
Douglas Pratt
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RELATIONSHIPS AND SPECIATION OF THE HAWAIIAN THRUSHES

H. Douglas Pratt

The Hawaiian Islands, separated from the nearest land masses by more than 4,000 km (2,500 mi) of open ocean, are among the most isolated islands in the world and are of relatively recent volcanic origin (Pliocene age for all main islands except Hawaii, which is Pleistocene). Their modern native land birds are believed to have evolved from only a few original colonizing species: one or two rails, a goose, a hawk, an owl, a crow, two honeyeaters, a small flycatcher, a warbler, a siskin-like finch, and a thrush (Mayr 1943). These colonizers are thought to have spread through the archipelago and adapted differentially to the environment of each island. When a new species formed, it could then reinvade a parent island. By such speciation and recolonization, a bird community of remarkable diversity evolved. Indeed, the Hawaiian honeycreepers (Drepanidinae), an endemic subfamily (Pratt 1979) related to cardueline finches (Raikow 1976), are among the most impressive avian examples of adaptive radiation. Much less spectacular than the oft-cited honeycreepers are the rather plain brown and gray native thrushes. Traditionally classified as an endemic genus, *Phaeornis,* the Hawaiian thrushes have not differentiated nearly as much as have the honeycreepers. They therefore provide an excellent opportunity to study adaptive radiation in its earliest stages.

MATERIALS AND METHODS

This study was part of a broad investigation of Hawaiian birds (Pratt 1979) that involved both specimen analysis and field observation. I originally gathered data on the thrushes to determine how many species should be recognized, and later extended the study to include the mainland (continental) ancestry of the group. The following discussions combine my own observations with the sparse literature on the appearance and natural history of the thrushes. The reader should understand that published data are limited but may represent all that will ever be known about some of these birds—most of them are rare or extinct (Berger 1981). My discussions of the Hawaiian birds' relationships to mainland thrushes are based on the literature and on my studies of museum skins and taped vocalizations.

I examined specimens at the Bernice P. Bishop Museum (BBM), American Museum of Natural History (AMNH), Louisiana State University Museum of Zoology (LSUMZ), and the Library of Natural Sounds (LNS), Cornell University. I conducted field work in Hawaii intermittently from 1974 to 1979. Most of my observations took place on the island of Hawaii, but from 28 June to 8 July 1975 I investigated the two thrush species in the Alakai Swamp on Kauai. I also participated in a successful search for the thrush of Molokai, 20–25 July 1975 (Scott et al. 1977), but did not personally see the bird. In the early part of the study I concentrated on collecting sound recordings of songs and call notes later used in playback experiments. I studied my own recordings, those made by Gauthey et al. (1968) on Kauai, and archived LNS sound specimens. All of these recordings are now in the LNS collection.

The Kamao (*Myadestes myadestinus*) of Kauai in lapalapa (*Cheirodendron kauaiense*), a favorite food source. Painting by H. Douglas Pratt.

THE HAWAIIAN THRUSHES: AN OVERVIEW

Six forms of *Phaeornis* from five different islands have been described, originally as separate species—*obscura* (Gmelin) 1789 of Hawaii; *lanaiensis* Wilson 1891 of Lanai; *rutha* Bryan 1908 of Molokai; *oahensis* Wilson and Evans 1899 of Oahu; and *myadestina* Stejneger 1887 and *palmeri* Rothschild 1893, both of Kauai. Figure 1 shows the distribution of these forms with their Hawaiian vernacular names. Since the Hawaiian names are taxonomically noncommittal, I shall make frequent use of them in the following discussions:

The Amaui (on Oahu) became extinct shortly after its discovery in 1826, and no specimens of it are known; the name *oahensis* was based on written descriptions only (Wilson and Evans 1890–99). The Hawaiians did not differentiate between the thrushes of Molokai and Lanai and used the name Olomao for both. Although never seen by ornithologists, a thrush probably also existed on Maui (Munro 1960). Kauai is the only island known to have more than one thrush species. For many years the smaller Puaiohi, *P. palmeri*, has been considered a monotypic species while the larger Kamao, *myadestina*, has been "lumped" with all the other forms under the name Hawaiian Thrush, *P. obscura*. Thus only two species are currently recognized in the genus, with the larger one having a different subspecies on each of the islands it inhabits.

Hawaiian thrushes are solitary, highly sedentary birds that live primarily in dense montane forests. On Kauai, both species are now confined to the Alakai Swamp, a boggy cloud-forested plateau in the central highlands. The Puaiohi has always been considered rare (Perkins 1903), but the Kamao was common until relatively recent times (Munro 1960). The Olomao was common in the small rainforest tract on Lanai until the 1920's, but then declined rapidly and is now believed to be extinct (Munro 1960). It barely holds on in a remnant of the original rainforest of eastern Molokai (Scott et al. 1977). In contrast, the Omao of Hawaii maintains a fairly high population and could even be considered locally abundant, especially in the rainforests of the windward Hamakua Coast and areas north and east of Hawaii Volcanoes National Park. It has, however, disappeared from some places where it formerly lived, such as the upper rainforests of the leeward Kona Coast (van Riper and Scott 1979). The Omao also occupies a wider range of habitats than do the other Hawaiian thrushes. I have found Omao often in scrubby ohia-lehua (*Metrosideros collina*) trees growing on relatively recent lava flows in the central "saddle" of the island. An isolated population of Omao lives also above tree line on Mauna Loa among low shrubs; the birds perch on rocks rather than trees (Dunmire 1961).

All Hawaiian thrushes eat small fruits, such as those of olapa (*Cheirodendron* spp.), but the birds also take insects, often by flycatching (hawking). The Puaiohi is primarily insectivorous (Perkins 1903). All the larger forms forage primarily in the forest canopy and only rarely go to the ground. The Puaiohi has most often been seen in the understory near, but not on, the ground. The many published illustrations that show Hawaiian thrushes on the ground are misleading and may partly account for the reluctance of some ornithologists to accept the idea that these island birds are closely related to the highly arboreal New World solitaires of the genus *Myadestes*.

