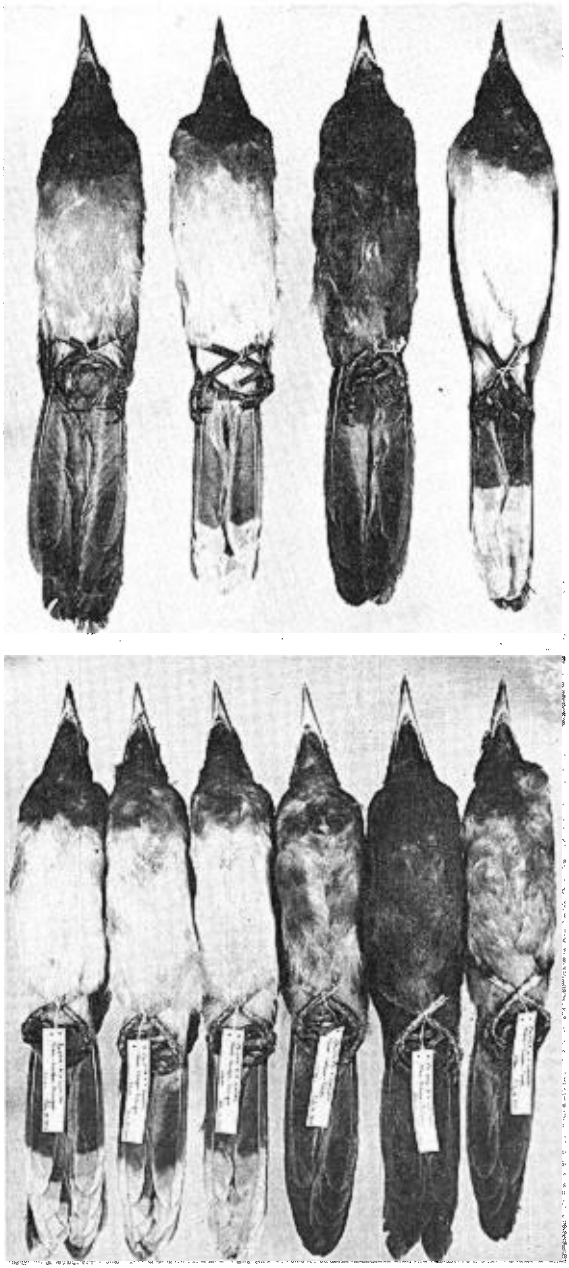


FIGURE 1. Distribution of *Psilorhinus morio.*

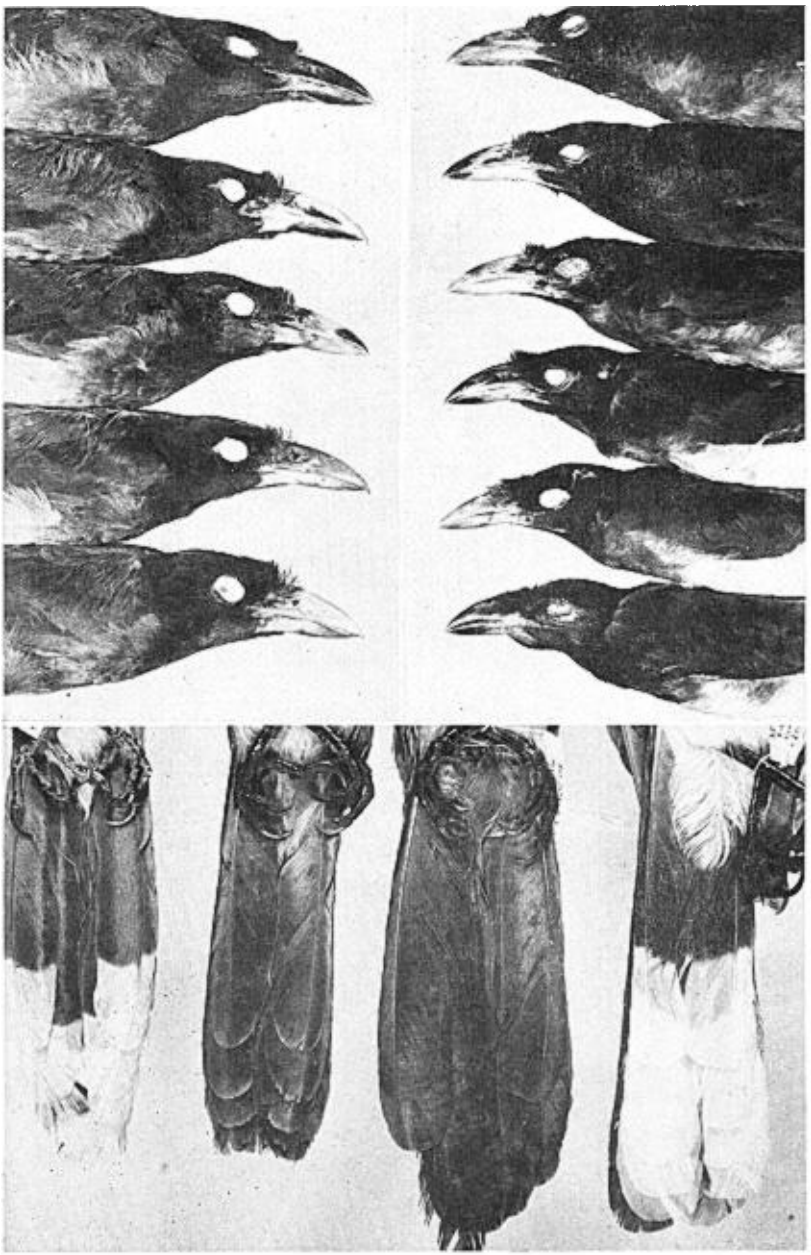
Throughout this report, "white-tipped morph" refers to the *"mexicanus"* phase, and "brown morph" is used for the *morio* type.

DESCRIPTIONS OF THE MORPHS

Brown jays are magpie-sized birds, measuring from 14 to 18 inches in length. Dorsally the two morphs are indistinguishable. The head and neck are dark sooty brown, grading to a lighter brown on the back, scapulars, rump, and upper tail coverts; dorsally the wings and tail are deep olive gray and usually have more or less of a bluish sheen. Ventrally the morphs differ conspicuously (Plate 14). In the brown morph the rectrices are uniformly brown; and the posterior



BROWN JAYS. *(Above)* Adult specimens showing color and pattern differences between morphs. From left to right: Male brown morph (Coatepec, Veracruz), female white-tipped morph (Catemaco, Veracruz), male brown (Teapa, Tabasco), male white-tipped (Palenque, Chiapas). *(Below)* Three juvenal white-tipped morphs from Palenque, Chiapas, and three brown morphs from Teapa, Tabasco. The second specimen from the right is a melanistic variant.



BROWN JAYS. Age and individual variation in color of bill. *(Left)* Adult males from central Veracruz (June-July). *(Right)* Juvenal males from Tabasco and Chiapas (July). *(Below)* Age variation in shape and size of rectrices. From left to right, two first-year and two adult female specimens.

under parts, including the under tail coverts and axillaries, range from brown to light grayish brown, the latter character being subject to a considerable degree of individual and geographic variation. In the white-tipped morph, rectrices 2 to 6 have conspicuous white-tips, but the central rectrices (1–1) are unmarked brown as in the brown morph. The posterior under parts of the white-tipped morph are cream white or white. In both morphs the breast is dark sooty brown, similar in shade to the back. A pale malar patch is indicated to some degree in all specimens, and occasionally it is well defined and grayish blue in color and there is an imperfectly developed light patch above the eye (Plate 15).

Juveniles are closely similar to adults in pattern (Plate 14), but the dark parts of the plumage are slightly paler. And in feather structure there is a conspicuous difference, the barbs being more widely spaced along the rhachis.

There is no appreciable sexual dimorphism in color or pattern, but females are significantly smaller than males in all dimensions.

The dark parts of the plumage fade rapidly with wear and exposure, so that only a few months after the fall molt the birds are brown rather than dark sooty brown. Prior to the time of the next fall molt the darker parts of the plumage may be grayish brown.

Age determination.—First-year birds may be distinguished from adults on the basis of a combination of criteria established for American jays by Pitelka (1945, 1958). The postjuvenal molt is incomplete, the juvenal rectrices, remiges, greater primary coverts, and a variable number of greater secondary coverts being retained. These differ in shape, structure, and, to some degree, in color from adult feathers (Plate 15). Also, they are at all times of the year more worn and faded than adult feathers, and even those feathers grown in the postjuvenal molt apparently are less resistant to wear and fading than are feathers of adult birds.

The importance of segregating age classes in systematic studies of Brown Jays is apparent from comparisons of measurements of adult and first-year individuals. Wing and tail average significantly shorter in first-year birds than in adults. Moreover, the data indicate that in this large species complete growth may not be attained by first-year birds undergoing their second fall (first postnuptial) molt. For example, 12- to 13-month-old first-year birds in postnuptial molt, collected in Veracruz in June and July, are smaller in length of bill and tarsus and weigh less than older birds.

The skull is completely ossified in all but a few first-year birds by June, at which time they are approximately one year old.

Color of soft parts.—Striking variability in coloration of the bill, tarsus, and toes is apparent in any representative series of *Psilorhinus* (Plate 15) and has been noted by many authors (*e.g.* Blake, 1953: 378). The color of the ring of skin surrounding the eye also is variable, as noted by Skutch (1935: 261), and a small patch of skin below the eye exhibits similar variation. These soft parts may be yellow, black, or parti-colored. My data on colors in birds of known age fully support Skutch's

claim, based on field observations, that these soft parts "turn black with age in an irregular fashion . . . taking two or more years to become entirely black."

In 1957, color and pattern of the soft parts were recorded for most specimens collected. These descriptions subsequently were grouped into categories of progressive development of black, permitting analysis of variation. Data on color pattern of the bill are summarized in table 1; age determinations are based on criteria described elsewhere.

According to Skutch (1935: 261), the nestling's bill, feet (tarsus and toes), and bill are uniformly yellow. Whether this is true of all nestlings is uncertain, but, in any event, in many juveniles the soft parts begin to darken very early. None of the juvenal specimens in table 1 was older than 3 months, and many, including some with partly black soft parts, had only recently fledged when collected and were no more than a month old. In fledged juveniles from one to three months old, the eye-ring is intense yellow, mustard yellow, black, or parti-colored yellow and black. Skin below the eye is yellow or greenish yellow; the tarsus, toes, and bill are yellow or parti-colored (Plate 15); the lining of the mouth is gray or flesh colored; and the iris is gray. Yellow of the soft parts varies from intense to dull grayish, and the tarsus and toes frequently have a greenish cast. The other extreme in coloration is seen in about 50 per cent of adult birds two or more years of age, in which the iris is solid brown, the mouth lining black, and the other soft parts uniformly black. In other adults and in first-year birds a seemingly unlimited variety of intermediate patterns is found (Plate 15). As regards bill, tarsus, and toes, there seem to be no regular patterns of replacement of yellow with black, although some trends are apparent from examination of large series of skins. Usually the iris is brown by the time a bird is one year old, but gray specks or patches may persist beyond the first year. Unlike the other soft parts, skin below the eye is never parti-colored; in intermediate condition it is gray-yellow.

There is a tendency for yellow to persist on the bill after other parts are uniformly black, but, even so, bill color (Table 1) serves as an index to stage of

TABLE 1

AGE, INDIVIDUAL, AND SEXUAL VARIATION IN COLOR OF BILL
(SPECIMENS FROM VERACRUZ, JUNE AND JULY, 1957)

			Per cent in various categories						
Sex and age	*Morph*	*No.*	*Yellow*	*Sub-yellow*	*¼ black*	*½ black*	*¾ black*	*Sub-black*	*Black*
♂ juvenile	Brown	15	33	27	13	27			
♀ juvenile	Brown	14	21	7	43	21	7		
♂ juvenile	White-tipped	3		33	33			33	
♀ juvenile	White-tipped	1	100						
Total juvenile		*33*	*27.3*	*18.2*	*27.3*	*21.2*	*3.0*	*3.0*	*0.0*
♂ first-year	Brown	3	33		33				33
♀ first-year	Brown	9	33	22	11		11	22	
♂ first-year	White-tipped	6	17	17	33		17	17	
♀ first-year	White-tipped	8	37		25	25			13
Total first-year		*26*	*30.8*	*11.5*	*23.1*	*7.7*	*7.7*	*11.5*	*7.7*
♂ adult	Brown	26	8	8		12	8	11	54
♀ adult	Brown	24			12		8	13	67
♂ adult	White-tipped	6		33		17			50
♀ adult	White-tipped	8			12	38			50
Total adult		*64*	*3.1*	*6.3*	*6.3*	*10.9*	*6.3*	*9.4*	*57.8*

development of black "adult" color of the soft parts generally. The categories in Table 1 are based on extent of black or yellow areas on the bill. All specimens were taken in Veracruz in June and July, 1957. The juveniles are from one to three months old; the first-year birds, all of which were in first postnuptial molt, are slightly older than one year; and the adults are at least two years old. Several points seem noteworthy.

