

BEHAVIORAL AND MORPHOLOGICAL CORRELATES OF HETEROCHRONY IN HISPANIOLAN PALM-TANAGERS¹

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Abstract. We documented the occurrence of heterochrony for morphological and behavioral characters in two species of Hispaniolan Palm-Tanager. *Phaenicophilus palmarum* is age-dimorphic in morphology and foraging behavior with 55% ($n = 126$) of specimens classified as juveniles. Juveniles differed from adults of their own species in five of eight foraging variables, average flight distance during a foraging bout, foraging height, use of broadleaf instead of pine substrates, and the presence of a gray instead of black crown. *Phaenicophilus poliocephalus* have gray crowns similar to those of *P. palmarum* juveniles and do not differ significantly from them for any of the eight foraging variables measured, choice of substrate, or average flight distance. They do differ from adult *P. palmarum* for four of eight foraging variables, average flight distance, and use of substrates. *Phaenicophilus poliocephalus* lacks a significant age-dimorphism in all behavioral and morphological characters measured. We classified only 15% ($n = 66$) of the specimens examined as juveniles based on morphology. This species tends to form groups of four to six individuals in the non-breeding season, in contrast to *P. palmarum* occurring singly or in pairs. *Phaenicophilus poliocephalus* is also smaller than adult *P. palmarum* for seven of 11 size-related features. We assessed the degree of gene flow across the narrow hybrid zone we documented and concluded, based on morphological variance analysis, that there was little introgression. The resemblance of *P. poliocephalus* to juvenile *P. palmarum* in general morphology and behavior, their smaller body size, and the increased tendency to form groups is consistent with a paedomorphic derivation of *P. poliocephalus* from *P. palmarum*.

Key words: Age-dimorphism; foraging behavior; heterochrony; Hispaniolan Palm-Tanagers; morphology; paedomorphosis; progenesis.

INTRODUCTION

The importance of heterochrony to the evolution of birds has received little attention since Gould's (1977) reformulation of Haeckel's model of ontogeny recapitulating phylogeny. Heterochrony, which involves shifts in developmental sequences, may be significant to the evolution and speciation of birds, particularly if it explains the differences in genetic and morphological diversity between birds and other vertebrates. Heterochrony by paedomorphosis can result in the retention of juvenile features in reproductively mature individuals and can be achieved either by progenesis or neoteny. Progenesis is characterized by early sexual maturation which often results in smaller body size. Neoteny, or delayed

somatic maturation, results in larger body size (Gould 1977) and increased variation in first age of reproduction. Gould's (1977) model of heterochrony provides a mechanism for rapid evolutionary change and speciation, often with little genetic divergence. Selection for change in one character often results in simultaneous change in non-selected but associated characters (Larson 1980). For example, juvenile behaviors associated with juvenile morphologies can be retained due to paedomorphosis (Geist 1971, Coppinger and Coppinger 1982, Lawton and Lawton 1986, Coppinger et al. 1987). Suites of characters can evolve without selection operating on every character. In addition, speciation between closely related forms may be facilitated by paedomorphosis.

Hispaniolan Palm-Tanagers represent a species pair in which heterochrony may have been essential to their relatively rapid evolution and speciation. Two recognized species of palm-tanagers, the Black-crowned Palm-Tanager, *Phaenicophilus palmarum*, and the Gray-crowned

