THE INTERPLAY OF SPECIES CONCEPTS, TAXONOMY, AND CONSERVATION: LESSONS FROM THE HAWAIIAN AVIFAUNA

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Abstract. The Hawaiian Islands, with their unique geological history and geographic position, provide an excellent natural laboratory in which to evaluate currently competing biological (BSC) and phylogenetic (PSC) concepts of the species. Although the BSC as historically applied in archipelagic situations is shown to be flawed in producing overlumped polytypic species, it nevertheless remains the preferable concept for most practical purposes. A review of the taxonomic history and species limits in Hawaiian birds under both concepts reveals that, when properly applied, the BSC yields a species total remarkably close to that produced under the PSC, contrary to what many proponents of the latter have supposed. We propose that the widespread adoption of the PSC for conservation purposes is potentially harmful. The PSC trivializes the species taxon and introduces new problems of deciding when a population becomes diagnosable, the possibility that species could appear and disappear in a reticulate fashion, and the likelihood that genetically diagnosable but phenotypically identical, and therefore not field identifiable, populations could be ranked as species. All of these problems negatively impact such things as constructing credible and politically defensible lists of endangered species, the prioritization of limited conservation resources, and the gathering of field data. We contend the BSC is arguably a more rational concept that better supports the activities of both scientific and nonprofessional observers. Biological species limits in oceanic archipelagoes worldwide need to be reevaluated using modern concepts and technologies before rational conservation decisions can be made.

Key Words: avian conservation; biological species; endangered species; Hawaiian Islands; phylogenetic species; polytypic species; species limits.

Avian systematists have recently joined in a great debate over the definition of species. The long-accepted biological species concept (BSC) of Mayr (1942a) has been challenged by a new one from the field of phylogenetic systematics, usually called the phylogenetic species concept (PSC). As defined by Cracraft (1983), a phylogenetic species is a population or cluster of individuals "diagnosably different from other such clusters, and within which there is a parental pattern of ancestry and descent." Because diagnosability can be established by "any feature or set of features, ranging from single fixed nucleotide substitutions to major phenotypic (but genetically based) features" (Zink and McKitrick 1995), the PSC would elevate virtually all isolated subspecies to species and add many more based on small populations with one or more distinctive traits. Zink and McKitrick (1995) and Zink (1997) summarized the debate and argue in favor of the PSC, whereas Mayr (1992), with recent support from Snow (1997) and Collar (1997), defended the BSC. For popular overviews of the controversy, see Myers (1988) and Sibley (1997).

Many might regard this debate as purely academic. Recently, however, some conservationists have suggested that the PSC would better serve their purposes than the BSC, showing that such esoteric pursuits do, indeed, have relevance in the "real world." Hazevoet (1996) has even charged that the BSC "promotes the extinction of endemic birds," by classifying many distinctive island forms as subspecies. Because conservation efforts often focus only on "full" species (Collar et al. 1994), there is some validity to Hazevoet's claim. In this review, we use the avifauna of the Hawaiian Islands to demonstrate: (1) that proper application of the BSC in archipelagic situations can produce a species list much closer to one based on the PSC than has been previously appreciated; (2) that the BSC itself is sound and that the many problems with it cited by some conservationists and systematists arise from misapplication of the concept rather than weaknesses of it; and (3) that the PSC suffers from its own problems in practice such that a shift to it could be worse for conservation than maintaining the BSC (Collar 1997).

Because Hawai'i is the most isolated oceanic archipelago, with numerous large and ecologically varied islands, it has long been regarded as a superb natural laboratory for the study of evolution and biogeography. With the possible exception of Galápagos's birds, Hawai'i's is the best studied of any insular avifauna, and represents a much later stage of evolution than that of Darwin's younger islands, with a much higher level of endemism. Unfortunately, the Hawaiian Islands have also suffered considerably more ecological degradation (for a review, see Pratt 1994; Van Riper and Scott *this volume*) than the Galápagos and have more extinct and endan-

gered birds than any comparable region. They also have the largest component of introduced species of any modern avifauna (Long 1981), but we will show that even alien birds can teach evolutionary lessons on islands. Thus Hawai'i's birds provide all the necessary ingredients for evaluating the relationship of the competing species concepts to each other and to conservation. They further provide an important counterpoint to Hazevoet's (1995) use of the Cape Verde Islands avifauna as evidence of the need to abandon the BSC.

