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## ECOGEOGRAPHIC PATTERNS OF MORPHOLOGICAL VARIATION IN ELEPAIOS (*CHASIEMPIS* spp.): BERGMANN'S, ALLEN'S, AND GLOGER'S RULES IN A MICROCOSM

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**ABSTRACT.**—Animals often exhibit predictable geographic variation in morphology, and such ecogeographic patterns reflect local adaptation to varying environmental conditions. The most common of these patterns are termed Bergmann's, Allen's, and Gloger's rules. I studied morphological variation in the Hawaii Elepaio (*Chasiempis sandwichensis*) and the Oahu Elepaio (*C. ibidis*), forest birds endemic to the Hawaiian Islands. I measured body size and plumage color of 223 live elepaios captured at 36 sites on Hawaii and 132 live elepaios captured at 23 sites on Oahu, and I examined 132 museum specimens from an additional 22 locations on Hawaii. I used multiple regressions to examine relationships of elepaio body size and plumage color to elevation and annual rainfall on each island. Size of Hawaii Elepaios varied among sites and was related to elevation and rainfall. Wing chord, tail length, and body mass had positive relationships with elevation, as predicted by Bergmann's rule. Proportional bill length and proportional tarsus length were inversely related to elevation, as predicted by Allen's rule. In Hawaii Elepaios, 17 of 20 plumage color variables were related to rainfall. Elepaios in wetter areas were more heavily pigmented and had fewer and smaller white markings, as predicted by Gloger's rule. Plumage color of Oahu Elepaios showed similar but weaker patterns and only two of 20 plumage characters were related to rainfall. All body-size and plumage-color measurements had smoothly clinal distributions, with no large gaps with respect to elevation or rainfall. Putative subspecies of the Hawaii Elepaio differed in mean value of several plumage characters, but there was overlap in plumage color among subspecies and variation within them, and none of the three subspecies was diagnosable from both other subspecies by any plumage character using the 75% rule. Elepaios differed morphologically among sites only a few kilometers apart because of their sedentary behavior and the steep gradients in temperature and elevation and limited climatic variation of the tropical environment of the Hawaiian Islands. Morphological variation in elepaios is smoothly clinal because there are few dispersal barriers and elepaios inhabit areas with a range of climates and vegetation. Although my results did not support the designation of subspecies within the Hawaii Elepaio, morphological and underlying genetic variation is important, and conservation of elepaios with varying phenotypes would preserve evolutionary potential and ability to adapt to climate change. *Received 28 July 2010, accepted 28 July 2011.*

Key words: *Chasiempis*, ecogeographic variation, elepaio, environmental gradients, local adaptation, morphological variation, subspecies diagnosis.

### Patrones Ecogeográficos de Variación Morfológica en *Chasiempis* spp.: Las Reglas de Bergmann, Allen y Gloger en un Microcosmos

**RESUMEN.**—Frecuentemente los animales presentan un patrón de variación geográfica en la morfología que es predecible, reflejando la adaptación local a las diversas condiciones ambientales. De estos patrones, los más comunes son las reglas de Bergmann, de Allen y de Gloger.

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Estudié la variación morfológica en *Chasiempis sandwichensis* y *C. ibidis*, aves de bosque endémicas de las islas de Hawái. Medí el tamaño del cuerpo y el color del plumaje de 223 individuos vivos capturados en 36 sitios en Hawái y de 132 individuos vivos capturados en 23 sitios en Oahu, y examiné 132 especímenes de museo de otros 22 lugares de Hawái. Utilicé una regresión múltiple para examinar las relaciones del tamaño del cuerpo y del color del plumaje de las aves con la altitud y las precipitaciones anuales en cada isla. Los tamaños de los individuos de *C. sandwichensis* varían entre sitios y se relacionaron con la altitud y las precipitaciones. La amplitud alar, la longitud de la cola y la masa corporal tuvieron una relación positiva con la elevación, según lo predicho por la regla de Bergmann. Las longitudes proporcionales del pico y del tarso estuvieron inversamente relacionadas con la elevación, según lo predicho por la regla de Allen. En *C. sandwichensis*, 17 de 20 variables del color del plumaje estuvieron relacionadas con la precipitación. Los individuos de *C. sandwichensis* de las zonas más húmedas presentaron pigmentaciones más fuertes con menos marcas blancas y más pequeñas, como predicho por la regla de Gloger. El color del plumaje de *C. ibidis* mostró patrones similares pero más débiles y sólo dos de 20 caracteres del plumaje estuvieron relacionados con la precipitación. Todas las mediciones del tamaño del cuerpo y del color del plumaje se distribuyeron gradualmente, sin grandes diferencias con respecto a la elevación o a la precipitación. Las subespecies putativas de *C. sandwichensis* difirieron en el valor medio de varios caracteres del plumaje, pero hubo superposición en el color del plumaje entre las subespecies y también hubo variación adentro de las subespecies, y ninguna de las tres subespecies se diferenció de las otras dos subespecies según algún carácter del plumaje, usando la regla del 75%. Las aves difirieron morfológicamente entre sitios a pocos kilómetros de distancia debido a su conducta sedentaria, a la existencia de gradientes abruptos de temperatura y de elevación, y a la variación climática limitada del ambiente tropical de las islas hawaianas. La variación morfológica en estas aves tiene una distribución gradual debido a que hay pocas barreras para la dispersión y a que las aves habitan zonas con una gran variedad de climas y vegetación. A pesar de que mis resultados no apoyan la designación de subespecies dentro de *C. sandwichensis*, la variación genética y morfológica subyacente es importante, y la conservación de estas aves con fenotipos variables preservaría su potencial de evolución y su capacidad de adaptación al cambio climático.

## INTRODUCTION

ASPECTS OF ANIMAL morphology such as body size and coloration often exhibit predictable geographic variation, and these ecogeographic patterns are thought to reflect local adaptations to varying environmental conditions (Mayr 1956; James 1970, 1991). Such patterns are widespread and have been described in numerous species of birds, mammals, reptiles, amphibians, and some invertebrates (Zink and Remsen 1986, Ashton et al. 2000, Ashton 2002, Millien et al. 2006, Olalla-Tárraga et al. 2006, Olson et al. 2009). The most common of these patterns have been formalized into ecogeographic rules, and for over a century they have spurred interdisciplinary research in evolutionary ecology, biogeography, and functional morphology.

Perhaps the best-known ecogeographic pattern is “Bergmann’s rule,” the tendency toward larger body size in colder climates. Bergmann (1847) originally described this relationship using relative body size of species within a genus, but since then it also has been applied to individuals or populations within a species (Blackburn et al.

1999, Ashton et al. 2000, Ashton 2002, Freckleton et al. 2003, Millien et al. 2006), and Olson et al. (2009) showed that it transcended higher taxonomic levels. The selective mechanism most often proposed to explain Bergmann’s rule is thermo-regulatory adaptation to varying environmental conditions; larger body size is selected in colder areas because the lower mass:surface area ratio results in less heat loss (Mayr 1956, James 1970), and smaller body size is favored in warmer environments because it allows greater heat dissipation (Brown and Lee 1969, McNab 1979). The universality of this mechanism has been questioned, however (Scholander 1955, McNab 1971, Geist 1987, Meiri and Dayan 2003), and fasting ability and seasonality and environmental predictability have been proposed as alternative mechanisms (Lindsey 1966, Boyce 1979, Lindstet and Boyce 1985), though the validity of Bergmann’s rule is not necessarily dependent on a single mechanism (Ashton 2002, Olson et al. 2009). Humidity may also play a role in Bergmann’s rule by influencing the rate of evaporative heat loss (James 1970, Aldrich and James 1991). Latitude and elevation are common proxies for temperature in studies of

Bergmann's rule (Ashton et al. 2000, Ashton 2002, Olson et al. 2009).

"Allen's rule" is related to Bergmann's and states that in endothermic animals the relative sizes of appendages such as limbs, ears, tail, and bill are smaller in colder environments (Allen 1877). As in Bergmann's rule, the mechanism most often proposed to explain this pattern is selection for thermoregulatory advantage. Smaller appendages lose less heat in cold environments, providing an energetic savings (Scholander 1955, Mayr 1956), and larger appendages can help to dissipate heat by serving as a radiator in hot environments (Tattersall et al. 2009). It has also been suggested that environmental temperature can directly influence appendage length by regulating growth, which indicates a possible ontogenetic component to this phenomenon (Serrat et al. 2008). Allen's rule has been reported most often in mammals (e.g., Griffing 1974, Lindsay 1987), but perhaps the most famous example comes from introduced populations of the House Sparrow (*Passer domesticus*) in North America (Johnston and Selander 1971, Fleischer and Johnston 1982). Symonds and Tattersall (2010) provided the strongest evidence of Allen's rule by demonstrating that in several groups of birds, bill size was larger in species inhabiting warmer environments.

The third major ecogeographic pattern is "Gloger's rule," in which animals in warm and humid environments tend to be more heavily pigmented than those in cold and dry environments (Gloger 1833). This relationship between coloration and climate has been described in a variety of birds and mammals in continental areas (Zink and Remsen 1986, Burtt and Ichida 2004). Most of the dark colors typical of animals exhibiting Gloger's rule are produced by melanin pigments (McGraw 2006), which are thought to serve a variety of functions, providing several possible mechanisms by which darker color could be advantageous in warmer and more humid environments. The amount of dark pigmentation could match environmental background color to reduce predation, with darker plumage being more cryptic in wetter environments (Zink and Remsen 1986). Production of darker feathers is costly (Griffith et al. 2006, McGraw 2006), and birds in extreme environments may be less able to produce them (Burtt 1999). Dark feathers absorb more solar energy than light feathers, which seemingly could provide a thermoregulatory advantage, but it has

been shown that this heat is largely lost to convection or conduction and that white feathers actually transfer more heat to the body (Walsberg et al. 1978, Walsberg 1982, Ward et al. 2002). Melanin has been shown to increase feather hardness and abrasion resistance, leading to improved feather condition and longer feather life (Barrowclough and Sibley 1980, Burtt 1986, Bonser 1995). Evidence that melanization deters ectoparasites is equivocal (Kose et al. 1999, Bush et al. 2006), but there is increasing evidence that melanin inhibits growth of feather-degrading bacteria (Burtt and Ichida 2004, Goldstein et al. 2004, Gunderson et al. 2008). Higher melanin content appears to be an adaptation to maintain feather condition and increase feather life in humid environments more conducive to bacterial growth and may play an important role in evolution of plumage color in birds (Clayton 1999, Grande et al. 2004, Gunderson 2008).

Bergmann's, Allen's, and Gloger's rules have been described primarily in continental areas at large geographic scales. However, interpretation of correlations between morphological characters and environmental variables such as temperature and precipitation has sometimes been hindered by covariation of these environmental variables across continents (Millien et al. 2006). It is unusual for a species to exhibit a wide range of morphological variation over short geographic distances. The Hawaiian Islands offer excellent opportunities for examining ecogeographic patterns of morphological variation because gradients in temperature and precipitation are largely independent within the archipelago. The island of Hawaii in particular, with its extremes of elevation and climate, represents a microcosm that offers an exceptional system in which to examine environmental correlates of morphological variation and adaptation.

The elepaio (*Chasiempis* spp.) are monarch flycatchers (Monarchidae) endemic to the Hawaiian Islands. Elepaio occur on Kauai, Oahu, and Hawaii but are absent from the four islands of the Maui Nui group (Maui, Molokai, Lanai, and Kahoolawe) in the center of the archipelago (VanderWerf 2007), even in the fossil record (Olson and James 1982, Burney et al. 2001). Each island form was originally described as a separate species: *Chasiempis sandwichensis* Gmelin 1789 on Hawaii; *C. sclateri* Ridgway 1882 on Kauai; and *C. ibidis* Stejneger 1887 (formerly *C. gayi* Wilson 1891; see Olson 1989) on Oahu. These taxa

were later reclassified as subspecies (Bryan and Greenway 1944) and were considered conspecific for many years (Berger 1981, American Ornithologists' Union [AOU] 1998, Pyle 2002), but some authorities continued to treat them as separate species on the basis of morphological and ecological differences (Olson and James 1982, Conant et al. 1998, Pratt and Pratt 2001). More recently, molecular evidence showed that elepaio on each island form monophyletic clades that warrant species classification (VanderWerf et al. 2009), and behavioral evidence from inter-island song-playback experiments demonstrated that song could serve as an isolating mechanism (VanderWerf 2007). The AOU accepted a taxonomic revision in which the island forms are again recognized as distinct species on the basis of a combination of morphological, ecological, molecular, and behavioral evidence (Chesser et al. 2010). The Kauai Elepaio and Hawaii Elepaio are fairly common and widespread (Fig. 1; Scott et al. 1986, Gorresen et al. 2009), but the Oahu Elepaio is listed as endangered and has a fragmented range that represents only 4% of the presumed prehistoric distribution (VanderWerf

et al. 2001, 2011; U.S. Fish and Wildlife Service [USFWS] 2006).

Elepaios exhibit substantial morphological variation among and within islands (Pratt 1980, VanderWerf 1998). Intra-island plumage-color variation is most pronounced on Hawaii, where two or three subspecies are recognized by some authorities on the basis of plumage color (Henshaw 1902; Pratt 1979, 1980). Elepaios in wet forests on the windward, eastern side of the island (*C. s. ridgwayi*; Fig. 1) tend to be darker and redder; those in drier forests on the leeward, western side (*C. s. sandwichensis*) tend to be paler and gray; and those in dry, high-elevation forest on Mauna Kea (*C. s. bryani*) are even paler and often have more white on the head (Pratt 1980). Similar, previously undescribed geographic plumage-color variation occurs in Oahu Elepaios. The present study also reports for the first time that Hawaii Elepaios exhibit substantial geographic variation in body size.

Pratt (1980) examined geographic color variation in the Hawaii Elepaio and described the apparent distribution of the three subspecies. Henshaw (1902) and Pratt (1980) also noted,

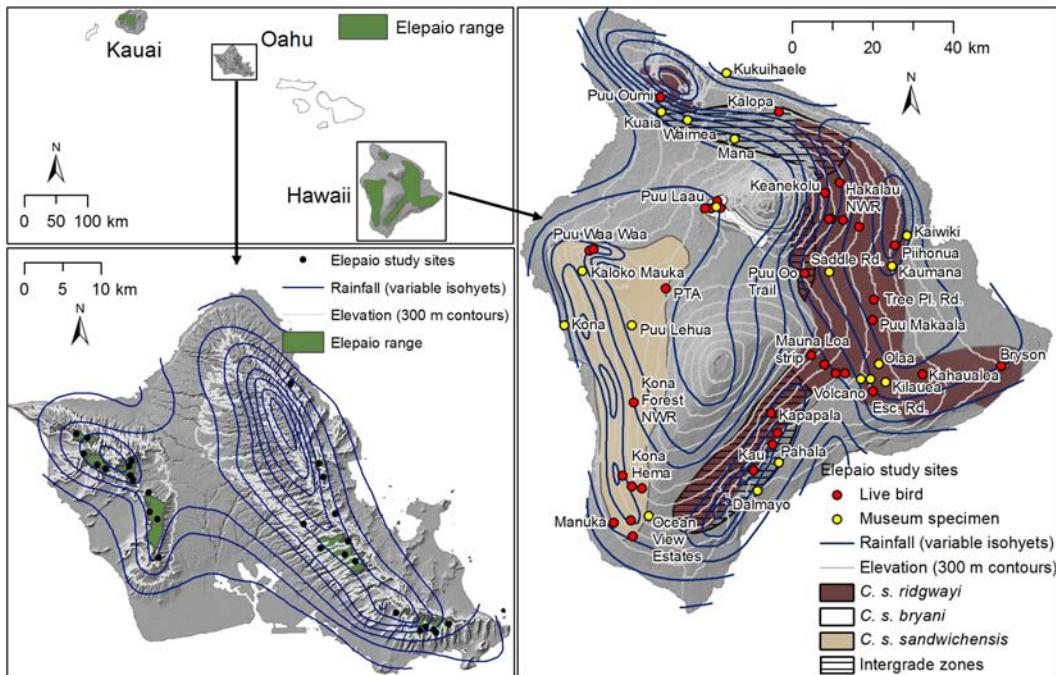


FIG. 1. Current range of elepaios, study-site locations, rainfall, and elevation. The range of elepaios has declined on all islands, especially at lower elevations. Several sites treated as intergrade zones lie outside the current range and were represented only by museum specimens.

however, the existence of several zones of intergradation, where elepaio showed mixed characters. Such intergradation was reported in the Kau area on the southern slope of Mauna Loa, in kipukas (pockets of forest within recent lava flows) in the Saddle Road area in the center of the island, and on the northern slope of Mauna Kea (Fig. 1). Not coincidentally, these are also areas where climate shifts most rapidly from wet to dry because of the rain shadow cast by massive volcanoes that block the prevailing northeasterly trade winds. Pratt (1980) also pointed out several areas where elepaio were known to occur but where no specimens had been collected. Understanding of geographic variation in elepaio coloration can be improved by further examination under a rigorous ecogeographic framework and by collection of data from additional locations. These patterns of variation are primarily of ecological interest, but examining the nature and extent of variation can also be useful in clarifying taxonomy.

The subject of avian subspecies has been controversial, with much debate about criteria for identifying subspecies and even the validity of the subspecies concept (Mayr 1982, Phillimore and Owens 2006, Rising 2007, Fitzpatrick 2010, James 2010, Winker 2010). Subspecies traditionally have been based on geographic discontinuities in phenotypic traits, but many taxa have been named along smooth clines in a single character, perhaps erroneously (Winker 2010). Several authors have emphasized the need for more objective and rigorous criteria in defining subspecies (Cicero and Johnson 2006, Rising 2007, Patten 2010, Remsen 2010). Amadon (1949) prescribed 75% as a minimum proportion of morphological differentiation between geographic areas or populations for them to qualify as subspecies. Patten and Unitt (2002) formalized the "75% rule" and provided a numerical index that can be used to test whether subspecies meet this criterion. If this rule is applied to continuously varying characters that are normally distributed, at least 75% of the distribution of a particular character must lie outside the distribution of that character in other populations for a population to be considered a subspecies (Patten and Unitt 2002). Although choosing a prescribed degree of differentiation is arbitrary, it provides a consistent framework for quantitatively addressing the interface between morphology and taxonomy.