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HISPANIOLA

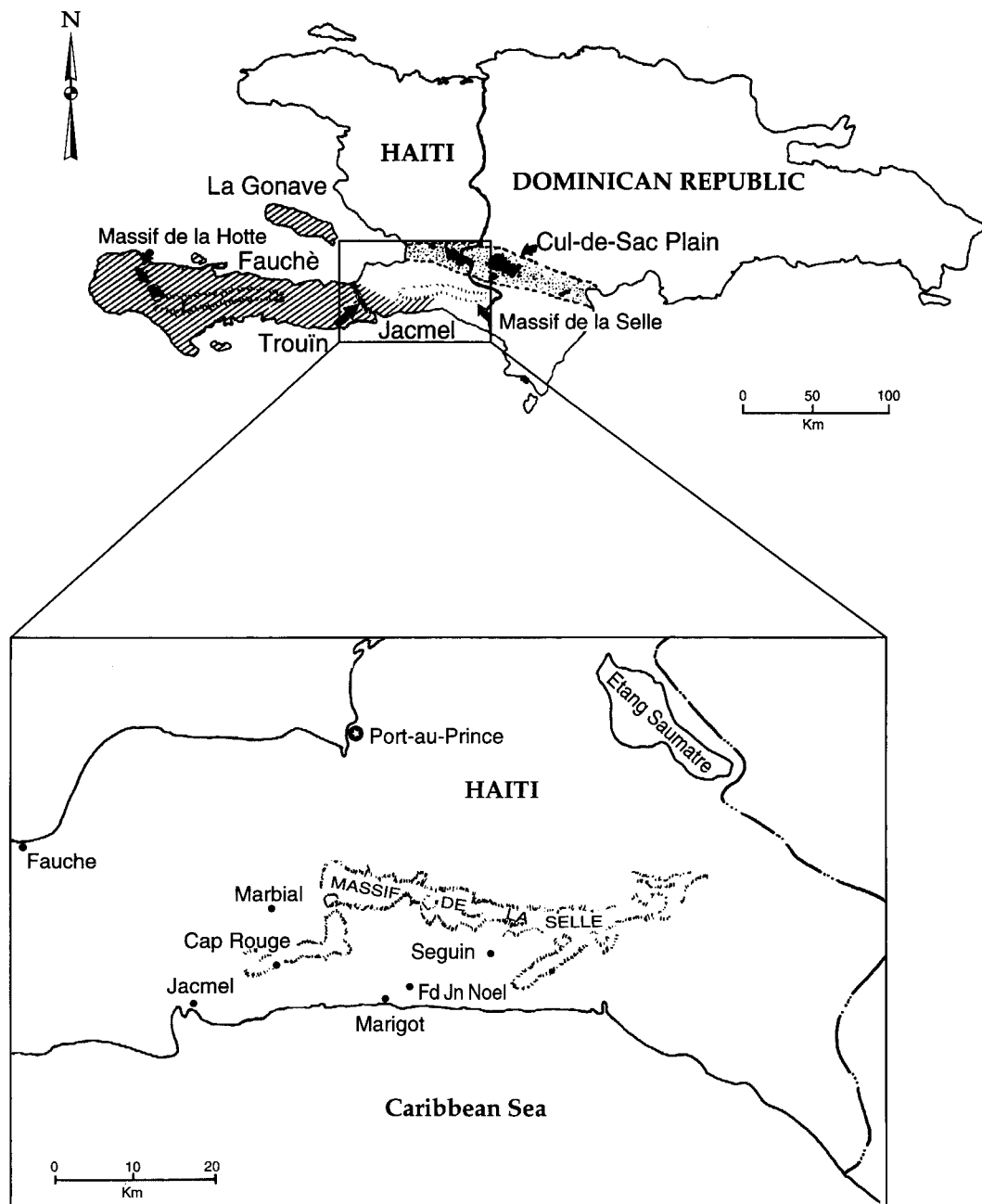


FIGURE 1. Map of the current distribution of Hispaniolan Palm-Tanagers. Shaded area represents the known distribution of *Phaenicophilus poliocephalus*; *P. palmarum* occurs throughout the rest of Hispaniola. Enlargement features the area of contact and hybridization bounded by Fond Jean Noel (Fd Jn Noel) in the east, Marigot on the Caribbean Sea to the south and includes a region southwest of Seguin. The western extent of the hybrid zone is still undefined but may extend into the valley between the Massif de La Selle and Cap Rouge. *P. poliocephalus* is known to occur in Marbial, along the Riviere Gosseline. Colonization during the late Pleistocene is thought to have occurred from the north island, either across the Cul-de-Sac Plain or the Trouin Valley. We do not currently have sufficient data to know whether *P. poliocephalus* is expanding east- and northward into the Massif de La Selle, or whether *P. palmarum* is expanding west- and southward.

Palm-Tanager, *P. poliocephalus*, are endemic to Hispaniola (Bond 1980). *Phaenicophilus palmarum* occurs throughout the island except on Isle La Gonave and the southern peninsula of Haiti, where *P. poliocephalus* occurs (Fig. 1). The two species were thought to meet but not overlap in the Trouin Valley (Wetmore and Swales 1931, Bond 1980). *P. poliocephalus* had been reported in the Dominican Republic (Dod 1981) and eastern Haiti, but these sightings were later found to be mistaken identifications of juvenile *P. palmarum* (Dod, pers. comm.). Bond (1986) proposed that if these tanagers did come into contact and hybridize, they should be considered conspecific. We document a hybrid zone farther east of the Trouin Valley, present evidence in favor of retaining the current species designations, and note the morphological similarity of adult *P. poliocephalus* to juvenile *P. palmarum*. The resemblance of *P. poliocephalus* to juvenile *P. palmarum*, the existence of an undescribed hybrid zone, their estimated recent divergence and the low gene flow between species (McDonald and Smith 1990) suggested that these taxa would be suitable to study the influence of heterochronic processes on the evolution and diversification of avian species, where it will not be confounded by significant differentiation due to long periods of isolation.

Our purpose was to investigate behavioral and morphological patterns in the Hispaniolan Palm-Tanagers and to determine the significance of heterochrony in their evolution. Specific objectives were as follows: (1) to evaluate the species status of these two taxa; (2) to test the hypothesis that *P. palmarum* is neotenic; (3) to describe the relationship between behavior and morphology in these species; and, (4) to determine whether *P. poliocephalus* is paedomorphic to *P. palmarum*. We suspect that heterochrony is an important mechanism for avian speciation, resulting in the absence of major genetic changes at structural gene loci (McDonald and Smith 1990). Heterochrony may explain why avian taxa are morphologically diverse but genetically conservative at structural gene loci when compared to other vertebrate classes (McDonald and Smith 1990).

DESCRIPTION OF BIRDS AND THEIR RANGES

Phaenicophilus palmarum has a yellow-green back, a gray nape, three white eye-spots on a black face mask, a black crown and a diffused

white chin and throat (Fig. 2). It is also characterized by an age-dimorphism in plumage. Juveniles have gray crowns that range from the same shade of gray on the nape to darker gray, depending on age (McDonald, pers. observ.). *Phaenicophilus poliocephalus* resembles juvenile *P. palmarum* by having gray crowns, but is distinguished from this species by a distinct white chin against a gray throat. Juvenile *P. palmarum* have been frequently confused with *P. poliocephalus* in the field by earlier workers (Dod 1981).

In July, 1983, *P. poliocephalus* was observed approximately 30 km east of the Trouin Valley (McDonald, pers. observ.). In May, 1985, a narrow hybrid zone was documented with specimen collections in the area north of Marigot, extending to about 4–5 km south of Seguin and bordered on the east by Fond Jean Noel (Fig. 1). The western extent of the hybrid zone is not known, although hybrids were not found along the Riviere Gosseline approximately 5–10 km east of Marbial. It is possible that hybrids occur in the valley between the Massif de La Selle and Cap Rouge. There were no *P. poliocephalus* or hybrids found in the Massif de La Selle. Both species occur in their respective ranges in all major habitats found in Haiti, including cloud forest, mixed pine, mesic broadleaf woodland, xeric thornscrub, desert, mangrove swamp, and disturbed rural and urban areas, while hybrids are found in a narrow band of mesic woodland, thornscrub, and disturbed rural area.

METHODS

MORPHOMETRIC ANALYSIS

Seventeen morphological variables (Fig. 2; App. I) were measured on fresh specimens before skin or skeletal preparations were made of *Phaenicophilus palmarum* ($n_1 = 22$), *P. poliocephalus* ($n_2 = 20$), and *P. palmarum* × *P. poliocephalus* hybrids ($N_3 = 14$) collected in Haiti (McDonald 1988; Table 1). Hybrid specimens and representatives of both parental species are deposited in the American Museum of Natural History in New York. The remaining individuals are deposited in the Florida Museum of Natural History. Additional museum specimens ($n_1 = 104$ and $n_2 = 46$) were included in the morphological analysis to increase the sample size for subsequent analyses. Hybrids were identified in the field by the intermediate extent of black on the crown and white on the chin.