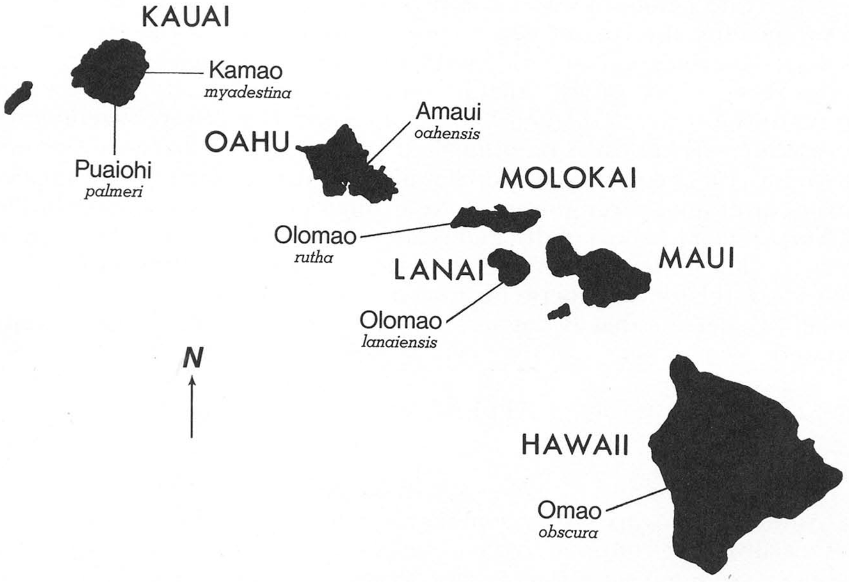

Figure 1. The Hawaiian Islands showing the distributions and native names of the six known forms of Hawaiian thrushes. Pronunciation of native names is as follows: consonants as in English; *a* as in father, *i* as in machine, *o* as in home, *u* as in lute, *ai* as eye, *ao* as *ow* in fowl, *au* as in Faust.

RELATIONSHIPS

The striking similarity of the Hawaiian thrushes to American solitaires were first noted by Stejneger (1887) in his description of *Phaeornis myadestina*. Later, Stejneger analyzed the relationships of *Phaeornis* and *Myadestes* in more detail. In comparing the Kamao with Townsend's Solitaire (*M. townsendi*), Stejneger (1889: 383) stated that "were it not for the different proportions of wing, tail, and legs, the two birds could hardly be separated generically." Other authors (Amadon 1942, Ripley 1952, Ames 1975) supported a close relationship of *Phaeornis* to *Myadestes,* but E. H. Bryan (1940) inexplicably associated *Phaeornis* with several Old World genera far removed from the American solitaires. Ripley (1962) later changed his opinion after hearing and seeing *Phaeornis* (probably only *obscura*) in the field. He thought that vocal behavior of the Hawaiian birds showed a close relationship with the nightingale-thrushes of the genus *Catharus.* Ripley (1964) placed *Phaeornis* next to *Catharus* in "Peters' Check-list."

The genus *Myadestes* comprises seven or nine species (depending on whose taxonomy one follows). All except Townsend's Solitaire are sedentary tropical birds. The genus is distributed from central Alaska south through Mexico, Central America, the West Indies, and the Andes of South America. Solitaires are usually considered to be aberrant thrushes, although Sibley's (1973) study of egg white proteins and Ames's (1975) work on syringeal morphology suggested that solitaires might be related to some other passerine group. More recently, Sibley and Ahlquist (in press) have evidence from DNA hybridization studies that shows solitaires to be thrushes after all.

The genus *Catharus* comprises 11 species that can be divided into two groups, the first of which contains four species—the Hermit (*C. guttatus*), Swainson's (*C. ustulatus*), and Gray-cheeked (*C. minimus*) thrushes, and the Veery (*C. fuscescens*)—that breed in temperate North America and migrate to the tropics (Dilger 1956). The second is a group of sedentary neotropical birds known as nightingale-thrushes, and it is to this subgroup that Ripley (1962) considered the Hawaiian thrushes related. Nightingale-thrushes are found throughout the Neotropics except for the West Indies and Amazonia. Members of this genus are typical thrushes in every respect.

The following comparisons are made to test Ripley's hypothesized close relationship between *Catharus* and *Phaeornis*, in contrast to Stejneger's assertion that *Phaeornis* and *Myadestes* can hardly be generically separated.

APPEARANCE

Coloration

Phaeornis and *Myadestes* are strikingly similar in plumage coloration. Adult solitaires are clad in somber tones of gray and brown, the brown tones usually being confined to the upper surface. A few species have white eye-rings and some have dark malar streaks. All but the Rufous-brown Solitaire (*M. leucogenys*) have the outer tail feathers tipped with white. In some species the white extends up the outer webs of the outer rectrices, giving the folded tail a white border, whereas in others the outer webs are paler than the inner ones, but are not white. The primaries are marked by a pale band at their base, and their outer webs form a pale rectangular patch on the folded wing. Only the Rufous-throated Solitaire (*M. genibarbis*) of the West Indies exhibits any striking patterns or color contrasts.

Immature *Myadestes,* very different from the adults, are dark and heavily "spotted" above and below in a manner unusual among thrushes. The feathers of the breast are pale in the center but have a dark border, and thus might better be called "scalloped" rather than spotted. Among New World thrushes, only the solitaires and bluebirds (*Sialia*) have such scalloping. Dorsal feathers of immature solitaires are brown or gray basally, with a darker border and a subterminal buffy spot. Species of solitaires differ subtly in hue, but vary only slightly from the pattern described.