Considerable individual variation is manifest in any one age or sex group; and while the majority of juveniles has the bill ¼ or less black, the bill of one specimen (collected on June 29) shows only a few small streaks of yellow ("sub-black"). Relatively little progress is made during the first year of life, since only 7.7 per cent of 26 year-old birds have all-black bills. The data suggest that in those individuals which as juveniles have bills ½ or more black, there is an increase in the area of black in their first year, whereas those with totally or predominantly yellow bills as juveniles do not progress. Thus, nearly equal percentages of juvenal and first-year birds fall in the "yellow," "sub-yellow," and "¼ black" categories, but a greater percentage of first-year than juvenal birds falls in the four more "advanced" categories. In two-year-old or older adults, 57.8 per cent have uniformly black bills, but a few (3.1 per cent) have totally yellow bills. Presumably a significant proportion of those adults having black soft parts are three or more years old. Age beyond the first postnuptial molt cannot be determined on the basis of presently known age criteria.

The data on bill color suggest, but do not prove, that progress is slightly more rapid in females than in males and in the brown morph than in the white-tipped morph. In adults, about 60 per cent of brown morphs, as compared to 50 per cent of white-tipped morphs, had uniformly black bills. This difference may not be significant because of the small size of the sample of the latter morph, but it is the kind of difference between morphs that may be expected, since morphic differences in plumage pattern, like the color changes of the soft parts, involve differential rates in deposition of black or brown (melanin) pigments.

Pitelka (1945: 256–258) has analyzed variation in changes in bill color from yellow to black in the jays *Aphelocoma unicolor* and *A. ultramarina*. In the latter species, "yellow color of the bill may disappear from the ages of slightly less than one year to more than two years." Of 216 specimens which were more than one year old, 49 per cent had some yellow on the lower mandible, suggesting a rate of change comparable to that of *Psilorhinus* in Veracruz. Unlike *Psilorhinus*, there is in *A. ultramarina* a tendency for males to acquire black bills before females.

Finally, it is obvious from the foregoing discussion that color of soft parts cannot be used as a criterion for age determination.

Survey of Evidence of Specific Status

Before proceeding further it may be desirable to review and evaluate the arguments of authors claiming specific status for the two types of jays.

The only cogent argument that *morio* and *mexicanus* are species given by Wetmore (1943) is that the white-tipped type occurs without geographic variation "through the area inhabited by two . . . subspecies of *Psilorhinus morio*." This statement obviously was based on the assumption that the white-tipped morph occurs north to

Tamaulipas; but, as explained elsewhere, in fact it almost surely does not. The fact that the brown type "does not occur south of Chiapas, while two races of *mexicanus* extend through the area from Guatemala to the Almirante region in Panama" is cited as another line of evidence that two species are involved, but actually this circumstance has no particular bearing on the problem. Monomorphic geographic populations or races are frequently found in species which elsewhere have polymorphic populations (Ford, 1945; Huxley, 1943; for examples in birds, see Mayr, 1942, Mayr and Stresemann, 1950, and Huxley, 1955).

One of the arguments of Lowery and Dalquest (1951) is not directed to the point here in question: "Since in the Upper Tropical Life-zone of central Veracruz only *morio* was found, and since, along the Río Coatzacoalcos, in southern Veracruz, only *mexicanus* was found, and since in the intermediate area, the coastal plain, the two forms occur together but retain their specific distinctions, the two jays seem to be full species, *instead of only subspecies,* as some authors have suggested. [Italics mine]" I am not aware that it has been suggested that the two types are subspecies in southeastern México; the problem is whether they are species or morphs. Incidentally, the "intermediate area" where the two types occur together is not confined to the coastal plain of central Veracruz.

Lowery and Dalquest state that "In the breeding season . . . when the birds are mated, the pairs that were observed closely consisted always of individuals of the same type only." Unfortunately they do not give details as to the number of pairs observed and the frequencies of the two types of jays in areas where their observations were made; without such information it is, of course, impossible to judge the significance of their observations. In my experience these jays are almost invariably found not in pairs but in groups, often consisting of both types, even during the breeding season (see beyond).

In summary, no conclusive argument for considering the two jays as separate species rather than morphs has been presented. Their conspicuous differences in coloration and the fact that no intermediates are known have been the chief reasons for classifying them as species.

DISTRIBUTION

Psilorhinus occurs in eastern México and Central America from Tamaulipas and Nuevo León, in northeastern México, south and east to northwestern Panamá (Fig. 1); the distribution apparently is continuous. Brown Jays are permanent residents and are common if not

abundant over the greater part of their range. They are, in fact, the most conspicuous element of the avifauna in many areas.

Brown Jays are markedly eurytopic, being found regularly from sea level to 4700 feet and, locally, up to 6600 feet (as at Puerto de Diablo, San Luis Potosí), where they occur in nearly all open woodland or forest types, both deciduous and evergreen. In México, at least, highest population densities are found at elevations below about 2000 feet. They are absent from the depths of undisturbed, mature rain forest, although they invade disturbed stands and are commonly found along rain forest edges (Skutch, 1935: 261; Pitelka, *et al.*, 1956; Lowery and Dalquest, 1951: 617; Howell, 1957: 97).

In Central America and in the Yucatán Peninsula, all Brown Jays are the white-tipped type; populations are monomorphic (Fig. 1). The easternmost localities for the brown type are Montecristo, eastern Tabasco, and Palenque, northern Chiapas. In the region from eastern Tabasco north to central Veracruz, including adjacent parts of Oaxaca and Chiapas, both morphs are found in varying ratios, and it is here that their relationships may be determined (Fig. 2). North of latitude 19°25′ in central Veracruz, all jays are of the brown type.

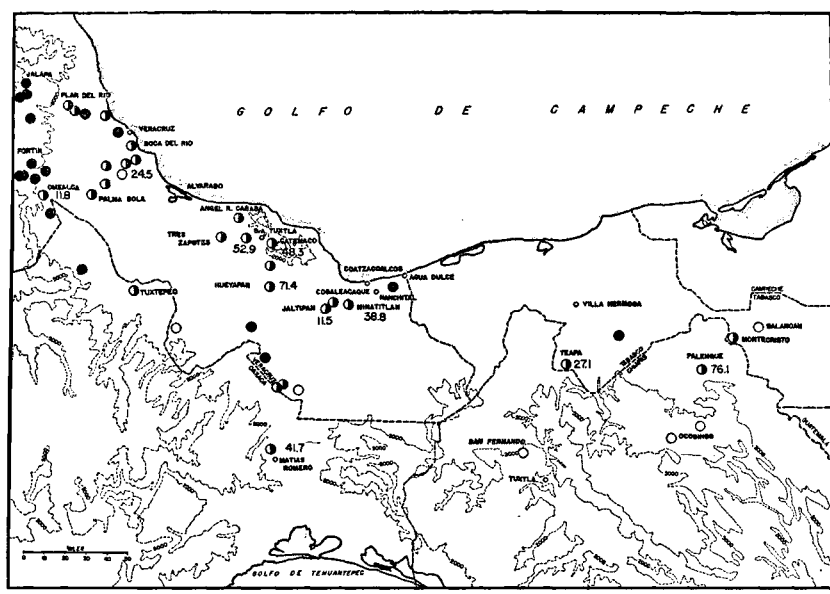


FIGURE 2. Distribution of *Psilorhinus morio* in central and southern Veracruz and adjacent areas. Dots represent records of the brown morph; circles, white-tipped morph; half-black symbols, both morphs from same locality. Numbers indicate percentages of white-tipped morphs in samples.

Northern limit of distribution of the white-tipped morph.—The northern limit of distribution of the white-tipped morph has been a matter of dispute and a source of misunderstanding. The fact that the type of *Psilorhinus mexicanus* Rüppell (1837) reportedly came from Tamaulipas ("Tamalipas") has been the basis for statements by some authors that the white-tipped morph occurs throughout the area occupied by two "races" of *morio (P. m. morio* and *P. m. fuliginosus).* But the occurrence of the white-tipped morph in Tamaulipas, or elsewhere in northeastern México north of central Veracruz, has never been confirmed. The Salvin and Godman (1887: 506) report of specimens of the white-tipped morph being obtained by Couch at Boquilla and China, Nuevo León, is simply erroneous. The specimens, which I have examined, are the brown morph (see also Ridgway, 1904: 300).

I have failed to record the white-tipped morph north of the coastal plain of central Veracruz. Hellmayr (1934: 15–16) questioned its occurrence in Tamaulipas, and Sutton (1951: 233) noted that: "In Tamaulipas, Nuevo León, and southeastern San Luis Potosí, I have seen literally hundreds of 'true' Brown Jays [brown morph], but not a single 'white-tipped' bird." Similarly, Mr. Irby Davis and Mr. Edgar Kincaid, who have had extensive field experience in northeastern México, have not recorded the white-tipped morph north of central Veracruz (personal communication with Kincaid). Until such time as reliable records of the white-tipped morph are available for northeastern México, I am inclined to regard Rüppell's report as erroneous (but for an alternative explanation, see pp. 406–407). The type of *mexicanus* may have come from Veracruz.

The northernmost point where the white-tipped morph can readily be found is in the vicinity of Boca del Río (Fig. 2), but it occurs in low frequency on the coastal plain of Veracruz up to 30 miles north of that locality. Lantz (1899: 222) reported that N. S. Goss collected a male at Rinconada in 1887; there is an adult in the British Museum (Natural History) taken at "Plan del Rio, Canton de Jalapa" in 1886; and in March, 1954, Kincaid (1954) saw one in company with six brown morphs in "semi-arid country" at the edge of a deep barranca near Plan del Río. On March 30, 1955, Davis and Kincaid (personal communication) saw a white-tipped morph flying with a brown morph at a point 53.6 miles southeast of Vega de Alatorre, Veracruz. And Mr. and Mrs. Ben Coffey (personal communication) recorded a white-tipped bird in this same area on May 30, 1951.

Lowery and Dalquest (1951: 617) reported a specimen of *mexicanus* taken 5 kilometers east-northeast of El Jobo, 600 feet, Veracruz, on October 19, 1947. El

Jobo is a village on the road from Teziutlán, Puebla, to the Gulf of México (Lowery and Dalquest, *op. cit.*: 542). This is about 55 miles northwest of the next northernmost locality for the white-tipped morph, Plan del Río, Veracruz. In response to an inquiry concerning this specimen, I received the following comments from Mr. Phillip W. Ogilvie, Acting Curator of Ornithology, Kansas Museum of Natural History: "The skeleton of *P. mexicanus* [K.U.No. 24966] . . . is not mentioned in Dalquest's itinerary nor in his species account. In his field catalog of specimens the bird is referred to as 'Brown Jay (black-tail).' I regret to say that this specimen seems to be missing. It may be of some help to know that this skeleton was reidentified in the museum systematic catalog . . . as *P. morio morio*. I find no initials by this reidentification and therefore cannot tell you on whose authority it was made." Unfortunately, the specimen from near El Jobo is a skeleton (male) and its identification could not be verified even if it were located, but it seems clear from Dalquest's notes that it represented the brown morph, not *mexicanus* as reported.