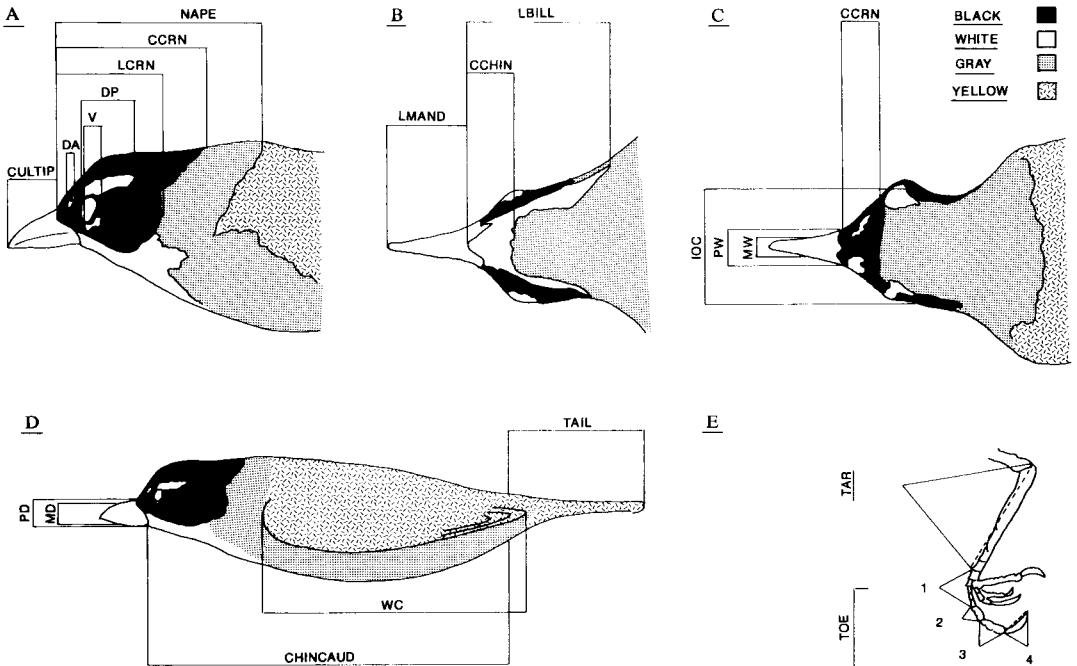


FIGURE 2. Description of morphological measurements taken for *Phaenicophilus*. Specimen abbreviations are defined in Appendix I. (A) represents a lateral view of *P. palmarum*; (B) and (C) are dorsal and ventral views of *P. poliocephalus*.

Analyses of age, sex, and species differences were conducted using Mann-Whitney U-tests for the morphological variables (Table 1). Analyses to determine whether there were significant differences in plumage or skeletal characters for museum vs. fresh specimens were done for crown, chin, left dorsal posterior eyespot (plumage character), wingchord, tarsus, length of culmen to tip of bill for size/skeletal characters. To determine whether there was significant geographic variation in these characters, difference matrices were calculated for crown and chin characters and their correlations to matrices of straight-line geographic distances between collecting sites were analyzed for significance, using a two-way Mantel analysis (Mantel 1967, Schnell et al. 1985). If variation in a character matrix corresponds to geographic variation, then it is likely that the change in character, such as extent of black on the crown, is a result of geographic variation, and not due to some other factor, e.g., speciation by pedomorphosis. For example, if the extent of black on the crown increases from the south to the north, then this character is likely the result

of geographic variation within a species, and not due to species-specific differences between taxa. Two-way Mantel analyses were used because early collections of individual *P. palmarum* were not scored for the chin character. Thus, the number of elements on the distance matrix was different for this character than for the crown character.

The value for the crown character for juvenile *P. palmarum* was set to zero for this analysis, because no black occurs on the crown until the final molt, even though the extent of gray on the crown could be measured. The value for the chin character in adult *P. palmarum* was set to average body length, because the white diffuses down the throat and entire ventral area of these birds. The average value for a species class was substituted for missing values and the degrees of freedom were adjusted accordingly. Homogeneity of variance for morphological traits was tested using the *F* test (Sokal and Rohlf 1969).

Juveniles of *P. palmarum*, but not of *P. poliocephalus*, are distinguishable in the field from adults. Juveniles were initially identified as fledg-

TABLE 1. Sample size (*n*), mean in mm, and standard error (SE) for 17 morphological variables of *Phaenicophilus palmarum* adult (BPA) and juvenile (BPI), *P. poliocephalus* (GPT), and their hybrids (HYB).

Variable	Species	<i>n</i>	Mean	±SE
Extent of black on crown ^{a,b}	BPA	91	26.48	0.26
	BPI	31	16.08	2.20
	GPT	57	6.08	0.44
	HYB	13	12.82	2.45
Lateral extent of face mask	BPA	90	22.66	0.18
	BPI	30	22.54	0.29
	GPT	54	22.35	0.14
	HYB	14	23.50	0.31
Length of nape from exposed culmen	BPA	90	38.24	0.45
	BPI	32	38.99	0.84
	GPT	56	38.68	0.65
	HYB	14	39.01	1.12
Width of white on chin ^b	BPA	94	19.34	3.78
	BPI	34	35.18	7.32
	GPT	56	10.33	0.31
	HYB	14	18.74	2.62
Lateral extent of malar stripe ^b	BPA	93	10.57	1.37
	BPI	29	23.06	1.82
	GPT	53	28.15	0.51
	HYB	14	29.02	1.37
Wingchord ^{a,b}	BPA	94	85.29	0.63
	BPI	33	81.00	0.78
	GPT	58	83.49	0.51
	HYB	13	85.73	1.21
Braincase length	BPA	79	22.04	0.21
	BPI	24	21.36	0.30
	GPT	52	21.30	0.17
	HYB	14	22.89	0.34
Bill length ^b	BPA	91	20.33	0.11
	BPI	32	20.34	0.18
	GPT	54	18.89	0.16
	HYB	14	19.25	0.27
Proximal bill width ^{b,c}	BPA	93	6.90	0.08
	BPI	33	6.68	0.14
	GPT	53	6.61	0.07
	HYB	14	6.64	0.12
Medial bill width ^c	BPA	92	3.41	0.03
	BPI	33	3.56	0.07
	GPT	53	3.39	0.05
	HYB	13	3.88	0.09
Proximal bill depth ^{a,b,c}	BPA	81	7.29	0.07
	BPI	33	6.90	0.10
	GPT	53	6.80	0.06
	HYB	13	7.05	0.15
Medial bill depth ^b	BPA	75	5.32	0.05
	BPI	32	5.30	0.08
	GPT	49	5.03	0.04
	HYB	14	5.32	0.07
Tarsus length	BPA	92	20.60	0.14
	BPI	31	19.70	0.22
	GPT	58	20.44	0.17
	HYB	13	20.88	0.23

TABLE 1. Continued.