A general description of the coloration of Hawaiian thrushes would repeat the foregoing almost verbatim, except that they are even more alike than are the solitaires. Color contrasts are less striking in the Hawaiian birds, but all have more-or-less white tips and pale outer webs to the tail feathers, and all have a pale wing patch exactly like that of solitaires. Adults never have spotted undersides, and the immature thrushes are dark brown and scalloped in precisely the same manner as are young solitaires. So similar are the Hawaiian thrushes to the solitaires that both adult and immature specimens of the thrushes can be easily "lost" in a tray of solitaire study skins (Figure 2). If the Hawaiian thrushes were placed in the genus *Myadestes,* their somewhat duller and less-contrasting plumage could be an illustration of trends noted elsewhere in island representatives of mainland genera (Grant 1965b), although the Rufous-throated, the most brightly plumaged solitaire, is a island dweller.

The plumage of the *Catharus* thrushes is also generally dull. Nightingale-thrushes often have red or orange bills, legs, and eyelids. Brightly colored bills also occur in some solitaires—the Andean (*Myadestes ralloides*), Black-faced (*M. melanops*), and Varied (*M. coloratus*)—but no solitaire has a brightly colored, fleshy eye-ring. Since bright eye-rings are generally common among thrushes, the lack of eye-rings in solitaires and Hawaiian thrushes may be noteworthy. All temperate region *Catharus* and some nightingale-thrushes have ventral spots in the adult plumage, and immature birds are heavily spotted (not scalloped) above and below. No *Catharus* shows any white in the tail or a pale patch at the base of the primaries on the closed wing.

Postures

Hawaiian thrushes characteristically perch upright, with the tail pointing downward and the wings often slightly drooped (Figure 3). I have never seen Hawaiian thrushes perch on the ground, although they apparently do so occasionally (Perkins 1903, Dunmire 1961). Solitaires also have an upright posture, unusual for thrushes. Their somewhat flycatcher-like stance is shown in well-executed illustrations such as those in Peterson and Chalif (1973), Bond (1974), and Ridgely (1976). *Catharus* thrushes perch in the somewhat horizontal posture characteristic of many thrushes. They often perch on the ground, and hop in the familiar manner of the American Robin (*Turdus migratorius*) (Bent 1949, Slud 1964).

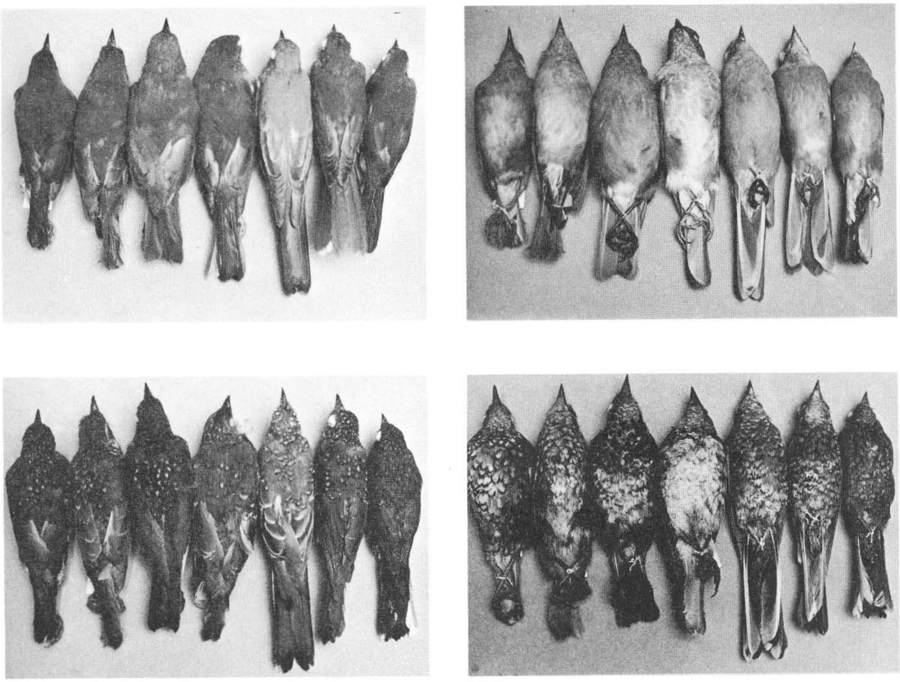

Figure 2. Study skins of Hawaiian thrushes and selected solitaires. Upper row, adults; lower row, immatures. Left, dorsal aspect; right, ventral aspect. Species, left to right in each photograph: *Myadestes* (*"Phaeornis"*) *palmeri, M. lanaiensis, M. obscurus, M. myadestinus* (all Hawaiian); *M. townsendi, M. occidentalis* (formerly *obscurus*), *M. ralloides* (all mainland species).

Figure 3. Characteristic postures of the Omao (*Myadestes obscurus*). Photographed at Keauhou Ranch, Island of Hawaii, by the author.

MORPHOLOGY

Bill

Solitaires clearly differ from typical thrushes in the shape of the bill, which is short and broad and resembles those of silky flycatchers (Sibley 1973). This bill shape apparently is an adaptation for combined flycatching and fruit-eating. Bills of Hawaiian thrushes are more variable among themselves than are those of solitaires. The extremes are represented by the two Kauai species. The bill of the larger Kamao (Figure 4, A) is, as Stejneger (1889: 384) states, "identical [to], though somewhat stouter and stronger" than those of solitaires (Figure 4, E-G). The bill of the Puaiohi (Figure 4, D) is the narrowest of all, and resembles the bills of typical thrushes. The morphological divergence of the two Kauai forms may have resulted from competition (Amadon 1947, Ripley 1962), since the isolated forms on Molokai, Lanai, and Hawaii have bills of intermediate shape (Figure 4, B-C). On islands with only one form of thrush, selection has probably favored a more generalized bill structure. Even the insular Cuban (*Myadestes elisabeth*) and Rufous-throated solitaires live alongside (are sympatric with) typical thrushes. In fact, if Kauai had not twice been colonized by thrushes, one that now eats mainly insects and the other mainly fruit, we might expect all *Phaeornis* to have evolved a more generalized bill type. Grant (1965a) has cited several examples of such broadening of feeding niche, accompanied by changes in bill shape, among birds of the Tres Marías Islands off Mexico. Evolution of the bills of Hawaiian thrushes could, of course, have proceeded in either direction, from long and narrow to short and broad, or vice versa. However, the closest resemblance to the bill shape of a mainland thrush is seen in the Kamao, whose bill is proportionately almost identical to the specialized bills of solitaires. I doubt that this bill shape evolved twice among thrushes, particularly in light of the other characters shared by *Phaeornis* and *Myadestes* that set them apart from other members of the family. Thus the divergence from the solitaire bill shape exhibited by the other Hawaiian thrushes in no way argues against considering the two groups congeneric. Such divergence could be predicted from the findings of Schoener (1965), who showed greater variation in bill size among West Indian representatives of several passerine families than among their mainland counterparts. In fact, generic separation of *Phaeornis* and *Myadestes* obscures an important example of evolutionary trends in bill structure in insular members of mainland genera.