Old literature records of the white-tipped morph at "Jalalpa," Veracruz (Cabanis, 1851, and a specimen in the British Museum (Natural History) from "Coatepec," in 1888) can, I believe, be discounted. This morph occurs on the coastal plain east of Jalapa, but there are no recent or reliable records of its presence in the vicinity of Jalapa or Coatepec, localities which have been rather extensively worked by ornithologists (Chapman, 1898; W. B. Davis, 1945; Lowery and Dalquest, 1951; Chester C. Lamb, in conversation; Selander, MS). Much the same may be said for old records of the white-tipped morph at "Mirador," Veracruz (Baird, *et al.*, 1875: 304–305; and a specimen collected by Nelson and Goldman in 1894).

EVIDENCE OF POLYMORPHISM

Irrefutable evidence of polymorphism is the finding of the different morphologic types regularly mated and producing progeny. In most birds this would be a relatively simple matter, but in *Psilorhinus* there is a series of complicating factors: (1) Brown Jays are secretive and wary in the vicinity of their nests and, hence, difficult to study, although they are extremely conspicuous and aggressive elsewhere; (2) the sexes cannot be distinguished in the field except by differences in behavior; and (3) first-year birds remain with their parents during their first year and longer, assisting them, as "helpers-at-the-nest," in raising a brood or broods in the following year (Skutch, 1935). The result is that Brown Jays are rarely found in isolated pairs even in the nesting season. Almost invariably they occur in small flocks, sometimes consisting of birds of three age groups, juvenal, first-year, and adult. Each "family" tends to remain distinct from others until the juveniles are well grown, but groups may readily join others when disturbed, as when a collector attempts to obtain all members of a group! Their occurrence in flocks is mentioned by many authors, for example, Wetmore (1943: 297), who found them "in little groups of 3 or 4 to 10" at Tres Zapotes, Veracruz.

Composition of groups.—At all nests watched by Skutch in Central America, he found at least one helper; and he mentioned one nest attended by a pair and five helpers, a situation which is not at all uncommon to judge from my experience with post-breeding groups in México. As Skutch's observations were made in Central America (Sierra de Merendón, between Guatemala and Honduras), where only the white-tipped jay occurs, they provide no evidence pertinent to the problem of relationship of the color types.

Skutch (1935: 265) reported that the helpers "seem in most cases to be yearling birds who will not have nests of their own until they are two years old." He also suggested that not all helpers are offspring of the mated pair in whose duties they assist, for the number of helpers in one group may exceed the clutch size. Skutch's claim that the helpers are first-year individuals was based on his observations that in breeding individuals the feet and bill average blacker than in non-breeding birds which assist them. My data on composition of groups, obtained by collecting some or all members, fully support Skutch's statements regarding age and reproductive status of the helpers. Because the young were fledging or had already fledged at the time of my arrival in México in June, 1957, I could not study birds at the nest. I was able to determine which two individuals of a given group were paired only by collecting most or all members of the group and examining them for evidence of breeding. However, even when watching birds at nests, it is difficult to identify the male parent with certainty, since the helpers, as well as the mated male, assist in nest building, bring food to the incubating female, and feed the young (Skutch, 1935: 95).

None of the first-year females had brood patches, and their ovaries were granular, whereas adult females invariably had brood patches and ovaries which contained larger follicles; the latter were termed "post-active." A brood patch is not present in males. The testes of first-year males apparently undergo some enlargement during the breeding season, but they are on the average smaller than those of adults. No more than one adult male and one adult female were collected from any group.

In Table 2 the composition of several family groups from the Boca del Río and Lake Catemaco regions is shown. I have selected from my records those cases in which I am confident that all birds collected or seen belonged to a single family group.

Numerous groups composed of both morphs were seen but not collected. Some examples follow: Lake Catemaco, June 23, 2 juvenal brown and 2 juvenal white-tipped birds together with a white-tipped morph having black soft parts (adult?) and a white-tipped individual

TABLE 2

COMPOSITION OF FAMILY GROUPS FROM BOCA DEL RÍO AND LAKE CATEMACO, VERACRUZ

Group and date	*Sex and age*	*Morph*	*Color of legs and feet*	*Color of bill*	*Cranium*[1]	*Length of testis (mm.)*	*Ovary*	*Brood-patch*	*Probable status in group*
1 June 12	♂ ad.	B	B	B	CO	17	—	—	Male parent
	♀ ad.	B	B	B	CO	—	Postactive	+	Female parent
	♂ 1 y	WT	¾ B	¼ B	CO	5	—	—	Helper
	♀ jv.	B	¼ B	¼ B	NCO	—	Inactive	—	Juvenile
	Other members of group not collected: one brown morph of undetermined age.								
2 June 12	♂ ad.	B	B	B	CO	"large"[2]	—	—	Male parent
	♀ ad.	B	B	B	CO	—	Postactive	+	Female parent
	Other members: juvenal white-tipped morph and a brown morph and a white-tipped morph of undetermined age.								
3 June 14	♀ 1 y	B	¼ B	¼ B	CO	—	Inactive	—	Helper
	♀ jv.	B	SY	SY	NCO	—	Inactive	—	Juvenile
	Other members: one white-tipped morph and 3 or 4 brown morphs of undetermined age.								
4 June 14	♂ ad.	B	?	?	CO	10	—	—	Male parent
	♀ ad.	B	B	B	CO	—	Postactive	+	Female parent
	♂ 1 y	B	B	B	CO	?	—	—	Helper
	♀ 1 y	WT	½ B	⅓ B	NCO	—	Inactive	—	Helper
	? jv.	B	Y	Y	NCO	—	—	—	Juvenile
	? jv.	B	Y	Y	NCO	—	—	—	Juvenile
	♂ jv.	B	Y	Y	NCO	3	—	—	Juvenile
	♂ jv.	B	Y	Y	NCO	3	—	—	Juvenile
	Other members: none.								
5 June 15	♀ ad.	WT	B	B	CO	—	Postactive	+	Female parent
	♂ jv.	B	Y	Y	NCO	3	—	—	Juvenile
	♀ jv.	B	Y	SY	NCO	—	Inactive	—	Juvenile
	Other members: one juvenal brown morph and one brown morph with black soft parts, possibly the male parent.								

TABLE 2 *(continued)*

COMPOSITION OF FAMILY GROUPS FROM BOCA DEL RÍO AND LAKE CATEMACO, VERACRUZ

Group and date	*Sex and age*	*Morph*	*Color of legs and feet*	*Color of bill*	*Cranium*[1]	*Length of testis (mm.)*	*Ovary*	*Brood-patch*	*Probable status in group*
6 June 26	♀ ad.	B	B	B	CO	—	Postactive	+	Female parent
	♀ 1 y	B	Y	SY	CO	—	Inactive	—	Helper
	♂ jv.	WT	SY	SY	NCO	3	—	—	Juvenile
	♀ jv.	B	SY	Y	NCO	—	Inactive	—	Juvenile
	♂? jv.	B	SY	SY	NCO	?	—	—	Juvenile
	♂ jv.	B	Y	Y	NCO	3	—	—	Juvenile
	Other members: two birds of undetermined morph-type and age.								
7 June 28	♀ ad.	WT	B	B	CO	—	Postactive	?	Female parent
	♀ 1 y	B	SY	Y	NCO	—	Inactive	—	Helper
	♂ jv.	B	¼ B	½ B	NCO	4	—	—	Juvenile
	♀ jv.	B	Y	SY	NCO	—	Inactive	—	Juvenile
	Other members: two or three birds of undetermined morph-type and age.								
8 June 28	♂ ad.	B	B	B	CO	7	—	—	Male parent
	♀ ad.	WT	½ B	½ B	CO	—	?	+	Female parent
	♀ 1 y	B	Y	SY	CO	—	Inactive	—	Helper
	Other members: none.								

[1] CO = completely ossified; NCO = not completely ossified.
[2] Testes demolished by shot.

with large yellow areas on the bill (first-year?); near Minatitlán, July 1, 5 brown and 1 white-tipped; 8 miles north of Matías Romero, July 10, 5 brown (including at least 1 juvenile) and 1 white-tipped; 10 miles north of Matías Romero, July 11, 1 adult (?) brown and 1 adult or first-year white-tipped with 2 juvenal brown; Angel R. Cabada, July 26, 6 brown and 2 white-tipped; Paso del Toro, July 26, 1 adult (?) brown with a white-tipped juvenile.

Older individuals were seen feeding juveniles of dissimilar morph-type on several occasions, as follows: San Andrés Tuxtla, June 23, juvenal white-tipped morph fed by an adult (?) brown; Minatitlán, July 2, juvenal white-tipped bird fed by first-year (?) brown; 10 miles north of Matías Romero, July 11, adult (?) white-tipped bird fed a juvenal brown; Tapalpa, near Santiago Tuxtla, July 26, adult (?) brown fed a juvenal white-tipped bird.

In June, family groups were more or less localized, being found in the same stands of trees on different days. By the first week in July, larger groups were forming and apparently wandering to a greater degree.

The data on composition of groups do not provide conclusive evidence as to the mode of inheritance of color differences. To solve this problem, cases in which similarly colored birds mate to produce offspring of the other morphic type or both types are needed. The association of a juvenal white-tipped morph with a post-breeding adult female brown morph and an adult male brown morph in group 2 strongly suggests that brown is dominant. It would be conclusive evidence were it not for the fact that the group included a white-tipped morph of undetermined age. It is possible, although improbable, that this bird was the male parent. If in fact the adult male and female pairs in groups 1 and 4 are the parents of the white-tipped first-year birds in their respective groups, brown is dominant to the white-tipped phase. However, as mentioned previously, there is some evidence that helpers may be associated with family groups other than their own.

Behavior.—As regards behavior, I found no difference between the morphs. Wetmore (1943) was equally impressed with their similarity, noting that "Possibly there are slight differences in note and habit between the two species of jays found at Tres Zapotes, but if so my period of observation in 1939 was not sufficient to allow me to detect them. It appeared at times that *morio* produced a louder snapping noise . . . but of this I was not certain. Both seemed equally inquisitive and vociferous, and both ranged through the same areas." I was unable to confirm Wetmore's suggested difference. The calls of the

two morphs were compared in the field, recorded on tape, and subsequently compared again. They are identical.

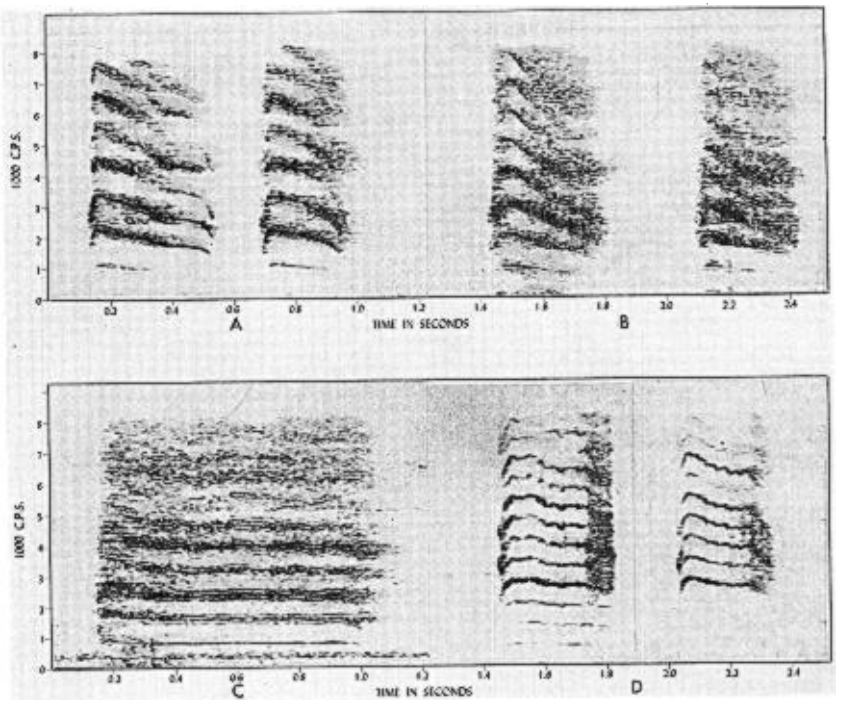
Wetmore noted that the furcular sac or pouch (a diverticulum of the interclavicular air-sac, see Sutton and Gilbert, 1942) of one of his specimens of the brown type "was a little smaller than those of the individuals of the other species examined and the sac seemed a little thicker walled." He was apparently correct in supposing that this represented individual variation, for I found no difference in structure of the pouch in the two morphs. There is, however, some age variation in structure. In juveniles the pouch itself is not firmly fused to the integument and may be pulled away with comparative ease, whereas in first-year and adult specimens, it cannot be separated from the integument.