The goals of the present study were to (1) further investigate geographic variation in elepaio

coloration, especially on Hawaii but also on Oahu; (2) describe previously unknown geographic variation in elepaio body size; (3) relate morphological variation to climate and behavior to elucidate selective forces that shape morphology; (4) evaluate elepaio taxonomy and validity of subspecies within the island of Hawaii using standardized morphological criteria; and (5) discuss why morphological variation is important in conservation.

## METHODS

*Study species.*—Elepaios are insectivorous, non-migratory, and adaptable, and pairs defend all-purpose territories year round (VanderWerf 1993, 1994, 1998, 2004). Their life histories are typical of many tropical, island, and south temperate birds (Martin 2002), characterized by high adult survival (>80% per year), long life span ( $\leq 19$  years), low fecundity (median clutch size = 2), and extended parental care (VanderWerf 2008, 2009). Elepaio are sedentary, and their dispersal is driven by intraspecific competition and territory availability. They usually disperse only far enough to find a vacant territory and rarely cross large areas of unforested habitat. Natal dispersal distances observed in Hawaii Elepaio were short but were longer in males ( $539 \pm 68$  m [SE]) than in females ( $357 \pm 82$  m), and instances of breeding dispersal have been <400 m (VanderWerf 2008). In dense populations, young birds usually act as floaters and do not acquire a territory and mate until their third year (VanderWerf 2004, 2008).

Elepaio are sexually mature and sometimes breed at 1 year of age, but they exhibit a 2-year delay in plumage maturation in both sexes (see cover; VanderWerf 2001, 2004). The subadult plumages function in status signaling and reduce aggression from dominant adults (VanderWerf and Freed 2003). Because the age-specific plumages differ in color and could confound comparisons among subspecies and sites, I used only birds in definitive (adult) plumage in analyses of geographic color variation. In definitive plumage, the ventral surface is white with darker streaks, the dorsal surface is brown (Hawaii and Oahu) or gray (Kauai), and the wing coverts, rump, tail, and throat feathers have conspicuous white tips (see cover). The first basic plumage is largely plain grayish-brown (Hawaii) or reddish-brown (Oahu and Kauai; see cover). The second basic plumage is more similar to definitive

plumage but differs in having only partly white tips to feathers on the wing coverts, rump, and throat, and in the somewhat browner breast and eyebrow (see cover; VanderWerf 2001).

Male elepaio are ~10% larger than females in most body measurements at a given site (VanderWerf 1998; see below), so the sexes had to be identified in order to study geographic size variation. I used several methods to distinguish males and females: reproductive condition—that is, presence of a brood patch (females only) or a cloacal protuberance (males only); color of the throat feathers in definitive plumage (more white in females; VanderWerf 2001); vocalizations (females rarely sing); and genetic sexing in a few cases.

Juvenile elepaio have shorter remiges and rectrices than adults (VanderWerf 1998), and these feathers are retained in the first basic plumage because the first prebasic (postjuvenile) molt is only partial (VanderWerf 2001). Wing chord and tail length of birds with juvenal and first subadult plumages are thus shorter and cannot be directly compared with those of older birds. I therefore used only males in definitive or second basic plumage in comparisons of size. It might be possible to correct for differences in size between age classes, but gradients of body size in relation to climate may differ between the sexes because male elepaio tend to disperse farther than females, as evidenced by direct observations and molecular genetics (VanderWerf 2008, VanderWerf et al. 2009).

**Study sites.**—The Hawaiian Islands are volcanic in origin and formed sequentially as the Pacific plate of the earth's crust moved northwest over a hot spot where magma from the mantle reaches the surface (Walker 1990, Carson and Clague 1995). Islands at the southeastern end of the chain are younger and generally higher and larger, with each island to the northwest progressively older and more eroded. Hawaii is the youngest and most volcanically active of the Hawaiian Islands and is composed of five distinct shield volcanoes that range in age from zero to 0.43 million years (Fig. 1): Mauna Kea at 4,205 m, Mauna Loa at 4,169 m, Hualalai at 2,521 m, Kohala at 1,670 m, and Kilauea at 1,248 m. Oahu is the second oldest of the main Hawaiian Islands at 3.7 million years and is composed of two roughly parallel mountain ranges, the Koolau in the east, which reaches a maximum elevation of 960 m at Konahuanui, and the Waianae in the west, with a maximum elevation of 1,220 m at Kaala.

Ambient temperatures in Hawaii exhibit wide variation over short distances because of the range of elevations yet are also extremely equitable over time because of the tropical location of the islands and the moderating influence of the Pacific Ocean. At a given location, the daily temperature variation throughout the year averages 5–8°C, and the seasonal temperature variation averages only 5°C at sea level (Juvik and Juvik 1998). By contrast, the lapse rate of temperature with increasing elevation is ~6.5°C per 1,000 m below 1,250 m and ~4°C per 1,000 m at higher elevations (Juvik and Juvik 1998). Most variation in temperature within the Hawaiian Islands is thus caused by elevation, and locations that are geographically very close can experience very different temperature regimes. Lowland forests bathed in warm humid air year round exist <20 km from the alpine slopes and snow-capped summits of Mauna Kea and Mauna Loa.

Pervading northeasterly trade winds that sweep moisture across the northern Pacific are forced upward by the massive volcanoes in Hawaii, causing condensation and high rainfall on the northern and eastern (windward) slopes of each island (Fig. 1). The rain shadow formed by each volcano causes their southern and western slopes to be generally drier, but convectional heating and sea breezes on these leeward slopes also cause cloud formation, leading to additional peaks in rainfall (Fig. 1). As with temperature, geographically close locations can experience very different amounts and patterns of rainfall. Annual rainfall ranges from ~0.4 m year<sup>-1</sup> along the western coasts of each island and at the highest elevations of Mauna Kea and Mauna Loa, to >6 m year<sup>-1</sup> on the eastern side of Hawaii and on the summit of the northern Koolau Mountains of Oahu. The northern and eastern slopes of each island are covered in dense rainforest, and the southern and western slopes support mesic forest and dry shrubland. On Hawaii, the forest becomes more open, drier, and stunted at higher elevations, giving way to subalpine shrubland and grassland above ~2,500 m, and eventually bare ash, cinder, and rock with only sparse vegetation toward the summits of Mauna Kea, Mauna Loa, and Hualalai. On Oahu, the upper slopes become progressively steeper, wetter, and more windswept, and the summits support low elfin forest and montane shrubland.

I collected data on body size and plumage color from 355 Hawaii Elepaio in 58 locations. Of

these, 223 were live birds captured in 37 locations and 132 were museum specimens collected in 22 locations. These sites encompassed the entire current range and the complete climatic breadth occupied by the species (Fig. 1). Twenty-six of the locations were within the range of *C. s. ridgwayi*, 16 in that of *C. s. sandwichensis*, 5 in that of *C. s. bryani*, and 11 in zones of intergradation between the subspecies (Fig. 1 and Appendix). In some cases, I sampled from multiple locations within larger areas that spanned a wide range of elevation or climate, such as Hawaii Volcanoes National Park, Hakalau Forest National Wildlife Refuge (NWR), Manuka Natural Area Reserve, Kau Forest Reserve, Mauna Kea Forest Reserve, and The Nature Conservancy's Kona Hema Preserve. Most sampling locations were separated by >5 km, except those representing *C. s. bryani*, which is currently restricted to 63 km<sup>2</sup> of high-elevation native forest on the western slope of Mauna Kea. The five locations representing that subspecies were separated by <5 km but differed in elevation by ≤500 m.

On Oahu, I collected data on body size and plumage color from 132 live elepaio in 23 locations representing all areas of the island in which the species still occurs (Fig. 1 and Appendix). The Oahu Elepaio has declined seriously in range, however, and it currently occupies only 4% of its presumed prehistoric distribution (VanderWerf et al. 2001). Because the Oahu Elepaio has been extirpated from the wettest and driest parts of the island, it was not possible to sample the entire climatic breadth it once occupied.

I examined specimens of the Hawaii Elepaio and Oahu Elepaio from the Bishop Museum in Honolulu, the American Museum of Natural History, and the Louisiana State University Museum of Natural Sciences. The locality information given for most specimens encompassed a large geographic area, such as "North Kona" or "Waianae Mountains, Oahu," and this was not specific enough to determine elevation or rainfall where the specimen was collected. In a few cases the elevation was provided on the specimen label, making it possible to determine elevation and rainfall for 43 museum specimens from five locations: Puu Laau, Kaumana, Volcano House, and two areas along Saddle Road. Data from other Hawaii Elepaio museum specimens were used only in comparisons of putative subspecies, for which elevation and rainfall data were not required. The Hawaii Elepaio has been extirpated

from several areas where birds were collected, making those specimens particularly valuable. No Oahu Elepaio museum specimens had locality information specific enough for inclusion in analyses of ecogeographic variation, and none came from an area outside the climatic range in which I sampled live birds.

I used elevation as a proxy for temperature because temperature data were available from only a small number of weather stations on each island. Elevation is often used in this way (Ashton 2002), and the relationship between elevation and temperature is especially strong in the Hawaiian Islands because of small daily and seasonal temperature variations. I measured elevation at each sampling location by taking a global positioning system (GPS) point and plotting it on a digital topographic map with elevation contours. Elevation at sampling locations on Hawaii ranged from 270 m at Bryson's in Puna and 360 m at Manuka Bay to 2,350 m in the Mauna Kea Forest Reserve, 1,950 m on Keanakolu Road just west of Hakalau Forest NWR, and 1,900 m on the Mauna Loa Strip Road in Hawaii Volcanoes National Park (Figs. 1 and 2). On Oahu the range of elevations sampled was narrower, from 150 m in Pia Valley to 640 m in Schofield Barracks, because the mountains on Oahu are not as high (Figs. 1 and 2).

I measured annual rainfall at each sampling location by using a geographic information system to plot GPS points on a digital topographic map with digital rainfall isohyets developed by Giambelluca et al. (1986). To obtain more precise measures of rainfall at sampling locations, I interpolated between isohyets on the basis of proportional distance to the two nearest isohyets. Annual rainfall at the locations sampled on Hawaii

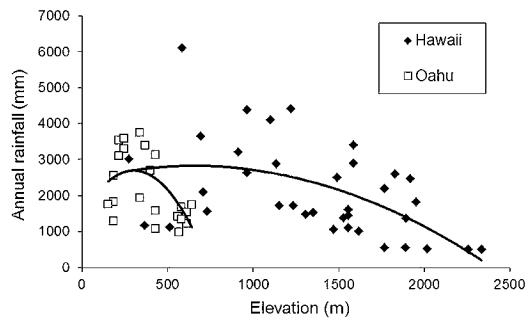


FIG. 2. Relationship of elevation and rainfall at sampling locations on Hawaii and Oahu, with best-fit polynomial regression lines. Rainfall was highest at middle elevations on both islands.

ranged from 490 mm at Puu Laau and 540 mm at Pohakuloa to 6,100 mm at Piihonua just west of Hilo, the wettest part of the island (Figs. 1 and 2). Annual rainfall at the locations sampled on Oahu ranged from 980 mm at Palehua to 3,750 mm at Waikane (Figs. 1 and 2).

In many parts of the world, orographic precipitation patterns make it difficult to separate the effects of elevation and rainfall on phenotypic variation. In Hawaii, these effects can be separated more easily because orographic precipitation patterns differ between the windward and leeward sides of each island. Rainfall increases with elevation on both aspects, but rainfall at a given elevation will be higher on the windward side of an island than on the leeward side (Gambellicca et al. 1986). I used linear and polynomial regression analyses to examine relationships between elevation and rainfall at study sites on Hawaii and Oahu. The relationship between elevation and rainfall was best described by a second-order polynomial function on both Hawaii ( $R^2 = 27.3\%$ ,  $F = 6.19$ ,  $P = 0.005$ ) and Oahu ( $R^2 = 35.8\%$ ,  $F = 5.57$ ,  $P = 0.01$ ), with rainfall highest at middle elevations (Fig. 2).

I assigned birds from each sampling location to subspecies following Pratt (1980), with birds from locations regarded as zones of intergradation not assigned to any subspecies. No specimens of Hawaii Elepaio exist from the Kohala area, and they were not considered by Pratt (1980). I assigned birds from Puu Oumi Natural Area Reserve in Kohala to *C. s. ridgwayi* because their plumage was typical of that subspecies, which is expected given the high rainfall in the area. I treated the following sites as being within zones of intergradation: Kalopa, Kapa-pala, Kau, Puu Oo Trail and other Saddle Road kipukas at higher elevations, Mana, Waimea, and Kuaia. Pratt regarded Kuaia as being near Hilo and, thus, within the range of *C. s. ridgwayi*, but I could find no such place name. It is possible that "Kuaia" is a misspelling of "Koaia," the common name of a tree (*Acacia koaia*) that is also sometimes used for a region on the southern slope of Kohala Volcano. Compared with the data used by Pratt (1980), my data set included a larger number of locations (58 vs. 23) and more complete geographic representation.

**Data collection.**—I captured elepaios in mist nets at each site, often using playbacks of recorded songs to attract them and increase the capture rate. Males are more active than females

in territorial defense and respond more aggressively to playbacks (VanderWerf and Freed 2003, VanderWerf 2007), and I captured more males than females. I banded each bird, weighed and measured it, inspected it for molt and breeding condition, measured plumage color, photographed it, and released it at the site of capture within 1 h. I also collected a small blood sample from the brachial vein of each bird for use in genetic and disease research. I measured every bird myself.

I quantified elepaio body size using five standard measurements: wing chord from base of the carpometacarpus to tip of the longest primary feather, with the wing bent 90° at the carpometacarpal joint and the primaries flattened but not straightened; tail length from tip of the longest (central) rectrix to where it emerged from the skin just posterior to the uropygial gland; bill length as exposed culmen, which is length of the maxilla from the tip to where it emerges from the skin on the forehead; tarsus length from the notch at the base of the tarsometatarsus to the distal edge of the last undivided scute on the anterior surface of the leg (i.e., "short" tarsus); and body mass with a 50-g spring scale. On museum specimens it was difficult to measure tarsus length or tail length without damaging the specimen, and body mass was not available, so I used only wing chord and bill length from museum specimens.

I quantified elepaio plumage color using 20 variables. I measured color of the brow, crown, back, and breast by visual comparison with Munsell color chips, yielding three variables for each of the four body regions (Munsell Color 1994; see below). I counted the number of feathers with white tips on the greater wing coverts and rectrices (on one side of the body), and measured the length of white tips on the greater wing coverts, median wing coverts, rump, and rectrices. Length of white feather tips varied somewhat within each body area. To reduce subjectivity and increase repeatability, I measured the longest tip on the wing coverts and rump, and length of the tip along the shaft of the outermost rectrix, which usually had the longest tip. I estimated proportion of the brow that was white to the nearest 10%. I scored the amount of streaking on the breast on a scale from 0 to 5, using the following definitions: 0 = no streaks; 1 = very light streaks or light streaks confined to sides of breast; 2 = light streaks extending across the breast but interspersed with white and not forming a solid

band; 3 = moderate streaks forming a solid band across the breast; 4 = heavy streaks extending onto the flanks; and 5 = very heavy streaks covering most or all of the ventral surface. On most museum specimens it was difficult to count the number of white tips on the median coverts or rectrices without damaging the specimen, so I did not do so.

In the Munsell system a color is described by three parameters: hue (spectral color or wavelength), value (darkness), and chroma (intensity or saturation). The notation for hue is a letter (Y for yellow, YR for yellow-red, R for red, etc.) preceded by a number from 0 to 10. Higher numbers represent equivalent decreases in wavelength, with 10 equal to 0 for the next lower-wavelength letter (i.e., 10YR = 0Y, with 5YR intermediate). Value is measured on a linear scale from 0, for black, to 10, for white. Chroma is measured on a linear scale from 0, for neutral gray, to 20 for extremely intense colors. For example, 10YR 5/8 would mean a color with a hue of 10 yellow-red, a value of 5, and a chroma of 8. The Munsell color system offers several advantages over the Smithe (1975) color system often used in ornithology: (1) the Munsell system provides more color choices than Smithe (1975), allowing distinction of finer differences and obviating the need for subjective adjectives; (2) each Munsell color differs from others by a standard and quantifiable amount, making measurements more suitable for statistical analyses; (3) in the Munsell system the three attributes of color are measured independently; and (4) the Munsell system does not use subjective English names and can be used internationally with little translation. The Smithe (1975) system provides examples of colors but does not actually measure them; to measure his color standards, Smithe (1974) relied on the Munsell system. Nevertheless, I also described the appearance of elepaio using Smithe (1975) colors to facilitate comparison with Pratt (1980).

**Analyses.**—I compared the size of male and female elepaio using a general linear model for each of the five variables (wing chord, tail length, bill length, tarsus length, and body mass), with sex and site as independent variables, using only sites where at least two birds of each sex were captured ( $n = 10$  sites). Size of males and females could not be compared across sites without also including site as a factor, because size varied with elevation.

I examined the relationship of body size and climate (Bergmann's rule) with a series of multiple regression analyses using elevation and rainfall at each site as independent variables and the average value of wing chord, tail length, bill length, tarsus length, or body mass at each site as the dependent variable. I investigated Bergmann's rule only on Hawaii because elevation range on Oahu was narrower and there was insufficient variation in size of Oahu Elepaio.

I examined the relationship between proportional appendage length and climate (Allen's rule) with a series of multiple regression analyses using elevation and rainfall at each site as independent variables and the ratio of each appendage length (wing chord, tail length, bill length, tarsus length) to body mass at each site as the dependent variable. I used the ratio of appendage length to body mass instead of simply appendage length to control for body size.