Variable	Species	<i>n</i>	Mean	±SE
Length of dorsal anterior eyespot ^b	BPA	93	5.68	0.09
	BPI	33	5.87	0.16
	GPT	55	4.98	0.12
	HYB	14	5.31	0.30
Length of dorsal posterior eyespot ^{b,c}	BPA	92	9.61	0.16
	BPI	30	10.00	0.34
	GPT	49	6.20	0.20
	HYB	12	7.91	0.48
Length of ventral eyespot ^b	BPA	87	5.69	0.13
	BPI	29	5.78	0.16
	GPT	53	4.18	0.17
	HYB	13	4.14	0.24
Length of tail ^{b,c,d}	BPA	93	68.00	0.40
	BPI	32	67.96	0.72
	GPT	58	66.79	0.56
	HYB	13	71.90	1.03

^a Significant differences in morphological character between BPA and BPI ($P < 0.01$ probability adjusted for multiple comparisons).

^b Significant differences between BPT and GPT.

^c Significant differences between sexes within BPT.

^d Significant differences between sexes within GPT.

lings when adults were seen feeding them. Once we established that juvenile *P. palmarum* had gray crowns but did not have a distinct white chin, juvenile *P. palmarum* could be distinguished from *P. poliocephalus* without difficulty. For our purposes, it was critical to determine the relationship between juvenile *P. palmarum* and *P. poliocephalus* and to determine the ranges of the two taxa. This determination hinged on whether juveniles in *P. poliocephalus* delayed maturation to the same extent as *P. palmarum*. Bias in most museum collections favors adults because juveniles are often in duller plumage (R. Zink, pers. comm.). The proportion of juveniles, as detected by a yellow wash in head plumage and rictal flanges (correlated with gonadal development), in the collections that were examined varied dramatically between the two *Phaenicophilus* species. Juvenile *P. palmarum* represented 55% ($n = 126$) of collected *P. palmarum*; juvenile *P. poliocephalus* represented only 15% ($n = 66$) of the collected specimens for this species. Because juveniles are easily identified in *P. palmarum* but not in *P. poliocephalus*, any bias due to collecting which favors adults should be greater in the former species, if juveniles take equal time to mature in both species. We interpret the higher proportion of juveniles in *P. palmarum* as evidence that this species delays maturation longer than does *P. poliocephalus*.

FORAGING BEHAVIOR

A modified version of the Cody stopwatch method (Cody 1968) was used to collect foraging data for the two species in Haiti. In addition to the foraging variables Cody (1968) collected, we included average activity (perch changes per unit time), food-catching attempts (FCA) per perch change, FCA per minute, food-catching successes (FCS) per minute, FCS/FCA (Table 2), as well as average distance per flight (Kepler 1977, Rabenold 1980). Multiple observations on some individuals doubtlessly were made because the birds were not individually marked (Table 2). We used the Mann-Whitney *U*-test to test for significant differences between variables, rather than a multivariate approach, because transformation of the data did not give a normal distribution.

Seventy-seven or more sites were visited to observe or collect tanagers. Three to five transects were run on many of these sites. We estimated the minimum number of individuals used in the foraging analyses by locating individuals on the transect and by keeping track of individuals observed at any one site. The estimated minimum number of individuals observed was 83 for *P. palmarum* (58 adults and 25 juveniles), and 84 for *P. poliocephalus*.

Substrates were identified by common Creole name (Pierre-Noel 1971) or classified more broadly (e.g., shrubs, broadleaf) for subsequent diversity calculations. Significant differences in substrate diversity between species and age-classes, computed using the Shannon Information Index (Pielou 1977), were evaluated with a *t*-test (Zar 1984).

Frequency data for flight distances were grouped into 3 m intervals, combining the observations that occurred in the intervals greater than 27 m. The frequency of foraging observations at different heights was calculated for each 1.8 m interval, up to 27 m, and combined for the intervals beyond that. Standardizations for differences in maximum height of the vegetation between habitats were made by dividing the foraging height by the height of the substrate.

DATA ANALYSIS

Statistical analyses were conducted using parametric or nonparametric tests from SAS or SPSS (SAS 1985, Norusis 1985). Data were standardized to a mean of 0 and a standard deviation of 1 to adjust for scaling differences among the vari-

ables to perform discriminant function analysis (DFA). Groups were identified *a priori* by species and age classes, including the hybrid class. DFA was performed to determine to what degree we could correctly classify individuals based on morphology.

We used Principal Component Analysis (PCA) for exploratory purposes only to determine what characters might be useful for differentiating the two species. We performed PCA with standardized and non-standardized variables, using either a correlation or a covariance matrix. Principal components were virtually uninterpretable with all methods except those using non-standardized variables and a covariance matrix. Principal components were accepted if they accounted for 5% or more of the variation. Coefficients of variation were higher for some of the morphological variables than for others.

Null hypotheses were rejected at $P \leq 0.05$; highly significant differences occurred at $P \leq 0.01$. Type 1 error was reduced when multiple comparisons of data were made using the same hypothesis with the formula: $1 - (0.95)^{1/n}$, where n is the number of comparisons (Harris 1975). This procedure adjusted the experimentwide error rate to $P_1 \leq 0.05$. Statistical differences between frequency distributions were evaluated using the Kolmogorov-Smirnov test for samples with nondiscrete categories (Sokal and Rohlf 1969). Otherwise, contingency χ^2 analysis was used. Comparisons of the tendency for the two species to form groups in the non-breeding season were evaluated by a modification of the Kolmogorov-Smirnov test, using a χ^2 statistic (Siegel 1956).

RESULTS

MORPHOLOGY

Of the six morphological characters examined, representing both plumage and skeletal features, only two were significantly smaller for the museum specimens than for fresh specimens. They were the lateral posterior eyespot in *P. palmarum* and the extent of black on the crown in *P. poliocephalus*. Because there were no consistent size differences between museum and fresh specimens for all features examined in both species, we included both fresh and museum specimens in our analyses as representing one population for each species.