The Brown Jay seems not to have a great variety of different calls. A characteristic call is a loud, low *pay-ah,* which is delivered repeatedly by members of groups as they move through the trees. As the birds become apprehensive at the approach of a human, or when they are "mobbing" a hawk, the *pay-ah* is gradually modified to a loud scream which is higher-pitched and more strongly accented (Plate 16). This has an obvious warning function. Sudden expansion of the furcular pouch as the call begins produces a low *pop,* which gives an almost explosive accent to the *pay* part of the call. The *pop* is not clearly audible at a distance and does not show well in sound spectrographs. Popping noises are sometimes made without the call, but their primary function is undoubtedly that of accenting the call. As a disturbed bird flies from a potential source of danger, the *pay-ah* calls rise in pitch and are given without the accenting *pop;* they are also given more rapidly. Once the warning call is sounded, all birds leave the immediate area. When scolding at low intensity, the *pay-ah* call may be extended in length to almost a full second (Plate 16).

The jays also make soft foraging notes that are difficult to describe, but which are unlike the usual ringing flock calls. Juveniles have a distinctive, short *hew* note and also call as do older birds, but more softly and at a higher pitch. They apparently do not scream or accent their calls with popping sounds, and their *pay-ah* note is often rendered *pay-ah-ah.*

The vocalizations of birds at Campeche were notably higher-pitched than those of birds heard elsewhere in México. This is correlated with their markedly smaller body size.

Size comparisons.—When specimens from any one region are segregated with respect to sex and age, there are no differences in size between the two color types. In Tabasco and Chiapas, both types are smaller than farther north (see Fig. 3). These facts have bearing on the problem of the relationship of the two color types and strongly support other lines of evidence indicating polymorphism. The prob-



SOUND SPECTROGRAPHS OF JAY CALLS. Calls of Brown Jay, *Psilorhinus,* recorded at Boca del Río, Veracruz, México: A, Two *pay-ah* calls of brown morph; B, Same call, white-tipped morph; C, Long version of call of brown morph. D, For comparison: Two calls of Blue Jay, *Cyanocitta cristata,* from Austin, Texas.

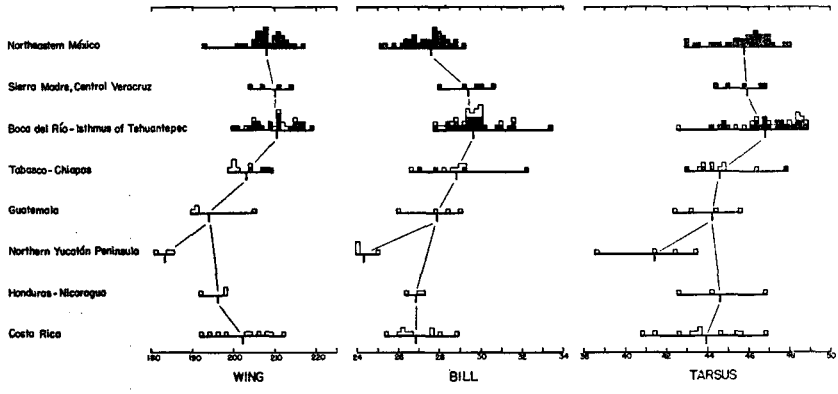


FIGURE 3. Individual and geographic variation in size in *Psilorhinus morio*. Black squares represent brown morph; open squares, white-tipped morph. Geographic contact between populations is indicated by narrow line connecting sample means. Measurements in millimeters.

ability of two species of identical size existing for any length of time in the same area without differences in habitat occurrence or feeding habits is remote. That two such species would vary geographically in precisely parallel fashion is equally improbable.

Molt.—All first-year and adult specimens taken in June and July were in fall molt, and careful comparisons of molt progress in specimens of the two morphs failed to reveal any significant difference.

MORPH-FREQUENCY AND RATIO-CLINES

Only a few authors have mentioned the relative frequency of the two morphs in particular areas, and no actual counts have been available for any locality within the range of the polymorphic population. During the summer of 1957, I made censuses in 13 different areas in eastern México from central Veracruz south to Palenque, Chiapas; these data are summarized in Table 3. Additional counts were made in northeastern México north of Veracruz and in Campeche. The data were obtained by recording all identified birds seen and/or collected at each locality. Any bias existing in these counts is in favor of the brown morph, since they were made at a time of the year when the tail feathers and other parts of the plumage were badly worn in many individuals. Thus, it is possible that some extremely worn white-tipped birds were mistakenly identified in the field as the brown morph. Counts made in fall or winter perhaps would be more accurate.

TABLE 3

MORPH-FREQUENCIES IN 1957

Locality	*Total number seen and/or collected*	*Per cent white-tipped morph*	*Period*
Coatepec region, Veracruz	35	0.0	June 7–9
Fortín region, Veracruz	36	0.0	July 27–29
Omealca, Veracruz	17	11.8	June 16
Boca del Río region, Veracruz	143	24.5	June 9–15
Riparian	111	19.8	
Coyol woodland[1]	32	40.6	
Angel R. Cabada-Santiago Tuxtla, Veracruz	17	52.9	July 26
Lake Catemaco, Veracruz	149	48.3	June 23–30 July 6–7, 26
Hueyapan region, Veracruz	14	71.4	July 7–8
Minatitlán, Veracruz	31	38.8	July 1–3
Jáltipan-Cosaleacaque region, Veracruz	26	11.5	July 3–5
Matías Romero region, Oaxaca	48	41.7	July 10–12
Teapa, Tabasco	48	27.1	July 15–17
Palenque, Chiapas	46	76.1	July 18–22

[1] 12 miles south of Boca del Río.

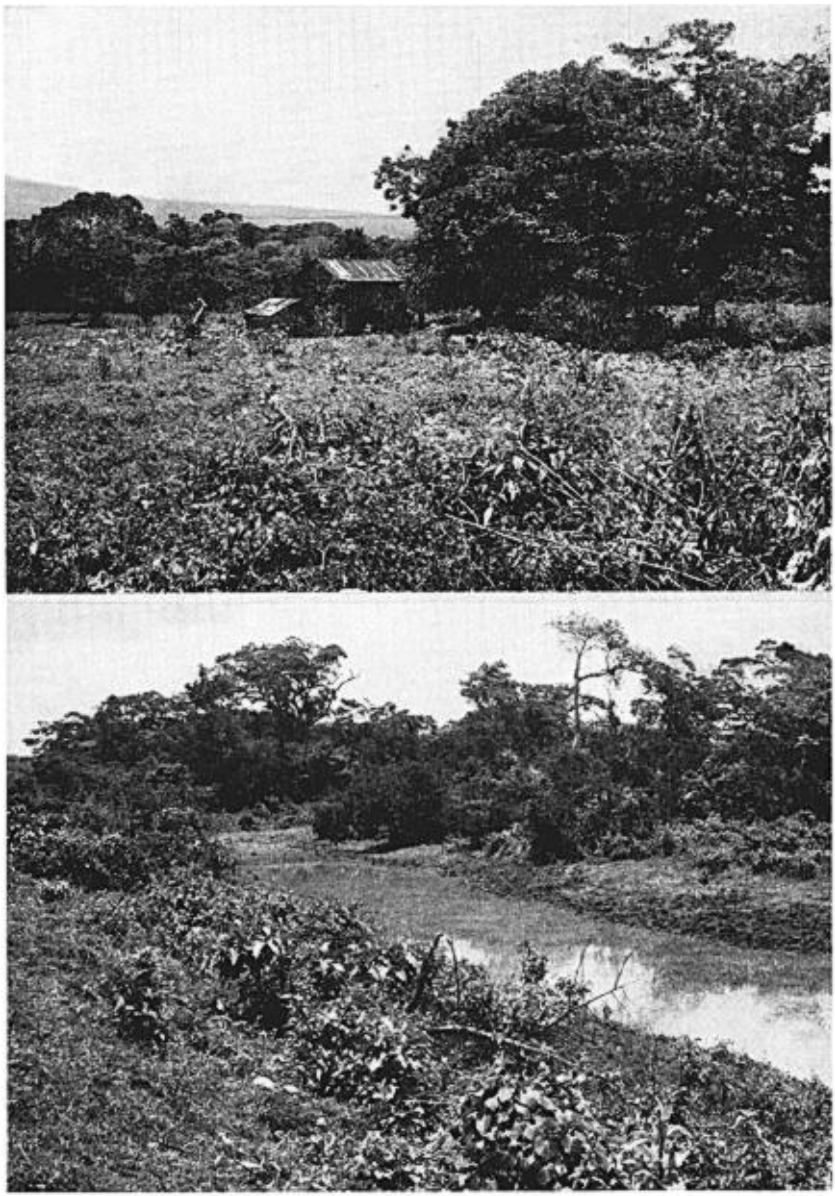
Fortín de las Flores-Boca del Río ratio-cline.—The population of *Psilorhinus* in the coffee zone of the Humid Upper Tropical Zone of the Fortín de las Flores-Córdoba region in west-central Veracruz is monomorphic brown. These localities are 3000 to 3500 feet in elevation in a region having an annual rainfall of 2270 millimeters, with no well-defined dry season (Contreras Arias, 1942). East of Córdoba the land slopes off to about 1330 feet at San Juan de la Punta (Cuitláhuac), which locality marks the division between the Humid Upper Tropical and Arid Lower Tropical zones; the latter zone extends to Boca del Río on the Gulf coast south of Veracruz City and south almost to the Isthmus of Tehuantepec (Lowery and Dalquest, 1951).

At Córdoba and Fortín, and in the Barranca Metlac a few kilometers north of Fortín, the Brown Jay is fairly common and widely distributed ecologically, although it is more often found in stands of forest bordering coffee groves than in other vegetation types (Plate 17). Of 36 birds seen or collected between July 27 and 29, 1957, all were the brown morph. The same region was visited for a short time in 1952 and 1954, and my notes show only records of the brown morph. Likewise, Lowery and Dalquest (1951: 618) did not encounter the white-tipped type here. Possibly it is occasionally found on the floor of the Barranca Metlac near Fortín, as residents of Rincón Brujo, a village in the Barranca reached by a side road leaving the Córdoba-Orizaba highway at Kilometer 326, were familiar with it and claimed to have seen it there.

It may be noted here that near Coatepec, approximately 40 miles north of Córdoba, at an elevation of 4680 feet, only the brown morph was recorded during a short visit in 1952 and from June 7 to 9, 1957. Vegetation at Coatepec is similar to that at Fortín and Córdoba.

Near Omealca, a small village near the Río Blanco, 6 miles southwest of San Juan de la Punta, at an elevation of 1370 feet, jays were common in riparian situations, citrus fruit orchards, banana groves, and other vegetation types. Climatic

(Above) Humid evergreen forest in Barranca Metlac, near Fortín de las Flores, Veracruz. Population at this locality is monomorphic brown. *(Below)* Coyol woodland 12 miles south of Boca del Río, Veracruz.



(Above) Habitat of *Psilorhinus* at Lake Catemaco, Veracruz. Approximately equal numbers of the two morphs occur in this region. *(Below)* Deciduous vegetation inhabited by *Psilorhinus* near Hueyapan, Veracruz.

data are not available for Omealca; but to judge from the growth forms of the dominant vegetation types, this is a region having a climate intermediate between those of the arid coastal plain to the east and the humid coffee zone to the west and north at higher elevations. Zonally the region is Upper Tropical. Of 17 jays seen here on June 16, 2 (11.8 per cent) were the white-tipped type.