Body Proportions

Stejneger (1889) could cite only the different proportions of wing, tail, and legs for making a generic distinction between *Phaeornis* and *Myadestes*. His analysis was based only on a comparison of the Kamao (*P. myadestina*) with several solitaires, but showed that some solitaires differed less from *Phaeornis* in these respects than they did from other *Myadestes*. Table 1 gives the wing/tail ratios of all the species in this complex that I examined. The relatively shorter tails of the Hawaiian birds can be seen as simply the extension of a trend established by the mainland forms. *M. townsendi, M. coloratus, M. genibarbis sibilans,* and *P. lanaiensis* have virtually identical wing/tail ratios; thus the character is useless for defining the two genera. Much greater gaps in the wing/tail ratio cline exist among various species of *Myadestes* than between *P. lanaiensis* and *M. townsendi*, and the

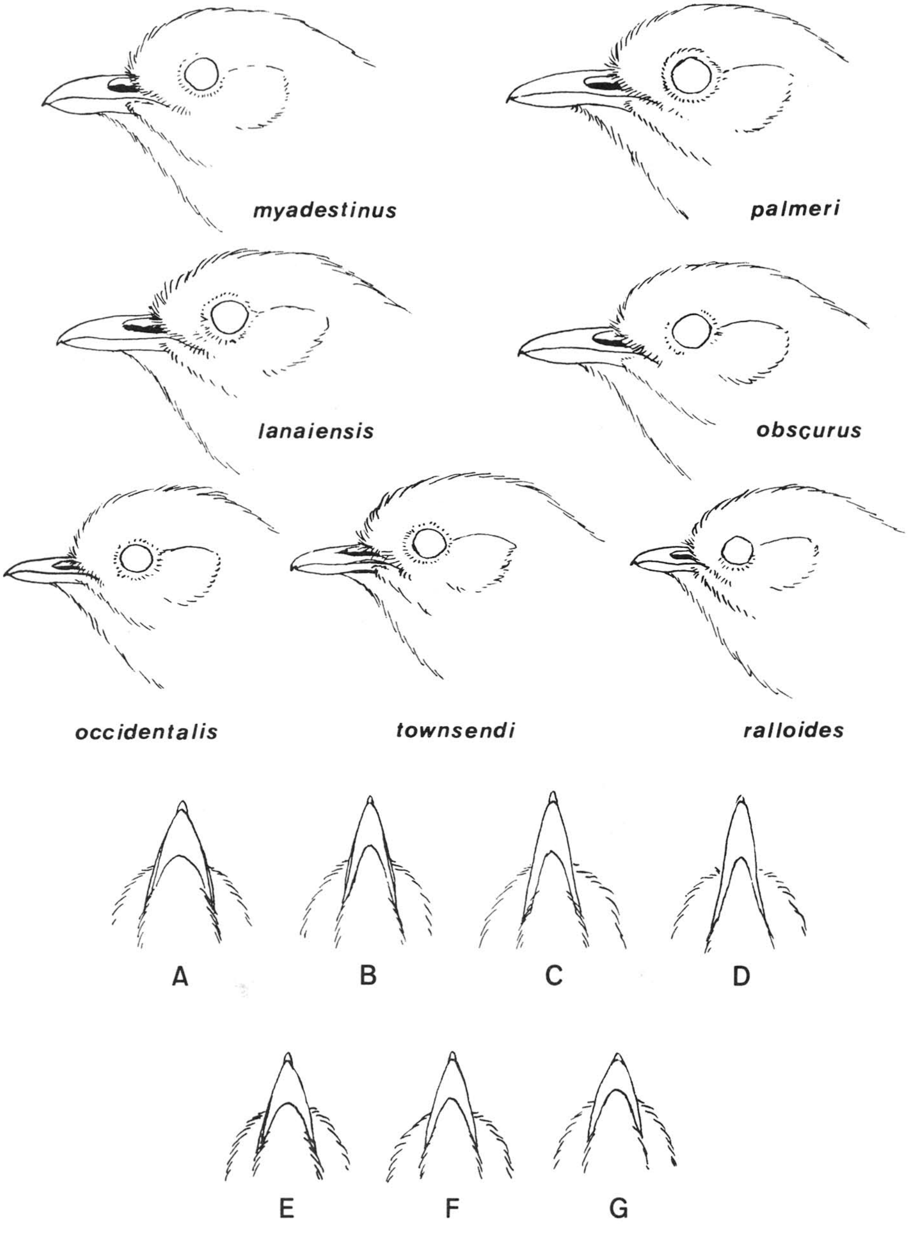

Figure 4. Bills of Hawaiian thrushes and representative solitaires. Ventral views (fourth and fifth rows): Hawaiian forms of *Myadestes* (*"Phaeornis"*) (A) *myadestinus,* (B) *obscurus,* (C) *lanaiensis,* (D) *palmeri;* mainland *Myadestes* (E) *occidentalis* (formerly *obscurus*), (F) *townsendi,* (G) *ralloides.* All to scale.

largest gaps of all occur within the Hawaiian group of species. The wing/tail ratios appear therefore to be following a pattern of divergence from their ancestral type similar to that of bill structure.

