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INTRA-ISLAND VARIATION IN THE 'ELEPAIO ON THE ISLAND OF HAWAI'I

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ABSTRACT.—The 'Elepaio (*Chasiempis sandwichensis*) exhibits great variation in plumage color on the Island of Hawai'i. Analysis of specimens from localities throughout the island reveals that the variation is geographically based, and that three subspecies can be distinguished: *C. s. bryani*, a pale form found at high elevation on the southwestern slopes of Mauna Kea; *C. s. ridgwayi*, a dark form found in wet windward forests; and *C. s. sandwichensis*, an intermediate form found in forests of the Kona region. Several zones of primary intergradation and one of possibly secondary intergradation occur, but appear to be narrow. The forms *C. s. sclateri* of Kaua'i and *C. s. gayi* of O'ahu exhibit no similar intra-island variation. Variation among the Hawai'i subspecies probably evolved in response to local variation in rainfall, and follows the predictions of Gloger's Rule, but the selective forces involved are obscure.

The 'Elepaio (*Chasiempis sandwichensis*) is a monarchine flycatcher that comprises a genus endemic to the Hawaiian Islands. 'Elepaios occur on Kaua'i, O'ahu, and Hawai'i, but are enigmatically absent from other seemingly suitable islands. Great plumage variation caused much early confusion as to the taxonomic status of the various forms. Some populations are sexually dimorphic as adults, and all exhibit distinctive immature plumages. Stejneger (1887) recognized five species but later workers (Wilson and Evans 1890–99, Rothschild 1893–1900, Henshaw 1902a, Perkins 1903, MacCaughey 1919) reduced the number to three: *C. sclateri* of Kaua'i, *C. gayi* of O'ahu, and *C. sandwichensis* of Hawai'i. Bryan and Greenway (1944) were apparently the first to consider all the forms conspecific, and this treatment has been followed in virtually all recent works. As subspecies, the three allopatric populations are strongly differentiated in color, but they are similar in habits, ecology, and vocalizations. Whether the plumage differences alone are potential isolating mechanisms is moot. The Kaua'i and O'ahu forms can be considered "megasubspecies" as defined by Amadon and Short (1976). Neither *C. (sandwichensis) sclateri* nor *C. (s.) gayi* shows any evidence of intra-island variation.

APPEARANCE OF THE BIRDS

Adult 'Elepaios on Hawai'i are brown above and white below with white wing-bars, rump, and tail tip. The breast and belly are more or less streaked with rufous–chestnut, and a contrasting eyebrow varies from deep rufous-chestnut to pure white. The throat feathers of males are black, tipped with white. The white tips wear away making some specimens appear entirely black-throated. In females the throat is often entirely white, and at most only a small area of black in the chin is present. Usually the white throat of females is separated from the rufous-streaked breast by a diffuse dark brown or black band. Immature birds of both sexes are plain gray-brown or dull reddish brown above, white below, and lack the bold white and chestnut markings of adults.

Striking variation occurs in the coloration of the head in adults, with males exhibiting more diversity than females. In birds at some localities, the eyebrow is pure white and quite broad, the white feathers of the throat very extensive, and an almost complete white collar encircles the neck. In most such individuals, no trace of rufous can be seen in the head region and the white is so extensive that the birds appear white-headed in the field. In contrast, other localities are inhabited by birds whose plumage above is a rich, dark chestnut, with the eyebrow a dark rufous like the color of the breast streaks. In these individuals the white tips of the throat feathers stand out in sharp contrast to the rest of the head plumage. Intermediates between these extremes occur at still other localities.

TAXONOMIC HISTORY

Henshaw (1902a) was the first to analyze variation among Hawai'i 'Elepaios. His study suffered from a lack of specimens from many parts of the island, but provided the first good evidence of geographically