On the coastal plain between San Juan de la Punta and the Gulf at Boca del Río, jays were encountered infrequently, and then usually in wooded arroyos or along the Río Atoyac. Woody vegetation over much of the coastal plain consists of shrubs and short trees which provide habitat not well-suited to these large jays. Annual rainfall is less than 1500 millimeters in many areas and is markedly seasonal. At Veracruz City, on the coast, annual rainfall is 1623 millimeters, and 86 per cent of it falls between June and October. However, along the rivers and streams, narrow stands of mangos, figs, guanacastes, and other large trees provide ideal habitat. In riparian vegetation in the vicinity of Boca del Río, the frequency of the white-tipped morph was 19.8 per cent; and 12 miles south of Boca del Río, in stands of coyols (Plate 17), a decidedly more xeric habitat type, the frequency was 40.6 per cent. The latter figure is based on a relatively small sample of birds and requires confirmation. Irby Davis (in conversation) reported a frequency of about 25 per cent white-tipped type in the La Piedra region, approximately 16 miles south of Boca del Río. The vegetation, as described by Davis (1952), is subhumid tropical grassland and wood mixture.

Catemaco region.—Headquarters were established at Playa Azul on the shore of Lake Catemaco, and studies were made at several points around the lake between elevations of 1000 and 1500 feet. Goldman (1951: 269) described this region as follows: "Cloud formations from over the Gulf discharge most of their moisture on the Sierra de San Martín, and the vicinity of Catemaco behind [west of] this mountain barrier is near the borderline between the Arid [Lower] and Humid [Upper] Tropical areas. The low hills, plains, and valleys about the western side of the lake are rather dry, being covered with small and sparse arboreal vegetation, and some open, grassy llanos are encountered. Elsewhere the heavy Humid Tropical forest prevails, descending to the water's edge along the eastern shore of the lake. Mahogany and Spanish cedar are among the forest trees."

Rainfall at San Andrés Tuxtla, about 5 miles east of Catemaco, is 2113 millimeters, and there is a dry season extending from January to May (Contreras Arias, 1942).

Brown Jays were found in greater numbers at Catemaco than at any other locality visited. They were abundant in fence rows, wooded arroyos, hillside woodland and forest bordering fields, and banana and citrus fruit trees (Plate 18). In smaller numbers they occurred also in coffee groves and disturbed stands of broadleafed evergreen forest on the eastern side of the lake. Apparently the great diversity of vegetation types in this region favors high population densities, but there were no differences between the morphs as regards habitat occurrence.

A total of 149 jays was recorded, of which 48.3 per cent were the white-tipped morph.

Between Angel R. Cabada and Santiago Tuxtla, 5 to 10 miles west-northwest of Catemaco, 8 brown and 9 white-tipped birds were counted on July 26; the percentage white-tipped is 52.9. These localities are at slightly lower elevations than Catemaco, but the vegetation types are similar.

Hueyapan region, Veracruz.—Collections and counts were made at Hueyapan, 20-25 miles south and inland from Lake Catemaco, on July 7 and 8. This area

lies within the rain shadow of the Tuxtla Mountains, in the Arid Lower Tropical Zone at an elevation of 300 feet. Jays were only moderately common here, frequenting deciduous woodland having a dense understory of thorny shrubs (Plate 18), a distinctly more xeric type of vegetation than those occupied by jays at Catemaco. Only 14 jays were counted, 71.4 per cent of which represented the white-tipped morph. These data suggest a higher frequency of this morph at Hueyapan than at Catemaco, but confirmation by a larger count is desirable.

Minatitlán and Jáltipan-Cosaleacaque regions, Isthmus of Tehuantepec.—On July 1, headquarters were established at Minatitlán and studies were made in this region through July 5. Censuses were made at a point 2 miles northeast of Minatitlán and at Jáltipan de Morelos and Cosaleacaque, villages 15 and 10 miles east, respectively, of Minatitlán. The climate of this general area is more or less intermediate between those of the Arid and Humid Lower Tropical life-zones. At Minatitlán rainfall is high (3085 millimeters) and there is no well-defined dry season; but, apparently because of edaphic factors, the dominant vegetation types are grassland and palm savannah. There are also numerous marshes and boggy areas supporting stands of tall mesic vegetation. Jays were common in these stands but were everywhere less numerous than at Catemaco. At Cosaleacaque and Jáltipan, jays were found in stands of mesic vegetation along the highway and in patches of tall forest between agricultural fields.

The white-tipped morph was relatively less common at Cosaleacaque and Jáltipan than at Minatitlán (see Table 3), but the census data are not entirely reliable because of the small size of the samples. Combining census data from the three localities, the percentage of the white-tipped type is 26.3, based on a total of 57 birds.

Nanchital-Agua Dulce region, Veracruz.—On July 2, I drove from Coatzacoalcos to Nanchital and thence east to Agua Dulce (Tonalá) on the Río Tonalá about 20 miles east of Coatzacoalcos. This region apparently is more humid than Minatitlán, and the abundant rainfall supports a tall evergreen forest having a notable development of epiphytes. The original vegetation is relatively undisturbed except for scattered small villages and roads which cut through the forest to provide access to oil wells. Jays were sparsely distributed here and only 8 were identified; all represented the brown morph. L. I. Davis and Morony (1953) reported the brown but not the white-tipped morph from a census plot in humid tropical grassland and woods mixture 17 miles east (by road) of Nanchital, and L. I. Davis (1955) noted the "complete absence of jays of any kind" in "virgin" lowland tropical forest 10 miles south (by road) of San José del Carmen, or about 30 miles south of Agua Dulce. Further investigation in this area is indicated; possibly the population is monomorphic brown.

Matías Romero region, Isthmus of Tehuantepec.—From July 10 to 12, jays were studied along the highway across the Isthmus of Tehuantepec. In humid and, locally, mesic evergreen tropical forest and woodland along the highway from 4.1 to 70 miles north of Matías Romero, 48 Brown Jays were collected or observed, 41.7 per cent of which were the white-tipped morph. Forests in this region are relatively undisturbed, and, as a result, jays are not so abundant as in the Catemaco region or other more heavily settled areas.

Lowery and Dalquest (1951: 618) report finding only the white-tipped type "along the Río Coatzacoalcos, in southern Veracruz." However, both morphs occur in this region, and the brown is at least as common as the white-tipped morph.

F. W. Loetscher, Jr., reports (in letter) that the brown morph was "overwhelmingly in the majority around Jesús Carranza" in August, 1937, and March, 1939; and Amadon and Eckelberry (1955: 76) found the brown in greater numbers than the white-tipped type along the Río Jaltepec, a tributary of the Río Coatzacoalcas.

The point of contact on the Isthmus between *Psilorhinus* and *Calocitta* was located by driving along the highway and stopping to investigate wooded arroyos. At a point 4.8 miles north of Matías Romero, a group of *Psilorhinus* consisting of 6 white-tipped and 3 brown morphs was present in a stand of forest composed of a mixture of humid and xeric elements. A small group of brown morphs was noted in a similar situation 4.1 miles north of Matías Romero. At a point 3 miles north of Matías Romero, a low ridge, the Continental Divide, was crossed. In the next arroyo, 2.3 miles north of Matías Romero, a family group of *Calocitta* was found in vegetation only slightly more xeric than that in which *Psilorhinus* occurred 1.8 miles to the north. Other groups of *Calocitta* were seen in typical Pacific coastal plain vegetation 15 miles south of Matías Romero.

The Green Jay *(Cyanocorax yncas)* was present with *Calocitta* in the arroyo 2.3 miles north of Matías Romero and is fairly common throughout the humid part of the Isthmus to the north, where it is sympatric with *Psilorhinus*. The Green Jay frequents understory vegetation, whereas the larger jays are more often found in the upper vegetational strata.

Teapa, Tabasco.—Teapa lies at an elevation of about 225 feet at the base of the mountains which form the highland plateau of central Chiapas (Fig. 2). Annual rainfall is 3967 millimeters and is rather well distributed throughout the year; April is the driest month, with 144 millimeters. Rain fell almost continuously during my stay in July.

On the hillsides just south of town, heavy rain forest has been partly cleared for coffee and pitaya, providing excellent habitat conditions for jays. Residents of Teapa reported that Brown Jays were also abundant in coffee fincas at higher elevations. On the coastal plain from one to three miles north of town, where rainfall is less abundant and the land is more extensively cultivated, jays were common in pastures, along streams, and in narrow stands of forest between milpas. The general aspect of the vegetation is closely similar to that at Omealca, Veracruz.

Morph-frequency was similar in the hills and on the coastal plain; 27.1 per cent of 48 birds recorded within a three-mile-radius of Teapa represented the white-tipped morph.

Nothing is known concerning morph-frequency on the extensive coastal plain of Tabasco north of Teapa. A few Brown Jays were heard 5 miles south of Villa Hermosa, on July 14, but the morph-type was not determined. *Cissiolopha yucatanica* was present at Villa Hermosa and Teapa, where it occupied the same types of habitat situations frequented by *Psilorhinus*. At both localities it is apparently less common than *Psilorhinus*.

Palenque, Chiapas.—Palenque lies at an elevation of 750 feet at the dividing line between forested foothills to the south and grassy plains to the north. Annual rainfall is approximately 3200 millimeters and there is no marked dry season. "The dense, humid, tropical forest of the mountain slopes and foothills gives place to a smaller growth on the plains, and large areas between Palenque and Monte Cristo are open savanna interrupted by, or alternating with, irregular patches and belts of timber" (Goldman, 1951: 108). Ecology of the rain forest in the vicinity of the archaeological ruins of Palenque was studied by Goodnight and Goodnight (1956), and Tashian (1952) reported on a small collection of birds from Palenque.

I found *Psilorhinus* scarce along rain forest edges at the ruins but not uncommon in forest remnants, cafetales, riparian growth, and meadows near town from July 18 to 22. The white-tipped morph predominated (Table 3), but 23.9 per cent of birds recorded were the brown morph.

There are records of white-tipped morphs from the mountains of central and northern Chiapas near San Fernando, Ocosingo, and El Real (Fig. 2). Rainfall is considerably less at these localities than at either Teapa or Palenque; at Ocosingo annual precipitation is 1666 millimeters (Contreras Arias, 1942).

GEOGRAPHIC VARIATION IN OTHER CHARACTERS

Morph-frequency is one of several geographically variable characters in *Psilorhinus*. There are other more or less independent patterns of geographic variation in color and in size.

Size.—Individual and geographic variation in length of wing, bill, and tarsus in adult males is shown in Figure 3. Wing length is uniform in México north of Tabasco and Chiapas, but there is some suggestion of slightly longer average wing length in polymorphic populations of central and southern Veracruz. In material from Central America (Guatemala, Honduras, Nicaragua, and Costa Rica), the wing is somewhat shorter, on the average, and birds from the northern Yucatán Peninsula have markedly shorter wings. A similar pattern of geographic variation is apparent in tail length.

There is close similarity in geographic patterns of variation in bill length and body weight. Birds from Veracruz, including the Sierra Madre and the lowlands, are significantly heavier and have longer bills than those from northeastern México north of Veracruz. Central American populations average lighter in weight and are shorter-billed. In the Yucatán population minimal size is manifest.

In tarsal length the polymorphic populations of Veracruz average slightly larger than those of northeastern México and the Sierra Madre of Veracruz. Again minimal size is seen in Yucatán birds. In all characters of size, the polymorphic population of Tabasco and Chiapas falls in a position intermediate between the adjacent large-sized, polymorphic population of Veracruz and the moderate-sized, monomorphic Guatemalan population.

Color.—An objective analysis of geographic variation in color has been possible through use of a Photovolt Meter registering percentage reflected light (see Blair, 1949, for details of the technique). Because the equipment is not designed to measure unfiltered (white) light, a red filter was used for all readings. The amount of light reflected from a porcelain block was taken as a standard of 100 per cent reflectance, and a piece of black velour paper served as a standard of 0 per cent reflectance. Small numbers are obtained for dark shades, large numbers for light shades. Results obtained with the Photovolt Meter (Fig. 4) agree closely with those of subjective evaluation of individual and geographic variation in darkness and lightness (value) of the areas of the specimens studied.

Individual and geographic variation in color of the abdomen and breast in adults was studied (Fig. 4). There is no significant sexual variation in color. The wide range of variation seen in any one sample results in some part from differences in degree of seasonal fading, but the data provide at least a good indication of geographic trends in color.