Ridgway (1907) used the greater tarsus length of *Phaeornis* as a key character to separate that genus from *Myadestes.* But the longer tarsus of *Phaeornis* is shown by Stejneger's (1889) data to represent just the extension of another morphological cline. A tendency toward greater tarsus length in island representatives of mainland genera has been demonstrated by Grant (1965a, 1966).

Internal Anatomy

Little is known of the internal anatomy of Hawaiian thrushes. Only specimens of the Omao (*P. obscura*) have been available for anatomical study and it is unlikely that the other species can or will ever be obtained because of their rarity or extinction.

Lucas (1894), in comparing skulls of the Omao and the Rufous-throated Solitaire, considered the two genera closely related. Indeed, he usually referred to them collectively when reconciling their placement in the thrush family. Since the Kamao is more solitaire-like in bill shape than the Omao, its skull might well reveal even greater similarities. Planned extraction of skulls from study skins by S. L. Olson (pers. comm.) may fill some of the gaps in our knowledge.

Morioka (1967) divided all thrushes into two groups on the basis of skeletal and muscular features. He found that *Phaeornis* and *Myadestes* belonged to the same group but he placed *Catharus* in the other. Morioka also showed that among the thrushes, only *Phaeornis* and *Myadestes* lack

TABLE 1

Wing and Tail Length Means and Wing/Tail Ratios of Solitaires (*Myadestes*) and Hawaiian Thrushes (“*Phaeornis*”)

	N	*Wing (mm)*	*Tail (mm)*	*Wing/Tail ratio*
“*Phaeornis*”				
palmeri	3	88	57	1.54
obscura	40	102	69	1.47
myadestina	20	106	80	1.33
lanaiensis	21	95	80	1.19
Myadestes				
townsendi	8	116	99	1.17
coloratus	8	88	75	1.17
genibarbis sibilans	6	87	75	1.16
leucogenys	6	104	92	1.13
melanops	8	87	78	1.12
ralloides	8	84	75	1.12
unicolor	8	95	89	1.07
elisabeth	7	89	84	1.06
genibarbis sanctaeluciae	6	92	87	1.06
genibarbis dominicanus	9	92	88	1.05
occidentalis (=*obscurus*) mainland forms	15	101	96	1.05
genibarbis solitarius	11	91	89	1.02
occidentalis insularis	4	96	96	1.00

ossified nasal septa and alinasal turbinals. Nor did he note any differences between *Phaeornis obscura* and *Myadestes* species that were greater than typical interspecific divergences. Olson (pers. comm.) has compared skulls of both adult and juvenile *Phaeornis* from the island of Hawaii with those of *Myadestes,* and he considers the two groups very similar in general appearance of the skull. Interestingly, he found the skull of a juvenile *Phaeornis* to be more like those of continental *Myadestes* than were those of adults.

Ames's (1975) study of the syrinx revealed another anatomical feature in which *Phaeornis* and *Myadestes* resemble each other but differ from other thrushes. In the Hawaiian birds, the syrinx is of the same unusual type as that of solitaires, but has diverged even further from the typical thrush syrinx.

In summary, the genera *Phaeornis* and *Myadestes* cannot be differentially diagnosed on morphological grounds. They are virtually indistinguishable in plumage, postures, and bill structure, and are similar in cranial and syringeal characters. Furthermore, in all of these characters the two groups share features that are different from those of typical thrushes. But because Ripley's (1962, 1964) classification was based mainly on vocalizations, an examination of those and other behavioral characters is warranted.

VOCALIZATIONS

Calls

Both the Omao and the Kamao utter a low-pitched, inquisitive raspy call that resembles the mewing call of the Gray Catbird (*Dumetella carolinensis*). In the Puaiohi, the homologous call is a harsh, almost toneless hiss. The larger Hawaiian thrushes also give a burry whistled call that sounds like a police whistle. As uttered by the Kamao, both calls are higher-pitched and less raspy than those of the Omao, and the "police whistle" has an ethereal quality produced by double-voicing of the notes. The call of the Rufous-throated Solitaire closely resembles that of the Kamao and has also been described as a police-whistle call (Lack 1976). Some nightingale-thrushes have a cat-like call note (Slud 1964), but none I have heard resemble the low rasp of the Hawaiian thrushes. However, one call of the Black-faced Solitaire sounds very much like the low-pitched Omao call. On the basis of call notes, then, Hawaiian thrushes are more like solitaires than like nightingale-thrushes.

Songs

The thrushes have been considered by most writers to be Hawaii's most skilled native songsters. Their songs differ considerably from island to island (Munro 1960), and thus are difficult to characterize as a group. The song of the Omao is rather unthrushlike and jerky but "pleasing and, at times, sweet" (Henshaw 1902: 29). The segment shown in Figure 5 is typical. The song comprises sharply up-and-down slurred whistles, without double-voicing. It therefore lacks the flutelike quality characteristic of many thrush songs. The song is loud, however, and echoes in the forest to such an extent that clear spectrograms are difficult to obtain. The song of the Kamao is entirely different from that of the Omao and has been described as resembling "that of an English thrush, but ... less powerful" (Palmer *in* Rothschild 1893–1900) and composed "of flute-like double