Highly significant differences between age-

classes within *P. palmarum* were detected for the extent of black on the crown, wingchord, and proximal depth of bill (Table 1). There were only six juvenile *P. poliocephalus* in the sample, thus making it statistically impossible to test for age differences in this species. The three variables listed above along with width of white on the chin, length of malar strip, bill length, bill mid-depth and proximal width, length of dorsal anterior, posterior and ventral eyespots, and tail length were significantly different between *P. palmarum* and *P. poliocephalus*. Significant differences between the sexes were detected within *P. palmarum* for proximal depth, proximal width, and mid-width of the bill, length of the dorsal posterior eyespot, and tail length. Sexes within *P. poliocephalus* differed only on tail length. Other differences in *P. poliocephalus* might have been detected if sample sizes were larger.

The first two principal components (PC) extracted from the data for 17 morphological variables (Table 1) explained 92.4% of the total variance. PC1 had high positive loadings (0.98) for the width of white on the chin and PC2 had high loadings (0.96) for the extent of black on the crown. Neither body size traits nor any other morphological variable had significant loadings for either PC1 or PC2. These data suggest that the two species are very similar. We used discriminant function analysis (DFA) to determine if we had classified all individuals correctly. DFA reclassified two of the *P. palmarum* individuals collected on the edge of the hybrid-contact zone near Fond Jean Noel as hybrids based on phenotype ($P = 0.984$ and $P = 0.998$). One hybrid clustered with the parental species on the crown character and may either represent a backcross or an outlier for one or more morphological characters, since DFA weights characters equally. No juvenile *P. palmarum* were misclassified as *P. poliocephalus* or vice versa. Two adult *P. palmarum* were misclassified as juveniles, but the probability of correct reclassifications was marginal ($P < 0.57$), so they were still considered adults in subsequent analyses.

We could detect no evidence for geographic variation, using Mantel Analysis. Neither the extent of black on the crown nor white on the chin was significantly correlated with geographic distance ($P > 0.05$). We did find that the crown character was significantly inversely correlated with the chin character (-0.73 , $P = 0.02$).

Three distinct morphs exist within *Phaenico-*

TABLE 2. Mean, sample size (in parentheses), and significance of differences for eight foraging behavior variables for adult (BPA) and juvenile (BPI) *P. palmarum* and (GPT) *P. poliocephalus*. Abbreviations are FCA = food-catching attempts and FCS = food-catching successes. Significance differences between pairwise comparisons of classes, as evaluated by Mann-Whitney *U*-tests, are designated by a dashed line with asterisks, where $P \leq 0.025$ (*), $P \leq 0.01$ (**), and $P \leq 0.001$ (***)

Variable	BPA	BPI	GPT
 ***		
Average activity	0.31 (270)	0.25 (100)	0.26 (170)
 ***		
Average speed	0.15 (269)	0.11 (100)	0.14 (169)
 *		
 **		
Duration of stop	4.09 (260)	5.30 (96)	4.23 (163)
 *		
Percent time stopped	0.87 (258)	0.87 (96)	0.86 (163)
FCA per minute	3.45 (230)	3.95 (84)	3.90 (136)
FCS per minute	2.05 (126)	1.80 (30)	1.53 (54)
Successes/attempts	0.59	0.46	0.39
 **		
FCA per perch change	0.26 (233)	0.37 (84)	0.30 (136)
 ***		

philus, with hybrids representing intermediates between the two parental species. Juvenile *P. palmarum* were distinct from adults for the extent of black on the crown and from *P. poliocephalus* for the width of white on the chin. Adult *P. palmarum* and *P. poliocephalus* were distinct from one another for both characters. Hybrids graded from one parental species to the other, though they resembled *P. poliocephalus* more closely. Juveniles were morphologically distinct from the hybrids and were not intergrades between the two parental species.

Homogeneity of morphological character variance between hybrids and each parental species was evaluated under the hypothesis that hybrids were no more variable than parentals. The variances of morphological characters were not related to the mean for either transformed or un-

transformed data. Variances for all characters between *P. palmarum* and the hybrids were not significantly different. Hybrid variances were highly significantly greater from those of *P. poliocephalus* for extent of black on crown ($F = 7.87$, $df = 2, 12$) and width of white on chin ($F = 18.8$, $df = 2, 12$).

FORAGING BEHAVIOR

No significant differences between juvenile *P. palmarum* and *P. poliocephalus* were found for the eight variables analyzed (Table 2). Adult and juvenile *P. palmarum* differed significantly for five variables, whereas adults of both species differed significantly for four variables (Table 2).

Homogeneity of variances for each of the eight foraging variables between *P. poliocephalus* and *P. palmarum* was evaluated under the hypothesis that *P. poliocephalus* observations should be more variable than juvenile *P. palmarum* observations if juvenile *P. poliocephalus* were included in the collection of the data but not correctly identified. Only one variable, average speed of foraging, showed significant heteroscedasticity between the two groups. To assess foraging differences more carefully and to remove the effects of different habitat types on the patterns, we analyzed foraging behavior for mixed pine habitat only. Significant differences in the use of substrate type between adult and juvenile *P. palmarum* ($\chi^2 = 14.8$, $df = 1$) and adult *P. palmarum* and *P. poliocephalus* ($\chi^2 = 16.4$, $df = 1$) were found (Fig. 3). *Phaenicophilus poliocephalus* did not differ from juveniles in substrate use ($\chi^2 = 0.07$, $df = 1$). Adult *P. palmarum* (BPA) foraged primarily in pine (58%) whereas juveniles (BPI) and *P. poliocephalus* (GPT) chose broadleaf trees and shrubs (67–69%). Foliage-gleaning was the predominant foraging mode for all groups (BPA = 67%, BPI = 68%, and GPT = 73%). The diversities of the substrates used by *P. poliocephalus* and juvenile *P. palmarum* were significantly lower than those of adult *P. palmarum* ($t = 3.6$, $df = 24$ and $t = 5.0$, $df = 48$, respectively). Foraging differences were a consequence of substrate use and not the mode of foraging.

Adult *P. palmarum* were highly significantly different from juveniles ($D_{max} = 0.16$) and from *P. poliocephalus* ($D_{max} = 0.19$) and juveniles were highly significantly different from *P. poliocephalus* ($D_{max} = 0.20$) in foraging heights. Juvenile *P. palmarum* occurred at equal or higher

heights when foraging than did adults in all habitats except mixed pine. The lower foraging heights of adult *P. palmarum* may result from differences in the vegetation structure of their habitat and/or resource distribution.