In Tamaulipas and Nuevo León, the abdomen is markedly lighter than in other

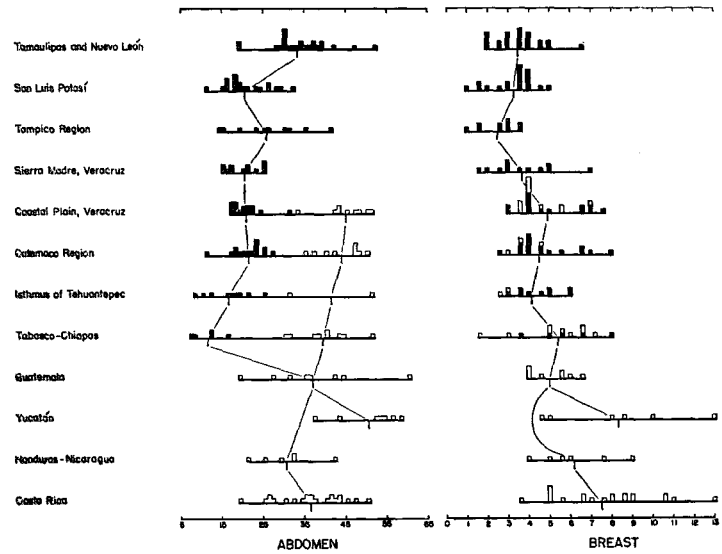


FIGURE 4. Individual and geographic variation in shade of abdomen and breast. Scale indicates percentage reflectance of red light. Black squares represent brown morph; open squares, white-tipped morph.

monomorphic brown populations or in brown morphs from Veracruz, Oaxaca, Tabasco, and Chiapas. The color is similar to that of monomorphic white-tipped birds from Central America. The "influence" of this light population is seen to some extent in the sample from the Tampico region. Brown morphs from San Luis Potosí south to the Catemaco region have dark abdomens; and there is a clinal increase in darkness south from the Catemaco region to Tabasco and Chiapas. In some specimens from Tabasco and Chiapas, the abdomen is nearly as dark as the breast and back.

In the white-tipped morph, abdominal color varies clinally from 45 on the coastal plain of Veracruz to about 31 in Honduras and Nicaragua and 30 in Costa Rica. It will be noted that in samples of the polymorphic populations there is no overlap in color between the morphs.

Breast color changes clinally from dark in northeastern México to light in Central America and the Yucatán Peninsula. The polymorphic populations apparently are slightly lighter than monomorphic populations to the north, and there is no significant difference in breast color between the morphs in any one population.

The fact that breast color is paler in birds from Tabasco and Chiapas than in those from the Isthmus of Tehuantepec and Lake Catemaco requires explanation. All but one specimen from Tabasco and Chiapas were collected in late July and are, on the average, more worn and faded than are specimens from the other regions. In all probability fresh adult specimens from Tabasco and Chiapas would average even darker than those from Veracruz. In any event, this is the case in juvenal specimens collected in June and July, 1957.

John Davis (1951) has called attention to geographic variation in intensity of

the bluish or glaucous sheen on the outer webs of the rectrices. This sheen is also present on the outer webs of the remiges and their greater upper coverts and on the inner web of rectrices 1-1. The character is best developed in northeastern México, being conspicuous in almost all specimens from Tamaulipas, Nuevo León, and San Luis Potosí. It is less intense, and occasionally all but absent, especially on the wings, in specimens from the Sierra Madre and lowlands of Veracruz. In specimens from Oaxaca, southern Veracruz, and Chiapas, it is usually barely visible. Practically no bluish cast is present in specimens from Central America and the Yucatán Peninsula. In Veracruz, Tabasco, and Chiapas, the character is equally well developed in both morphic types.

Another character showing geographic variation is degree of development of the triangular malar patch. The patch is most conspicuous in birds from Costa Rica and the Yucatán Peninsula, where it frequently has a gray or bluish cast. It is relatively inconspicuous in birds from Guatemala, Chiapas, Tabasco, Oaxaca, and Veracruz, and it is only slightly more apparent, on the average, in birds from northeastern México. In occasional variants of either morph from Veracruz, the patch is as conspicuous as in specimens from Costa Rica and Yucatán (Ridgway, 1904: 302).

POLYMORPHISM: TRANSIENT OR BALANCED?

As pointed out by Ford (1940, 1945), genetically controlled polymorphism includes two different conditions: (1) *transient polymorphism,* in which an advantageous gene is in the process of spreading through a population, and (2) *balanced polymorphism,* in which an advantageous gene is maintained at some fixed level of frequency in a given population by a balance of selective agencies. The former is a temporary condition maintained only during the time that a gene is in the process of replacing its allelomorph, whereas balanced polymorphism is characterized by stability of morph-ratios in time. The simplest stable equilibrium occurs when a heterozygote has a selective advantage over either homozygote. Various examples of these phenomena are cited by Ford (1945).

If polymorphism in *Psilorhinus* is transient, we may expect to find evidence of change in morph-frequencies in already polymorphic populations and/or extension of range of one or both morphs. Conclusive evidence is not presently available and will not be for some time to come, but the few data bearing on the problem suggest that polymorphism in *Psilorhinus* is balanced.

In 1939, Wetmore (1943: 297) found the two morphs "in about equal number" at Tres Zapotes, Veracruz, and, as noted elsewhere, in 1957 the percentage of the white-tipped morph in the adjacent Catemaco region was 48.3. The two areas differ climatically, so perhaps comparisons ought not to be made; but at the present time this is the nearest we can come to comparing frequencies in different years for any locality within the range of the polymorphic populations.

It is possible that the white-tipped morph formerly occurred in low frequency

in northeastern México and in the Sierra Madre of central Veracruz, where today populations apparently are monomorphic brown. This is suggested by Rüppell's record of the white-tipped morph in Tamaulipas and old records of it at "Jalapa," "Coatepec," and "Mirador" (see pp. 392–3). Rüppell's specimen was taken sometime prior to 1837. The "Jalapa" specimen was collected over 106 years ago (reported in 1851 by Cabanis); the "Coatepec" specimen was collected in 1888; and the first "Mirador" specimen was taken prior to 1887. Nelson and Goldman also collected a white-tipped morph at "Mirador" on February 3, 1894. However, considering the looser practices in labeling and reporting of specimens collected in México in the 1800's, it would be most unwise to assume that changes in gene-frequency have occurred in these areas on the basis of these early records. Many species of birds which in Veracruz are in fact restricted to xeric habitats on the coastal plain have been erroneously reported from "Jalapa" and "Mirador" (see remarks by Chapman, 1898: 16–18).

Little is known concerning the degree of stability of the southern limit of distribution of the brown morph. A specimen from Montecristo, Tabasco, was collected by Nelson and Goldman on May 3, 1900. In 1939, Eizi Matuda and three assistants collected from May 9 to 20 at Balancán, Tabasco, a town on the Río San Juan Pedro approximately 15 miles east of Montecristo (Brodkorb, 1943). Matuda's collection included four specimens of the white-tipped but none of the brown. It is probable, therefore, that the brown morph had not extended its range beyond Montecristo in the interval from 1900 to 1939. Further work is badly needed here, as elsewhere in México, before the problem of transient or balanced polymorphism is finally resolved.

DISCUSSION

Study of patterns of ratio-clines may be expected to provide clues to environmental selective agencies maintaining balanced polymorphism (Huxley, 1955). In *Psilorhinus* it is obvious that the subject is fairly complex and will require further investigation, but sufficient data are available to justify a tentative interpretation. Before proceeding, it may be well to point out that the obvious color differences distinguishing the morphs probably do not have great significance in themselves. The particular character or characters being selected may well be of a physiological nature, perhaps having to do with temperature or humidity tolerance. Most known polymorphisms involve apparent non-adaptive correlates of physiological or fitness characters having selective value (Huxley, 1955: 311). On the other hand, the brown morph is relatively less conspicuous against a background of dark, evergreen vegetation than is the white-tipped morph, and the light colors of the latter may be more advantageous in xeric habitats. Therefore, the possibility that color and pattern types themselves have differential adaptive values, at least in some areas, cannot be completely ruled out.

If we consider only the polymorphic population occurring from central Veracruz south and east to Teapa, Tabasco, it appears that

there is a general relation between morph-ratios and climate. Temperature varies little over much of the range of the polymorphic population, but there are major variations in rainfall and atmospheric humidity. Relatively large percentages of the white-tipped morph are found in populations in arid or mesic environments, and a predominance of the brown morph is seen in the more humid areas.

In the field this relationship was first evident in the transect from Boca del Río up the eastern slope of the Sierra Madre of central Veracruz through Omealca to the Fortín-Córdoba region. In this situation it is unlikely that altitude itself has any direct effect, but precisely what factor or combination of factors acts as a selective agency is unknown. The apparent higher percentage of the white-tipped morph in xeric coyol woodland south of Boca del Río, as compared to that in the more mesic riparian vegetation along the Río Atoyac, is of interest in this connection. In this region riparian stands of trees provide avenues of dispersal between the Sierra Madre and the mesic lowlands near the coast, whereas the coyol woodland is relatively more isolated from the brown populations in the mountains. This introduces an important aspect of the problem being considered. The relative frequency of the two morphs in any one limited area will depend, among other things, on the interaction and balance of local selective forces and gene-exchange with populations in adjacent areas in which selective forces and, hence, the morphic composition of the population, may differ considerably. These facts must be considered in interpreting the significance of morph-frequencies at different localities.

At Lake Catemaco, mesic conditions exist, and, to judge from the abundance of jays, provide optimum habitat for the species. The two morphs are about equally common. At Hueyapan, in a decidedly more xeric environment, the white-tipped morph seemingly predominates. Considering general climatic conditions at Minatitlán, a percentage of 38.8 for the white-tipped morph is not surprising, but the Jáltipan-Cosaleacaque ratio is unexpectedly low in white-tipped morphs. A ratio of 50:50 would seem more in line with expectations based on observations at Catemaco and elsewhere to the north. The percentage of white-tipped morphs (41.7) in the Matías Romero region is not far out of line, although a rather lower frequency might be expected considering the relatively humid climate of that region.

At Teapa, conditions are even more humid than at Fortín de las Flores and Catemaco, and, on this basis, following the hypothesis suggested, a monomorphic brown population might be expected. However, the town lies only a few miles inland from mesic savannah on the coastal plain, so that influx of genes may be expected (see, also, beyond).

The high frequency (76.1 per cent) of the white-tipped morph recorded at Palenque is way out of line and totally unexpected, but this does not necessarily negate the hypothesis. Even neglecting morph-frequencies, the Palenque population obviously is genetically different from those in Veracruz; this is evidenced in body size and in color of upper parts and breast. Morphologically, the population approaches populations of medium-sized birds of Guatemala and

Central America, which are monomorphic white-tipped. It is possible that the brown gene or super-gene (Ford, 1955) has distinctly lower survival value on the genetic background or "genetic environment" (Mayr, 1954) of the Palenque population than on backgrounds of other polymorphic populations. Moreover, it is unlikely that environmental selective forces are the same at Palenque as at Fortín, several hundred miles to the north. This same explanation would also help account for the high percentage of white-tipped morphs in the morphologically similar population at Teapa, Tabasco.

In Guatemala and other parts of Central America, Brown Jays occur in regions fully as humid as those in Veracruz, and also in mesic and xeric environments, but the populations are uniformly white-tipped. We may presume that either (1) the brown gene or super-gene is disadvantageous in these regions on the genetic background of these populations, or (2) the brown gene has not yet reached these populations. The former seems more probable. There are many species in which dimorph-clines connect monomorphic populations (Ford, 1945: 82). A polymorphic situation may be advantageous in one part of the range of a species but not in other parts.

North of central Veracruz, Brown Jays inhabit humid areas, as at Xilitla, San Luis Potosí, and xeric environments, as in Tamaulipas and Nuevo León, yet these populations are uniformly monomorphic brown. Again the question arises as to why the other morph is absent, and the suggestions made in reference to the Central American situation may well apply, but in reverse. It is possibly significant that in Tamaulipas and Nuevo León, where jays occur in particularly xeric habitats, birds have light abdomens; they approach in this character the white-tipped morph of Veracruz, although the tail is not white-tipped. Perhaps similar physiological adaptations to arid habitats have been made in both areas, but in the former case without development of the genetic mechanism responsible for visible polymorphism.