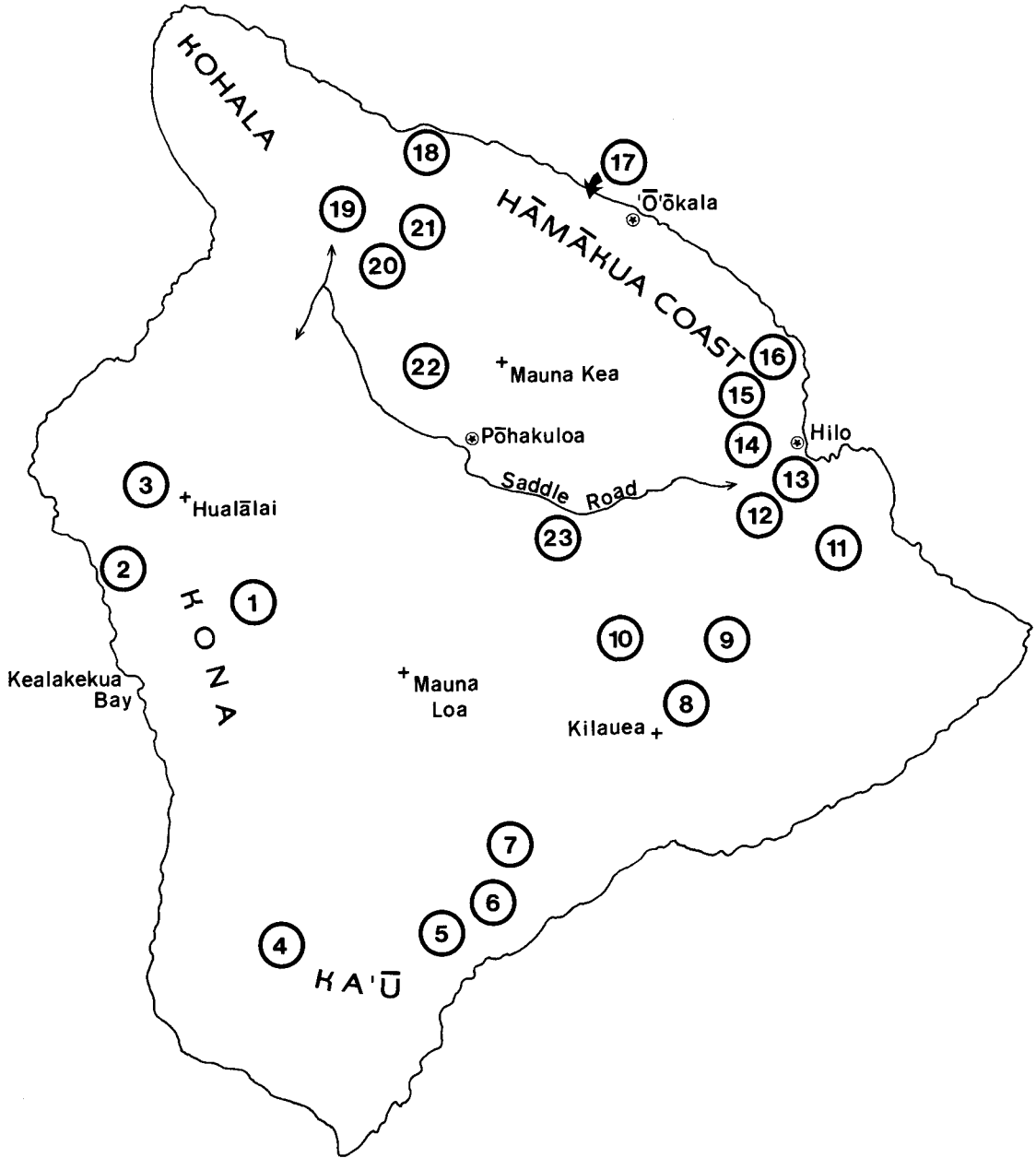

FIGURE 1. Map of the island of Hawai'i showing localities of specimens of *Chasiempis sandwichensis* used in this study and several other important localities. (1) Pu'u Lehua, (2) Keauhou (Kona), (3) Kaloko Mauka, (4) Ocean View Estates, (5) Dalway's, (6) Pāhala, (7) Kapāpala, (8) Volcano/Kīlauea, (9) Ōla'a, (10) Keauhou Ranch, (11) Kea'au, (12) Kaūmana, (13) Waiakea, (14) Kaiwiki, (15) Kuaia, (16) Honomū, (17) Pa'auilo, (18) Kukuihaele, (19) Waimea, (20) Horner's Ranch, (21) Mānā, (22) Pu'u Lā'au, (23) several kīpukas along the Saddle Road.

based variation. He recognized two subspecies: *C. s. ridgwayi*, a chestnut-browed form on the wet windward side of the island; and *C. s. sandwichensis*, a paler-browed form on the rest of the island. He designated the range of *C. s. ridgwayi* as lying between 'Ō'ōkala and Volcano. His extensive series of specimens from this area showed great uniformity. Henshaw (1902a) also collected extensively at Pu'u Lehua in Kona, where he encountered a form with a more or less white eyebrow. He considered this form to be the nominate one, since the specimens upon which the name was based probably came from Kealakekua Bay in Kona (Henshaw 1902a). His collection also included birds from a few localities in Ka'ū, but basically was from only two parts of the island. This fact may account for the reluctance of subsequent authors to use his sub-

TABLE 1. Key to color characters of male 'Elepaios from the island of Hawai'i. Capitalized color names are from Smithe (1975).

Character	Character states	Specimens
A. Breast color	1. Chestnut to Amber	BBM 3896
	2. Amber	BBM 3889
	3. pale Amber	BBM 3942
	4. between Amber and Antique Brown	LSUMZ 81726
	5. Antique Brown	LSUMZ 81713
B. Breast streaks	1. No streaks, uniform color	BBM 3896
	2. Breast band broken posteriorly	BBM 3932
	3. Complete streaks in center only	BBM 3949
	4. Heavily streaked	LSUMZ 81726
	5. Streaks confined to sides, center clear	LSUMZ 81713
C. Auricular color	1. between Chestnut and Amber	BBM 3896
	2. Cinnamon-Rufous	BBM 3907
	3. Tawny	BBM 3894
	4. Cinnamon-Brown	BBM 3905
	5. Olive-Brown	LSUMZ 81713
D. Back color	1. dark Cinnamon-Brown	BBM 3852
	2. Cinnamon-Brown	BBM 3924
	3. Antique Brown	BBM 3780
	4. grayish Antique Brown	BBM 7210
	5. Olive-Brown	LSUMZ 81712
E. Color of eyestripe and side of head	1. Between Chestnut and Amber	BBM 3896
	2. Amber	BBM 3889
	3. between Tawny and Cinnamon-Rufous	BBM 3852
	4. white tinged Cinnamon-Rufous	BBM 3808
	5. white	LSUMZ 81725
F. Amount of black in lores	1. extensive	BBM 3728
	2. less extensive	BBM 3848
	3. moderate amount	BBM 3845
	4. trace	BBM 3849
	5. none	LSUMZ 81713
G. Crown color	1. dark reddish Amber	BBM 3822
	2. Amber	BBM 3734
	3. Cinnamon-Brown	BBM 3749
	4. dark Cinnamon-Brown	LSUMZ 81736
	5. Brownish Olive	LSUMZ 81725