I examined the relationship of plumage color and rainfall (Gloger's rule) with a series of regression analyses using annual rainfall at each site as the independent variable and the average value of each of the 20 plumage variables at each site as the dependent variable. I used Munsell measures of value and chroma without modification, but measures of hue were first converted to a numerical scale (white = 0, 2.5Y = 1, 10YR = 2, 7.5YR = 3, 5YR = 4, and 2.5YR = 5). I chose numerical values for hue such that colors that were less reddish had lower values.

I applied the Dunn-Šidák correction for multiple comparisons in all analyses. For example, in analyses of plumage color, I used an alpha level of 0.0026 to test significance of the relationship in each of the 20 variables.

To investigate the validity of Hawaii Elepaio subspecies, I conducted pairwise diagnosability tests on each plumage variable based on the 75% rule, using an index provided by Patten and Unit (2002):  $D_{12} = x_2 - S_2(t_{0.25, df2}) - x_1 - S_1(t_{0.01, df1})$ , where  $D_{12}$  is the index between populations 1 and 2, population 2 has the larger mean,  $x$  is the sample mean, and  $S$  is the sample standard deviation. The  $t$  values were determined for  $\alpha = 0.01$  and the degrees of freedom of population 1 ( $df_1 = n_1 - 1$ , where  $n_1$  is the sample size for population 1) and  $\alpha = 0.25$  and  $df_2 = n_2 - 1$ . If  $D_{12} \geq 0$ , population 1 was diagnosable from population 2; if  $D_{12} < 0$ , population 1 was not diagnosable from population 2. I excluded birds from zones of intergradation.

## RESULTS

*Body size and appendage length.*—Male Hawaii Elepaio were larger than females in all five body measurements, including wing chord, tail length, bill length, tarsus length, and body mass (Table 1 and Fig. 3). The difference in size between males and females varied somewhat among sites, probably because of sampling error, but males were consistently larger in all five measurements. Because size varied with both sex and site, I used only males in subsequent analyses of ecogeographic size variation.

Size of male Hawaii Elepaio varied substantially among sites. The difference in size between sites with the smallest and largest average measurements was 10% in wing chord (70.0–77.0 mm), 21% in tail length (59.3–71.5 mm), 11% in tarsus length (21.9–24.3 mm), 17% in bill length (12.3–14.4 mm), and 21% in body mass (14.5–17.6 g).

This variation was related to elevation and, to a lesser degree, rainfall. Multiple regression analyses showed that wing chord, tail length, and body mass were related to climate and that, in most cases, this relationship was caused primarily by elevation and not rainfall (Table 2 and Figs. 4 and 5). Wing chord, tail length, and body mass had positive relationships with elevation but were not related to rainfall. Tail length had a negative relationship with rainfall. Bill length showed a negative trend with elevation, but the relationship was not quite significant. All body-size measurements had continuous, smoothly clinal distributions, with no large gaps or breaks with respect to elevation or rainfall (Figs. 4 and 5). Variation in body size of Oahu Elepaio was not examined because they occurred over a narrower range of elevations and exhibited insufficient variation.

Variation in proportional appendage length of male Hawaii Elepaio also was related to climate. Multiple regression analyses showed that proportional bill length and proportional tarsus length were inversely related to elevation and that proportional tail length was inversely related to rainfall (Table 3 and Fig. 6).

*Plumage color.*—Plumage color of male Hawaii Elepaio varied among sites in several ways, and much of the variation was related to annual rainfall, which was a significant predictor for 17 of 20 plumage variables (Table 4 and Fig. 7). Each variable had a continuous, smoothly clinal distribution with respect to rainfall and did not exhibit large gaps or breaks. Elepaio in wetter areas were generally darker and redder and had fewer and smaller white markings. Specifically, birds in wetter areas had fewer white tips on the tail and greater wing coverts, and white tips on the greater wing coverts, median wing coverts, rump, and tail were shorter in areas with higher rainfall. The amount of white in the brow also declined with rainfall, with birds in the wettest areas having no white in the brow and many birds in the driest areas having completely white brows. The amount of breast streaking was greater in areas of high rainfall, with birds in the wettest areas having dark reddish-brown streaks that extended across the entire ventral surface from the throat to the flanks, and birds in the driest areas having pale tan streaks confined to the sides of the upper breast. In areas with higher rainfall, the hue or spectral color of the brow, crown, back, and breast was more red; the value of the brow, crown, and breast was lower (darker); and the chroma of the brow and crown was higher (more intense).

Using colors from Smith (1975; capitalized) closest to the Munsell measures, birds in the

TABLE 1. Comparison of body-size measurements in male and female Hawaii Elepaio at 10 sites, based on general linear models with sex and site as independent variables. Degrees of freedom (df) vary because not all measurements were taken on every bird at each site. Size of males and females could not be compared across sites without also including site as a factor because size varied with elevation.

Variable	Sex			Site		
	df	F	P	df	F	P
Wing chord	1 and 172	313.36	<0.001	9 and 172	13.98	<0.001
Tail length	1 and 80	27.50	<0.001	9 and 80	9.54	<0.001
Bill length	1 and 172	28.27	<0.001	9 and 172	5.09	<0.001
Tarsus length	1 and 172	79.24	<0.001	9 and 172	3.33	0.001
Body mass	1 and 171	157.30	<0.001	9 and 171	5.78	<0.001

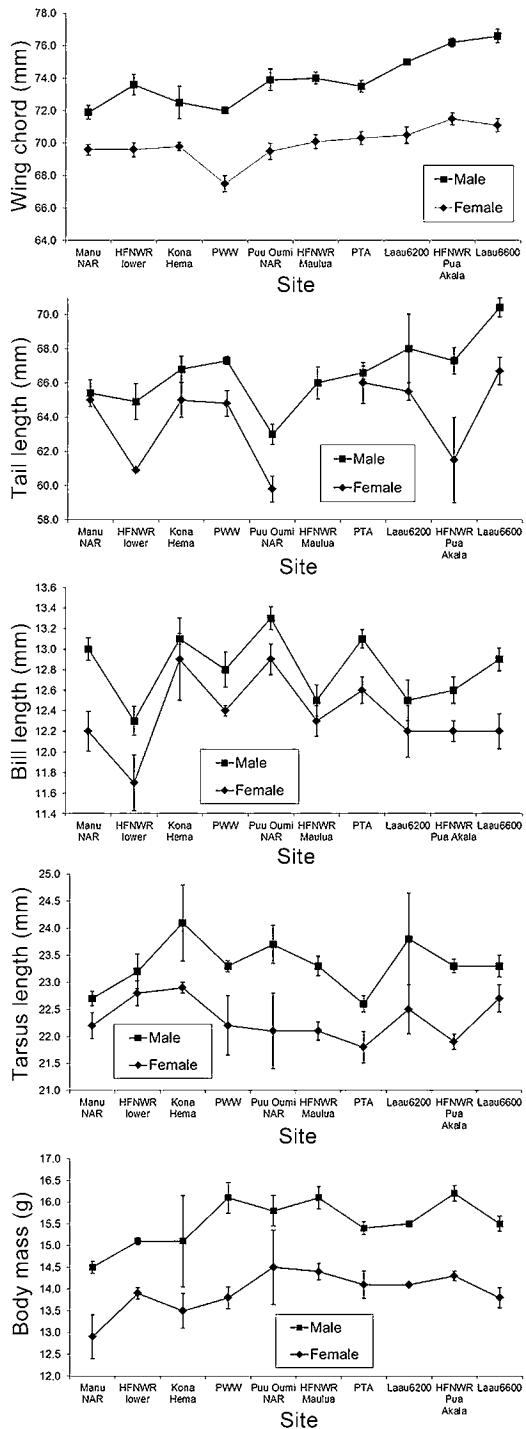


FIG. 3. Body-size measurements in male and female Hawaii Elepaio at 10 sites. Males were larger than females in all five characters examined. For results of general linear models, see Table 1.

wettest areas had a brow ranging from bright Russet to dark Chestnut, a crown and back of Fuscous or Raw Umber, a completely dark Amber breast, and short white tips on the wing coverts, rump, and tail. Birds in dry areas had a brow ranging from Cinnamon to Rufous, often mixed with white or entirely white, a Burnt Umber or Olive Brown back and crown, streaks of Antique Brown confined to the sides of the breast, and broad white tips on the wing coverts, rump, and tail.

Plumage color of Oahu Elepaios also was related to rainfall and showed geographic patterns similar to those on Hawaii, but the relationships were generally weaker and only 2 of 19 plumage characters were significantly associated with annual rainfall (Table 4 and Fig. 7). The range of variation in rainfall and in most plumage variables was smaller on Oahu. Two variables, numbers of white tips on the median wing coverts and the rectrices, exhibited almost no variation. One variable, back chroma, showed a stronger relationship with rainfall on Oahu than on Hawaii.

**Subspecific variation and diagnosis.**—The mean values of several plumage characters differed among putative subspecies on Hawaii. For example, greater-covert tip length, amount of white in the brow, and brow value differed between *C. s. bryani* and *C. s. ridgwayi* (Fig. 8). However, diagnosability tests using the 75% rule index of Patten and Unit (2002) indicated that none of the subspecies was diagnosable from both other subspecies using any of the 20 plumage characters examined (Table 5). *Chasiempis s. ridgwayi* and *C. s. bryani* were diagnosable using greater-covert tip length, amount of white in the brow, and brow value, but *C. s. sandwichensis* was intermediate in each case and none of those characters could be used to distinguish *C. s. bryani* from *C. s. sandwichensis* or *C. s. sandwichensis* from *C. s. ridgwayi* (Fig. 9). Similarly, *C. s. sandwichensis* and *C. s. ridgwayi* could be distinguished by breast hue, but neither could be distinguished from *C. s. bryani* at the 75% level using this character.

Difficulty in distinguishing the subspecies resulted from overlap among subspecies and from individuals that exhibited plumage color atypical of their putative subspecies. For example, 8 of 47 individuals (17%) of *C. s. bryani* did not have the pale, largely ( $\geq 90\%$ ) white brow described as characteristic of this subspecies, and some individuals of other subspecies (not including zones of intergradation) had a

TABLE 2. Relationships of body size to elevation and annual rainfall in male Hawaii Elepaios, based on multiple regression analyses of five body measurements at each site. Individuals at higher elevations were larger in wing chord, tail length, and body mass, as predicted by Bergmann's rule. Rainfall was a significant predictor only of tail length. Values marked with an asterisk were significant at  $\alpha = 0.05$  with the Dunn-Šidák correction for multiple comparisons.

Measurement	df	F	$R^2$	T		P	
				Elevation	Rainfall	Elevation	Rainfall
Wing chord	2 and 37	24.29*	56.8	6.19	0.55	<0.001*	0.58
Tail length	2 and 32	57.67*	78.3	6.07	-4.72	<0.001*	<0.001*
Bill length	2 and 37	5.36	22.5	-3.26	-1.50	0.02	0.14
Tarsus length	2 and 33	2.76	14.3	0.38	-1.86	0.70	0.07
Body mass	2 and 33	7.44*	31.1	3.56	0.36	0.001*	0.72

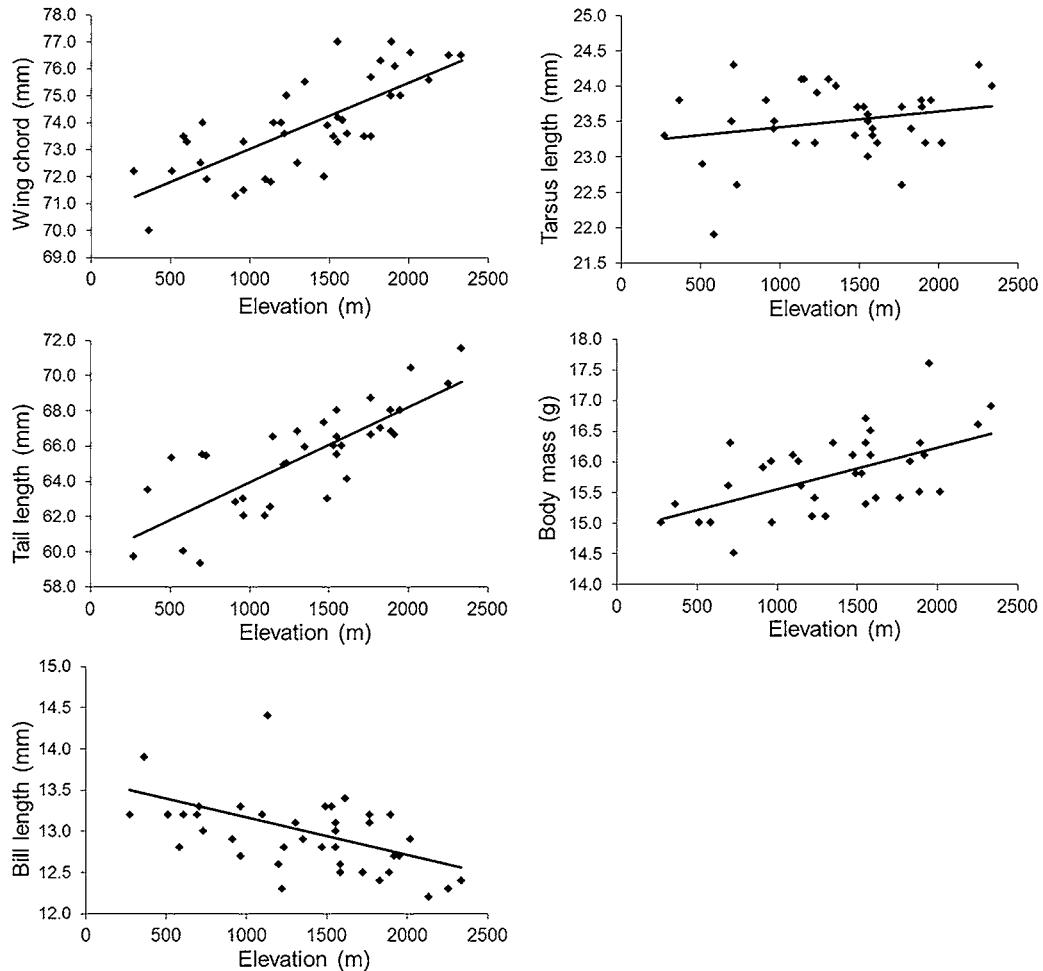


FIG. 4. Relationship of body size to elevation in male Hawaii Elepaios. Elepaios at higher elevations were larger in wing chord, tail length, and body mass, as predicted by Bergmann's rule, but elevation was not a significant predictor of bill length or tarsus length. For results of regression analyses, see Table 2.

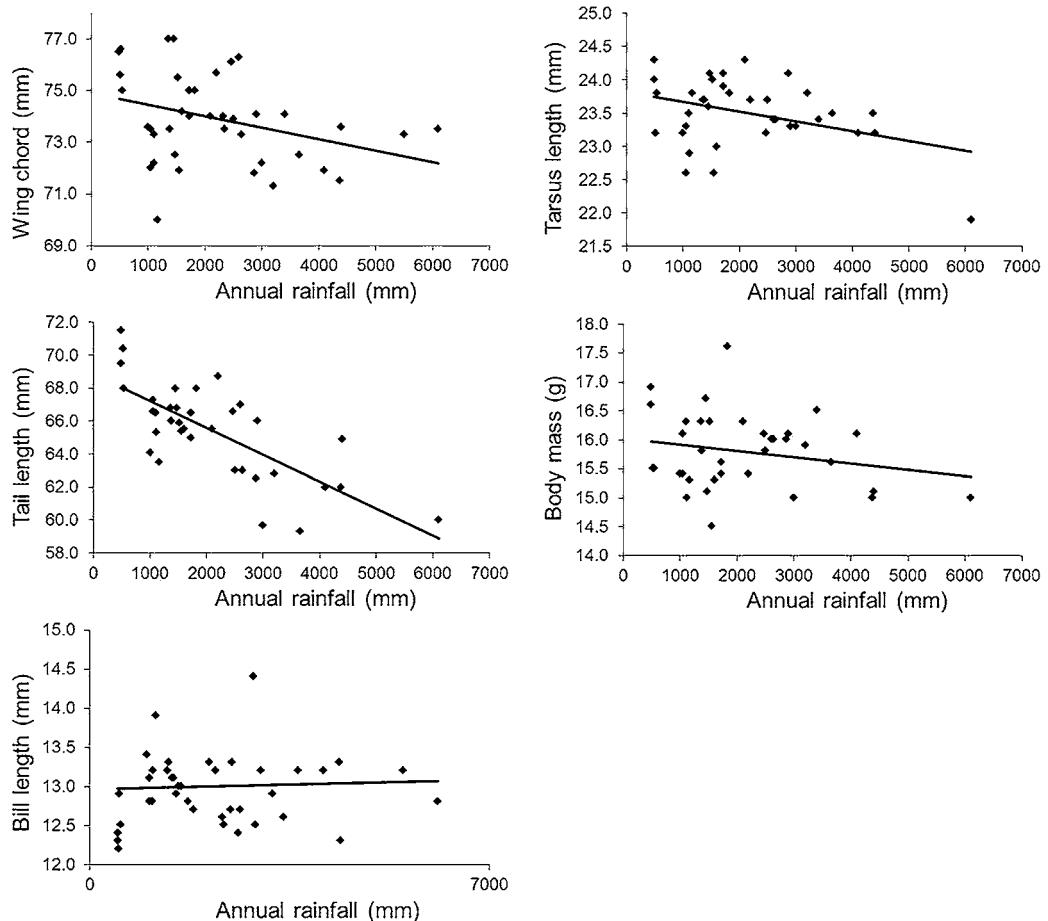


FIG. 5. Relationship of body size to annual rainfall in male Hawaii Elepaios. Tail length was shorter in areas of higher rainfall, perhaps reflecting Bergmann's rule, but rainfall was not a significant predictor of other morphological characters. For results of regression analyses, see Table 2.

largely white brow, including 33 of 107 individuals (31%) of *C. s. sandwichensis* and 8 of 156 individuals (5%) of *C. s. ridgwayi* (Fig. 9B). Two of the birds from Puu Laau that did not have mostly white brows or extensive white markings were paratypes used by Pratt (1979) in the description of *C. s. bryani* (specimen nos. LSU81709 and LSU81720; Fig. 10H). Birds that exhibited a largely white brow and extensive white markings were found in multiple locations, some of which were not geographically close to the putative range of *C. s. bryani*, including Pohakuloa Training Area, Puu Waa Waa, Kona Forest NWR, Kona Hema Preserve (Fig. 10E), Manuka, and Ocean View Estates (Fig. 10G) in the range of *C. s. sandwichensis*, and Hakalau Forest NWR (Fig. 10F) and the

Mauna Loa Strip of Hawaii Volcanoes National Park in the range of *C. s. ridgwayi*.