The frequency distribution of flight distances for adult *P. palmarum* differed significantly from the distributions for juveniles ($D_{max} = 0.21$) and for *P. poliocephalus* ($D_{max} = 0.19$). Juveniles did not differ significantly from *P. poliocephalus* ($D_{max} = 0.15$) in the distribution of flight distances. This frequency pattern is true for all habitats sampled, supporting the hypothesis that juvenile *P. palmarum* and *P. poliocephalus* perceive resources within habitats differently from adult *P. palmarum*. These differences may result from differential dispersion of resources within habitats. For example, in mixed pine, shrubs are not as closely spaced as are pine trees.

Species that retain the juvenile morphology of their antecedents are predicted to be relatively more social than their antecedents because of reduced intraspecific aggression (Lawton and Lawton 1986). We tested the tendency within each species to form groups (>2 individuals) in the non-breeding season (August–April) against the same tendency during the breeding season because family groups are expected to be common during the breeding but not the non-breeding season. A significantly greater tendency to form groups in the breeding rather than the non-breeding season occurred for *P. palmarum* ($\chi^2 = 3.9$, $df = 1$). Differences were not observed between seasons for *P. poliocephalus*. Therefore, the distributions of the number of individuals observed together on transects in the non-breeding season were compared between *P. palmarum* and *P. poliocephalus*. *Phaenicophilus poliocephalus* had a significantly greater tendency to be observed in groups of more than two individuals than did *P. palmarum* in the non-breeding season ($\chi^2 = 7.3$, $df = 2$).

DISCUSSION

Several hypotheses can explain the close similarity between two taxa. They include lack of divergence, geographic variation within a species, character displacement, and/or heterochrony. Because the two taxa were originally chosen for study on the basis of their close relationship, many of the similarities are doubtlessly due to lack of divergence. This observation is consistent

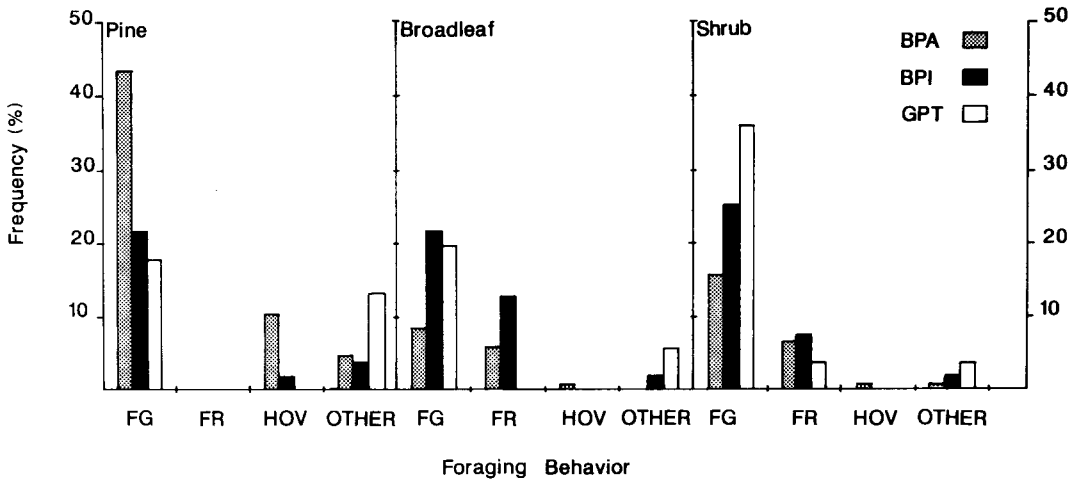


FIGURE 3. Frequency of different types of foraging behavior and substrate use within a mixed pine habitat for three forms of *Phaenicophilus*. Abbreviations as follows: BPA = adult and BPI = juvenile *P. palmarum*; GPT = *P. poliocephalus*; FG = foliage gleaning; FR = frugivory; HOV = hover-gleaning; OTHER = all other foraging behavior.

with their recent estimated divergence in the late Pleistocene (McDonald and Smith 1990). The two taxa are primarily characterized by differences in the extent of black on the crown and the extent of white on the chin. This close resemblance in morphology is further documented by the lack of significant loadings on many of the morphological characters on the first two principal components, suggesting no significant differences in other morphological characters. The differences between species occurred even when the age-dimorphism observed in *P. palmarum* was taken into account.

Extensive gene flow due to hybridization might explain similarities between species. We evaluated the extent of backcrossing between the two taxa, using Lerner's model (1954) for the 17 morphological variables measured in this study (Table 1). Lerner (1954) documented that variation of morphological characters in F₁s is no greater than for either parental species in a hybrid cross. Backcrossing and crosses between F₁s (i.e., F₂) result in higher morphological variation for the hybrids than for parentals. Variances of crown and chin characters, two features that are species-specific, were significantly higher for the hybrids than for *P. poliocephalus*; hybrids were no more variable than *P. palmarum* for any morphological character. The general lack of significant differences in the degree of morphological variation between hybrids and either of the parental spe-

cies suggests that extensive introgression is not likely (Lerner 1954). The pattern of higher variance in hybrids than in *P. poliocephalus* for the two species-specific features is a result of the low variation of these features observed in *P. poliocephalus* and the relatively high variance in *P. palmarum* (Table 1). A cross between these two taxa will result in F₁s with a variance for morphological features intermediate or less than that of the parentals. The apparent absence of introgression and the narrowness of the hybrid zone, in conjunction with low gene flow (McDonald and Smith 1990), suggests that selection against hybrids is occurring. Therefore, the taxa can be considered good species; hybridization does not explain the morphological patterns.

The variation within the crown and chin characters and the frequency of the occurrence might be explained by geographic variation within one species. However, there is no significant correlation of crown and chin characters with geographic variation, as detected by Mantel analysis. In addition, the putative hybrids, which are intermediate in morphology, occur in areas where the two taxa are sympatric. Thus, hybrids do not occur in a unique habitat distinct from that of the two species of *Phaenicophilus*. Nor is there any evidence for character displacement (McDonald 1988). These results suggest that neither geographic variation within a species nor character displacement between species suitably

explain the patterns we observed for these two characters in *Phaenicophilus*. A simpler model is more appropriate.