specific designations. Nevertheless, his collections are now extremely valuable in documenting the distribution of color variants of the 'Elepaio in areas where the species no longer exists.

In 1974 I observed what I at first took to be an albinistic 'Elepaio at Pu'u Lā'au on the northwest slope of Mauna Kea. Further investigation revealed not only that all 'Elepaios at this locality were similarly colored but that no specimens from the area existed in collections. After obtaining a series of specimens, I described the Pu'u Lā'au population as a new subspecies, *C. s. bryani* (Pratt 1979a). The present study documents the distributions of the three named subspecies of *C. sandwichensis* on the island of Hawai'i.

METHODS

I compared the type series of *Chasiempis sandwichensis bryani* with other specimens collected on the island in 1976–78 and with older specimens in the Bernice P. Bishop Museum, Honolulu (BBM), American Museum of Natural History (AMNH), National Museum of Natural History (USNM), Museum of Vertebrate Zoology, Berkeley (MVZ), and Louisiana State University Museum of Zoology (LSUMZ). The total sample contained 136 adult males and 118 adult females from 23 localities (Fig. 1).

Color variation was documented by use of a series of reference specimens for each character. The specimens were designated 1 to 5 to show a gradation of the character. A description of these character states and the museum numbers of the reference specimens are given in Table 1 (males) and Table 2 (females). More parameters were available for males than for females in the color analysis. Mensural data included length of exposed culmen, width of bill at base, wing chord, and tail length.

Figure 1 shows numbered localities from which 'Elepaios were examined and other geographical features mentioned herein. Proper names are given for all sites except for 23, which groups together several isolated forests (kīpukas) along the Saddle Road between 1,494 and 1,743 m elevation. Some of the numbered localities undoubtedly represent samples from fairly large areas. For example, most of Henshaw's Kona specimens are labelled "Puluhua" (= Pu'u Lehua) but his account (Henshaw 1902b) reveals that he ranged far from this base of operations. Thus his Kona series