## DISCUSSION

*Ecogeographic variation in elepaio morphology.*—Hawaii Elepaios and, to a lesser extent, Oahu Elepaios exhibited substantial geographic variation in body size and plumage color, and much of this variation was related to climate. Variation in Hawaii Elepaio plumage color has been studied (Henshaw 1902, Pratt 1980), but variations in plumage color of Oahu Elepaios and body size of Hawaii Elepaios have not been described previously. Patterns of morphological variation in both species were smoothly clinal, with all measures of body size and plumage

TABLE 3. Relationships of proportional appendage length to elevation and rainfall in male Hawaii Elepaio, based on regression analyses of the ratios of wing length, tail length, bill length, and tarsus length to body mass. Birds at higher elevations had proportionally shorter bills and tarsi, as predicted by Allen's rule, but proportional wing length and tail length were not related to elevation.  $P$  values marked with an asterisk were significant at  $\alpha = 0.0125$  with the Dunn-Šidák correction for multiple comparisons.

Ratio	df	$F$	$R^2$	T		P	
				Elevation	Rainfall	Elevation	Rainfall
Wing chord:body mass	2 and 33	0.20	1.2	-0.63	-0.20	0.53	0.85
Tail length:body mass	2 and 32	4.95	23.6	0.28	-2.59	0.78	0.014
Bill length:body mass	2 and 33	10.82*	39.6	-4.58	-1.43	<0.001*	0.16
Tarsus length:body mass	2 and 33	7.16*	30.2	-3.78	-1.69	0.001*	0.10

color varying continuously with respect to elevation and rainfall and no large gaps in their distribution. These two clinal patterns combined to create a complex array of phenotypes across the landscape.

Similar patterns of morphological variation have been described in numerous species of birds, mammals, reptiles, and other groups (Zink and Remsen 1986, Ashton 2002, Freckleton et al. 2003, Millien et al. 2006). Among birds, the range of morphological variation exhibited by elepaio is similar to that in several other species, such as Song Sparrows (*Melospiza melodia*; Aldrich 1984,

Burtt and Ichida 2004, Patten and Pruett 2009) and Savannah Sparrows (*Passerculus sandwichensis*; Rising 2001, Rising et al. 2009). However, this degree of variation over such a small geographic area is unusual. The maximum distance between sampling points on Hawaii was <100 km (Fig. 1), but these locations ranged in elevation from 360 m to >2,300 m, and annual rainfall ranged from 0.5 m to >6 m (Appendix). The largest and palest elepaio in the arid, subalpine woodland at Puu Laau were separated by only 30–40 km from the smallest, darkest birds in dense rainforest at Piihonua in the Hilo Forest Reserve and lower

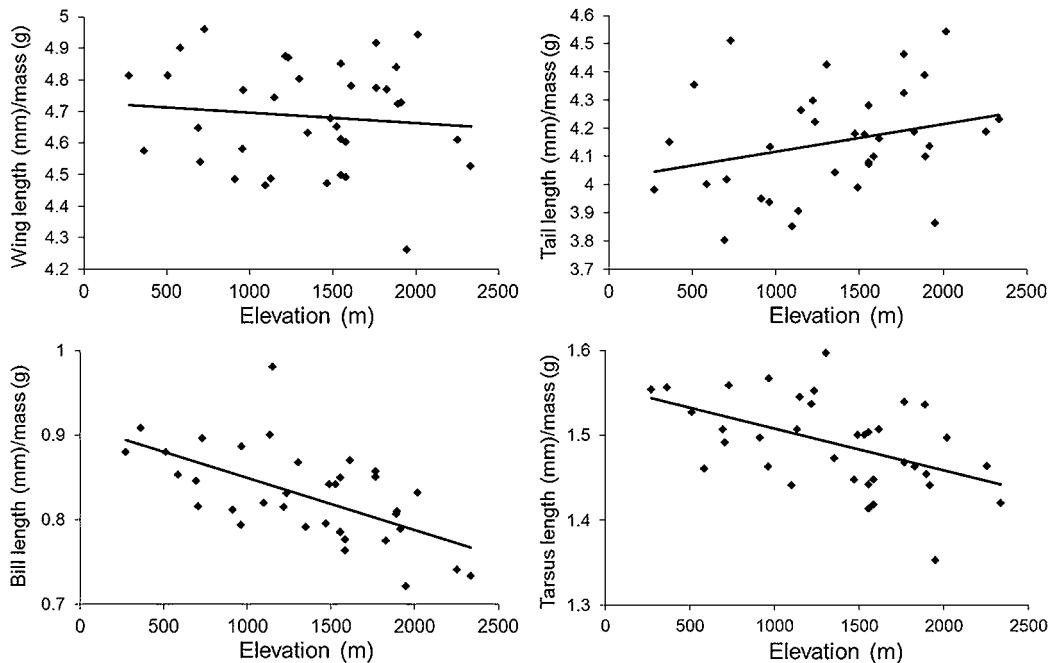


FIG. 6. Relationship of proportional appendage length to elevation in male Hawaii Elepaio. Elepaio at higher elevations had proportionally shorter bills and tarsi, as predicted by Allen's rule, but proportional wing length and tail length were not related to elevation. For results of regression analyses, see Table 3.

TABLE 4. Relationship of rainfall and plumage color in Hawaii Elepaios and Oahu Elepaios, based on regression analyses of 20 plumage color variables. Elepaios in wetter areas were darker, redder, and had less extensive white markings than those in drier climates, as predicted by Gloger's rule. *P* values marked with an asterisk were significant at  $\alpha = 0.0026$  with the Dunn-Šidák correction for multiple comparisons.

Variable	<i>R</i> <sup>2</sup>		<i>F</i> <sup>a</sup>		<i>F</i> <sup>b</sup>		<i>P</i>	
	Hawaii	Oahu	Hawaii	Oahu	Hawaii	Oahu	Hawaii	Oahu
Number white tips greater coverts	32.5	1.3	18.80	0.27	<0.001*	0.61		
White tip length greater coverts	66.2	24.0	76.38	6.63	<0.001*	0.018		
White tip length median coverts	49.3	1.2	37.88	0.25	<0.001*	0.62		
White tip length rump	28.2	12	15.29	2.86	<0.001*	0.11		
Number white tips rectrices	51.4	—	35.91	—	<0.001*	—		
White tip length outer rectrix	65.6	25.9	74.48	7.32	<0.001*	0.013		
Brow percentage white	58.0	10.9	53.78	2.58	<0.001*	0.12		
Brow hue	67.4	67.6	80.52	43.72	<0.001*	<0.001*		
Brow value	58.3	5.7	54.43	1.26	<0.001*	0.27		
Brow chroma	32.3	3.2	18.63	0.68	<0.001*	0.42		
Crown hue	65.9	28.7	75.33	8.46	<0.001*	0.008		
Crown value	32.3	0.1	18.65	0.01	<0.001*	0.91		
Crown chroma	32.3	2.3	18.62	0.50	<0.001*	0.49		
Back hue	62.7	30.7	65.54	9.28	<0.001*	0.006		
Back value	7.6	0.2	3.19	0.04	0.21	0.82		
Back chroma	0.3	36.3	0.10	11.95	0.75	0.002*		
Breast hue	57.9	21.5	53.60	5.74	<0.001*	0.026		
Breast value	33.8	0.2	19.95	0.05	<0.001*	0.82		
Breast chroma	4.6	8.6	1.86	1.97	0.18	0.18		
Breast streaking score	67.0	1.1	79.28	0.24	<0.001*	0.63		

<sup>a</sup>df = 1 and 39.

<sup>b</sup>df = 1 and 21.

Hakalau Forest NWR. The only other bird species known to have similar morphological variation over an area of comparable size is the Mascarene White-eye (*Zosterops borbonicus*) on Reunion (Gill 1973), and many parallels exist between that species and the two elepaios. All are adaptable and sedentary, and the islands on which they occur are roughly similar in size, elevation, terrain, and latitude and have similarly steep gradients in temperature and climate (Gill 1973). Among Hawaiian species, elepaios are not unique in this respect; geology and environmental variation in the Hawaiian Islands have shaped the evolutionary ecology of many groups of animals and plants, producing some of the best-known examples of adaptive radiation and diversification (Fleischer et al. 1998, Holland and Hadfield 2004, Cowie and Holland 2008, Givnish et al. 2008, Percy et al. 2008).

The ecogeographic patterns of morphological variation in elepaios are also compelling because they were replicated on two islands, Hawaii and Oahu. Although the range of morphological variation observed on Oahu was smaller, the Oahu

Elepaio has declined substantially and no longer occupies the wettest or driest portions of the island (Fig. 1; VanderWerf et al. 2001). The Oahu Elepaio probably exhibited a wider range of morphological variation before its distribution was reduced by loss of forest habitat, mosquito-borne diseases, introduced predators, and other human impacts (VanderWerf and Smith 2002, VanderWerf et al. 2006, VanderWerf 2009). No specimens of Oahu Elepaio were collected in areas wetter or drier than the areas in which they still occur. The Kauai Elepaio may exhibit similar variation but has not been examined in detail.

*Bergmann's rule and a corollary to Janzen's rule.*—The main Hawaiian Islands lie within tropical latitudes, but they experience considerable climatic variation because of their wide range of elevations, and the limited seasonality causes steep temperature gradients to persist year round. The highest elevations where the Hawaii Elepaio occur, above 2,500 m on the western slope of Mauna Kea, experience freezing temperatures in all months, and the potential for heat loss may be increased by

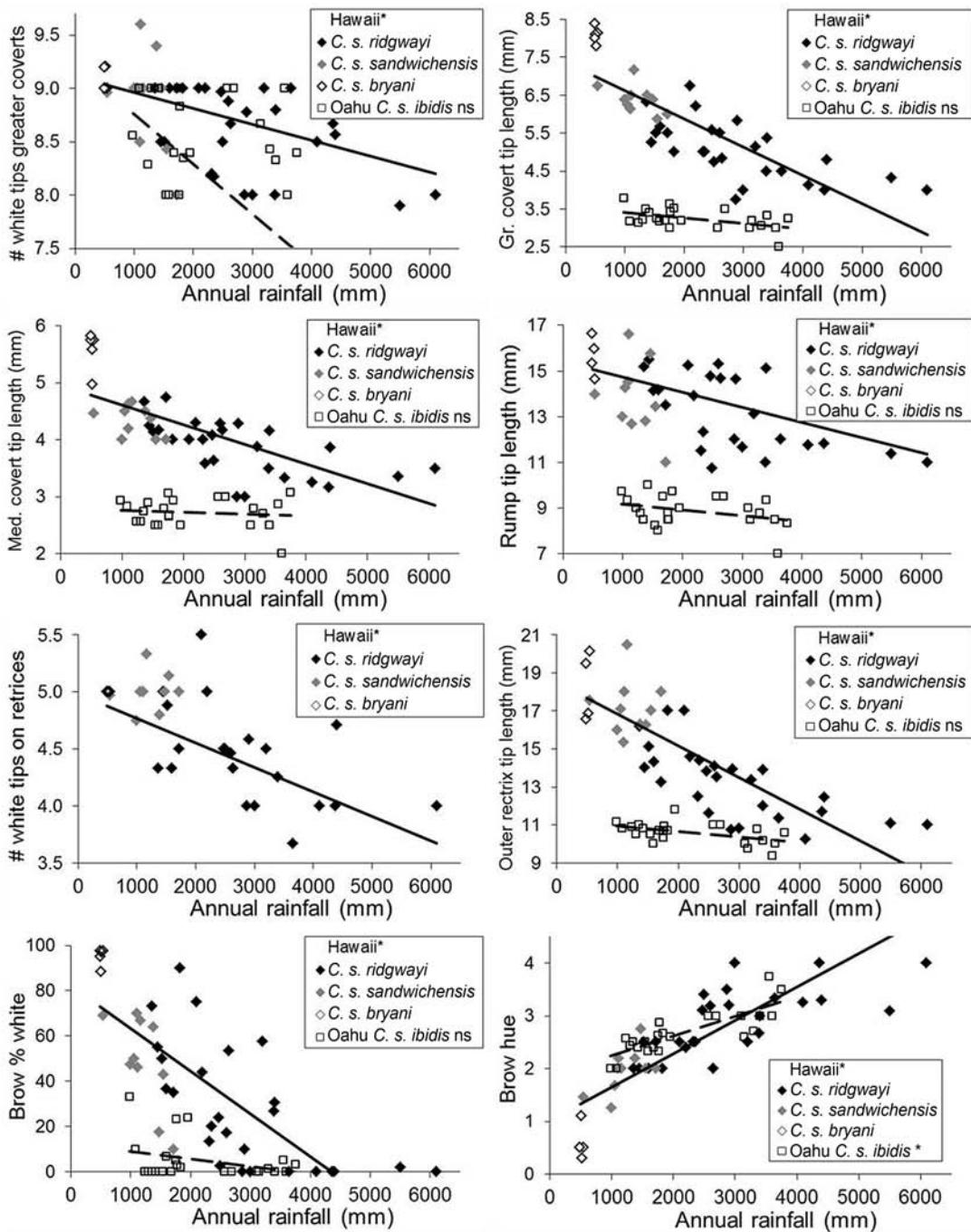


FIG. 7. Relationship of plumage color and annual rainfall in Hawaii Elepaios and Oahu Elepaios. Elepaios were more heavily pigmented in areas with higher rainfall on both islands, as predicted by Gloger's rule. Rainfall was a significant predictor for 17 of 20 plumage characters in Hawaii Elepaios and 2 of 20 in Oahu Elepaios. Significant relationships ( $P < 0.0026$ ) are indicated by an asterisk; ns = regressions that were not significant. For results of regression analyses, see Table 4. Figure 7 is continued on the next two pages.

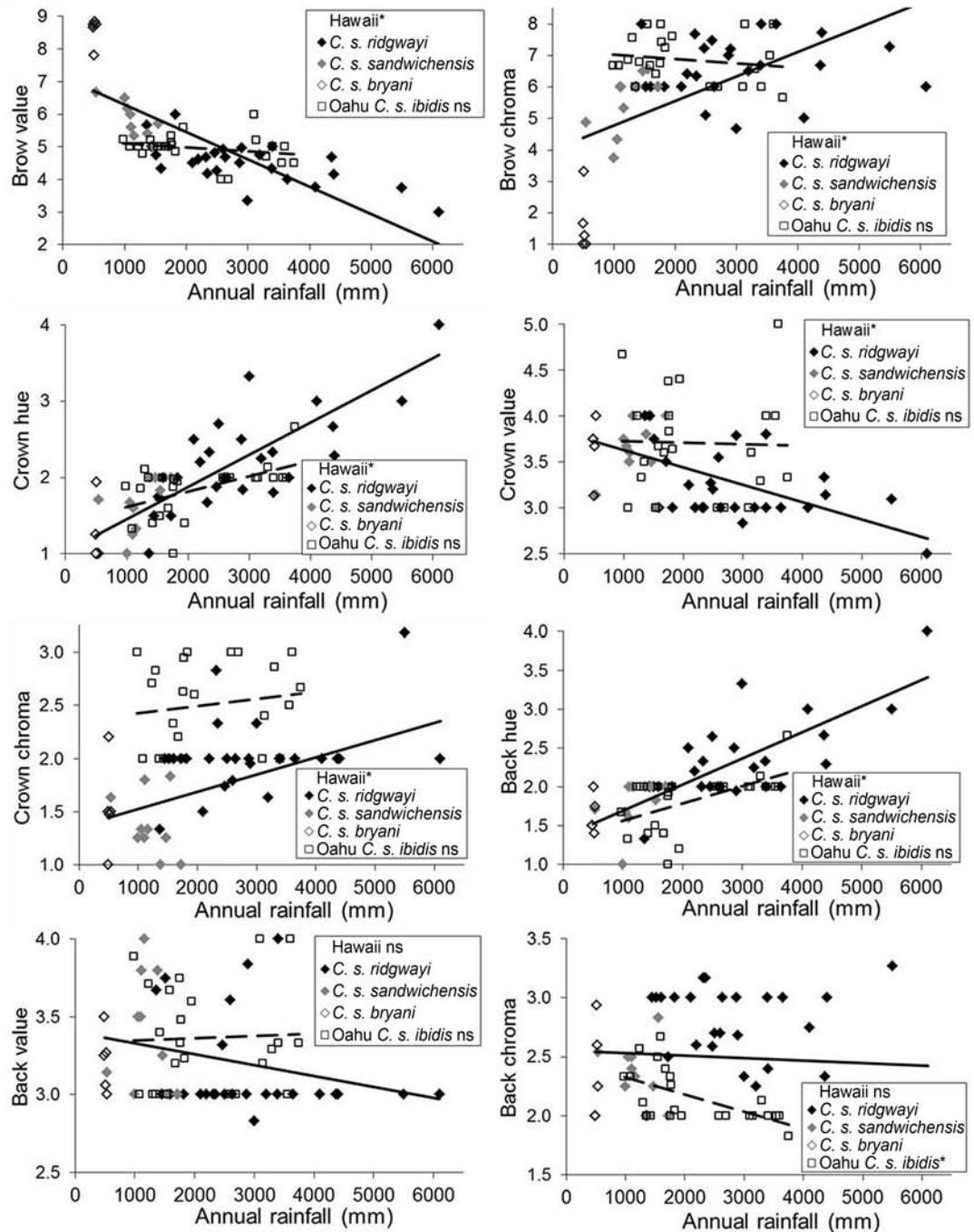
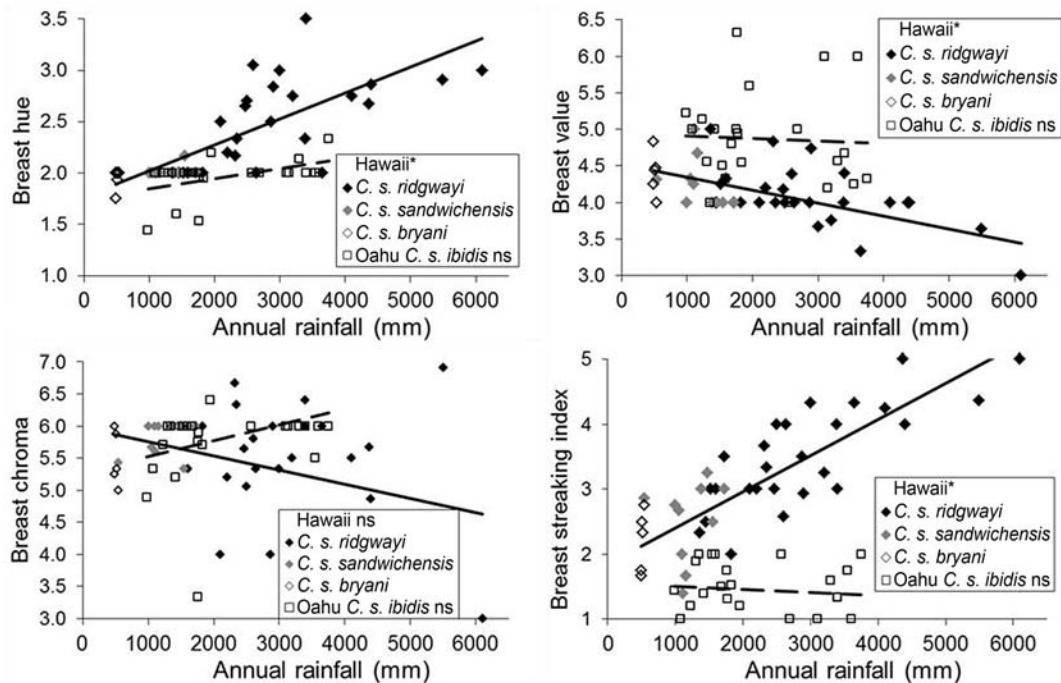


FIG. 7. Continued.

strong winds and open woodland habitat that allows substantial air flow and convective heat loss overnight. By contrast, the low-elevation rainforests inhabited by the Hawaii Elepaio

at Piihonua and Puna are warm all year and throughout the day, are very humid, and experience limited air flow and convective heat loss because of the dense forest canopy.