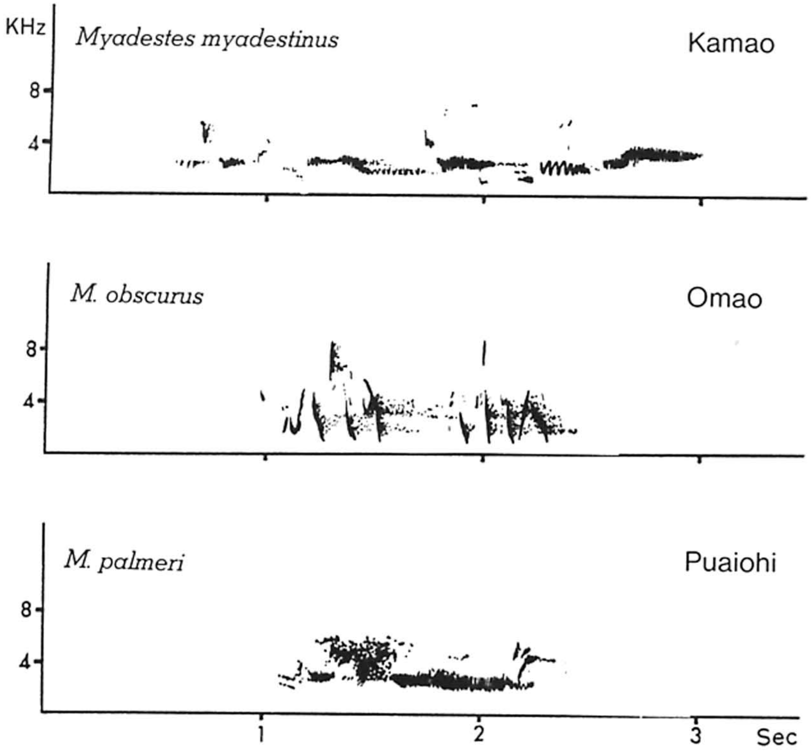

Figure 5. Songs of three species of Hawaiian thrushes. Recording data as follows: Kamao (LNS 5012) by the author, 2 July 1975, Alakai Swamp, Kauai; Omao (LNS 5166) by the author, 17 August 1975, Keauhou Ranch, Hawaii; Puaiohi (LNS 5898) by Gauthey et al. (1968), 1 June 1968, Alakai Swamp, Kauai. These diagrams are ink tracings of spectrograms made on the Spectral Dynamics Model SD301-C Real Time Analyzer with a range of 0–10,000 Hz and a band width of 120 Hz.

notes" (Richardson and Bowles 1964). The double-voicing can be seen in the example given in Figure 5. The song lacks the sharp ascending and descending whistles of the Omao and is characterized by rapid frequency modulations of narrow amplitude that produce a burry quality, like that of some of the call notes. The song of the Puaiohi (as recorded by Gauthey et al. 1968) is much less musical than the songs of the other two Hawaiian thrushes. It is wheezy and high-pitched, like the squeaking of a metal wheel in need of lubrication, but it contains some notes that resemble elements of the Kamao's much longer and more elaborate song. All three known Hawaiian thrush songs are reiterated between pauses of varying length. The examples shown in Figure 5 are single segments extracted from lengthy series of songs and pauses. The Olomao has an "irregular . . . somewhat jerky, though always melodious" (W. A. Bryan 1908: 174) song on Molokai, but on Lanai it apparently was "no singer at all" (Munro 1960: 74). No recordings exist of the song of the Olomao.

Ripley (1962) claimed that in "song and apparently in habits" Hawaiian thrushes were "far closer to *Catharus* especially the central American nightingale-thrush group" than to *Myadestes*. Obviously, he considered the songs of solitaires to be noticeably different from those of nightingale-thrushes. I listened to recorded examples of the songs of five species of *Myadestes,* the four temperate zone *Catharus,* and five species of nightingale-thrush. In general, and to my ears, *Catharus* songs are simpler than those of solitaires and the temperate zone species have longer more complex songs than do the nightingale-thrushes. Despite these generalizations, songs of some nightingale-thrushes closely resemble the songs of some solitaires. Spotted Nightingale-thrush (*C. dryas*) and Black-faced Solitaire songs can hardly be distinguished. Thus, although the two groups can be generally characterized on the basis of song, the differences are neither clear-cut nor consistent and are, in my opinion, of only limited taxonomic value. The song of the Kamao resembles that of Townsend's Solitaire more than it does that of any other mainland species, but this may or may not be important.

The behavior associated with singing may provide more phylogenetically significant data than does song alone. Solitaires and Hawaiian thrushes choose song perches high in the forest canopy (Bent 1948, Skutch 1967, pers. obs.), whereas *Catharus* thrushes usually sing on or near the ground (Bent 1949, Skutch 1960). Singing in flight is unusual among thrushes in general (Skutch 1960), but almost all writers have mentioned that Hawaiian thrushes sometimes sing on the wing. I have seen this behavior in both the Kamao and Omao. The birds often end a bout of singing in the treetops with an upward flight, a brief period of singing on the wing or "skylarking," and a sudden dive into the forest understory. Similar behavior has been noted in the Puaiohi (Perkins 1903). Townsend's Solitaire (Bent 1949, Bailey and Niedrach 1965) and the Brown-backed Solitaire (Gunn and Gulledge 1977) have a virtually identical song flight. In the genus *Catharus,* only the Gray-cheeked Thrush is known to have a song flight, which is apparently not similar to the song flights of solitaires and Hawaiian thrushes (Bent 1949).

Nesting

A possible Olomao nest in a fork about 9 m (30 ft) high in an ohia-lehua tree was reported by W. A. Bryan (1908), but the first confirmed nest of a Hawaiian thrush was that of an Omao (Berger 1969). It was located about 1.3 m (4.3 ft) above the ground against the trunk of a tree fern. More recently, other Omao nests have been found in niches or cavities in trees (van Riper and Scott 1979). All were bulky constructions of various plant materials. No nests of Hawaiian thrushes have yet been found on the ground, but the alpine population of the Omao would have to use terrestrial sites.

The best-known nest of the genus *Myadestes* is that of Townsend's Solitaire. Often the nest is built on or near the ground, frequently in a recess in a steep bank with an overhanging shelter (Bent 1949). Similar nest sites have been reported for the Cuban and Rufous-throated solitaires of the West Indies (Bond 1974), for the Black-faced and Brown-backed (*M. occidentalis = obscurus;* see beyond) solitaires in Central America (Skutch 1967), and for the Andean Solitaire in Colombia (Wallace 1965). Other low sites include a nook in the side of a leaning moss-covered tree (Skutch 1967) and a cavity in a stub or the heart of a tree fern (Bond 1974). The Rufous-throated Solitaire sometimes chooses higher nest sites in trees, such as in a bromeliad about 15 m (49 ft) above the ground or in a tree fork at 4 m (13 ft) (Cruz 1976). These nests are all bulky and structurally similar to those of

Hawaiian thrushes (Berger 1969, van Riper and Scott 1979).