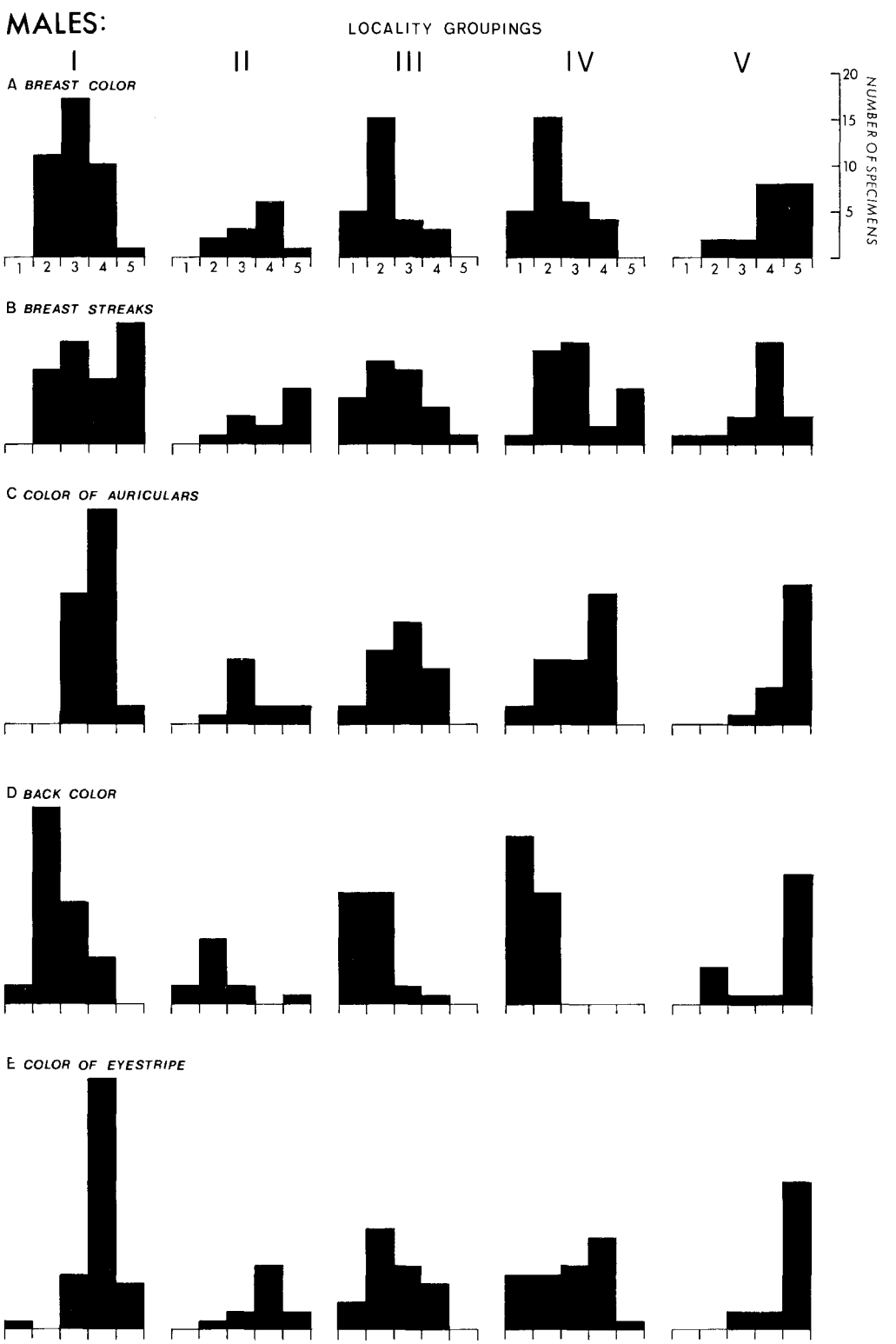

FIGURE 2. Distributions of color characters among samples of *Chasiempis sandwichensis* from five groupings of localities on the island of Hawai'i. Character states 1–5 as in Tables 1 and 2; locality groupings given in Methods.

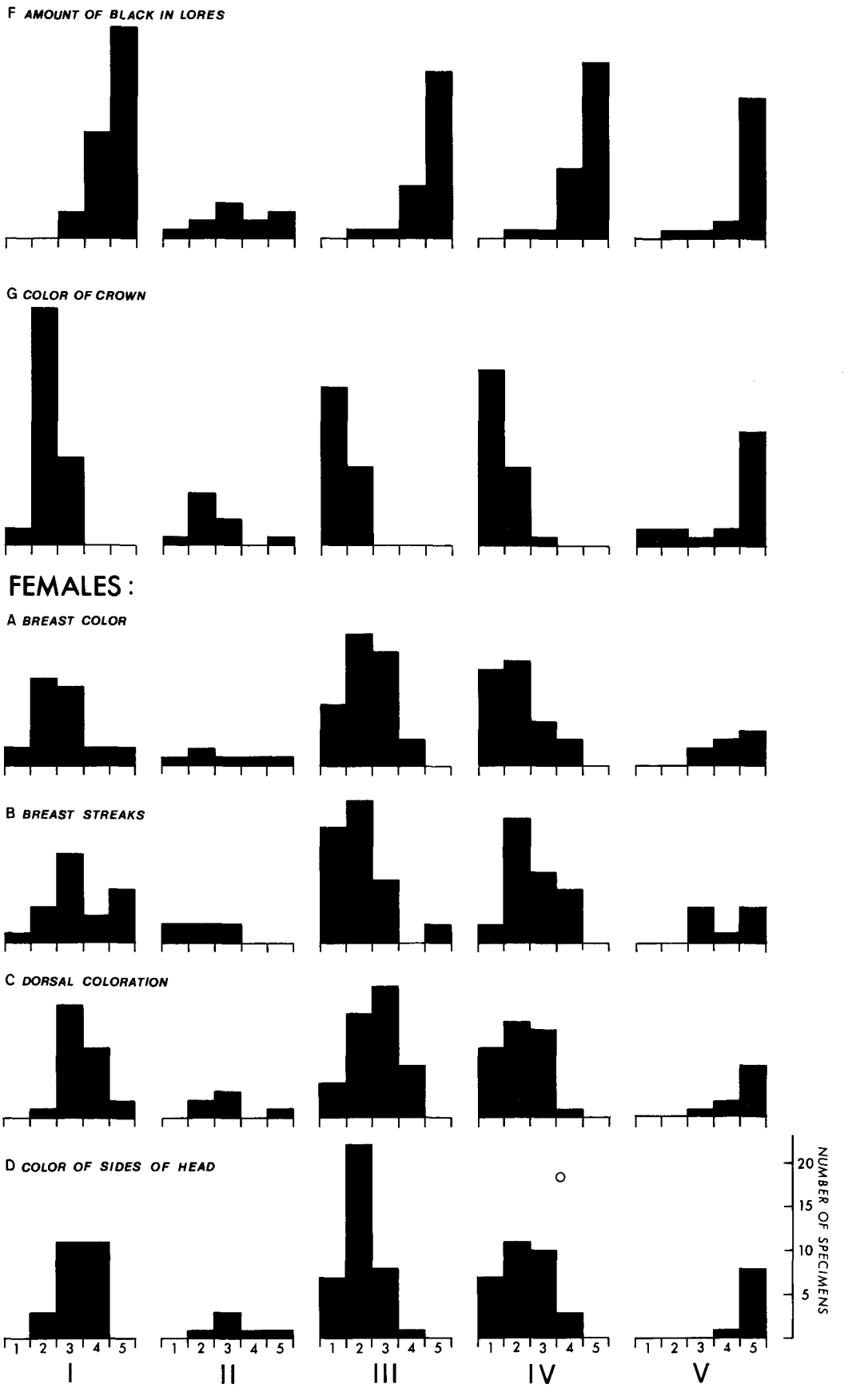
F AMOUNT OF BLACK IN LORES
G COLOR OF CROWN
FEMALES:
A BREAST COLOR
B BREAST STREAKS
C DORSAL COLORATION
D COLOR OF SIDES OF HEAD
NUMBER OF SPECIMENS
20
15
10
5
1 2 3 4 5
I
II
III
IV
V