FIG. 7. *Continued.*

Most examples of Bergmann's rule come from temperate continental species, and several authors have commented that climatic seasonality may promote geographic size variation (Lindstet and Boyce 1985, Murphy 1985, Graves 1991). However, in tropical areas where sufficient climatic variation exists as a result of varying topography, reduced seasonality could promote morphological variation in resident species through local adaptation. This rationale is similar to Janzen's (1967) argument for why mountain passes are more effective barriers to dispersal in the tropics. This idea is based on the fact that lower seasonal variation in ambient temperature in the tropics reduces overlap in thermal regimes between low- and high-altitude sites. Janzen (1967) predicted that mountain passes therefore represent greater physiological barriers to dispersal for lowland tropical organisms, which should favor narrower distributions in the tropics and an increase in species turnover along altitudinal gradients. McCain (2009) tested the most important prediction of Janzen's rule and confirmed that in most groups of vertebrate animals, tropical species indeed have narrower elevational ranges. Janzen's (1967) argument also included assumptions that tropical organisms have a narrower

thermal tolerance than temperate species and are less likely to evolve in response to climatic variation, but Ghalambor et al. (2006) showed that tropical species inhabiting high altitudes can have broad climatic tolerance and that the ability of tropical species to evolve in response to climate has not been adequately tested. Elepaio appear to be particularly plastic with respect to climate and have readily evolved in response to climatic variation. Mountain passes have not served as barriers to dispersal by the Hawaii Elepaio (VanderWerf et al. 2009), but other aspects of Janzen's rule help explain the small-scale morphological adaptations they exhibit. A corollary to Janzen's rule appears to be that, in species that are able to evolve in response to climatic variation, mountain passes cause greater morphological variation and finer-scale local adaptation in the tropics.

Previous studies have reported that Bergmann's rule is more common in resident than in migratory species (Zink and Remsen 1986; but see Ashton 2002), but this pattern may be reversed in temperate and tropical species. Tropical resident species would be more likely to exhibit Bergmann's rule because they are subject to a single, consistent thermal regime throughout the

TABLE 5. Diagnosability indexes of Hawaii Elepaio subspecies using the 75% rule as prescribed by Patten and Unitt (2002). Values >0 (marked with an asterisk) indicate characters that distinguished ≥75% of individuals in two samples. *Chasiempis sandwichensis ridgwayi* and *C. s. bryani* were distinguished by length of white tips on the greater coverts, amount of white in the brow, and brow value, and *C. s. ridgwayi* and *C. s. sandwichensis* were distinguished by breast hue, but none of the subspecies could be distinguished from both other subspecies at the 75% level using any character.

Character	<i>C. s. ridgwayi</i> vs. <i>C. s. sandwichensis</i>	<i>C. s. sandwichensis</i> vs. <i>C. s. bryani</i>	<i>C. s. ridgwayi</i> vs. <i>C. s. bryani</i>
Number white tips greater coverts	-1.41	-2.45	-1.28
White tip length greater coverts	-1.24	-1.90	0.14*
Number white tips median coverts	-1.15	-1.38	-1.16
White tip length median coverts	-1.35	-1.20	-0.54
White tip length rump	-7.42	-6.32	-6.59
Number white tips rectrices	-1.00	-0.77	-0.76
White tip length outer rectrix	-3.26	-8.78	-2.71
Brow percentage white	-44.45	-55.06	3.10*
Brow hue	-1.19	-1.74	0.27
Brow value	-1.46	-3.40	0.64*
Brow chroma	-5.25	-5.23	-2.85
Crown hue	-0.93	-1.12	-0.74
Crown value	-1.45	-1.33	-1.29
Crown chroma	-2.21	-1.85	-1.47
Back hue	-0.83	-1.29	-0.88
Back value	-1.36	-1.23	-1.22
Back chroma	-1.80	-1.53	-1.37
Breast hue	0.06*	-0.51	-0.14
Breast value	-1.77	-1.62	-1.58
Breast chroma	-2.60	-2.60	-2.51
Breast streaking score	-1.88	-2.02	-1.34

year, whereas temperate residents would experience a much wider climatic range that could inhibit thermoregulatory adaptation via body size. Migrants also experience varying climates during their travels and often migrate to escape seasonal climatic variation. Elepaios are resident and sedentary, and their variation in body size and plumage color is closely tied to the narrow climatic range experienced by individuals. By contrast, two widespread species of Hawaiian honeycreepers, the Apapane (*Himatione sanguinea*) and Iiwi (*Vestiaria coccinea*), are less sedentary and exhibit no morphological variation within or even among islands (MacMillen and Carpenter 1980, Ralph and Fancy 1995, Pratt 2005), presumably because higher gene flow has prevented local morphological adaptation.

Ambient temperature is the climatic variable most often associated with body size (Ashton 2002, Millien et al. 2006), but the thermal environment experienced by organisms is also influenced by other factors. Temperature and humidity were important predictors of body size in House Sparrows (Johnston and Selander 1971) and American

Robins (*Turdus migratorius*; Aldrich and James 1991). More sophisticated measures of thermal environment have been developed, such as operative temperature (Bakken 1992), but the data required to calculate such measures are often not available from a sufficient number of sites at a landscape scale. In Hawaii Elepaios, temperature was a better indicator than rainfall of most body measurements and appeared to be more important overall, but rainfall was a better predictor of tail length and appeared to play some role.

Thermoregulatory adaptation and fasting ability are the two mechanisms most often proposed for Bergmann's rule (Scholander 1955, Mayr 1956, James 1970, Boyce 1979), but testing and distinguishing these mechanisms has been difficult (McNab 1971, Dunbrack and Ramsay 1993, Ashton 2002, Olson et al. 2009). Fasting endurance is related to fat deposition (Lindstet and Boyce 1985), but elepaios at all elevations rarely had significant fat deposits and usually had a fat score of zero or trace (E. VanderWerf unpubl. data), which suggests that fat deposition and, thus, fasting endurance were not related to temperature.

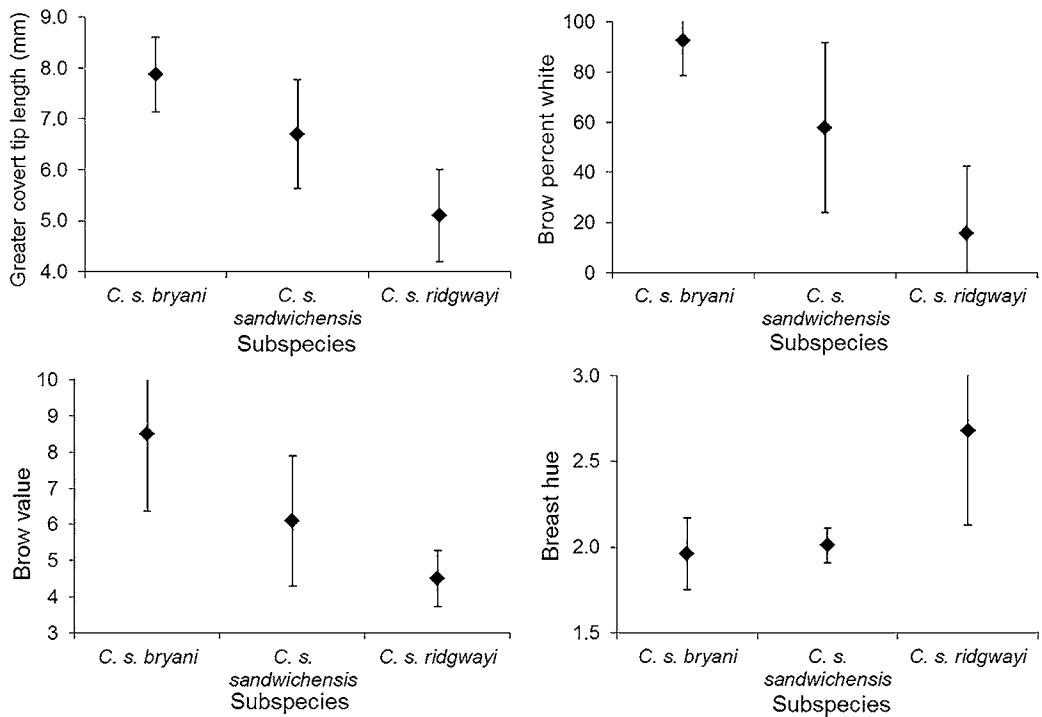


FIG. 8. Mean ( $\pm$  SD) values of four plumage color variables in three putative Hawaii Elepaio subspecies. *Chasiempis sandwichensis bryani* and *C. s. ridgwayi* differed in mean greater-covert tip length, amount of white in the brow, and brow value, and *C. s. ridgwayi* and *C. s. sandwichensis* differed in breast hue, but none of these variables could be used to distinguish all three subspecies.

Fasting endurance has been proposed primarily on the basis of studies of mammals (Lindstet and Boyce 1985, Millar and Hickling 1990, Dunbrack and Ramsay 1993). Birds, except for long-distance migrants, may deposit fat to a lesser degree than mammals because of the weight constraints imposed by flight. Resident insectivorous birds like elepaios may have more difficulty than migratory species or nectarivorous or frugivorous species in accumulating energy reserves, and the selective mechanism for Bergmann's rule may differ not only between birds and mammals, but also among birds in different feeding guilds and with different movement patterns.

**Allen's rule.**—Elepaios conformed to Allen's rule for bill length and tarsus length but not for wing length or tail length, which is perhaps not surprising. Heat loss in birds occurs primarily from unfeathered areas, typically the bill, face, legs, and feet (Steen and Steen 1965, Phillips and Sanborn 1994, Symonds and Tattersall 2010). Although the wings are the largest appendage in most birds and have large surface area, they are

well insulated with feathers and lose little heat. Tail length in most birds is determined primarily by length of the rectrices, and heat loss through the keratinous tissue of these feathers is minimal. The bony tissue of the tail is reduced in birds to the pygostyle, and muscles and associated tissues that control and supply the tail do not extend far from the body core. By contrast, the bill, legs, and feet are bare of feathers and uninsulated in most birds and allow substantial heat exchange with the environment (Phillips and Heath 1995, Symonds and Tattersall 2010). Negative relationships between bill length and temperature or latitude have been found in several bird species (Snow 1954, Laiolo and Rolando 2001, Symonds and Tattersall 2010), and the bill is known to be an important surface for heat exchange (Hagan and Heath 1980, Midtgard 1984). In the Toco Toucan (*Ramphastos toco*), a tropical species with a particularly large bill, Tattersall et al. (2009) showed that 30–60% of body heat was lost through the bill and that the bill served as an important thermoregulatory organ through which heat exchange

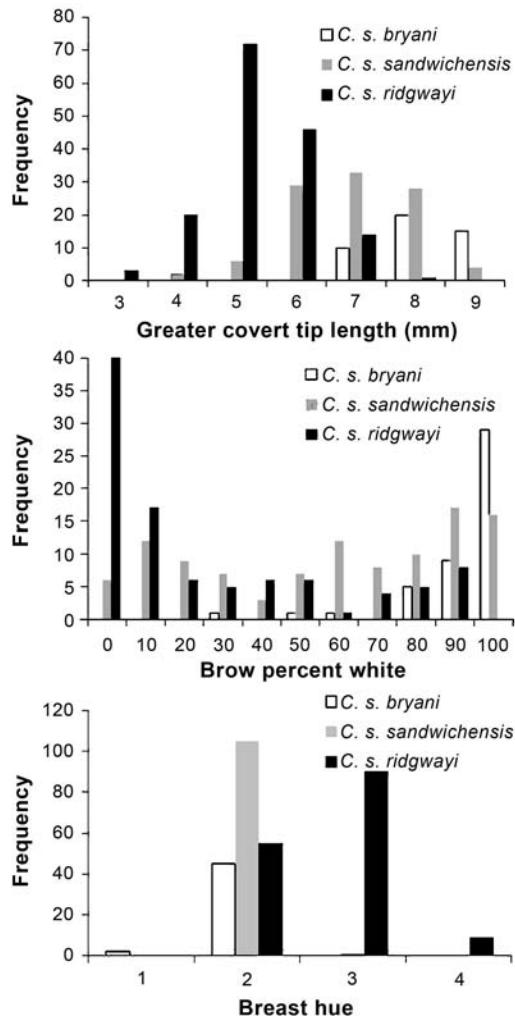


FIG. 9. Histograms of Hawaii Elepaio (A) greater-covert tip length, (B) amount of white in the brow, and (C) breast hue, by subspecies. *Chasiempis sandwichensis bryani* was diagnosable from *C. s. ridgwayi* by each of these characters, but *C. s. sandwichensis* was intermediate in each, and no subspecies was diagnosable from both other subspecies.

was regulated by variable blood flow. The legs and feet also provide large uninsulated surfaces for heat exchange, and since they are often in direct contact with solid substrates that have higher specific heat than air, they have high potential for heat exchange. Inverse relationships between temperature and leg length have been reported in several species, particularly seabirds, gulls, terns, and shorebirds (Cartar and Morrison 2005, Nudds and Oswald 2007, Symonds and

Tattersall 2010). Although most studies of Allen's rule have focused on limbs, particularly the legs, Symonds and Tattersall (2010) argued that bird bills may illustrate Allen's rule more strongly because heat loss through the legs is minimized through counter-current vascular heat-exchange systems (Ederstrom and Brumleve 1964, Johansen and Millard 1973). No such vascular counter-current heat exchange is known in the bill, which makes it a greater potential source of heat exchange and, thus, more subject to selection and local adaptation in response to varying thermal environments.

**Gloger's rule.**—The underlying cause of plumage color variation in elepaio is not certain, but most mechanisms can be ruled out by various evidence, leaving resistance to microbial feather degradation as the most likely explanation. Thermoregulation is unlikely to be the cause of plumage color variation because elepaio have paler plumage and larger white markings in areas that are both hot and dry and cold and dry. Furthermore, the white markings cover only a small portion of the plumage; if heat absorption or reflectance were of primary importance, one would expect these markings to be more extensive. Predation on adult elepaio is rare and annual survival is high, >80% (VanderWerf 2008, 2009). Moreover, there is no reason to suspect that predator abundance or predation pressure is higher in wet or dry habitats. The main extant predator of the Hawaii Elepaio is the Hawaiian Hawk (*Buteo solitarius*; VanderWerf 1998), which occurs throughout the range of the Hawaii Elepaio and is common in areas of both high and low rainfall (Klavitter et al. 2003). The Hawaiian Short-eared Owl (*Asio flammeus sandwichensis*) may prey on elepaio occasionally (Snetsinger et al. 1994), but it and other avian predators, such as the extinct *Grallistrix* owls (Olson and James 1991), also are or were widespread. Energetic variation does not explain the plumage differences among locations, or those among age classes, because the contrasting white marks on the wing coverts, rump, and tail that characterize adult plumage are caused by lack of pigment and, thus, are not physiologically costly to produce (VanderWerf 2001, VanderWerf and Freed 2003).