AVIAN TAXONOMY IN HAWAI'I

Most recognizable forms of Hawaiian birds were first described as separate species under the Linnean typological or morphological species concept. Even some forms no longer regarded as subspecies were so described (e.g., the three populations of *Hemignathus virens wilsoni*; Wilson and Evans 1890–1899). All authors of the "classical period" of Hawaiian bird research (Wilson and Evans 1890–1899, Rothschild 1893–1900, Bryan 1901, Henshaw 1902a, Perkins 1903) used a morphological species concept, although all were evolutionists. Perkins's (1903) "family tree" of the Hawaiian honeycreepers, an endemic taxon variously ranked as the Drepanididae, Drepanidinae, or Drepanidini, was the first phylogenetic treatment of any Hawaiian birds. After the flurry of ornithological research in the islands around the turn of the twentieth century, a period of neglect ensued, with only a few scattered notes and papers on Hawaiian birds appearing over the next four decades, and avian taxonomy remained static.

Elsewhere during this quiescent period, systematists, with ornithologists prominent among them, were formulating the "modern synthesis" that culminated in Mayr's (1942a) classical definition of the biological species that has been memorized by generations of biologists. The BSC is operational, rather than morphological, and is based on the ability or inability of populations to interbreed freely. It introduced the concept of polytypic species (comprising several subspecies) for clusters of morphological "species" that could or would interbreed in nature. It thereby created the vexing problem of how to classify distinctive isolated (allopatric) forms whose ability or willingness to interbreed cannot be objectively demonstrated. Mayr (1942a) suggested the use of "potential isolating mechanisms" to gain inferences as to what might happen during a hypothetical future period of contact. He also suggested that systematists look to the degree of difference between related sympatric species as a guideline to evaluate allopatric forms in a given group. We will show that

properly applied, these precepts lead to species lists that can be corroborated by other procedures, such as phylogenetic analyses and genetic studies. However, early practitioners of the BSC too often ignored their own fundamental guidelines and engaged in hasty lumping of vaguely similar forms. One wag has dubbed the period "Lumparama." In many cases, no reasons other than general similarity and geographic separation were ever stated for lumping closely related forms previously considered separate species (see numerous examples in Mayr and Short 1970). It was taxonomy by decree.

Virtually all mid-century authors treated geographically replacing island populations the same as such populations on continents, even when differences were striking and consistent. However, subsequent genetic studies (e.g., Boag 1988) showed that island colonization is a unique phenomenon that differs fundamentally from the kind of isolation that results from habitat fragmentation, glacial cycles, and other continental phenomena. Diamond (1977) showed that speciation differed on islands as compared to continents, but his study suffered from the state of knowledge of the time in that several assumptions he made about Hawai'i in particular (e.g., that intraisland subspeciation has not occurred on islands smaller than New Zealand, but see Pratt 1980; that the Hawaiian Crow, *Corvus hawaiiensis,* represents a single colonization with no subsequent intra-archipelagal dispersal, but see Olson and James 1982b) have been shown to be false. The failure to appreciate the different character of insular allopatry was a basic misunderstanding that contributed to overlumping many island taxa.

The problem was exacerbated by Mayr's (1942a, 1969) clearly stated belief that allopatric populations of uncertain status should be considered subspecies. The "when in doubt, lump" precept may be appropriate for closely related isolates on continents (Snow 1997), but we will show that for traditional studies of archipelagic speciation, exactly the opposite bias ("when in doubt, split") is more likely to result in a species list that will stand up to independent corroboration. Indeed, every recent study of strikingly marked insular "subspecies" of which we are aware has revealed potential behavioral or ecological isolating mechanisms to support recognition of the forms as separate biological species. Although Mayr (1942a) introduced the concept of the superspecies for strongly differentiated allopatric species (allospecies), he stated that (p. 170): "It would be an abuse of this concept if an author were to call every polytypic species, composed of insular and thus well-marked subspecies, a superspecies." Again, it

now appears that the real abuse of the superspecies concept is its under use in insular situations. Subsequently, Sibley and Monroe (1990) modified the Mayrian definitions for the BSC and recognized many well-marked island "subspecies" as allospecies. Even Mayr himself (E. Mayr and J. Diamond, unpubl. data) has elevated many of his earlier (Mayr 1945) subspecies to allospecies.