TABLE 2. Key to color characters of female 'Elepaios from the island of Hawai'i. Capitalized color names are from Smithe (1975).

Character	Character states	Specimens
A. Breast color	1. Amber	BBM 3888
	2. between Tawny and Cinnamon	BBM 3919
	3. Tawny	BBM 3813
	4. between Tawny and Antique Brown	BBM 3778
	5. Antique Brown	LSUMZ 81732
B. Breast streaks	1. no streaks, breast uniform	BBM 3920
	2. breast color broken posteriorly	BBM 3909
	3. breast entirely streaked	BBM 3794
	4. streaks confined to sides	BBM 3811
	5. few streaks, on sides only	LSUMZ 81715
C. Dorsal color	1. dark Cinnamon-Brown	BBM 3899
	2. dark Antique Brown	BBM 3910
	3. Antique Brown	BBM 3847
	4. between Antique Brown and Cinnamon	BBM 3953
	5. between Olive Brown and Cinnamon-Brown	LSUMZ 81723
D. Color of sides of head	1. dark Cinnamon-Rufous	BBM 3887
	2. Cinnamon	BBM 3879
	3. pale Cinnamon	BBM 3943
	4. white tinged with Cinnamon	BBM 3817
	5. white	LSUMZ 81710

represents a larger area than his single place name would indicate. Other such designations that probably refer to large areas are Volcano (8), 'Ōla'a (9), Kaūmana (12), and Waimea (19). I could not tell the exact location represented by two names, "Kuaia" (15) and Horner's Ranch (20), but I deduced an approximate location from the collection dates of surrounding localities. The 23 places cover well the areas where 'Elepaios occurred historically on the island, but a few areas of difficult access remain unsampled. Two particularly important such areas are the forests of the Kohala region at the northern end of the island and the wet upper forests of Ka'ū.

The localities fall naturally into five geographical clusters (Fig. 1) as follows: (I) Hualālai-Kona, 1–3; (II) Ka'ū, 4–7; (III) Volcano-'Ōla'a, 8–10; (IV) Hāmākua Coast, 11–16; and (V) Mauna Kea, 19–22. Localities 17, 18, and 23 were purposely not included in the groupings. The other groupings were considered single localities in the computer analysis of the data. The samples were too small for the use of otherwise appropriate nonparametric statistical tests. I used the parametric Duncan's Multiple Range Test (Duncan 1955) even though the data are not strictly parametric. Differences were considered significant at the 0.05 level.

Words of Hawaiian origin used in this paper are written using the orthography of the *Atlas of Hawaii* (Armstrong 1973) and the Pukui and Elbert (1971) *Hawaiian Dictionary*. Taxonomy follows Pratt (1979b).

RESULTS

Mean scores of the five locality groupings for plumage color characters are given in Table 3, and Figure 2 shows the distribution of character states within each sample. For males, Groups I and II differ significantly from each other only in the amount of black in the lores (Character F) and in tail length (K). Groups III and IV are morphologically indistinguishable. If these two pairs are combined as single units, a clear picture (Fig. 3) of intra-island variation in male 'Elepaios emerges. For each character, those populations showing no significant differences are connected by lines. For example, Character A (breast color) is not different in populations I+II and V, but both of these populations differ in this character from III+IV. Each of the three populations has at least two diagnostic plumage characters. Mensural data show little appreciable differentiation.

Females are much less variable than males. Figure 4 diagrams the relationship among the five geographic groups of the four variable plumage characters. Other

TABLE 3. Mean color scores of 'Elepaios from five groups of localities on the island of Hawai'i.

	Locality groupings[b]				
Character[a]	I	II	III	IV	V
Males					
A	3.0	3.5	2.2	2.3	4.1
B	3.6	4.1	2.7	3.1	3.8
C	3.7	3.4	2.8	3.1	4.7
D	2.5	2.3	1.7	1.4	4.3
E	3.9	3.8	2.5	2.8	4.7
F	4.5	3.3	4.6	4.6	4.7
G	2.2	2.5	1.3	1.4	4.1
Females					
A	2.7	2.8	2.3	2.0	4.2
B	3.4	2.0	2.0	2.5	4.0
C	3.4	3.0	2.6	2.1	4.5
D	3.3	3.3	2.1	2.3	4.9

[a] For descriptions of characters and meanings of scores, see Tables 1 and 2.
[b] Locality groupings given in Methods.