Several species of feather-degrading bacteria have been found on feathers of a variety of bird species, and they appear to be pervasive (Burtt and Ichida 2004, Whitaker et al. 2005), but the identity and prevalence of such bacteria may vary

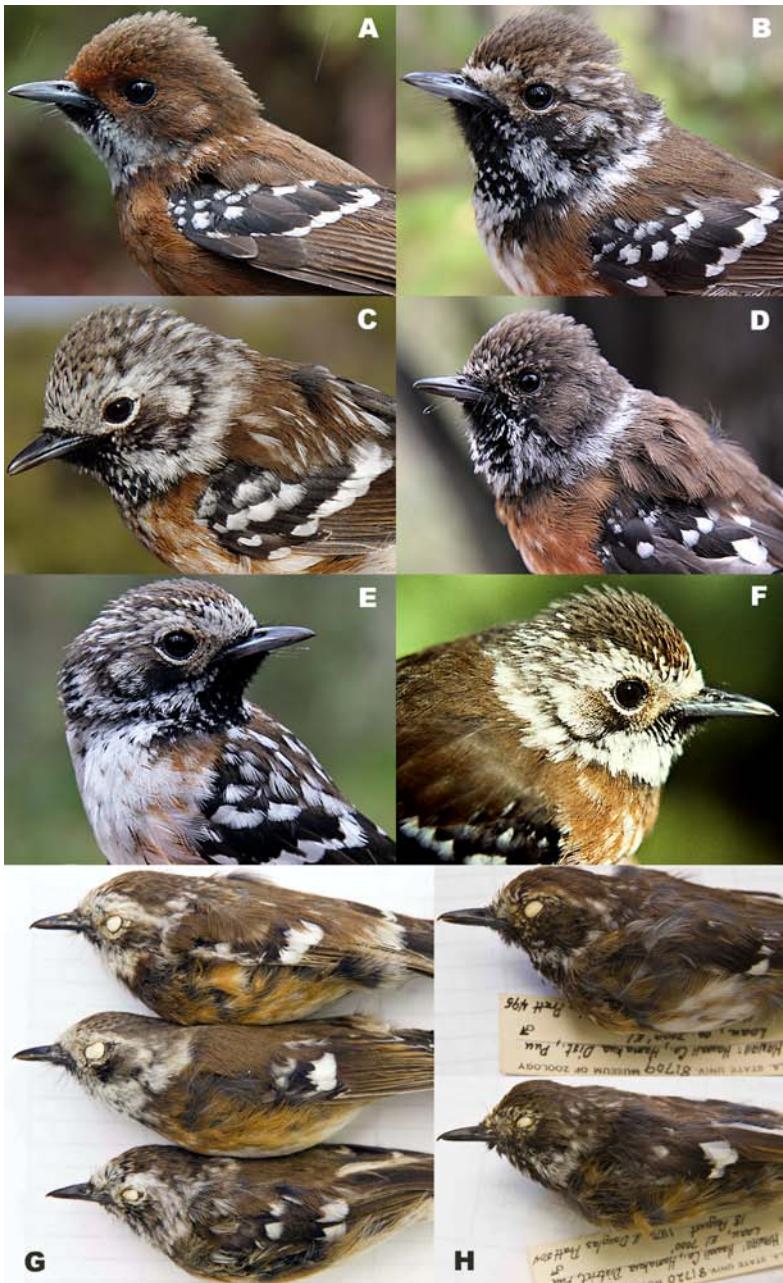


FIG. 10. Photographs of Hawaii Elepaio, illustrating variation and overlap in plumage color among subspecies. (A) Typical male *Chasiempis sandwichensis ridgwayi* from Puu Makaala, a wet site. (B) Typical male *C. s. sandwichensis* from Kona Forest National Wildlife Refuge (NWR), a moderate-rainfall site. (C) Typical male *C. s. bryani* from Puu Laau, a dry site. (D) Male from Puu Laau atypical of *C. s. bryani*. (E) Male from Kona Hema Preserve, where birds are considered *C. s. sandwichensis*, but more typical of *C. s. bryani*. (F) Female from Hakalau Forest NWR, a wet site where birds are considered *C. s. ridgwayi*, but more typical of *C. s. bryani*. (G) Two typical female *C. s. bryani* specimens from Puu Laau and a female from Ocean View Estates. (H) Two male specimens from Puu Laau that are paratypes of *C. s. bryani* yet are dark, have only partly white brows, and have heavy breast streaks.

considerably among and within species (Gunderson 2008). I collected 48 Hawaii Elepaio feather samples that were tested for *Bacillus licheniformis*, but no feather-degrading bacteria were cultured from them (E. Burtt pers. comm.). Several soil samples collected from elepaio habitat also failed to produce any *Bacillus*. However, the cultivation techniques used were highly selective of the genus *Bacillus* and narrowed the range of bacteria that could have been detected (Gunderson 2008). More inclusive cultivation methods have yielded higher prevalence of feather-degrading bacteria in some birds (Shawkey et al. 2007) and greater diversity of bacterial species in others (Shawkey et al. 2005), and they might be productive with elepaios and other Hawaiian birds. Some fungal species are also known to have keratinolytic properties and could have a similar effect on avian plumage (Gunderson 2008).

*Relation of morphology, genetics, and behavior.*—Geographic variation and, ultimately, speciation depend on a complex interaction of gene flow, local adaptation, and environmental gradients (Coyne and Orr 2004, Nosil et al. 2009). Local adaptation may be inhibited by gene flow from the center of a species range toward its periphery as a result of varying environmental conditions. Similarly, the steepness of environmental gradients responsible for selection of certain characters can influence the geographic scale over which an optimal phenotype persists. Although these arguments were originally used as mechanisms to explain the limits of a species range, they can also be applied to patterns of intraspecific variation in locally adapted characters.

Body size and plumage color of the Hawaii Elepaio varied over small geographic areas, and this spatially compressed morphological adaptation was caused by an adaptive landscape formed by steep gradients in temperature and humidity. This landscape varies geographically because rainfall and temperature gradients are not parallel and are created by multiple volcanoes, resulting in a complex environment in which elepaios are exceptionally plastic. The extent to which phenotypic variation and local adaptation has evolved in the Hawaii Elepaio is also related to their dispersal behavior and mating system. Elepaio dispersal is driven by intraspecific competition and territory availability; young birds usually disperse only far enough to find a vacant territory and a mate, which in dense populations is typically only a few hundred meters (VanderWerf 2008). The short dispersal distances limit

gene flow, producing adaptation to local environmental conditions at a small geographic scale. The limited dispersal and localized phenotypic variation of Hawaii Elepaios also was reflected in their genetic population structure; mitochondrial DNA (mtDNA) showed significant structure, but most of the variation was partitioned among sites within the ranges of putative subspecies, not among the subspecies (VanderWerf et al. 2009).

Morphological variation of elepaios within each island was smoothly clinal because there were few barriers to dispersal at a landscape scale and because elepaios are adaptable and inhabit areas with a wide range of climates and vegetation types (Cicero and Johnson 2006). There were no large breaks in elepaio size or coloration because there are no large barriers that have prevented gene flow from occurring throughout each island. On Hawaii, areas of bare lava from recent volcanic events and unforested alpine areas on Mauna Kea and Mauna Loa may inhibit elepaio dispersal to some extent, but continuous forest encircling these volcanoes at lower elevations provided a pathway for gene flow around the island (VanderWerf et al. 2009).

The sedentary behavior of elepaios also affects cultural transmission and geographic variation of their songs, which in turn can influence mate choice. Young oscine passerines usually learn songs from adult tutors early in their developmental period (Catchpole and Slater 1995) and retain a long-lasting memory of the tutor's song that largely shapes their own song (Phan et al. 2006). VanderWerf (2007) used inter-island song-playback experiments to show that elepaios on Kauai, Oahu, and Hawaii responded more strongly to playbacks of songs from their own island and suggested that song could serve as a behavioral reproductive isolating mechanism. Similar experiments within islands revealed that elepaios responded more strongly to songs from their own region than to songs from more distant parts of the island (E. VanderWerf unpubl. data). These local song dialects may be reinforced by the sociobiology of elepaios, in which young birds usually disperse only far enough to find a vacant territory and a mate.

*Variation and subspecies.*—The putative subspecies of Hawaii Elepaio were not diagnosable using the 75% rule as prescribed by Patten and Unit (2002), but this does not mean that morphological variation in elepaios is unimportant or that the described subspecies are without value.

The subject of avian subspecies has been controversial, with widely varying viewpoints about the value and purpose of subspecific taxonomy that stem largely from adherence to different species concepts (James 2010, Winker 2010). Another source of contention has been the naming of subspecies along smooth clines, where in theory an unlimited number of subspecies could be named provided that sample sizes from each location were sufficiently large (Patten and Unitt 2002). This has occurred to varying degrees in several North American bird species, including the Sage Sparrow (*Amphispiza belli*; Patten and Unitt 2002, Cicero and Johnson 2006), Savannah Sparrow (Rising 2007), and Yellow-throated Warbler (*Dendroica dominica*; McKay 2008), and also in the Hawaii Elepaio. More sophisticated methods of attempting to distinguish subspecies have been devised (Patten 2010), but because all aspects of Hawaii Elepaio plumage variation were smoothly clinal, it is unlikely that other techniques would reveal greater differentiation. Nevertheless, the described subspecies represent historical advances in studies of *Chasiempis* and have helped increase our understanding of geographic variation, which Cicero (2010) reported was also important in the Sage Sparrow. Fitzpatrick (2010) argued that subspecies, even if not biologically valid, provide a convenient means of describing variation, and this view is relevant to the Hawaii Elepaio. Referring to elepaios as “*C. s. bryani*” is simpler than describing them as “pale, white-headed birds from high-elevation dry forests on Mauna Kea.” In the following section, I discuss how variation in Hawaii Elepaio morphology is not always concordant with the putative subspecies, though I continue to use the subspecies names for convenience.

The clinal nature of variation in Hawaii Elepaio morphology was less evident previously because data were available from fewer locations that encompassed less of the species range (Pratt 1980: fig. 1). Addition of data from intervening locations sampled in the present study showed that variation was not so discrete and that the zones of intergradation were broader than was previously recognized (Fig. 1). Some overlap can be expected among subspecies, but this should occur along narrow contact zones. The zone of intergradation was particularly broad in the Kau area on the southeast flank of Mauna Loa. Rainfall in this area is generally lower toward the west, but it declines in a complex pattern that results from the

interaction of rain shadows cast by Mauna Loa and Kilauea, forming a second rainfall peak in central Kau (Fig. 1). The appearance of elepaios across this region mirrored the complex climate, with darker birds in the Volcano region grading into paler birds in the rain shadow near Kapapala and on the higher slopes of Mauna Loa, then becoming darker again farther west around the second rainfall peak in central Kau. Henshaw (1902) and Pratt (1980) recognized elepaios from Kau and Kapapala as intergrades, and the results of the present study reveal that this zone of intergradation is broader and more complex than was previously realized.

The clinal nature of Hawaii Elepaio morphological variation has also been obscured by extensive habitat loss and disappearance of elepaios from some portions of their former range. For example, elepaios that inhabit high-elevation dry forests of Mamane (*Sophora chrysophylla*) and Naio (*Myoporum sandwicense*) on the western slope of Mauna Kea near Puu Laau have been described as a separate subspecies, *C. s. bryani* (Pratt 1979). These birds occupy the coldest, driest habitat of any elepaios and thus represent an extreme form of the dry forest phenotype that is characterized by less pigmentation and generally paler plumage (Pratt 1980). However, Mamane-Naio forest was formerly more widespread and has been reduced by clearing for ranching and browsing by cattle and feral sheep. These actions have greatly decreased the distribution of the Palila (*Loxioides bailleui*), an endangered Hawaiian honeycreeper that is specialized in foraging on Mamane seed pods and whose present range coincides with that of *C. s. bryani* (Leonard et al. 2008). The ranges of both Palila and *C. s. bryani* have been truncated because their habitat is now largely confined to the upper slopes of Mauna Kea, particularly the western slope. When forest cover was more continuous, the *C. s. bryani* plumage type would have been more widespread and would have graded into areas of higher rainfall to the north, west, and south. Vestiges of this pattern are still evident in the form of plumage color variation within *C. s. bryani*. Pratt (1980) stated that “all Elepaios at this locality were similarly colored,” but this is not true. Two of 17 specimens from Puu Laau described as paratypes of *C. s. bryani* and several live birds examined during the present study did not exhibit the pale plumage and white head purported to be characteristic of this subspecies (Fig. 10D, H). These seemingly

atypical individuals are not aberrant and should not be overlooked; they represent an interesting legacy of dispersal and genetic introgression that occurred until the area became isolated by loss of forest habitat in the past 150 years.

Another remnant of Mamane–Naio dry forest occurs at the U.S. Army Pohakuloa Training Area (PTA), which is located 20 km south of Puu Laau and supports a small and declining elepaio population that is now isolated by open habitat and has not been described previously. Some of this isolation is the result of volcanic activity from Mauna Loa and Hualalai volcanoes, but isolation has been greatly increased by loss of forest habitat to military training, cattle ranching, and browsing by feral sheep and goats. Most elepaios in this area were fairly pale and typical of *C. s. sandwichensis*, but some had the largely white head thought to be characteristic of *C. s. bryani* and others were darker and more similar to individuals of *C. s. ridgwayi* found farther east. This variation is perhaps not surprising given the location of Pohakuloa on a broad central plateau among three high volcanoes. As at Puu Laau, the variability of elepaios at PTA represents a legacy of prior dispersal from all directions that occurred when forest habitat was more continuous.

Kalopa State Park, on the northwestern slope of Mauna Kea, contains the last remnant population in a region regarded by Henshaw (1902) and Pratt (1980) to be a zone of overlap between *C. s. ridgwayi* and *C. s. bryani*. This area is located in a transition from the wet forest that covers the eastern slopes of Mauna Kea to its drier western aspect. Elepaios from Kalopa did have some white in the brow, like *C. s. bryani*, and were somewhat larger than expected given the elevation, which suggests that there has been gene flow from higher on Mauna Kea. Most of the native forest in the upper elevations of northern Hamakua and Waimea has been destroyed, however, and Kalopa is now isolated from the main population of *C. s. ridgwayi* to the southeast and from the Mamane–Naio forest occupied by *C. s. bryani* to the south. It seems unlikely that there is currently any gene flow or that this tiny population remnant, which in 2007 consisted of four single males, will be rescued by immigration. Elepaios from Mana and Waimea were regarded by Pratt (1980) as belonging to *C. s. bryani*, but the only three specimens from these locations were actually quite dark and more similar to *C. s. ridgwayi*, which suggests that they may have been collected

farther east and labeled with the locality where the collector had stayed the night. I treated Mana and Waimea as being within the zone of intergradation.

Elepaios in the Kona region on the western side of Hawaii, regarded as *C. s. sandwichensis*, also exhibited substantial color variation that confounded subspecific categorization. These birds were paler, on average, as first noted by Henshaw (1902), but some individuals from wetter areas in Kona, such as The Nature Conservancy's Kona Hema Preserve and the Kona Forest NWR, were similar in many respects to *C. s. ridgwayi*. Perhaps most striking, some birds from lower Manuka Natural Area Reserve and Ocean View Estates were virtually indistinguishable from *C. s. bryani* (Fig. 10G). These sites are as dry as Puu Laau, the type locality for *C. s. bryani*, so the similarity of elepaios inhabiting these sites should not be surprising. Elepaios with plumage similar to that described for *C. s. bryani* were also found in other areas with dry climate, including the upper elevations of Mauna Loa in Hawaii Volcanoes National Park and the upper elevations of Hakalau Forest NWR (Fig. 10F).

The lack of consistent genetic differences among the putative subspecies in the loci examined thus far does not imply that genetic variation does not exist in the Hawaii Elepaio or that such variation is unimportant. In fact, VanderWerf et al. (2009) found significant variation in the mtDNA ND2 gene and the nuclear LDH gene of the Hawaii Elepaio, but in both loci most variation was partitioned among sites within the putative subspecies, not among the subspecies. Neutral genetic markers such as mtDNA are less likely to correspond with phenotypic variation, and evidence from mtDNA alone is insufficient to state that observed phenotypic variation is unimportant or not adaptive (Funk and Omland 2003, Mumme et al. 2006, Rising 2007, Edwards and Bensch 2009). Ballentine and Greenberg (2010) found that phenotypic differences between populations of the Swamp Sparrow (*Melospiza georgiana*) were under genetic control and likely were adaptive, despite lack of differentiation in mtDNA. Similarly, Pruett and Winker (2010) found that mtDNA reflected little information about Song Sparrow subspecies, but they concluded that differences in body mass and microsatellite allele frequencies supported continued recognition of subspecific units for taxonomy and conservation because they may represent recently

diverged populations that have not been isolated long enough for complete lineage sorting using mtDNA markers yet have accrued important biological diversity below the level of full species. In the Hawaii Elepaio, mtDNA already has revealed significant variation that corresponds with phenotypic patterns and likely reflects, but is not responsible for, adaptive differentiation. Examination of additional nuclear markers might reveal further differentiation, but it likely would occur at small geographic scales and, thus, still not coincide with putative subspecies.

*Conservation and management implications.*—The ability of a population to adapt to environmental change is dependent on sufficient genetic variation. Protecting the diversity of habitats responsible for maintaining local adaptations in elepaio morphology will help maximize their evolutionary potential and ability to cope with change. However, preservation of the environmental gradients alone is not sufficient to ensure evolutionary potential; extirpation of locally adapted populations and the haplotypes they carry may cause permanent loss of biodiversity and compromise evolutionary potential (Ballentine and Greenberg 2010). Such loss probably has already occurred in the Oahu Elepaio. Global climate change is expected to cause warmer and drier conditions, on average, in the Hawaiian Islands (U.S. Environmental Protection Agency 1998, Benning et al. 2002, Christensen et al. 2007) and is likely to exacerbate many existing threats to Hawaiian forest birds. Conservation of elepaio phenotypes already adapted to these conditions might enhance long-term survival of *Chasiempis* species, and conservation of phenotypic variation in general will maximize their ability to adapt to unforeseen changes in the future.

Translocation or release of captive-bred elepaios to areas where they have been extirpated or declined can be an appropriate management strategy to restore populations or stabilize numbers (USFWS 2006), but birds should be taken from areas with habitat and climate as similar as possible to that of the target area in order to preserve and benefit from any local adaptation in plumage color, body size, and other characters and so that locally evolved phenotypes are not compromised.