The first review of the Hawaiian avifauna to apply the "modern synthesis" was that of Bryan and Greenway (1944), who combined many geographically replacing morphological species. Amadon (1950) carried the process further, lumping many strikingly differentiated island forms into large polytypic species (his work dealt mainly with the honeycreepers, but he reviewed the other land and freshwater species in an appendix). His classification exemplifies mid-century evolutionary thinking. For example, Amadon (1950) considered plumage color relatively unimportant as an isolating mechanism, despite the fact that birds are highly visual organisms. The de-emphasis of coloration as a guideline to species limits was undoubtedly influenced by numerous hybridization studies during the period that lumped such different-looking continental forms as the three North American flickers (*Colaptes* spp.; Short 1965), the various "dark-eyed" juncos (*Junco* spp.; Mayr 1942b), "Black-crested" and Tufted titmice (*Baeolophus* spp.; Dixon 1955), Australian magpies (*Gymnorhina* spp.), silvereyes (*Zosterops* spp.), and many others (reviewed by Ford 1987), the "Northern" orioles (*Icterus* spp.; Sibley and Short 1964), Black-headed and Rose-breasted grosbeaks (*Pheucticus* spp.; West 1962), Eastern and Spotted towhees (*Pipilo* spp.; Sibley and West 1959), and numerous others. Some of these studies have withstood subsequent scrutiny, but many have not. The trend of the era led to lumping of such other taxa as Glossy and White-faced ibises (*Plegadis* spp.; Palmer 1962), Palearctic and Nearctic Green-winged Teal (*Anas* spp.; Delacour and Mayr 1945), "Black-shouldered" kites (*Elanus* spp.; Parkes 1958), the three "yellow-bellied" sapsuckers (*Sphyrapicus* spp.; Howell 1952), and Holarctic rosy-finches (*Leucosticte* spp.; Mayr 1927, French 1959), based solely on inference rather than actual studies. Most of the latter lumpings have subsequently been shown to be erroneous or ill-advised. We will show that, among Hawaiian birds, behavioral and genetic studies virtually always support the premise that those that *look* different, *are* different. Interestingly, although Amadon (1950) was applying the BSC, his work largely ignored the relatively little biological data available at the time and was based almost

entirely on museum skins. But his study was state-of-the-art, and we should not be surprised that some of his polytypic "species" have subsequently been shown to be amalgams of several biological species (see section on 'Alauahios below). Amadon's (1950) classification of Hawaiian birds remained the standard for three decades.

The 1970s saw a renaissance in ornithological field studies in Hawai'i. Many observers, including the authors, confronted by overwhelming potential isolating mechanisms among many very strikingly marked "subspecies," began to question Amadon's (1950) taxonomy. H. Douglas Pratt conducted a complete review of available data from a variety of lines of inquiry and combined it with new information on vocalizations (Pratt 1996b), foraging behavior, nesting habits, and ecology to produce the first complete taxonomic revision of the endemic avifauna (Pratt 1979) since Amadon (1950). First appearing in a dissertation, his classification was the basis of that published by Berger (1981), who did not accept all of Pratt's splits at the species level. Berger's (and hence most of Pratt's) taxonomy was then adopted by the American Ornithologists' Union (AOU) Check-list (AOU 1983), which has been followed by most subsequent authors. Pratt et al. (1987) adopted all of Pratt's (1979) species limits, and in a series of papers expanding on his dissertation, Pratt (1982, 1987, 1989, 1992b) defended them, and all were eventually adopted by the AOU (1985, 1991, 1993, 1995).