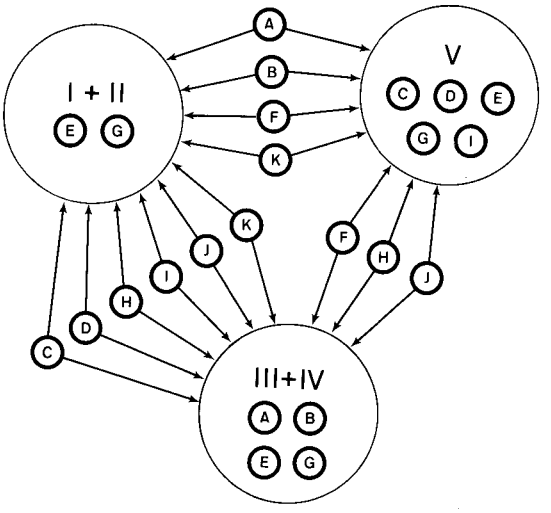

FIGURE 3. Diagrammatic representation of character distributions among male 'Elepaios on the island of Hawai'i. The lettered arrows connect populations that do not differ significantly in the character indicated. When a population differs from all others for a given character, the letter is enclosed within the numbered circle for that population. Plumage characters (A–G) are given in Table 1. Mensural characters are (H) bill length, (I) bill width, (J) wing chord, and (K) tail length. Roman numerals indicate locality groupings as given in Methods.

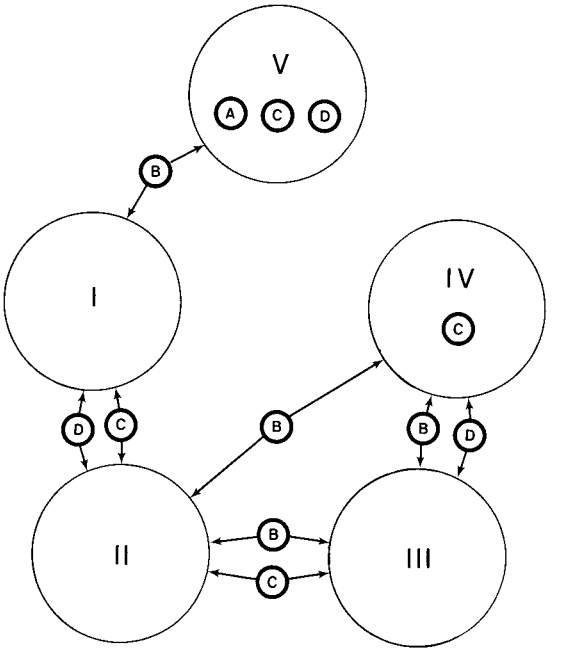

FIGURE 4. Diagrammatic representation of character distributions among female 'Elepaios on the island of Hawai'i. Letters indicate characters as given in Table 2. For interpretation of symbols, see Figure 3.

characters exhibit no geographical variation. The pattern shown is essentially the same as that for males, but is less obvious because of the small number of characters available. As with males, the Mauna Kea population stands clearly apart from the others. The I+II and III+IV groupings are less obvious, however, as are the distinctions between populations I+II and III+IV. But the most striking character, color of the eyebrow and face (D), follows the pattern found in the males.

The pattern of geographic variation revealed here supports the recognition of the three described subspecies of 'Elepaio on the island. Also, the range of *C. s. bryani* is expanded by the inclusion of older specimens from lower elevations adjacent to the range first described for the subspecies (Pratt 1979a). Because of habitat loss, 'Elepaios no longer occur in these areas. Similarly, the distributions shown in Figure 5 of the other two races include lowland areas now largely sugar cane fields or pastureland. The gap shown in the central part of the island probably reflects natural patterns of distribution. Areas of intergradation are indicated by cross-hatching. Question marks indicate areas where 'Elepaios are known to occur, but which have not been sampled.

Henshaw (1902a) described a zone of intergradation between *C. s. ridgwayi* and *C. s. sandwichensis* (then including *bryani*) north of 'Ō'ōkala on the Hāmākua Coast. Specimens from the area are few but revealing. One male (MVZ 21445) from Pa'auilo about 10 km north along the coast from 'Ō'ōkala is clearly intermediate in several characters. It generally resembles *C. s. ridgwayi,* but has a slightly rusty tinged white eyebrow that forms an almost complete collar around the back of the head as in *C. s. bryani.* Another male (MVZ 7028), taken the same day at the same place, shows much less influence of *bryani* in the color of the eyebrow but does have a few white feathers scattered among the rufous ones, and has a trace of a pale collar.

Henshaw (1902a) also considered his specimens from Ka'ū to be intergrades, and indeed the small series from Pāhala (4 males, 3 females) and Kapāpala (3 males, 2 females) shows intermediacy in various characters. Since these specimens were included in the statistical analysis, they may account for the greater degree of similarity between *sandwichensis* and *ridgwayi* than between either of these and *bryani* (Figs. 3, 4).