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#### LITERATURE CITED

- ALDRICH, J. W. 1984. Ecogeographical variation in size and proportions of Song Sparrows (*Melospiza melodia*). *Ornithological Monographs*, no. 35.
- ALDRICH, J. W., AND F. C. JAMES. 1991. Ecogeographic variation in the American Robin (*Turdus migratorius*). *Auk* 108:230–249.
- ALLEN, J. A. 1877. The influence of physical conditions in the genesis of species. *Radical Review* 1:108–140.
- AMADON, D. 1949. The seventy-five per cent rule for subspecies. *Condor* 51:250–258.
- AMERICAN ORNITHOLOGISTS' UNION. 1998. Check-list of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.
- ASHTON, K. G. 2002. Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. *Global Ecology & Biogeography* 11:505–523.
- ASHTON, K. G., M. C. TRACY, AND A. DE QUEIROZ. 2000. Is Bergmann's rule valid for mammals? *American Naturalist* 156:390–415.
- BAKKEN, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist* 32:194–216.
- BALLENTINE, B., AND R. GREENBERG. 2010. Common garden experiment reveals genetic control of phenotypic divergence between Swamp Sparrow subspecies that lack divergence in neutral genotypes. *PLoS ONE* 5(4): e10229.
- BARROWCLOUGH, G. F., AND F. C. SIBLEY. 1980. Feather pigmentation and abrasion: Test of a hypothesis. *Auk* 97:881–883.
- BENNING, T. L., D. LAPOINTE, C. T. ATKINSON, AND P. M. VITOUSEK. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian

- Islands: Modeling the fate of endemic birds using a geographic information system. *Proceedings of the National Academy of Sciences USA* 99:14246–14249.
- BERGER, A. J. 1981. Hawaiian Birdlife, 2nd ed. University of Hawaii Press, Honolulu.
- BERGMANN, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, Göttingen 3:595–708.
- BLACKBURN, T. M., K. J. GASTON, AND N. LODER. 1999. Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distributions* 5:165–174.
- BONSER, R. H. C. 1995. Melanin and the abrasion resistance of feathers. *Condor* 97:590–591.
- BOYCE, M. S. 1979. Seasonality and patterns of natural selection for life histories. *American Naturalist* 114:569–583.
- BROWN, J. H., AND A. K. LEE. 1969. Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). *Evolution* 23:329–338.
- BRYAN, E. H., JR., AND J. C. GREENWAY, JR. 1944. Check-list of the birds of the Hawaiian Islands. *Bulletin of the Museum of Comparative Zoology* 94:92–140.
- BURNEY, D. A., H. F. JAMES, L. P. BURNEY, S. L. OLSON, W. KIKUCHI, W. L. WAGNER, M. BURNEY, D. McCLOSKEY, D. KIKUCHI, F. V. GRADY, AND OTHERS. 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecological Monographs* 71:615–641.
- BURTT, E. H., JR. 1986. An analysis of physical, physiological and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monographs*, no. 38.
- BURTT, E. H., JR. 1999. Rules to bird by: Gloger's and Allen's. *Birding* 31:362–365.
- BURTT, E. H., JR., AND J. M. ICHIDA. 2004. Gloger's rule, feather-degrading bacteria, and color variation among Song Sparrows. *Condor* 106:681–686.
- BUSH, S. E., D. KIM, B. R. MOYER, J. LEVER, AND D. H. CLAYTON. 2006. Is melanin a defense against feather-feeding lice? *Auk* 123:153–161.
- CARSON, H. L., AND D. A. CLAGUE. 1995. Geology and biogeography of the Hawaiian Islands. Pages 14–29 in *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago* (W. L. Wagner and V. A. Funk, Eds.). Smithsonian Institution Press, Washington, D.C.
- CARTAR, R. V., AND R. I. G. MORRISON. 2005. Metabolic correlates of leg length in breeding Arctic shorebirds: The cost of getting high. *Journal of Biogeography* 32:377–382.
- CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. *Bird Song: Biological Themes and Variations*. Cambridge University Press, Cambridge, United Kingdom.
- CHESSER, R. T., R. C. BANKS, F. K. BARKER, C. CICERO, J. L. DUNN, A. W. KRATTER, I. J. LOVETTE, P. C. RASMUSSEN, J. V. REMSEN, JR., J. D. RISING, AND OTHERS. 2010. Fifty-first supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 127:726–744.
- CHRISTENSEN, J. H., B. HEWITSON, A. BUSUIOC, A. CHEN, X. GAO, I. HELD, R. JONES, R. K. KOLLI, W.-T. KWON, R. LAPRISE, AND OTHERS. 2007. Regional Climate Projections. Pages 847–940 in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- CICERO, C. 2010. The significance of subspecies: A case study of Sage Sparrows (Emberizidae, *Amphispiza belli*). Pages 103–113 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). Ornithological Monographs, no. 67.
- CICERO, C., AND N. K. JOHNSON. 2006. Diagnosability of subspecies: Lessons from Sage Sparrows (*Amphispiza belli*) for analysis of geographic variation in birds. *Auk* 123:266–274.
- CLAYTON, D. H. 1999. Feather-busting bacteria. *Auk* 116:302–304.
- CONANT, S., H. D. PRATT, AND R. J. SHALLENBERGER. 1998. Reflections on a 1975 expedition to the lost world of the Alaka'i and other notes on the natural history, systematics, and conservation of Kaua'i birds. *Wilson Bulletin* 110:1–22.
- COWIE, R. H., AND B. S. HOLLAND. 2008. Molecular biogeography and diversification of the endemic terrestrial fauna on the Hawaiian Islands. *Philosophical Transactions of the Royal Society of London, Series B* 363:3363–3376.
- COYNE, J. A., AND H. A. ORR. 2004. *Speciation*. Sinauer Associates, Sunderland, Massachusetts.
- DUNBRACK, R. L., AND M. A. RAMSAY. 1993. The allometry of mammalian adaptations to seasonal environments: A critique of the fasting endurance hypothesis. *Oikos* 66:336–342.
- EDERSTROM, H. E., AND S. J. BRUMLEVE. 1964. Temperature gradients in the legs of cold-acclimatized pheasants. *American Journal of Physiology* 207:457–459.
- EDWARDS, S., AND S. BEN SCH. 2009. Looking forwards or looking backwards in avian phylogeography? A comment on Zink and Barrowclough 2008. *Molecular Ecology* 18:2930–2933.
- FITZPATRICK, J. W. 2010. Subspecies are for convenience. Pages 54–61 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). Ornithological Monographs, no. 67.
- FLEISCHER, R. C., AND R. F. JOHNSTON. 1982. Natural selection on body size and proportions in House Sparrows. *Nature* 298:747–749.
- FLEISCHER, R. C., C. E. MCINTOSH, AND C. L. TARR. 1998. Evolution on a volcanic conveyor belt: Using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology* 7:533–545.

- FRECKLETON, R. P., P. H. HARVEY, AND M. PAGEL. 2003. Bergmann's rule and body size in mammals. *American Naturalist* 161:821–825.
- FUNK, D. J., AND K. E. OMLAND. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 34:397–423.
- GEIST, V. 1987. Bergmann's rule is invalid. *Canadian Journal of Zoology* 65:1035–1038.
- GHALAMBOR, C. K., R. B. HUEY, P. R. MARTIN, J. J. TEWKSBURY, AND G. WANG. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* 46:5–17.
- GIAMBELLUCA, T. W., M. A. NULLET, AND T. A. SCHROEDER. 1986. Hawaii Rainfall Atlas. Report R76, Hawaii Division of Water and Land Development, Department of Land and Natural Resources, Honolulu.
- GILL, F. B. 1973. Intra-island variation in the Mascarene White-eye *Zosterops borbonica*. *Ornithological Monographs*, no. 12.
- GIVNISH, T. J., K. C. MILLAM, A. R. MAST, T. B. PATERSON, T. J. THEIM, A. L. HIPP, J. M. HENSS, J. F. SMITH, K. R. WOOD, AND K. J. SYTSMA. 2008. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society of London, Series B* 276:407–416.
- GLOGER, C. L. 1833. Das Abändern der Vögel durch Einfluss des Klimas. Breslau, Germany.
- GOLDSTEIN, G., K. R. FLORY, B. A. BROWNE, S. MAJID, J. M. ICHIDA, AND E. H. BURTT, JR. 2004. Bacterial degradation of black and white feathers. *Auk* 121:656–659.
- GORRESEN, P. M., R. J. CAMP, M. H. REYNOLDS, B. L. WOODWORTH, AND T. K. PRATT. 2009. Status and trends of native Hawaiian songbirds. Pages 108–136 in *Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna* (T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, and B. L. Woodworth, Eds.). Yale University Press, New Haven, Connecticut.
- GRANDE, J. M., J. J. NEGRO, AND M. J. TORRES. 2004. The evolution of bird plumage colouration: A role for feather-degrading bacteria? *Ardeola* 51:375–383.
- GRAVES, G. R. 1991. Bergmann's rule near the equator: Latitudinal clines in body size of Andean birds. *Proceedings of the National Academy of Sciences USA* 88:2322–2325.
- GRIFFING, J. P. 1974. Body measurements of black-tailed jackrabbits of southeastern New Mexico with implications of Allen's rule. *Journal of Mammalogy* 55:674–678.
- GRIFFITH, S. C., T. H. PARKER, AND V. A. OLSON. 2006. Melanin- versus carotenoid-based sexual signals: Is the difference really so black and red? *Animal Behaviour* 71:749–763.
- GUNDERSON, A. R. 2008. Feather-degrading bacteria: A new frontier in avian and host-parasite research? *Auk* 125:972–979.
- GUNDERSON, A. R., A. M. FRAME, J. P. SWADDLE, AND M. H. FORSYTH. 2008. Resistance of melanized feathers to bacterial degradation: Is it really so black and white? *Journal of Avian Biology* 39:539–545.
- HAGAN, A. A., AND J. E. HEATH. 1980. Regulation of heat loss in the duck by vasomotion in the bill. *Journal of Thermal Biology* 5:95–101.
- HENSHAW, H. W. 1902. The elepaio of Hawaii. *Auk* 19:221–232.
- HOLLAND, B. S., AND M. G. HADFIELD. 2004. Origin and diversification of the endemic Hawaiian tree snails (Achatinellinae: Achatinellidae) based on molecular evidence. *Molecular Phylogenetics and Evolution* 32:588–600.
- JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51:365–390.
- JAMES, F. C. 1991. Complementary descriptive and experimental studies of clinal variation in birds. *American Zoologist* 31:694–706.
- JAMES, F. C. 2010. Avian subspecies: Introduction. Pages 1–5 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). *Ornithological Monographs*, no. 67.
- JANZEN, D. H. 1967. Why mountain passes are higher in the tropics. *American Naturalist* 101:233–249.
- JOHANSEN, K., AND R. W. MILLARD. 1973. Vascular responses to temperature in the foot of the Giant Fulmar, *Macronectes giganteus*. *Journal of Comparative Physiology* 85:47–64.
- JOHNSTON, R. F., AND R. K. SELANDER. 1971. Evolution in the House Sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1–28.
- JUVIK, S. P., AND J. O. JUVIK, Eds. 1998. *Atlas of Hawai'i*, 3rd ed. University of Hawaii Press, Honolulu.
- KLAVITTER, J. L., J. M. MARZLUFF, AND M. S. VEKASY. 2003. Abundance and demography of the Hawaiian Hawk: Is delisting warranted? *Journal of Wildlife Management* 67:165–176.
- KOSE, M., R. MÄND, AND A. P. MØLLER. 1999. Sexual selection for white tail spots in the Barn Swallow in relation to habitat choice by feather lice. *Animal Behaviour* 58:1201–1205.
- LAIOLI, P., AND A. ROLANDO. 2001. Ecogeographic correlates of morphometric variation in the Red-billed Chough *Pyrhocorax pyrrhocorax* and the Alpine Chough *Pyrhocorax graculus*. *Ibis* 143:602–616.
- LEONARD, D. L., JR., P. C. BANKO, K. W. BRINCK, C. FARMER, AND R. J. CAMP. 2008. Recent surveys indicate rapid decline of Palila population. *'Elepaio* 68:27–30.
- LINDSAY, S. L. 1987. Geographic size and non-size variation in Rocky Mountain *Tamiasciurus hudsonicus*: Significance in relation to Allen's rule and vicariant biogeography. *Journal of Mammalogy* 68:39–48.
- LINDSEY, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. *Evolution* 20:456–465.
- LINDSTET, S. L., AND M. S. BOYCE. 1985. Seasonality, fasting endurance, and body size in mammals. *American Naturalist* 125:873–878.

- MACMILLEN, R. E., AND F. L. CARPENTER. 1980. Evening roosting flights of the honeycreepers *Himatione sanguinea* and *Vestiaria coccinea* on Hawaii. *Auk* 97:28–37.
- MARTIN, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London, Series B* 269:309–316.
- MAYR, E. 1956. Geographical character gradients and climatic adaptation. *Evolution* 10:105–108.
- MAYR, E. 1982. Of what use are subspecies? *Auk* 99: 593–595.
- MCCAIN, C. M. 2009. Vertebrate range sizes indicate that mountains may be ‘higher’ in the tropics. *Ecology Letters* 12:550–560.
- McGRAW, K. J. 2006. Mechanics of melanin-based coloration. Pages 243–294 in *Bird Coloration*, vol. 1: Mechanisms and Measurements (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.
- MCKAY, B. D. 2008. Phenotypic variation is clinal in the Yellow-throated Warbler. *Condor* 110:569–574.
- MCNAB, B. K. 1971. On the ecological significance of Bergmann’s rule. *Ecology* 52:845–854.
- MCNAB, B. K. 1979. The influence of body size on the energetics and distribution of fossorial burrowing mammals. *Ecology* 60:1010–1021.
- MEIRI, S., AND T. DAYAN. 2003. On the validity of Bergmann’s rule. *Journal of Biogeography* 30:331–351.
- MIDTGARD, U. 1984. Blood vessels and the occurrence of arteriovenous anastomoses in cephalic heat loss areas of Mallards, *Anas platyrhynchos* (Aves). *Zoology* 104:323–335.
- MILLAR, J. S., AND G. J. HICKLING. 1990. Fasting endurance and the evolution of mammalian body size. *Functional Ecology* 4:5–12.
- MILLIEN, V., S. K. LYONS, L. OLSON, F. A. SMITH, A. B. WILSON, AND Y. YOM-TOV. 2006. Ecotypic variation in the context of global climate change: Revisiting the rules. *Ecology Letters* 9:853–869.
- MUMME, R. L., M. L. GALATOWITSCH, P. G. JABLONSKI, T. M. STAWARCZYK, AND J. P. CYGAN. 2006. Evolutionary significance of geographic variation in a plumage-based foraging adaptation: An experimental test in the Slate-throated Redstart (*Myioborus miniatus*). *Evolution* 60:1086–1097.
- MUNSELL COLOR. 1994. Munsell Soil Color Charts. Macbeth Division of Kollmorgen Instruments Corporation, New Windsor, New York.
- MURPHY, E. C. 1985. Bergmann’s rule, seasonality, and geographic variation in body size of House Sparrows. *Evolution* 39:1327–1334.
- NOSIL, P., L. J. HARMON, AND O. SEEHAUSEN. 2009. Ecological explanations for (incomplete) speciation. *Trends in Ecology & Evolution* 24:145–156.
- NUDDS, R. L., AND S. A. OSWALD. 2007. An interspecific test of Allen’s rule: Evolutionary implications for endothermic species. *Evolution* 61:2839–2848.
- OLALLA-TÁRRAGA, M. Á., M. Á. RODRÍGUEZ, AND B. A. HAWKINS. 2006. Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography* 33:781–793.
- OLSON, S. L. 1989. Two overlooked holotypes of the Hawaiian Flycatcher *Chasiempis* described by Leonhard Stejneger (Aves: Myiagrinae). *Proceedings of the Biological Society of Washington* 102:555–558.
- OLSON, S. L., AND H. F. JAMES. 1982. Prodromus of the fossil avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology*, no. 365.
- OLSON, S. L., AND H. F. JAMES. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part I. Non-passeriformes. *Ornithological Monographs*, no. 45.
- OLSON, V. A., R. G. DAVIES, C. D. L. ORME, G. H. THOMAS, S. MEIRI, T. M. BLACKBURN, K. J. GASTON, I. P. F. OWENS, AND P. M. BENNETT. 2009. Global biogeography and ecology of body size in birds. *Ecology Letters* 12:249–259.
- PATTEN, M. A. 2010. Null expectations in subspecies diagnosis. Pages 35–41 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). *Ornithological Monographs*, no. 67.
- PATTEN, M. A., AND C. L. PRUETT. 2009. The Song Sparrow, *Melospiza melodia*, as a ring species: Patterns of geographic variation, a revision of subspecies, and implications for speciation. *Systematics and Biodiversity* 7:33–62.
- PATTEN, M. A., AND P. UNITT. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk* 119:26–35.
- PERCY, D. M., A. M. GARVER, W. L. WAGNER, H. F. JAMES, C. W. CUNNINGHAM, S. E. MILLER, AND R. C. FLEISCHER. 2008. Progressive island colonization and ancient origin of Hawaiian *Metrosideros* (Myrtaceae). *Proceedings of the Royal Society of London, Series B* 275:1479–1490.
- PHAN, M. L., P. L. PYTTE, AND D. S. VICARIO. 2006. Early auditory experience generates long-lasting memories that may subserve vocal learning in songbirds. *Proceedings of the National Academy of Sciences USA* 103:1088–1093.
- PHILLIMORE, A. B., AND I. P. F. OWENS. 2006. Are subspecies useful in evolutionary and conservation biology? *Proceedings of the Royal Society of London, Series B* 273:1049–1053.
- PHILLIPS, P. K., AND J. E. HEATH. 1995. Dependency of surface temperature regulation on body size in terrestrial mammals. *Journal of Thermal Biology* 20:281–289.
- PHILLIPS, P. K., AND A. F. SANBORN. 1994. An infrared, thermographic study of surface-temperature in three ratites: Ostrich, Emu and Double-wattled Cassowary. *Journal of Thermal Biology* 19:423–430.
- PRATT, H. D. 1979. A new subspecies of the elepaio *Chasiempis sandwichensis*, from the island of Hawaii. *Bulletin of the British Ornithologists’ Club* 99:105–108.