Nightingale-thrushes build small compact nests in low shrubbery (Skutch 1960, Wallace 1965), and the temperate *Catharus* often nest also on the ground but never in cavities or niches (Bent 1949, Harrison 1978). These nests bear little similarity to those of Hawaiian thrushes.

The eggs of solitaires are white to pale blue, liberally spotted with reddish brown, with the spots often concentrated toward the larger end (Skutch 1967, Bent 1949). The eggs of Townsend's Solitaire are "entirely different from the eggs of other North American thrushes" (Bent 1949: 320) as can be readily seen in a recently published plate (Harrison 1978). Thus the similarity of the eggs of the Omao and Puaiohi (as described by Berger 1981) to those of solitaires may be noteworthy. Lack (1958), however, considered egg color useless as an indicator of relationships among thrushes.

TAXONOMY

Because no morphological, behavioral, or ecological characters distinguish *Phaeornis* from *Myadestes,* I see no justification for maintaining the two as separate genera. I therefore formally propose *Phaeornis* Sclater 1859 as a junior synonym of *Myadestes* Swainson 1838.

One consequence of acknowledging that Hawaiian thrushes are solitaires is that the long-established scientific name of the Brown-backed Solitaire, *M. obscurus* Lafresnaye 1839, must yield to the priority of *Myadestes obscurus* (Gmelin) 1789, now the name of the Omao. According to nomenclatural rules, the Brown-backed Solitaire will now be called *M. occidentalis* Stejneger 1882, and the former nominate subspecies must be renamed (Pratt in press).

POSSIBLE ANCESTRY

Townsend's Solitaire is more like the Hawaiian thrushes than is any other mainland *Myadestes.* Its song resembles that of the Kamao, its wing/tail ratio is almost identical to that of the Olomao, and it exhibits alpine adaptations similar to those of the Mauna Loa population of the Omao. These characteristics suggest that the Hawaiian thrushes as a group may be descended from the same ancestral species as is *Myadestes townsendi.* Townsend's is also the only migratory solitaire and thus represents the evolutionary line most likely to colonize a remote island; during migration Townsend's Solitaires sometimes forsake their solitary habits and gather in aggregations or flocks (Bent 1949, Phillips et al. 1964), ideal for island colonizations. In winter, Townsend's Solitaires also wander widely in "family groups," following variable food supplies (Bent 1949).

SPECIATION AMONG HAWAIIAN SOLITAIRES

The key to the interrelationships of the Hawaiian solitaires lies in determining which of the two Kauai species is the more recent colonizer. Amadon (1947) proposed a scenario in which the Puaiohi (*M. palmeri*) reached Kauai first and, because of the relative isolation of that island, diverged to the species level. A second invasion by the same ancestral species then occurred, giving rise to the Kamao (*M. myadestinus*). Amadon considered the Kauai example to be a typical double-invasion phenomenon, with subsequent character displacement. However, in bill shape, diet, and vocalizations the Kamao is the most clearly myadestine member of the Hawaiian solitaire group, whereas the Puaiohi is the most divergent in these same characters. For Amadon's hypothesis to be valid, the ancestral characters of the Kamao would have to have been lost and then regained after the second invasion of Kauai.

I favor a simpler scenario that would have the Kamao retaining its solitaire-like characters throughout its history. Thus it would represent a direct link to the mainland ancestor of all Hawaiian *Myadestes*. Kauai may well have been the site of the first landfall by *Myadestes* in the islands, since it is farther north and therefore closer to a possible source area (recall that modern Townsend's Solitaires breed to tree line in central Alaska). All historical records of continental passerines in the archipelago have come from the small islands that lie north and west of Kauai; none have ever been recorded among the main islands (Berger 1981). Modern theories of island colonization suggest that invading species usually spread rapidly throughout an archipelago before undergoing major divergence (Ricklefs and Cox 1972). Thus a single species of *Myadestes* may originally have occurred throughout the islands. At least one of the island forms diverged sufficiently to become a new species, and then reinvaded Kauai to share it successfully with the first colonizer. Thus the Kauai example is not a typical double-invasion phenomenon as Amadon (1947) suggested, because the two *Myadestes* are from different source areas, one more-or-less directly from the mainland, the other from within the archipelago. (The remoteness of the Hawaiian Islands makes two invasions from the mainland highly unlikely.) I believe the Puaiohi represents the second invader. Its longer and narrower bill, insectivorous diet, and distinct vocalizations simply extend the trends away from continental characteristics seen in the solitaires of the other islands.

If my scenario is correct, then logically a minimum of three solitaire species must be (or have been) present in Hawaii, unless the Puaiohi is conspecific with the allopatric forms. No one has ever suggested the latter possibility, because the Puaiohi is so distinctive within the complex. Most authors have overlooked the fact that the Kamao is equally distinctive, particularly with regard to vocalizations.

Vocalization Experiments

To test the possibility that potential reproductive isolating mechanisms exist among the Hawaiian *Myadestes* that live on separate islands, I conducted a series of vocal playback experiments on the island of Hawaii. On 28 and 29 April 1977 I visited Keauhou Ranch (which lies between Kilauea Forest Reserve and Hawaii Volcanoes National Park) where Omao were abundant and many were singing vigorously. I had prepared tapes of Kamao call notes and songs from recordings I made in 1975 on Kauai, and also tapes of homologous vocalizations of the Omao from Keauhou Ranch. Before I began experimenting with the Kauai tapes, I tested responsiveness of singing Omao to playbacks of previously recorded Omao songs and calls.