Heterochrony that occurs as a result of pedomorphic processes can explain both the pattern of resemblance of individuals of one species to juveniles of the other species (Wake 1966, Geist 1971) and delayed maturation within a species (Lawton and Lawton 1986, Foster 1987). Age-dimorphism in characters usually accompanies delayed maturation. *Phaenicophilus palmarum* shows a striking age-dimorphism and is likely an example of a species characterized by delayed maturation. The systematic consequences of heterochrony could be a species retaining the juvenile characters of an antecedent species, as may be the case for *Phaenicophilus poliocephalus*. For this to occur, there must be significant character differences between the adults and juveniles of the antecedent species. Such a dimorphism is often associated with differences in resource exploitation by the adult and juvenile age-classes when resources are periodically limiting (e.g., Northern Harrier, *Circus cyaneus*; Hammerstrom 1986).

Juvenile *P. palmarum* were significantly different from adults in the extent of black on the crown, wingchord, and proximal depth of bill. Gray crowns in juveniles darken with age. Although gray-crowned *P. palmarum* were not observed breeding, dark gray-crowned individuals have been collected at the beginning of the breeding season in late March or early April; some individuals probably delay maturation through their first breeding season. At least 10% of tanager species delay molt into adult plumages through the first breeding season (Isler and Isler 1987), and some species are known to breed in subadult plumage and therefore, are neotenic (Lawton and Lawton 1986). Thus, *Phaenicophilus palmarum* is most likely a neotenic species, and one reflection of this is the observed age-dimorphism. The principal difficulty in establishing whether *P. poliocephalus* is pedomorphic to *P. palmarum* rests with determining the polarity of their evolution, i.e., which species is derived from which. We present genetic and morphological evidence elsewhere (McDonald 1988, McDonald and Smith 1990) that strongly support our contention that *P. poliocephalus* is derived from *P. palmarum*, and therefore, must be pedomorphic to it.

Paedomorphosis results in the retention of ju-

venile morphologies and could have consequences for other characters, such as social behavior. There is evidence in Red-winged Blackbirds, *Agelaius phoeniceus*, that subadult plumage reduces intraspecific aggression (Rohwer 1978). Species derived from other species by pedomorphosis should be more social relative to their antecedents as a result of reduced intraspecific aggression (Lawton and Lawton 1986). Data on mountain sheep support this prediction (Geist 1971). *Phaenicophilus poliocephalus* was observed in groups of 4–6 individuals during the non-breeding season, whereas *P. palmarum* was observed singly or in pairs. This tendency to form groups in *P. poliocephalus* is consistent with the hypothesis that gray crowns may reduce intraspecific aggression. Additional predictions involving body size follow from this general pedomorphic model.

Gould's (1977) primary distinction between progenesis and neoteny depends upon selection that alters first age of reproduction and changes body size. Neoteny would be expected to result in larger adult body size due to delayed maturation. In contrast, progenesis (i.e., earlier sexual maturation) results in smaller body size, due to slower somatic growth after sexual maturation (Gould 1977). Development arrested at an early stage often results in smaller individuals (Larson 1980, Alberch 1989). Three hypotheses concerning the relation of body size between the two species were evaluated as follows: (1.) Adult *P. palmarum* are larger than post-fledgling juveniles, (2.) Adult *P. palmarum* are larger than adult *P. poliocephalus*, (3.) Juvenile *P. palmarum* are no larger than adult *P. poliocephalus*. The first hypothesis needs to be tested because post-fledgling juveniles can often be as large or larger than adults in birds. The second hypothesis tests the prediction that arrested development occurs early enough in the ontogeny of the derived species relative to the antecedent that the adults of the derived species will be smaller. The third hypothesis tests the prediction that adults of the derived species and juveniles of the antecedent species are comparable in size.

Juvenile *P. palmarum* are significantly smaller (one-tailed test) than adults in wingchord, braincase length, and proximal depth of bill ($P_1 < 0.025$). *Phaenicophilus poliocephalus* is significantly smaller than juvenile *P. palmarum* in bill length, medial depth of the bill, and length of second toe (one-tailed test), and is smaller than

adults for the same three characters as well as wingchord, braincase length, and proximal bill width and depth (one-tailed test). Data from juveniles of differing ages were pooled because the criterion for designating juvenile *P. palmarum* was the presence of a gray crown; therefore, elevated variances for various characters might be expected to confound the tests for size differences. However, variances were homogeneous between the juvenile and adult classes. Juveniles were significantly smaller than adults in three of the eleven size-related characters. That *P. poliocephalus* was significantly smaller than adult *P. palmarum* in seven of the eleven characters as predicted, supports the hypothesis of evolution by progenesis for this species.

It is the pattern and direction of size differences that are important to our argument that *poliocephalus* is not only paedomorphic to *palmarum*, but that it is progenetic. Only under the progenetic hypothesis (Gould 1977) do we expect *poliocephalus* to be smaller than *palmarum*. If *poliocephalus* were neotenic, ancestral, or recapitulatory to *palmarum*, we would expect it to be larger or the same size. The size differences and the direction of the size change is concordant with other patterns we discussed and fits most parsimoniously with the model of heterochrony, and particularly with progenesis. The average first age of reproduction and/or its variance should also be lower in *P. poliocephalus* than in *P. palmarum*, but the necessary data to test this prediction are lacking.

Gould's (1977) model stresses the importance of selection on one character leading to simultaneous change in other associated characters. The retention of juvenile behavior in *P. poliocephalus* is most likely a consequence of the association of behavior with juvenile morphology (Coppinger et al. 1987). Juvenile *P. palmarum* differ significantly in their foraging behavior from and are less efficient than adults. This is a common observation in birds and has been attributed to the lack of experience of juveniles (Orians 1969, Recher and Recher 1969, Stevens 1985, Sutherland et al. 1983). Juvenile *P. palmarum* are significantly slower, spend more time stopped, and try more food-catching attempts per perch change than adults, but the success-to-attempts ratio is lower (Table 2). Significant differences between juveniles and adults were not observed in the type of foraging behavior; they are both primarily insectivorous. Significant differences

were observed in the choice of substrates. In mixed pine habitat, juveniles used broadleaf rather than pine substrates (Fig. 3). In mesic woodland, juveniles had a significantly lower substrate diversity than did adults. Foraging height, flight distances, and horizontal substrate use were also significantly different between adults and juveniles. Differences in foraging behavior are probably not a simple function of learning but effectively result in partitioning the foraging space between birds of different age-classes. Juveniles and adults use the same foraging behavior but in different parts of their habitat.