Shortly after H. Douglas Pratt's work became widely known, another new classification appeared in the form of a review of recently discovered subfossil Hawaiian bird remains (Olson and James 1982b). As further discoveries came to light, these authors revised their classification and presented an updated version in tabular form (Olson and James 1991). Their arrangement of genera differs irreconcilably (Conant et al. 1998, Pratt *this volume*) with that of Pratt (1979) and the AOU Check-list (AOU 1998) as revised, but at the species level the two classifications differ only slightly and could eventually agree totally. In a footnote, Olson and James (1991) expressed the view that "distinctive, allopatric, insular forms" are best regarded as species. Their species-level taxonomy is thus the closest yet to application of the PSC to the Hawaiian avifauna.

During the 1970s, the first systematic studies of Hawaiian birds using the new technique of cladistics appeared. Raikow's (1977, 1986) anatomical studies produced the first cladistic phylogeny of Hawaiian honeycreepers (Pratt [1979] was influenced by this technique, but his first classification was not strictly cladistic). Since

then, virtually all analyses of Hawaiian bird evolution have been cladistic. Until recently, cladistic methods did not affect decisions at the species level, but the PSC is itself an outgrowth of cladistic thinking (Cracraft 1983, Zink 1997). The recent split of the Oʻahu ʻAmakihi (*Hemignathus flavus*; see below) was based solely on a reconstruction of phylogenetic history through the study of mitochondrial DNA and shows that some decisions by proponents of the BSC come surprisingly close to PSC reasoning. Among Hawaiian birds, genetic studies at the molecular level have usually supported species limits determined by more traditional methods and are an important independent corroboration of them (Johnson et al. 1989; Tarr and Fleischer 1993, 1995; Fleischer et al. 1998). Indeed, many recent splits were not accepted until biochemical data supported them, but such data are not, in the operational sense of the BSC, biological (Greenwood 1997). Rather, biochemical systematists may base their decisions on the Mayrian technique of comparing degrees of difference, in this case genetic, between allopatric forms and those between related sympatric ones, or on measurements of the length of time allopatric populations have been evolving independently. Thus they implicitly subscribe to the BSC but deal with data that are outside the realm of traditional isolating mechanisms.

THE SPECIES OF HAWAIIAN BIRDS

The following is a review of all historically known Hawaiian land and freshwater birds and one nesting seabird whose species limits have been controversial. It shows that a near consensus on species limits has developed during the past decade. All lines of inquiry have contributed to it, and the result is a species list, based on the BSC, that differs little from one based on the PSC. It also suggests that in practice, application of the PSC is not as simple as it first appears.

HAWAIIAN PETREL

The Hawaiian petrel breeds in barren alpine zones of the Hawaiian Islands, with the main colony near the summit of Haleakalā on Maui. The birds' range at sea is poorly documented, but they are believed to remain in the central Pacific near Hawaiʻi year-round (Pratt et al. 1987). From the earliest days of its discovery, the similarity of the Hawaiian Petrel to the Dark-rumped Petrel (*Pterodroma phaeopygia*) of the Galápagos was obvious, and virtually all taxonomists regarded it as an allopatric subspecies *P. p. sandwichensis*. With the advent of technology that allowed detailed vocal comparisons of the two populations, differences in voice became apparent. Tomkins and Milne (1991) suggested that these differences were sufficient to be regarded as isolating mechanisms between species, and Sibley and Monroe (1993) recognized the Hawaiian Petrel (*P. sandwichensis*) as distinct. This case demonstrates a longstanding and increasing appreciation among BSC proponents of vocalizations as isolating mechanisms. Recently, strong genetic divergence of the two petrels was demonstrated using allozyme electrophoresis (Browne et al. 1997) and as yet unpublished mtDNA studies (G. Nunn fide R. Fleischer, pers. comm) had similar results. Because of their genetic diagnosability and geographic separation, the two forms would clearly qualify as phylogenetic species.