The raspy, cat-like Omao call elicited no response whatever. Singing birds continued uninterrupted, and birds giving the same call did not alter their behavior when the tape was played. The higher-pitched call was also ignored. This latter result was surprising in light of Perkins' (1903) statement that Omao could be attracted by imitation of that call. Response to the Omao song was, however, immediate and obvious. First the experimental subject, singing vigorously, flew upward from its perch and then dived into the forest understory near the playback speaker. Then the Omao approached silently in a series of short flights as if attempting a surreptitious investigation. When only a short distance from the speaker, the bird stared intently at the sound source, but did not appear agitated. In fact, the wing-shivering, characteristic of Hawaiian thrushes, ceased during the bird's approach to the recorded sound. The bird remained, seemingly oblivious to human presence, as long as the playback continued. When the tape ended, the Omao flew back into the canopy and resumed singing.

Having established that the birds were responsive to song playback, I began playing the Kamao tape first, followed by the Omao recordings—a method similar to that used by Raitt and Hardy (1970) in their study of two Mexican species of *Catharus.* In the first experiment I played the Kamao tape for an apparently territorial, vigorously singing Omao. Neither the two different call notes nor the complex Kamao song (Figure 5) elicited any response, or even any indication that the bird heard the tape. The subject's vocalizations continued until the taped Omao song began. The bird then ceased singing abruptly and flew directly to an open perch about 4 m (13 ft) above the playback speaker. Its approach to the speaker then closely matched that previously described. I conducted nine such playback experiments during the two-day period, involving nine different individuals. None of these birds responded in any way to recordings of the Kamao. Seven responded vigorously to subsequent presentation of the Omao song; two others responded to neither tape. At the time I did not have a recording of the Puaiohi song, but it is so different from the songs of the Omao and Kamao that response to it by either of those species seems unlikely.

Conclusions

Lanyon (1967) interpreted the same kinds of responses to taped vocalizations by flycatchers as indicating that forms with nonoverlapping ranges were separate species, although they were morphologically similar. Like flychatchers, many thrush species are similar in appearance but differ vocally (Dilger 1956, Raitt and Hardy 1970). Thus it is reasonable to interpret vocal differences among allopatric Hawaiian solitaires as potential isolating mechanisms, and I conclude that the Puaiohi, the Omao, and the Kamao are distinct species.

The solitaires of Oahu, Molokai, and Lanai are problematical. The Lanai and Molokai birds were originally considered a single taxon (*lanaiensis*) and bore the single native name, Olomao. W. A. Bryan (1908) gave the epithet *rutha* to the Molokai population on the basis of slight differences in color and measurements. Later Munro (1960), with years of field experience on Lanai, pointed out that the two forms differed vocally, in that *lanaiensis* did not sing at all but gave only call notes. I re-examined Bryan's type series of *rutha* in the Bishop Museum, and compared the skins with more recently collected specimens from Lanai. I cannot see the color differences he noted. Perhaps the apparent differences were artifacts resulting from the comparison of a then–fresh series from Molokai with older Lanai specimens. Nor could I detect any important differences in measurements of the two populations. Thus to distinguish the two taxa, we are left only with Munro's (1960) report of the lack of song in *lanaiensis.*

Molokai, Lanai, and Maui were united during the last glaciation and may have separated as recently as 10,000 years ago (Juvik and Austring 1979). Probably a single form of *Myadestes* inhabited the conjoined island, and thus the populations on Lanai and Molokai have had relatively little time for differentiation. I believe *rutha* and *lanaiensis* must be considered the same species; their differing vocal behavior, however, justifies recognizing them as subspecies. But should they be considered conspecific with any of the other Hawaiian *Myadestes?* The Olomao (*lanaiensis* + *rutha*) is as distinct morphologically in the complex as are the Omao, Kamao, and Puaiohi. Earlier writers considered the song (on Molokai at least) distinctive as well. Thus I believe the best course is to recognize the Olomao as a separate species, *M. lanaiensis,* with subspecies on Lanai (*M. l. lanaiensis*) and on Molokai (*M. l. rutha*).

The extinct Amaui of Oahu conceivably could have been conspecific with one of the three certain species, or with the Molokai and Lanai forms. In the absence of specimens, its status must be considered hypothetical. Perhaps recently discovered fossil solitaires from Oahu (S. L. Olson pers. comm.) will help to solve the problem. In the meantime, I recommend that the Amaui appear in checklists as a questionable species *Myadestes ?oahensis.*

The Hawaiian solitaires (thrushes) are an excellent example of island evolution. Although they retain enough of their ancestral characters to indicate their relationships, they exhibit all levels of speciation, and have begun the process of interisland cross-colonization that has led to spectacular adaptive radiations in such groups as the Hawaiian honeycreepers. The solitaires are thus instructive in demonstrating how such evolutionary phenomena began.

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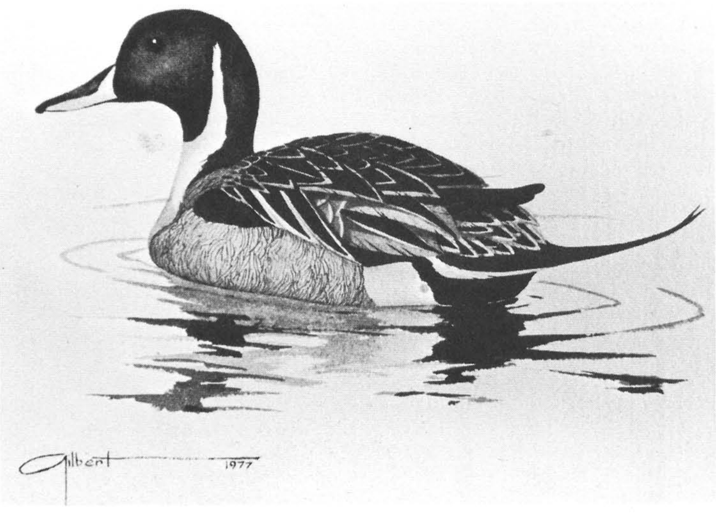
LOUISIANA STATE UNIVERSITY
BATON ROUGE, LOUISIANA 70893



Pintail, *Anas acuta.* Painting by George E. Gilbert, courtesy of John Steed.