Arrested morphology in the derived species should correspond to retention of juvenile behaviors (Geist 1971, Lawton and Lawton 1986, Coppinger et al. 1987). Adult *Phaenicophilus poliocephalus* resemble juvenile *P. palmarum* in foraging behavior. A lack of experience in foraging is not a likely explanation for behavior in adult *P. poliocephalus*. *Phaenicophilus poliocephalus* uses broadleaf substrates in mixed pine habitat as do juvenile *P. palmarum* and has significantly lower substrate diversity in mesic woodland than do adult *P. palmarum*. Competition between *P. poliocephalus* and adult *P. palmarum* is not a likely explanation, either. The zone of contact between the two forms is narrow. Moreover, the mixed pine habitats in which the foraging data were collected were separated by a distance of 100 km or more. Differences between *P. poliocephalus* and juvenile *P. palmarum* in patterns of foraging height and horizontal use of the substrate suggest that similarity of other foraging behavior is not a result of similar selective regimes because their habitats differ. The behavioral similarities probably result from retaining juvenile behaviors which are associated with arrested morphological development in *P. poliocephalus*.

Critical to our argument is that *P. poliocephalus* adults resemble juvenile *palmarum*. It is conceivable that juvenile *poliocephalus* differ from adults of their own species; that does not affect our argument about heterochrony. It implies something else is occurring. We did not find evidence of this age-dimorphism in morphology, genetics, or in predicted heteroscedasticity of the pooled foraging data for *poliocephalus*. Given that so few museum specimens were characterized as juveniles for this species, we suspect that errors in our analysis would be in favor of adult behavior.

Phaenicophilus poliocephalus is most likely derived from and is progenetic to *P. palmarum*. The smaller size, retention of juvenile morphology and foraging characteristics, and the propensity to form groups in *P. poliocephalus* support this conclusion. The retention of these juvenile patterns cannot be simply explained by selection for every character, especially because juvenile *P. palmarum* are less efficient foragers than adult *P. palmarum* and, therefore, selection would not favor these behaviors. The retention of juvenile foraging behavior and smaller size of *P. poliocephalus* is probably a consequence of arrested development in morphology. Selection for early maturation in *P. poliocephalus* was probably concomitant with the retention of gray crowns, which may reduce intraspecific aggression. Reduction in intraspecific aggression may have resulted in changes in the degree of sociality between species of *Phaenicophilus*, which can have significant consequences for the subsequent evolution and ecology of *P. poliocephalus*.

We propose elsewhere (McDonald and Smith 1990) that *P. poliocephalus* is most likely derived from a small founding population, composed mostly of juvenile *P. palmarum*, colonizing the south island of Haiti during Pleistocene glacier melts, when sea levels rose, and Hispaniola was divided in two or more islands. Our genetic model (McDonald and Smith 1990) supports a small founding population composed mostly of juveniles and is consistent with subsequent speciation by regulatory gene changes, as expected in paedomorphic derivations. Necessary prerequisites for this scenario are an antecedent species with significant differences between age-classes in genetic variability and selection in the new habitat for early reproductive maturation. Here we present evidence that *P. palmarum* is age-dimorphic in behavior and morphology corresponding to the genetic patterns, that *P. poliocephalus* has retained the juvenile behavior and morphology of its purported antecedent, and that these patterns support the hypothesis that the derivation is heterochronic. We emphasize that retention of juvenile behavior results from arrested development and not selection. We predict that there are many more examples, particularly for the tanagers, where heterochronic speciation can be documented by investigating the phenotypic and genetic patterns among species.

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APPENDIX I

DESCRIPTION OF MORPHOLOGICAL MEASUREMENTS

Measurements were taken with a Helios caliper to the nearest 0.01 mm. Nomenclature based on Baldwin et al. (1931).

Extent of black on forehead and crown (CCRN): Exposed culmen to central edge of black on crown at nape. Only black crowns were analyzed; crowns of juvenile *P. palmarum*, which were of varying shades of gray, were measured (when crown was distinct from gray nape), but not used in the morphological analysis. CCRN for juveniles was set = 0. Hybrids were not intermediate in shade of gray on the crown, as expected, but were intermediate in extent of black on the crown.

Crown to nape (NAPE): Exposed culmen to distal edge of gray on nape.

Crown to left (LCRN), right edge of mask (RCRN): Exposed culmen to left or right edge of black on face mask, lateral to head.

Braincase (BRNC): Exposed culmen to occiput. This measurement could only be taken on fresh specimens or where the back of the skull was not removed in preparation.

Eyespots: Length of the three facial eyespots, right and left, was taken as the longest axis on the eyespots. The eyespots are designated as (1) Dorsal Anterior (DA)-eyespot dorsal anterior to the eye, (2) Dorsal Posterior (DP)-eyespot dorsal to the eye and posterior to the DA, (3) Ventral (V)-eyespot ventral to eye.

Length of white on chin (CCHIN): Angle of gony on lower mandible to posterior edge of white on chin along midline of bird. In *P. palmarum*, there was often no distinction between chin and throat. When this occurred, CCHIN was set equal to CHINCAUD.

Lateral extension of white on throat (LBILL, RBILL): Angle of gony to lateral extension of white below rami.

Body length (CHINCAUD): Angle of gony to insertion of first rectrices at base of tail.

Bill length (CULTIP): Exposed culmen to tip of bill.

Bill depth: The depth of the bill at the base, or proximal depth (PD), was measured from the exposed culmen

to the lower edge of the ramus below. Mid-depth (MD) was taken at one-half length of the bill, from the upper edge of the mandible to the lower edge of the lower mandible.

Bill width: The proximal width (PW) of the bill was taken at the edge of the exposed culmen, across both mandibles. The mid-width (MW) was taken at one-half length of the bill from the exposed culmen.

Length of the lower mandible (LMAND): From the juncture of the gonys to the tip of the lower mandible.

Wingchord (WC): Chord measured from the most anterior portion of the wrist joint to the tip of the longest primary, on the unflattened wing.

Tarsus (TAR): Taken from the middle joint between the tibia and metatarsus in back of the leg to the most distal undivided scute located above the junction of the metatarsus and the middle toe.

Middle toe + claw (TOE): (1) Taken from the junction of the middle toe and the metatarsus to the first joint, (2) first joint to second joint, (3) second joint to base of claw, (4) chord from base of claw to tip of claw.

Tail length (TAIL): From the point of insertion of the two middle rectrices on the body to the tip of the longest rectrix, when the tail is closed.