ENDEMIC DUCKS

The Hawaiian Islands have two endemic ducks that are apparent derivatives of the Mallard (*Anas platyrhynchos*). The form *wyvilliana* (Hawaiian Duck, hereafter referred to as Koloa) is known historically from the main islands, whereas *laysanensis* was historically restricted to Laysan. Both endemics were originally described as separate species, but Bryan and Greenway (1944), Munro (1944), and Amadon (1950) considered them conspecific but distinct from the Mallard. Delacour and Mayr (1945) lumped them all. For the next two decades most authors (e.g., Brock 1951a, Bailey 1956, Warner 1963) followed the former taxonomy, but Ripley (1960) advocated species status for the Laysan Duck while keeping the Koloa a subspecies of Mallard. Alternatively, Berger (1972) considered both endemics full species, whereas Weller (1980) again lumped both with the Mallard. Virtually all of these varied treatments resulted from subjective treatment of morphological characters with little consideration given to some rather obvious potential isolating mechanisms. For example, Mallards and their relatives are notorious hybridizers, especially in captivity. Yet Ripley (1960) indicated that captive Laysan Ducks failed to hybridize with Koloa when they had the opportunity. In a recent survey of waterfowl collections worldwide, only three of 46 collections holding Laysan Ducks reported that *laysanensis* hybridized with another duck species (M. Reynolds, pers. comm.). Ripley (1960) further described numerous ecological peculiarities of the Laysan Duck, but based his taxonomic reasoning solely on morphological characters such as distinctive downy plumage. For the Koloa, Pratt (1979) pointed out that migratory ducks form pair bonds on the wintering grounds, a fact overlooked by previous treatments of this complex. Koloa breed year-round (Swedberg 1967) and form pairs within sight of occasional

wild Mallards. Swedberg (1967) further states that even on small ponds the local ducks tend to avoid wintering migrants, another obvious behavioral isolating mechanism. The near total genetic swamping of Koloa by domestic Mallards on Oʻahu (Browne et al. 1993) does not negate the inference gained from earlier, more natural situations. Species status for the two endemic ducks is now also supported by both laboratory and paleontological studies. Browne et al. (1993), using allozyme electrophoresis, proposed that *A. wyvilliana* and *A. laysanensis* are sister taxa, separate from *A. platyrhynchos*. Discovery of subfossil remains of what appeared to be *laysansensis* on the main Hawaiian Islands (Olson and Ziegler 1995) suggested prehistoric sympatry with *wyvilliana*. Sequencing of mt-DNA from the subfossil bones (Cooper et al. 1996, Cooper 1997, Rhymer *this volume*) indicated that they were close to the Laysan Duck but not the Koloa, strongly suggesting former sympatry. Rhymer's (*this volume*) results differ from those of Browne et al. (1993) in showing a close Mallard/Koloa relationship, with the Laysan Duck very distinct genetically. Whatever their phylogeny, these three forms appear to be good species under virtually any species concept.

HAWAIIAN COOT

All authors after Bryan and Greenway (1944) considered the Hawaiian Coot a subspecies of the American Coot (*Fulica americana*) until Pratt (1987) showed that its differences were of the same degree as those of other allospecies of the worldwide coot superspecies, and involved characters important in species recognition. He suggested it be classified as *F. alai* as originally described, and was followed by Sibley and Monroe (1990), Olson and James (1991), and the AOU (1993). Because it has consistent diagnostic characters that distinguish it from other coots, the Hawaiian Coot is also a phylogenetic species.

HAWAIIAN STILT

Like the coot, the endemic stilt of the Hawaiian Islands has been regarded by most authors as a subspecies of its North American counterpart, the Black-necked Stilt (*Himantopus mexicanus*). It is behaviorally quite similar but has many distinctive plumage features (Pratt et al. 1987) as well as adaptations to the unique Hawaiian environment. Mayr and Short (1970) recognized eight species of stilt in the superspecies *H. himantopus,* including the Hawaiian *H. knudseni,* rather than engage in "partial dubious lumping with insufficient knowledge." They stated that some forms "will undoubtedly prove

conspecific," and virtually no one followed their split. Olson and James (1991), without comment, ranked the Hawaiian Stilt as a full species. In light of what we now know about discrete plumage differences as indicators of relationship among island birds, that decision was probably sound. Under the PSC, the Hawaiian Stilt would unquestionably be a separate species because of its diagnostic plumage differences, and now molecular data (Fleischer and McIntosh *this volume*) show large genetic divergence as well. It likely is a valid biological species.