Just north of the northern limit of the white-tipped morph in Veracruz, the Sierra closely approaches the Gulf coast and the climate is humid on the coastal plain (Fig. 2). If in central Veracruz genotypes which have the white-tipped gene are disadvantageous under humid conditions, this humid zone would serve as a barrier, or at least a "bottle-neck," to dispersal of genes into more northern populations. The effect would be to lessen the rate of flow of white-tipped genes into these populations, thereby decreasing the probability of their reaching areas in which they might not be subject to elimination by counter-selection, if indeed such areas exist. There is, it should be

noted, no comparable "bottle-neck" to gene dispersal at the other end of the polymorph area.

Corvid evolution and relationships in México and Central America are not by any means well understood, but it seems quite certain that *Psilorhinus* is closely related to *Cyanocorax* (Amadon, 1944). Because white tips to the tail and pale under parts are basic pattern components of a number of jays of the genus *Cyanocorax,* it is highly probable that the white-tipped morph of *Psilorhinus* is morphologically "primitive" and the brown represents a secondary modification of the white-tipped pattern. Moreover, another close relative of the Brown Jay is *Calocitta,* with which it has hybridized in Chiapas (Pitelka, *et al.,* 1956). This jay is blue dorsally and has white posterior under parts and tips to the tail. Since *Calocitta* is a xeric-adapted species, there is a good possibility that the ancestor of the Brown Jay, perhaps a *Calocitta*-like form, was adapted to xeric or mesic rather than humid environments, and that the adaptation of the Brown Jay to humid habitat types was a secondary development.

It is possible that the present pattern of polymorphism was originally established by secondary contact and introgressive hybridization between a monomorphic brown population which evolved in humid environments in northeastern México and originally xeric- or mesic-adapted white-tipped birds occupying Central America or southeastern México. Later, perhaps, the brown population moved into xeric environments in Tamaulipas and other areas, where in ventral coloration it approaches the white-tipped type. Similarly, the white-tipped Central American populations could have managed to inhabit humid vegetation types without making the particular genetic adjustments accompanied by brown morphism. All of this is highly speculative. In any event, however, the fact that polymorphism is shown over an extensive area and that there is a complex ratio-cline connecting "pure" monomorphic populations on either side of this area tends to rule out the possibility that polymorphism is maintained merely by gene-flow from centers in which one or the other of the types is at an advantage (Ford, 1945: 80, 82). Polymorphism in *Psilorhinus* is apparently balanced, but as yet no information is available concerning the intrinsic balance mechanism.

NOMENCLATURE AND SUBSPECIES

The correct name of the Brown Jay is *Psilorhinus morio* (Wagler); the type locality, formerly believed to be Jalapa (see J. Davis, 1951), apparently is Alvarado, Veracruz (Stresemann, 1954: 89).

In my opinion, formal recognition of subspecies in *P. morio* is of

questionable value. However, if subspecies are to be recognized, I suggest the following arrangement, which is based mainly on two geographically variable characters, size and presence or absence of polymorphism.

Psilorhinus morio morio (Wagler)

Pica Morio Wagler, 1829, Isis von Oken, col. 751 (Mexico = Alvarado, Veracruz)

Psilorhinus morio palliatus van Rossem, 1934, Bull. Mus. Comp. Zool., 77: 415 (Ciudad Victoria, Tamaulipas)

Characters.—Large size; monomorphic brown.

Range.—Northeastern México from Tamaulipas and Nuevo León south to central Veracruz (latitude 19°25′), and in Sierra Madre of Veracruz above 2000 feet elevation south at least to Córdoba.

Psilorhinus morio fuliginosus (Lesson)

Pica fuliginosa Lesson, 1830, Traite d'Ornith., livr. 5: 333 ("Mexique"; type lost)

Psilorhinus mexicanus Rüppell, 1837, Mus. Senckenb., 2, heft. 2: 189 ("Tamalipas" = Tamaulipas = central or southern Veracruz (?); based on white-tipped morph)

Characters.—Large size; polymorphic.

Range.—Southeastern México from coastal plain of central Veracruz south and east to eastern Tabasco (Montecristo) and northern Chiapas (Palenque).

Psilorhinus morio cyanogenys Sharpe

Psilorhinus cyanogenys Sharpe, 1877, Cat. Birds Brit. Mus., 3: 140 ("Pearl-Bay Lagoon, Mosquito" = Pearl Cay Lagoon, Nicaragua)

Psilorhinus mexicanus captus Kennard and Peters, 1927, Proc. New Engl. Zool. Cl., 10:2 (Chiriquicito, northwestern Panamá)

Characters.—Medium size; monomorphic white-tipped.

Range.—Extreme eastern Tabasco (Balancán) south and east through Central America (except El Salvador) to the Almirante region, Panamá.

Remarks.—*P. m. captus* reportedly differs from *P. m. cyanogenys* in minor details of ventral coloration and in having smaller white tail-patches. These characters, particularly the latter, should be checked in series of specimens segregated as to age. I have seen only a single specimen, a juvenile, from the Almirante region; it is closely similar to specimens from Costa Rica.

A specimen from Palma Real, Ocosingo, Chiapas, is similar in all respects to birds from Guatemala. If the population of the highlands of central Chiapas proves to be monomorphic white-tipped, this bird and others from the same region may arbitrarily be referred to *P. m. cyanogenys.*

Psilorhinus morio vociferus (Cabot)

Corvus vociferus Cabot, 1843, Proc. Boston Soc. Nat. Hist., 1: 155 (Yucatan)

Characters.—Like *P. m. cyanogenys* in being monomorphic white-tipped, but smaller and paler, with posterior under parts whiter and lacking gray on thighs.

Range.—Northern Yucatán Peninsula in Yucatán, Quintana Roo, and Campeche.

Remarks.—Paynter (1955: 213), who examined a considerable number of specimens of *P. m. vociferus,* notes that it may be distinguished from *cyanogenys* "most easily, by the total lack of gray on the thighs." *P. m. vociferus* intergrades with

P. m. cyanogenys in southern Campeche and along the Río Hondo between Quintana Roo and British Honduras (Paynter, *op. cit.*, 213–214). Paynter was correct in supposing that Traylor's (1941) specimen from Matamoros, Campeche, is not typical of either race. The bird, a first-year female, is intermediate in size and color between Guatemalan specimens *(cyanogenys)* and those from the northern Yucatán Peninsula. Paynter reported an intergrade from 20 miles north of Escárcega. Traylor's specimen (adult female) from Pacaytún, about 50 miles southwest of Matamoros, is "typical" *P. m. cyanogenys*.

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SUMMARY

Relationships of two nominal species of jays, the Brown Jay *(Psilorhinus morio)* and the White-tipped Brown Jay *(P. mexicanus)*, in eastern México were studied. Evidence is marshalled to show that the two are color phases (morphs) of a single species.

North of latitude 19°25′ in central Veracruz all jays are the brown morph; from central Veracruz south to eastern Tabasco both morphs are found together in varying frequency-ratios; and populations in Central America and the Yucatán Peninsula are monomorphic white-tipped. Within the range of the polymorphic populations both types are identical in size, are found in the same family group, are constantly associated, and show no differences in habitat occurrence or behavior. Available evidence from composition of family groups suggests that brown is genetically dominant over the white-tipped pattern.

Study of patterns of ratio-clines, based on censuses at 13 localities in Veracruz, Oaxaca, Chiapas, and Tabasco, shows a general relation between morph-ratios and climate. Within the polymorphic range, relatively high frequencies of the white-tipped morph are found in arid and mesic regions, and a predominance of the brown morph is seen in more humid areas. Elsewhere within the species' range, however, monomorphic populations of either type occupy both humid and xeric regions.

The obvious color and pattern differences between the morphs are believed to be non- or weakly-adaptive correlates of underlying physiological characters, such as temperature or humidity tolerance, having differential selective values. The extent of the area over which polymorphism exists and the complexity of ratio-clines within this area indicate that polymorphism is not maintained merely by gene-flow from adjacent monomorphic populations. Polymorphism in *Psilorhinus* may have been originally established by secondary contact and hybridization between monomorphic populations, but, in any event, it is now apparently balanced.

LITERATURE CITED

AMADON, D. 1944. The genera of Corvidae and their relationships. Amer. Mus. Nov. 1251: 1–21.

AMADON, D., and ECKELBERRY, D. R. 1955. Observations on Mexican birds. Condor, **57**: 65–80.

BAIRD, S. F., BREWER, T. M., and RIDGWAY, R. 1875. A history of North American birds. Landbirds, vol. 2. Little, Brown, and Co., Boston, 590 pp.

BLAIR, W. F. 1949. Shade of pelage color in two populations of kangaroo rats and remarks on the status of *Dipodomys merriami ambiguus*. Journ. Mamm., **30**: 388–390.

BLAKE, E. R. 1953. Birds of Mexico. Univ. Chicago Press, Chicago, 644 pp.

BRODKORB, P. 1943. Birds from the gulf lowlands of southern Mexico. Mus. Zool. Univ. Mich., Misc. Publ. 55: 88 pp.

CABANIS, J. 1851. Museum Heineanum. 1 Theil. Halberstadt, 175 pp.

CHAPMAN, F. M. 1898. Notes on birds observed at Jalapa and Las Vigas, Vera Cruz, Mexico. Amer. Mus. Nat. Hist., Bull. 10: 15–43.

CONTRERAS ARIAS, A. 1942. Mapa de las provincias climatológicas de la República Mexicana. Instituto Geográfico, México, D. F.

DAVIS, J. 1951. Notes on the nomenclature of the brown jays. Condor, **53**: 152–153.

DAVIS, L. I. 1952. Coastal prairie. Sixteenth breeding-bird census. Audubon Field Notes, **6**: 324.

DAVIS, L. I. 1955. Tropical rain forest. Nineteenth breeding-bird census. Audubon Field Notes, **9**: 425–426.

DAVIS, L. I., and MORONY, J., JR. 1953. Tropical prairie. Seventeenth breeding-bird census. Audubon Field Notes, **7**.

DAVIS, W. B. 1945. Notes on Veracruzan birds. Auk, **62**: 272–286.

EISENMANN, E. 1955. The species of Middle American birds. Trans. Linnaean Soc. N. Y., **7**: 128 pp.

EISENMANN, E. 1957. Notes on birds of the province of Bocas del Toro, Panama. Condor, **59**: 247–262.

FORD, E. B. 1940. Polymorphism and taxonomy. Pp. 493–513 *in* J. Huxley (ed.), The new systematics. Oxford Univ. Press, London.

FORD, E .B. 1945. Polymorphism. Biol. Rev. Cambridge Phil. Soc., **20**: 73–88.

FORD, E. B. 1955. Rapid evolution and the conditions which make it possible. Cold Spring Harbor Symp. on Quant. Biol., 20: 230–238.

GOLDMAN, E. A. 1951. Biological investigations in México. Smithsonian Misc. Publ., 115: 476 pp.

GOODNIGHT, C. J., and GOODNIGHT, M. L. 1956. Some observations in a tropical rain forest in Chiapas, Mexico. Ecology, **37**: 139–150.

HELLMAYR, C. E. 1934. Catalogue of birds of the Americas. Field Mus. Nat. Hist., Zool. Ser., **13**, pt. 7: 531 pp.

HOWELL, T. R. 1957. Birds of a second-growth rain forest area of Nicaragua. Condor, **59**: 73–111.

HUXLEY, J. 1943. Evolution: The modern synthesis. Harper Bros., New York, 645 pp.

HUXLEY, J. 1955. Morphism in birds. Acta XI Congressus Internationalis Ornithologici Basel, 1954: 309–328.

KINCAID, E. 1954. The 1954 Irby Davis expedition to Mexico. Part 1. Texas Ornith. Newsletter, **2**: 2-14 (mimeographed).

LANTZ, D. E. 1899. A list of birds collected by Col. N. S. Goss in Mexico and Central America. Trans. Kansas Acad. Sci., **16**: 218–224.

LAWRENCE, G. N. 1876. Catalogue of birds collected by Prof. Sumichrast, in southwestern Mexico, and now in the National Museum at Washington, D. C. U. S. Natl. Mus. Bull., 4: 56 pp.

LOWERY, G. H., JR., and DALQUEST, W. W. 1951. Birds from the state of Veracruz, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 3: 531–649.

MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York, 334 pp.

MAYR, E. 1954. Change of genetic environment and evolution. Pp. 157–180 *in* J. Huxley, A. C. Hardy, and E. B. Ford (eds.), Evolution as a process. George Allen and Unwin, Ltd., London.