A particularly interesting zone of intergradation (Locality 23) occurs in the saddle

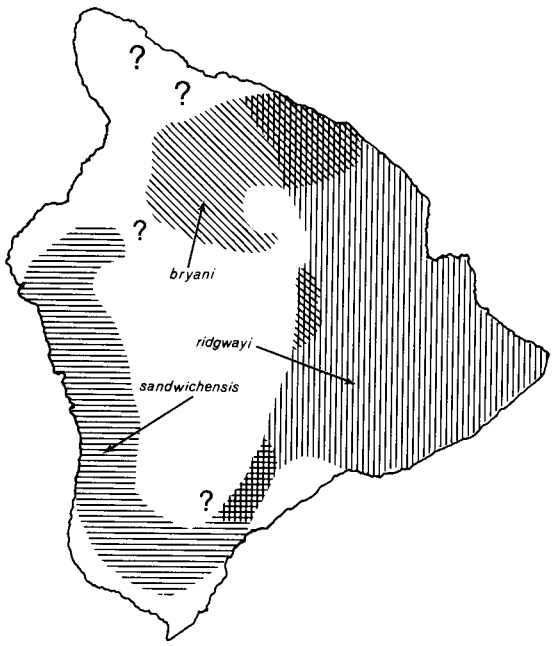

FIGURE 5. Approximate distributions of the three subspecies of *Chasiempis sandwichensis* on the island of Hawai'i. Question marks indicate areas where 'Elepaios are known to occur but which are not represented by specimens. Locality 18 (Fig. 1) is represented by a single enigmatic specimen and is thus not included in any of the ranges shown. Cross-hatching indicates intergradation.

between Mauna Kea and Mauna Loa. Here a gap of approximately 10 km occurs in the distribution of the 'Elepaio. Apparently the present range of *C. s. bryani* corresponds closely to that of the Palila (*Loxioides bailleui*) on Mauna Kea (van Riper et al. 1978). 'Elepaios do not occur, or are very scarce, in the seemingly suitable scrub forest of the flat region known as Pōhakuloa. From the southeast, the range of *C. s. ridgwayi* extends to the upper limit of wet forests. At the upper forest fringe, lava flows have dissected the wooded areas and produced numerous forest islands known as kīpukas. 'Elepaios are rare here. I could obtain at most only two specimens in any single kīpuka. By chance, the specimens include only one male, and it is a typical specimen of *ridgwayi*. The six females, however, show varying degrees of intergradation in the color of the eyebrow. Female *ridgwayi* only rarely show appreciable amounts of white over the eye, but one specimen (LSUMZ 81443) from a kīpuka at 1,494 m has only a slight tinge of rufous in an otherwise white eyebrow. But another bird from the same elevation (LSUMZ 81728) shows no evidence of intergradation. At the uppermost elevation (1,743 m) before the distributional hiatus, three specimens (LSUMZ 81731, 81732, 81733) all possess eyebrows of mingled rufous and white feathers, but in a small kīpuka at 1,597 m I obtained a bird (LSUMZ 81730) that represents the dark extreme for every plumage character! Apparently these forest islands function in a manner similar to actual islands, receiving chance immigrants from the nearby "mainland" forests. Thus some kīpukas are populated by pure *ridgwayi*, while others have apparently received genetic input from *bryani* or perhaps even *sandwichensis*. An important consideration here is that 'Elepaios seem to be rather sedentary.

DISCUSSION

Evolutionary divergence within the confines of a single small island is rare. On Jamaica (11,784 sq. km), the hummingbird *Trochilus polytmus* has evolved two forms that have been treated as subspecies (Gill et al. 1973) or full species (Schuchmann 1978). On the Indian Ocean island of Reunion (2,590 sq. km) the white-eye *Zosterops borbonica* exhibits a mosaic of color and size variation and was originally divided into four subspecies (Storer and Gill 1966). Gill (1973) later advocated that the various forms of this white-eye be considered a single variable taxon. Nevertheless, the variation shown by *Z. borbonica* on Reunion is essentially the same evolutionary phenomenon exhibited by the 'Elepaio on Hawai'i (10,458 sq. km), and indeed Gill (1973: 56) suggested Hawai'i as a likely place to look for such phenomena. Apparently climatological and ecological diversity even on a small island can lead to a speciation event.

As on Jamaica and Reunion, the intra-island variation on Hawai'i appears to be completely autochthonous. Despite differences among them, the three Hawai'i forms of the 'Elepaio are more similar to each other than any of them is to the Kaua'i or O'ahu subspecies. The Hawaiian example, however, differs from that on Jamaica (Schuchmann 1978) in being mainly the result of primary divergence with continual contact between the populations. Only the kīpukas of the saddle area show evidence of secondary contact and even then, the forms involved intergrade clinally elsewhere on the island. Because 'Elepaios apparently do not disperse widely, adaptations to local conditions can easily become fixed in local populations.