HAWAIIAN SOLITAIRES

The relationship of the Hawaiian thrushes (Turdinae) to the American solitaires (*Myadestes*) was hypothesized by the earliest researchers (Stejneger 1887, 1889) but was not generally accepted until Pratt (1982) reviewed and amplified the evidence supporting it. This classification has subsequently been corroborated by new osteological comparisons (Olson 1996) and genetic studies (Fleischer and McIntosh *this volume*). The various forms exhibit only slight variation in plumage, but differ strongly in bill morphology and vocalizations. They might all have been considered conspecific except for the fact that two of them are sympatric on Kauaʻi. The smaller of those, the Puaiohi (*M. palmeri*), has always been considered a separate species, but mid-century workers regarded all the others as conspecific. Pratt (1982) documented the vocal differences mentioned by early researchers and showed by playback experiments that these were effective isolating mechanisms, at least between the Kāmaʻo (*M. myadestinus*) of Kauaʻi and the ʻŌmaʻo (*M. obscurus*) of Hawaiʻi. The status of the then rare (and probably now extinct) form of Molokaʻi (see Reynolds and Snetsinger *this volume*) and the extinct forms of Oʻahu and Lānaʻi had to be assessed by inference. Pratt (1982) recognized the Olomaʻo (*M. lanaiensis*) as a species on the basis of its reportedly distinctive song. He found that the named subspecies on Lānaʻi (nominate) and Molokaʻi (*M. lanaiensis rutha*) could not be differentiated on the basis of plumage, but maintained the subspecies because of a reported difference in vocal behavior. Munro (1944) reported that the Molokaʻi bird sang and the Lānaʻi one did not. This difference disappeared, however, when Olomaʻo on Molokaʻi fell silent as they became rare and thinly distributed (pers. obs. based on reports of various field workers). Although the bird has been observed, its song has not been heard for decades. Because the Oʻahu specimens had been lost, Pratt (1982) only tentatively recognized the ʻĀmaui (*M. woahensis*) as an additional species. Following rediscovery of the two known speci-

mens of the latter, Olson (1996) re-evaluated the O'ahu form and considered it a subspecies of *M. lanaiensis* pending comparison with subfossil remains from Maui (which lost its solitaire before the arrival of ornithologists). He emended the name to *M. lanaiensis woahensis*. If this arrangement stands up to further scrutiny, it will represent a pattern of speciation unique in the Hawaiian Islands. Whether the three populations of Oloma'o are phylogenetic species is difficult to say, given our limited knowledge of them, but the O'ahu form has a stronger claim to status under the PSC than the other two because of its slightly different coloration and longer period of isolation (Moloka'i and Lāna'i were joined with Maui to form Maui Nui during the last glaciation).

'ELEPAIOS

Hawai'i's monarchine flycatchers comprise the endemic genus *Chasiempis* and are distributed on Kaua'i (*sclateri*), O'ahu (*ibidis*; formerly *gayi* but see Olson 1989), and Hawai'i (*sandwichensis*), but are enigmatically absent from the Maui Nui cluster. The three island forms are strikingly different in coloration, but their voices, ecology, and general behavior are rather similar. Also, *sandwichensis* exhibits considerable intraisland variation and has three named forms (nominate, *ridgwayi*, and *bryani*) with zones of intergradation (Pratt 1980). The three major forms were first lumped by Bryan and Greenway (1944), and until very recently no one had challenged that classification. Pratt (1980) regarded them as megasubspecies (Amadon and Short 1976) to emphasize the two different levels of differentiation. Reflecting their previously stated beliefs about distinctive island forms, Olson and James (1991) recognized three species without elaboration, and Olson (1996) maintained that classification. Conant et al. (1998) were the first to document behavioral and ecological differences among 'elepaios. They showed that the obvious and diagnostic plumage differences are reinforced by other, more subtle potential isolating mechanisms. Conant et al. (1998) recommended biological species status for the Kaua'i 'Elepaio (*C. sclateri*), O'ahu 'Elepaio (*C. ibidis*), and Hawai'i 'Elepaio (*C. sandwichensis*), and we endorse their conclusion.