- PRATT, H. D. 1980. Intra-island variation in the 'elepaio on the island of Hawai'i. *Condor* 82:449–458.
- PRATT, H. D. 2005. The Hawaiian Honeycreepers: Drepanidinae. Oxford University Press, Oxford, United Kingdom.
- PRATT, H. D., AND T. K. PRATT. 2001. The interplay of species concepts, taxonomy, and conservation: Lessons from the Hawaiian avifauna. Pages 68–80 in *Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna* (J. M. Scott, S. Conant, and C. Van Riper III, Eds.). Studies in Avian Biology, no. 22.
- PRUETT, C. L., AND K. WINKER. 2010. Alaska Song Sparrows (*Melospiza melodia*) demonstrate that genetic marker and method of analysis matter in subspecies assessments. Pages 162–171 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). Ornithological Monographs, no. 67.
- PYLE, R. L. 2002. Checklist of the birds of Hawaii—2002. 'Elepaio 62:137–148.
- RALPH, C. J., AND S. G. FANCY. 1995. Demography and movements of Apapane and Iiwi in Hawaii. *Condor* 97:729–742.
- REMSEN, J. V., JR. 2010. Subspecies as a meaningful taxonomic rank in avian classification. Pages 62–78 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). Ornithological Monographs, no. 67.
- RISING, J. D. 2001. Geographic variation in size and shape of Savannah Sparrows (*Passerculus sandwichensis*). *Studies in Avian Biology*, no. 23.
- RISING, J. D. 2007. Named subspecies and their significance in contemporary ornithology. Pages 45–54 in *Festschrift for Ned K. Johnson: Geographic Variation and Evolution in Birds* (C. Cicero and J. V. Remsen, Jr., Eds.). Ornithological Monographs, no. 63.
- RISING, J. D., D. A. JACKSON, AND H. B. FOKIDIS. 2009. Geographic variation in plumage pattern and coloration of Savannah Sparrows. *Wilson Journal of Ornithology* 121:253–264.
- SCHOLANDER, P. F. 1955. Evolution of climatic adaptation in homeotherms. *Evolution* 9:15–26.
- SCOTT, J. M., S. MOUNTAINSPRING, F. L. RAMSEY, AND C. B. KEPLER. 1986. Forest bird communities of the Hawaiian Islands: Their dynamics, ecology, and conservation. *Studies in Avian Biology*, no. 9.
- SERRAT, M. A., D. KING, AND C. O. LOVEJOY. 2008. Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proceedings of the National Academy of Sciences USA* 105:19348–19353.
- SHAWKEY, M. D., K. L. MILLS, C. DALE, AND G. E. HILL. 2005. Microbial diversity of wild bird feathers revealed through culture-based and culture-independent techniques. *Microbial Ecology* 50:40–47.
- SHAWKEY, M. D., S. R. PILLAI, G. E. HILL, L. M. STEFFERMAN, AND S. R. ROBERTS. 2007. Bacteria as an agent for change in structural plumage color: Correlational and experimental evidence. *American Naturalist* 169:S112–S121.
- SMITHE, F. B. 1974. *Naturalist's Color Guide Supplement*. American Museum of Natural History, New York.
- SMITHE, F. B. 1975. *Naturalist's Color Guide*. American Museum of Natural History, New York.
- SNETSINGER, T. J., S. G. FANCY, J. C. SIMON, AND J. D. JACOBI. 1994. Diets of owls and feral cats in Hawai'i. 'Elepaio 54:47–50.
- SNOW, D. W. 1954. Trends in geographical variation in palaeartic members of the genus *Parus*. *Evolution* 8:19–28.
- STEEN, I., AND J. B. STEEN. 1965. The importance of the legs in the thermoregulation of birds. *Acta Physiologica Scandinavica* 63:285–291.
- STEJNEGER, L. 1887. Birds of Kauai Island, Hawaiian Archipelago, collected by Mr. Valdemar Knudsen, with descriptions of new species. *Proceedings of the United States National Museum* 10:75–102.
- SYMONDS, M. R. E., AND G. J. TATTERSALL. 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. *American Naturalist* 176:188–197.
- TATTERSALL, G. J., D. V. ANDRADE, AND A. S. ABE. 2009. Heat exchange from the toucan bill reveals a controllable vascular thermal radiator. *Science* 325:468–470.
- U.S. ENVIRONMENTAL PROTECTION AGENCY. 1998. Climate change and Hawaii. EPA 236-F-98-007e.
- U.S. FISH AND WILDLIFE SERVICE. 2006. Final revised recovery plan for Hawaiian forest birds. U.S. Fish and Wildlife Service, Portland, Oregon.
- VANDERWERF, E. A. 1993. Scales of habitat selection by foraging 'elepaio in undisturbed and human-altered Hawaiian forests. *Condor* 95:961–971.
- VANDERWERF, E. A. 1994. Intraspecific variation in elepaio foraging behavior in Hawaiian forests of different structure. *Auk* 111:917–932.
- VANDERWERF, E. A. 1998. Elepaio (*Chasiempis sandwichensis*). In *The Birds of North America*, no. 344 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia, and American Ornithologists' Union, D.C.
- VANDERWERF, E. A. 2001. Two-year delay in plumage maturation of male and female 'elepaio. *Condor* 103:756–766.
- VANDERWERF, E. A. 2004. Demography of Hawai'i 'Elepaio: Variation with habitat disturbance and population density. *Ecology* 85:770–783.
- VANDERWERF, E. A. 2007. Biogeography of 'elepaio: Evidence from inter-island song playbacks. *Wilson Journal of Ornithology* 119:325–333.
- VANDERWERF, E. A. 2008. Sources of variation in survival, recruitment, and natal dispersal of the Hawai'i 'Elepaio. *Condor* 110:241–250.
- VANDERWERF, E. A. 2009. Importance of nest predation by alien rodents and avian poxvirus in conservation of Oahu Elepaio. *Journal of Wildlife Management* 73:737–746.

- VANDERWERF, E. A., M. D. BURT, J. L. ROHRER, AND S. M. MOSHER. 2006. Distribution and prevalence of mosquito-borne diseases in O'ahu 'Elepaio. *Condor* 108:770–777.
- VANDERWERF, E. A., AND L. A. FREED. 2003. 'Elepaio subadult plumages reduce aggression through graded status signaling, not mimicry. *Journal of Field Ornithology* 74:406–415.
- VANDERWERF, E. A., S. M. MOSHER, M. D. BURT, AND P. E. TAYLOR. 2011. Current distribution and abundance of O'ahu 'Elepaio (*Chasiempis ibidis*) in the Waianae Mountains. *Pacific Science* 65:311–319.
- VANDERWERF, E. A., J. L. ROHRER, D. G. SMITH, AND M. D. BURT. 2001. Current distribution and abundance of the O'ahu 'Elepaio. *Wilson Bulletin* 113:10–16.
- VANDERWERF, E. A., AND D. G. SMITH. 2002. Effects of alien rodent control on demography of the O'ahu 'Elepaio, an endangered Hawaiian forest bird. *Pacific Conservation Biology* 8:73–81.
- VANDERWERF, E. A., L. C. YOUNG, N. W. YEUNG, AND D. B. CARLON. 2009. Stepping stone speciation in Hawaii's flycatchers: Molecular divergence supports new island endemics within the elepaio. *Conservation Genetics* 11:1283–1298.
- WALKER, G. P. L. 1990. Geology and volcanology of the Hawaiian Islands. *Pacific Science* 44:315–347.
- WALSBURG, G. E. 1982. Coat color, solar heat gain, and conspicuousness in the Phainopepla. *Auk* 99:495–502.
- WALSBURG, G. E., G. S. CAMPBELL, AND J. R. KING. 1978. Animal coat color and radiative heat gain: A re-evaluation. *Journal of Comparative Physiology B* 126:211–222.
- WARD, J. M., J. D. BLOUNT, G. D. RUXTON, AND D. C. HOUSTON. 2002. The adaptive significance of dark plumage for birds in desert environments. *Ardea* 90:311–323.
- WHITAKER, J. M., D. A. CRISTOL, AND M. H. FORSYTH. 2005. Prevalence and genetic diversity of *Bacillus licheniformis* in avian plumage. *Journal of Field Ornithology* 76:264–270.
- WINKER, K. 2010. Subspecies represent geographically partitioned variation, a gold mine of evolutionary biology, and a challenge for conservation. Pages 6–23 in *Avian Subspecies* (K. Winker and S. M. Haig, Eds.). *Ornithological Monographs*, no. 67.
- ZINK, R. M., AND J. V. REMSEN, JR. 1986. Evolutionary processes and patterns of geographic variation in birds. Pages 1–69 in *Current Ornithology*, vol. 4 (R. F. Johnston, Ed.). Plenum Press, New York.

APPENDIX. Elevation and rainfall at locations from which elepaio were examined. Abbreviations: FR = forest reserve, GMA = game management area, NAR = natural area reserve, NP = national park, NWR = national wildlife refuge, and SP = state park. Location names for museum specimens in quotes are as written on specimen label; the exact location was unknown in some cases. Location names in parentheses correspond to Figure 1.

Island	Subspecies	Location	Data source	Elevation (m)	Annual rainfall (mm)
Hawaii	<i>Chasiempis sandwichensis</i>	Kaloko Mauka	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. sandwichensis</i>	"Kawaloa, Kona" (Kona)	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. sandwichensis</i>	"Keauhou, Kona" (Kona)	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. sandwichensis</i>	"Kona", "North Kona" (Kona)	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. sandwichensis</i>	Kona Forest NWR	Live birds	1,616	1,000
Hawaii	<i>C. s. sandwichensis</i>	Kona Hema Preserve middle	Live birds	1,305	1,470
Hawaii	<i>C. s. sandwichensis</i>	Kona Hema Preserve Papa section	Live birds	1,152	1,720
Hawaii	<i>C. s. sandwichensis</i>	Kona Hema Preserve upper	Live birds	1,530	1,380
Hawaii	<i>C. s. sandwichensis</i>	Manuka Bay Road	Live birds	366	1,160
Hawaii	<i>C. s. sandwichensis</i>	Manuka NAR	Live birds	732	1,550
Hawaii	<i>C. s. sandwichensis</i>	Manuka Road to the Sea	Live birds	512	1,110
Hawaii	<i>C. s. sandwichensis</i>	Ocean View Estates	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. sandwichensis</i>	Pohakuloa Training Area (PTA)	Live birds	1,768	540
Hawaii	<i>C. s. sandwichensis</i>	"Pulahua", "Pulehua" (Puu Lehua)	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. sandwichensis</i>	Puu Waa Waa Wildlife Sanctuary middle	Live birds	1,472	1,050
Hawaii	<i>C. s. sandwichensis</i>	Puu Waa Waa Wildlife Sanctuary upper	Live birds	1,555	1,100
Hawaii	<i>C. s. ridgwayi</i>	Bryson's, Puna	Live birds	274	3,000
Hawaii	<i>C. s. ridgwayi</i>	Hakalau Forest NWR Maulua	Live birds	1,585	2,900
Hawaii	<i>C. s. ridgwayi</i>	Hakalau Forest NWR lower Pua Akala	Live birds	1,585	3,400
Hawaii	<i>C. s. ridgwayi</i>	Hakalau Forest NWR middle Pua Akala	Live birds	1,829	2,600
Hawaii	<i>C. s. ridgwayi</i>	Hakalau Forest NWR upper Pua Akala	Live birds	1,918	2,470
Hawaii	<i>C. s. ridgwayi</i>	Hakalau Forest NWR World Union	Live birds	1,220	4,400
Hawaii	<i>C. s. ridgwayi</i>	Hawaii Volcanoes NP Escape Road	Live birds	1,134	2,870
Hawaii	<i>C. s. ridgwayi</i>	Hawaii Volcanoes NP Kipuka Puaulu	Live birds	1,235	1,720
Hawaii	<i>C. s. ridgwayi</i>	Hawaii Volcanoes NP Mauna Loa Strip mile 1	Live birds	1,352	1,520
Hawaii	<i>C. s. ridgwayi</i>	Hawaii Volcanoes NP Mauna Loa Strip mile 5	Live birds	1,555	1,450
Hawaii	<i>C. s. ridgwayi</i>	Hawaii Volcanoes NP Mauna Loa Strip mile 8	Live birds	1,896	1,360
Hawaii	<i>C. s. ridgwayi</i>	Kahaualea NAR	Live birds	695	3,650
Hawaii	<i>C. s. ridgwayi</i>	Kaiwiki	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. ridgwayi</i>	Kalopa SP	Live birds	707	2,100
Hawaii	<i>C. s. ridgwayi</i>	Kaumana	Museum specimens	610	5,500
Hawaii	<i>C. s. ridgwayi</i>	Keanekolu Road	Live birds	1,951	1,825
Hawaii	<i>C. s. ridgwayi</i>	Kilauea	Museum specimens	Unknown	Unknown

(continued)

## APPENDIX. Continued.

Island	Subspecies	Location	Data source	Elevation (m)	Annual rainfall (mm)
Hawaii	<i>C. s. ridgwayi</i>	Kukuihaele, Hamakua	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. ridgwayi</i>	Olaa	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. ridgwayi</i>	Pihonua, Hilo FR	Live birds	585	6,100
Hawaii	<i>C. s. ridgwayi</i>	Puu Makaala NAR	Live birds	1,100	4,100
Hawaii	<i>C. s. ridgwayi</i>	Puu Oumi NAR	Live birds	1,492	2,500
Hawaii	<i>C. s. ridgwayi</i>	Saddle Road kipukas	Museum specimens	1,530	3,390
Hawaii	<i>C. s. ridgwayi</i>	Tree Planting Road, Upper Waiakea FR	Live birds	966	4,370
Hawaii	<i>C. s. ridgwayi</i>	Volcano	Museum specimens	Unknown	Unknown
Hawaii	<i>C. s. ridgwayi</i>	Volcano House	Museum specimens	1,200	2,320
Hawaii	<i>C. s. bryani</i>	Kaohe GMA lower (Puu Laau)	Live birds	1,890	540
Hawaii	<i>C. s. bryani</i>	Kaohe GMA middle (Puu Laau)	Live birds	2,018	520
Hawaii	<i>C. s. bryani</i>	Puu Laau	Museum specimens	2,133	510
Hawaii	<i>C. s. bryani</i>	Mauna Kea FR lower (Puu Laau)	Live birds	2,256	490
Hawaii	<i>C. s. bryani</i>	Mauna Kea FR middle (Puu Laau)	Live birds	2,335	490
Hawaii	Intergrade	Kalopa SP	Live birds	707	2,100
Hawaii	Intergrade	Kapapala	Museum specimens	Unknown	Unknown
Hawaii	Intergrade	Kapapala FR	Live birds	1,555	1,600
Hawaii	Intergrade	Kau, Dalmayo	Museum specimens	Unknown	Unknown
Hawaii	Intergrade	Kau FR Alii Spring (Kau)	Live birds	914	3,200
Hawaii	Intergrade	Kau FR Wood Valley (Kau)	Live birds	963	2,640
Hawaii	Intergrade	"Kuaia" (Koaia)	Museum specimens	Unknown	Unknown
Hawaii	Intergrade	Mana	Museum specimens	Unknown	Unknown
Hawaii	Intergrade	Pahala	Museum specimens	Unknown	Unknown
Hawaii	Intergrade	Puu Oo Trail, Upper Waiakea FR	Both	1,768	2,200
Hawaii	Intergrade	Waimea	Museum specimens	Unknown	Unknown
Oahu	<i>C. s. ibidis</i>	Aiea Ridge	Live birds	396	2,690
Oahu	<i>C. s. ibidis</i>	Ewa FR Waimano	Live birds	213	3,100
Oahu	<i>C. s. ibidis</i>	Hauula FR	Live birds	183	2,570
Oahu	<i>C. s. ibidis</i>	Honolulu Watershed FR Hawaii Loa Ridge	Live birds	335	1,950
Oahu	<i>C. s. ibidis</i>	Honolulu Watershed FR Kulioouou	Live birds	183	1,300
Oahu	<i>C. s. ibidis</i>	Honolulu Watershed FR Pia Valley	Live birds	152	1,770
Oahu	<i>C. s. ibidis</i>	Honolulu Watershed FR Wailupe Valley	Live birds	183	1,830
Oahu	<i>C. s. ibidis</i>	Honolulu Watershed FR Wiliwilinui Ridge	Live birds	427	1,590
Oahu	<i>C. s. ibidis</i>	Honolulu Watershed FR Woodlawn Trail	Live birds	244	3,600

(continued)

## APPENDIX. Continued.

Island	Subspecies	Location	Data source	Elevation (m)	Annual rainfall (mm)
Oahu	<i>C. s. ibidis</i>	Honouliuli Preserve	Live birds	610	1,230
Oahu	<i>C. s. ibidis</i>	Lualualei Naval Magazine	Live birds	427	1,080
Oahu	<i>C. s. ibidis</i>	Makaha Valley	Live birds	579	1,680
Oahu	<i>C. s. ibidis</i>	Makua Valley Military Reservation	Live birds	557	1,420
Oahu	<i>C. s. ibidis</i>	Moanalua Valley	Live birds	244	3,300
Oahu	<i>C. s. ibidis</i>	North Halawa Valley	Live birds	427	3,140
Oahu	<i>C. s. ibidis</i>	Pahole NAR	Live birds	610	1,540
Oahu	<i>C. s. ibidis</i>	Palehua	Live birds	564	980
Oahu	<i>C. s. ibidis</i>	Schofield Barracks South Range	Live birds	579	1,350
Oahu	<i>C. s. ibidis</i>	Schofield Barracks West Range	Live birds	640	1,755
Oahu	<i>C. s. ibidis</i>	South Halawa Valley	Live birds	366	3,400
Oahu	<i>C. s. ibidis</i>	Waiahole FR	Live birds	213	3,550
Oahu	<i>C. s. ibidis</i>	Waianae Kai FR	Live birds	640	1,760
Oahu	<i>C. s. ibidis</i>	Waikane Valley	Live birds	335	3,750