The variation in the 'Elepaio on Hawai'i appears to be related to rainfall. The range

of *C. s. ridgwayi* corresponds almost exactly to the windward parts of the island that receive over 190 cm of annual rainfall. This area at its heart receives over 762 cm of rain, and in such very wet areas the darkest plumage variants occur. Local populations are not uniform, however, and no smooth clines associated with rainfall can be discerned. Similar variation in local populations can be seen in *C. s. sandwichensis*, with the pale extremes occurring in the drier areas of southern Ka'ū. Some specimens from this area possess plumage characters similar to those of *C. s. bryani*. The latter race is apparently adapted to xeric habitats that receive annual rainfall of less than 76 cm.

'Elepaios on the island of Hawai'i provide the only clear expression of Gloger's Rule among Hawaiian birds, and may give insight into the selective basis of the rule. That such ecogeographic trends exist is well documented (Mayr 1956), but the selective forces involved are a matter of controversy. Concealment has often been regarded as the main adaptive advantage of dark pigmentation in humid habitats (Cott 1957). The island of Hawai'i has two large avian predators that hunt visually, the Hawaiian Hawk (*Buteo solitarius*) and the diurnal Short-eared Owl (*Asio flammeus*). Predation thus could have been a factor in selection for concealing coloration on the island. O'ahu and Kaua'i 'Elepaios show no variation within their respective islands where only the owl occurs. However, the effectiveness of the hawk as a predator of small birds such as the 'Elepaio is probably not great. Certainly the hawk must have fed on birds before rats were introduced by aboriginal Hawaiians, but in historic times it has fed mainly on arthropods and introduced rodents (Henshaw 1902b, Munro 1960, Tomich 1971, Berger 1972). Henshaw (1902b: 81) found 'Apapane (*Himatione sanguinea*) and 'Amakihi (*Hemignathus virens*) remains in the stomachs of two hawks, and he and Munro (1960), Baldwin (1969) and Tomich (1971) reported limited predation on exotic bird species. No instance of predation on the 'Elepaio by the Hawaiian Hawk is known and because 'Elepaios are sedentary birds of the understory, such predation seems particularly unlikely.

Another possible basis for the observed color variation may be that proposed by Hamilton and Heppner (1967), who hypothesized that selection would favor dark pigmentation as a heat-absorbing mechanism in areas of reduced sunlight. Heppner (1970) presented experimental evidence of differential heat absorption by dark and light-colored individuals of the same species. Paler coloration would presumably be selected for in open, sunny areas such as the high leeward slopes of Mauna Kea where *C. s. bryani* occurs. A similar expression of Gloger's Rule has been documented (Bowers 1960) for the Wrentit (*Chamaea fasciata*), a bird of somewhat similar habits to the 'Elepaio and probably also an infrequent victim of predation. Bowers (1960) concluded that the variation in Wrentits was due to "natural selection" but did not specify the forces that may have been involved. Perhaps further studies of intra-island variation of *Chasiempis* will reveal more precise correlations of color pattern with environmental factors. At present, the selective forces involved are obscure.

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RECENT PUBLICATIONS

Neural Mechanisms of Behavior in the Pigeon.—Edited by A. M. Granda and J. H. Maxwell. 1979. Plenum Press, New York and London. 436 p. Vision and the visual system have been intensively studied in the domestic pigeon, a convenient experimental animal for such research. This book presents a current view of the field, being the proceedings of a 1977 conference. Its 22 papers are arranged so as to give an increasingly finely resolved view of the neural mechanisms underlying the bird's observed behavior. The opening chapters discuss the sensory cues that are integrated to facilitate such large behavioral complexes as navigation and the perception of color, patterns, and time. Subsequent papers examine the neural complexes governing vision and then the tissues themselves, particularly the retina. The retinal oil droplets and their functional significance in color processing are treated by several authors. The volume concludes with detailed anatomical views of the major visual networks, along with the integration of that anatomy into an understanding of specific forms of behavior. Illustrations, lists of references, index.

Perspectives in Ethology, Volume 3. Social Behavior.—Edited by P. P. G. Bateson and Peter H. Klopfer. 1978. Plenum Press, New York and London. 263 p. Like its predecessors, this volume is a collection of articles on salient topics in social biology. Studies on the genetics, ecology, development, and regulation of social behavior are followed by chapters on the development of status and hierarchy, early social relationships, and on predation and competition. Only Robert A. Wallace's chapter, "Social behavior on islands," is explicitly about birds. Nevertheless, ornithologists who are interested in the comparative study of behavior will find stimulation in these essays. Lists of references; index.

Vocal Communication in Birds. Studies in Biology no. 115.—Clive K. Catchpole. 1979. University Park Press, Baltimore. 68 p. Paper. $5.95. This booklet is one of a series on biological topics published by the Institute of Biology (41 Queen's Gate, London SW7 5HU, U.K.). Written at a college level, they are intended to provide authoritative and up-to-date treatment in depth, as is no longer possible in textbooks. Chapters in the present work deal with the communication system, methods of sound recording and analysis, nature and functions of calls and song, development of song and dialects, and the evolution of song. The underlying theme "is not only to show how birds communicate with their vocalizations but also to suggest wherever possible why they have been selected for during evolution." Appropriately for the book's use in teaching, it emphasizes the experimental approach and points out areas deserving more research. Diagrams, audiospectrograms, list of references.