Whether the three subspecies of the Hawai'i 'Elepaio would be considered phylogenetic species is problematical because some of their observed intergradation may be primary and clinal rather than secondary (Pratt 1980). The three forms were presumably in constant genetic contact in the recent past, but because of habitat destruction the very distinctive Mauna Kea population (*C. sandwichensis bryani*) is now an isolate (Scott et al. 1986) with distinctive ecology as well as plumage. Preliminary studies of one zone of intergradation between *C. sandwichensis bryani* and *C. sandwichensis ridgwayi* on the southeastern flank of the mountain have found evidence of secondary contact with possibly some assortative mating (E. VanderWerf, pers. comm.). Thus *C. sandwichensis bryani* may be in the very earliest stage of speciation by the BSC. In a PSC view, none of the three intraisland variants would be recognized taxonomically while they remained in genetic contact, but presumably "*C. bryani*" is now a phylogenetic species.

MILLERBIRDS

The only Old World warblers (Sylviinae) native to the Hawaiian Islands are restricted to the Northwestern Hawaiian Islands. The extinct Laysan Millerbird (*Acrocephalus familiaris*) and the endangered Nihoa Millerbird (*A. kingi*) have long been considered conspecific, but Olson and Ziegler (1995) split them without elaboration. Biological support for such a split is presented by Morin et al. (1997), although they maintained the single species. Certainly the differences between them are of the same degree as those existing between other Pacific island *Acrocephalus* (Pratt et al. 1987), and separate species status is probably warranted. They clearly are phylogenetic species. The question has more than academic significance because of recent proposals to introduce Nihoa Millerbirds to Laysan (M. P. Morin and S. L. Conant, pers. comms.). If they are a different species from the original Laysan bird, the proposal should perhaps be reconsidered.

DREPANIDINE FINCHES

The finches of Laysan and Nihoa present an instructive example of differing appearance as an indicator of biological isolating mechanisms. They differ strikingly in overall size as well as relative size of bill. Plumages are similar but diagnostically different with females more divergent than males. Amadon (1950) and other midcentury authors regarded them as conspecific, but Banks and Laybourne (1977) split them after reporting very different molt and maturational sequences. Other authors (e.g., Ely and Clapp 1973, Clapp et al. 1977) reported differences in nesting behavior, and Pratt (1979, 1996a) described vocal differences. Because of the many potential isolating mechanisms, all recent authors have recognized both Laysan Finch (*Telespiza cantans*) and Nihoa Finch (*T. ultima*) as both biological and phylogenetic species. Recently, proof of biological species status was reported by James and Olson (1991), who found

fossil remains of both species together on Moloka'i. Genetically, the two differ to the degree expected between pairs of closely related but biologically distinct species (Fleischer et al. 1998). These finches are one of many examples in which plumage differences that were dismissed by mid-century workers accurately predicted biological species status.

'AMAKIHIS

This is a group of small, black-lored olive green birds with down curved, short bills. The extinct Greater 'Amakihi (*Hemignathus sagittirostris*) of the island of Hawai'i had a longer, straighter bill and was probably a close relative, although some authors place it in the monotypic genus *Viridonia*. The 'Anianiau (*H. parvus*), a Kaua'i endemic, has a shorter, straighter bill and rather different coloration and, despite its occasional designation as "Lesser 'Amakihi," is probably not very closely related. Conant et al. (1998) reevaluated the morphological data and placed the 'Anianiau in the monotypic genus *Magumma*, and Fleischer et al. (1998) found genetic evidence to support their treatment. Both of these birds appear to have influenced the evolution of "typical" 'amakihis by character displacement: the Hawai'i form *H. virens virens* has the shortest bill in the complex, whereas the Kaua'i 'Amakihi (*H. kauaiensis*) has the longest (Pratt 1979). Mid-century authors regarded all typical 'amakihis as conspecific but almost always noted the much larger bill of the Kaua'i bird. The bill is both longer and heavier with virtually no overlap in measurements with any other form (Conant et al. 1998). The larger bill results in different feeding behavior and general ecology. Vocalizations of the Kaua'i 'Amakihi are also distinctive (Pratt et al. 1987, Pratt 1996b). Nevertheless, Berger (1981), and the AOU (1983), failed to follow Pratt's (1979) split. After biochemical data (Johnson et al. 1989, Tarr and Fleischer 1993) corroborated Pratt's findings, the split was accepted (AOU 1995), although the Check-list Committee cited no "traditional" data in support of the change. Conant et al. (1998) summarized the numerous potential isolating mechanisms of the Kaua'i 'Amakihi.