MAYR, E., and STRESEMANN, E. 1950. Polymorphism in the chat genus Oenanthe (Aves). Evolution, **4**: 291–300.

MILLER, A. H., FRIEDMANN, H., GRISCOM, L., and MOORE, R. T. 1957. Distributional check-list of the birds of Mexico. Pacific Coast Avi., 33: 435 pp.

PAYNTER, R. A., JR. 1955. The ornithogeography of the Yucatan Peninsula. Peabody Mus. Nat. Hist., Yale Univ., Bull. 9: 347 pp.

PITELKA, F. A. 1945. Pterylography, molt, and age determination of American jays of the genus *Aphelocoma*. Condor, **47**: 229–260.

PITELKA, F. A. 1958. Timing of molt in Steller jays of the Queen Charlotte Islands, British Columbia. Condor, **60**: 38–49.

PITELKA, F. A., SELANDER, R. K., and ALVAREZ DEL TORO, M. 1956. A hybrid jay from Chiapas, Mexico. Condor, **58**: 98–106.

RIDGWAY, R. 1904. Birds of North and Middle America. U. S. Natl. Mus. Bull., **50**, pt. 3: 801 pp.

SALVIN, C., and GODMAN, F. D. 1887. Biologia Centrali-Americana. Aves, vol. 1. Taylor and Francis, London, 512 pp.

SCLATER, P. L. 1859. On a series of birds collected in the vicinity of Jalapa, in southern Mexico. Proc. Zool. Soc. London, pt. **28**: 362–369.

SKUTCH, A. F. 1935. Helpers at the nest. Auk, **60**: 257–273.

STRESEMANN, E. 1954. Ferdinand Deppe's travels in Mexico, 1824–1829. Condor, **56**: 86–92.

SUTTON, G. M. 1951. Mexican birds, first impressions. Univ. Oklahoma Press, Norman, 282 pp.

SUTTON, G. M., and GILBERT, P. W. 1942. The brown jay's furcular pouch. Condor, **44**: 160–165.

TASHIAN, R. E. 1952. Some birds from the Palenque region of northeastern Chiapas, Mexico. Auk, **69**: 60–66.

TRAYLOR, M. A., JR. 1941. Birds from the Yucatan Peninsula. Field Mus. Natl. Hist., Publ. 493, Zool. Ser., **24**: 195–225.

WETMORE, A. 1943. The birds of southern Veracruz, Mexico. Proc. U. S. Nat. Mus., **93**: 215–340.

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APPENDIX

List of Specimens Examined

Sample 1. Tamualipas and Nuevo León; 50 specimens; all brown morph.

Tamaulipas: Camargo, 2 (♀ adult and ♀ first-year, collected on January 16, 1902, by Nelson and Goldman); Villagrán, 3; 5 mi. S Villagrán, 1; Río Pilón, 2; Ciudad Victoria, 5; Alicia, 60 mi. S Victoria, 1; Río de Corona, 1000 ft., 20 km. NNW Ciudad Victoria, 1; Santa Engracia, 6; 1 mi. N Magueyes, 1; Cañon de Galeana, 1; Río Sabinas, near Gómez Farías, 2; Cañon Guiaves (?), 2500 ft., 1; 10 mi. S Linares, 1; 14 km. S Mante, 1; Arroyo los Miradores, 1 km. W Km. 619, 22 mi. N Limón, 1. *Nuevo León:* Monterrey, 6; Hacienda de las Escobas, 1; Cerro de la Silla, 3; Montemorelos, 2; San Diego, Río San Juan, 1; Boquilla, 6; China, 1; no further locality, 1.

Sample 2. San Luis Potosí; 29 specimens; all brown morph.

San Luis Potosí: El Naciemento del Coy, 1; Ebano, 2; Cerco de Ebano, 2.5 mi. SSE Ajinche, 1; Hacienda Limón, 10 mi. W Ebano, 1; 4 mi. beyond Ajinche on road to Oviedo, Ebano region, 2; 19 km. W Ebano, 1; Paso de Botella, 1500 ft., 5 mi. SW Sta. María Acapulco, 2; Valles, 3; Tamuín region, 1; 1 mi. S. Tamuín Station, 1; Xilitla, 2000 ft., 3; 1 mi. W Xilitla, 2400 ft., 1; 4 mi. E Xilitla, 1000 ft., 1; 3 mi. W Naranjo, 2; E of Tamazunchale, 1; El Sol, 1 mi. N Tamazunchale, 1; 4 mi. E Tamazunchale, 1; El Banito, 1; Puerto de Diablo, 6600 ft., Cerro Coneja reg., 1; Puente de Dios, Río Santa María 2.

Sample 3. Tampico region, southern Tamaulipas and northern Veracruz; 18 specimens; all brown morph.

Tamaulipas: Tampico, 10; Cervantes, 2. *Veracruz*: Tamesí River near Rayón, 2; 30 mi. S Tampico, 2; 40 mi. S Tampico, 1; 30 mi. N Tuxpan, 1.

Sample 4. Sierra Madre, central Veracruz; 22 specimens; all brown morph.

Veracruz: 3 mi. S. Jalapa, 1; Coatepec, 4500 ft., 2; Mirador, 1; Potrero Viejo, 10 mi. E Córdoba, 1750 ft., 1; Ojochico, 7; Fortín de las Flores, 6; 2 mi. N Fortín, 3200 ft., 1; Barranca Metlac, 1; Río Atoyac, 8 km. NW Potrero, 2.

Sample 5. Coastal plain, central Veracruz; 37 specimens; both morphs.

BROWN MORPH; 22 SPECIMENS

Veracruz: Palma Sola, 1000-1200 ft., SE Cuitláhuac, 3; Puente Nacional, 3; 9 mi. SSW[=S] Boca del Río, 7; 14 mi. SSW Boca del Río, 3; 12 mi. S Boca del Rio, 6.

WHITE-TIPPED MORPH; 15 SPECIMENS

Veracruz: Palma Sola, 1200-1250 ft., SE Cuitláhuac, 3; Arroyo de Piedra, 1.7 mi. NE La Capilla, 1; "Mirador," 1; 3 km. W Boca del Río, 1; 14 mi. SSW Boca del Río, 3; 9 mi. SSW[=S] Boca del Río, 1; 12 mi. S Boca del Río, 3; 20 mi. S Veracruz City, 1; Río Blanco, 20 km. WNW Piedras Negras, 1.

Sample 6. Catemaco region, Veracruz; 48 specimens; both morphs.

BROWN MORPH; 32 SPECIMENS

Veracruz: Catemaco, 5; Lake Catemaco at Playa Azul, 11; Lake Catemaco at Coyame, 9; 10 mi. SW Catemaco, 1; Angel R. Cabada, 3; Hueyapan, 3.

WHITE-TIPPED MORPH; 16 SPECIMENS

Veracruz: Catemaco, 5; Lake Catemaco at Playa Azul, 6; Lake Catemaco at Coyame, 3; 10 mi. SW Catemaco, 4; Santiago Tuxtla, 1; Angel R. Cabada, 1; Hueyapan 1.

Sample 7. Isthmus of Tehuantepec, southern Veracruz and Oaxaca; 21 specimens; both morphs.

BROWN MORPH; 17 SPECIMENS

Veracruz: Achotal, 1; Jáltipan, 4; Cosaleacaque, 10 mi. W Minatitlán, 4; 2 mi. NE Minatitlán, 2; Pasa Nueva, 1. *Oaxaca:* 4 mi. N Matías Romero, 4; Guichicovi, 1.

WHITE-TIPPED MORPH; 4 SPECIMENS

Veracruz: Jáltipan, 1; 2 mi. NE Minatitlán, 2; Pasa Nueva, 1.

Sample 8. Tabasco and Ciapas; 28 specimens; both morphs.

BROWN MORPH; 10 SPECIMENS

Tabasco: Teapa, 7; Montecristo, 1. *Chiapas*: Palenque, 2.

WHITE-TIPPED MORPH; 18 SPECIMENS

Tabasco: Teapa, 1; Montecristo, 1. *Chiapas*: Palenque, 13; Palma Real, Ocosingo, 1; 5.4 mi. NW San Fernando, 2000 ft., 2.

Sample 9. Guatemala; 18 specimens; all white-tipped morph.

Guatemala: Los Amates, Izabel, 5; Bobos, Izabel, 1; Remate, Petén, 1; Macanché, Petén, 1; Chuntuqui, Petén, 1; Panzos, 1; Puebla, 1; Finca Chama, 1; Miles Rock, 1; Coban to Clusec, 2; no further locality, 3.

Sample 10. Yucatán, northern Campeche, and northern Quintana Roo; 14 specimens; all white-tipped morph.

Yucatán: Xocempich, 3; Chichén Itzá, 3; San Felipe, 1; no further locality, 2. *Campeche:* 15 mi. S Campeche, 2; Canasayab, 1; San Juan, 1. *Quintana Roo*: La Vega, 1.

Sample 11. Honduras and Nicaragua; 14 specimens; all white-tipped morph.

Honduras: Truxillo, 1; Chamelicón, 2; La Ceiba, 1; El Boquerón, Catamacas, 1; Alto Guaymaca, Tegucigalpa, 3000 ft., 1; Balfate, Prov. Colón, 1. *Nicaragua:* Segovia R., 4; Managua Río, 1; Matagalpa, 1; San Rafael del Norte, 4000 ft., 1.

Sample 12. Costa Rica; 39 specimens; all white-tipped morph.

Costa Rica: Copey, 1; "Sibahue," 1; San José, 4; Volcán de Irazú, 1; Talamanca, 2; Guayabo, 9; Bonilla, 1; Santa María de Dota, 3; Carillo, 1000 ft., 1; Aginares, slope Vol. Turrialba, 3800 ft., 1; San Isidro, Vol. Irazú, 1; Agua Caliente, 4500 ft., 1; Limón, 1; Juan Viñas, 1; Coliblanco, 1; Peralta, 1; La Lola, Madre de Dios, 3; Parás, 1045 m., 7 km. W San José, Prov. San José, 1; no further locality, 5.

Additional Specimens Examined

BROWN MORPH

Oaxaca: Tuxtepec, 3; Palo Blanco, 3 km. Oeste Tuxtepec, 1. "Tamaulipas," 1; "City of Mexico," 1; "Hacienda Santa Gratias," 1.

WHITE-TIPPED MORPH

Oaxaca: Tuxtepec, 2. *Chiapas*: 5.4 mi. NW San Fernando, 2000 ft., 2; "Mexico," 1. *Campeche*: Matamoros, 1; "Pacaitun"[=Pacaytún], 1. *Quintana Roo*: Coba, 1. *Panamá*: Boca[=Bocas] del Toro, Almirante, 1. There is a specimen in the British Museum (Natural History) from Playa Vicente, Veracruz (*fide* Pitelka, in letter).

Selected Additional Locality Records from the Literature

BROWN MORPH

Veracruz: Tres Zapotes (Wetmore, 1943: 296); Río Blanco, 20 km. W Piedras Negras, 400 ft. (Lowery and Dalquest, 1951: 617); Jalapa (Sclater, 1859: 365); Rinconada (Lantz, 1899: 222); 17 mi. E (by road) Nanchital (L. I. Davis and Morony, 1953). *Tabasco:* Río Macuspana (reported by Rovirosa in vol. 7 of Naturaleza, 1887: 367, *fide* Brodkorb, 1943: 71). *Oaxaca:* Soyaltepec (Miller, *et al.*, 1957: 130). *Puebla:* 30 mi. E Huauchinango (Miller, *et al.*, 1957: 130).

WHITE-TIPPED MORPH

Veracruz: Rinconada (Lantz, 1899: 222); 1 km. E Mecayucan, 200 ft., 20 mi. ESE Jesús Carranza, 400 ft. (Lowery and Dalquest, 1951: 617); Tres Zapotes (Wetmore, 1943: 297); along Río Jaltepec where highway crosses (Amadon and Eckelberry, 1955: 76). *Oaxaca:* Ridgway (1904) apparently was in error in listing Guichicovi as a locality for the white-tipped morph. The record is based on a specimen reported by Lawrence (1876: 25) as *P. morio*. Also, the locality is in Oaxaca, not Chiapas as indicated by Ridgway.