Surprisingly, Tarr and Fleischer's (1993) analysis of restriction-site variation in mtDNA showed that the O'ahu 'Amakihi (*H. chloris*), which had never been considered a biological species in modern times, was genetically distant from the morphologically, ecologically, and vocally similar 'amakihis of Maui Nui and Hawai'i. Furthermore, their evidence indicated that the O'ahu birds were the sister taxon to *H. kauaiensis* and therefore could not be conspecific those of Maui Nui and Hawai'i. On this basis, the AOU (1995) accorded the O'ahu 'Amakihi species status. Then Fleischer et al. (1998) altered their earlier branching-sequence hypothesis as the result of a new analysis involving sequencing of mtDNA. They now believe the O'ahu taxon is, after all, sister taxon to the Maui/Hawai'i forms. Still, the genetic distance between the O'ahu 'Amakihi and its sister taxa is of the same order of magnitude as that between the Kaua'i and Maui/Hawai'i forms, so the species status of the O'ahu 'Amakihi is valid. This example shows why caution is dictated in making taxonomic innovations based solely on a single genetic study. The AOU (1995) decision, though now upheld for different reasons, could easily have proven incorrect and may have been premature.

Interestingly, the only clue that the O'ahu bird might be a separate species prior to the DNA studies was its distinctive plumage. Again, the character considered least important by mid-century workers was, in fact, the most telling. Male O'ahu 'Amakihi are more yellow below and more strikingly two-toned than other 'amakihis, with the typical pale eyebrow reduced to a small supraloral spot. Females are even more distinctive in being much less yellow or olive than others and especially in retaining as adults the pale wingbars seen in juveniles of all forms. O'ahu 'Amakihi can be distinguished from those of other islands with virtually 100% accuracy on plumage characters alone. Vocal differences, such as a higher pitched song (Pratt 1996b), may also exist but have not been adequately investigated.

The same cannot be said of the remaining two forms. Separate names were originally proposed for the populations on Moloka'i, Lāna'i, and Maui, but both Amadon (1950) and Pratt (1979) found them inseparable. As a group they differ on average from Hawai'i birds in coloration and bill length (longer), but overlap is so broad that only extreme individuals could be diagnosed on characters alone (Pratt 1979). Thus they form a biological subspecies *H. virens wilsoni*. Whether practitioners of the PSC would consider this form a species is unclear because despite their obviously divergent histories, they are not completely diagnosable on phenotypic characters.

'AKIALOAS

'Akialoas look like giant 'amakihis with extremely long bills. All forms are extinct, making biological assessment difficult. Forms are known historically from Kaua'i, O'ahu, Lāna'i, and Hawai'i, but those from the central islands are known only from a handful of specimens. Their classification has produced a nomenclatural

tangle (Olson and James 1995), and their systematics is as yet unsettled. Most authors (e.g., Berger 1981, AOU 1983, Pratt et al. 1987, Sibley and Monroe 1990) follow Pratt (1979) in placing 'akialoas in a large genus *Hemignathus* defined on the basis of a suite of synapomorphies (Conant et al. 1998) in coloration, plumage sequence, and degree of sexual dimorphism, bill shape, and vocalizations, but Olson and James (1995) segregate them in their own genus *Akialoa.* (For a defense of "greater" *Hemignathus,* see Conant et al. 1998). At the species level, the situation is historically complicated. Bryan and Greenway (1944) lumped all forms, but Amadon (1950) recognized two species on the basis of the strikingly different relative bill lengths of the Kaua'i and Hawai'i forms. Having seen only two immature specimens of the Lāna'i form and none of the O'ahu one, he included both with the shorter-billed Hawai'i birds as *Hemignathus obscurus* and separated the Kaua'i 'Akialoa (*H. procerus* emended to *H. stejnegeri* by Olson and James 1995). Pratt (1979) and Olson and James (1982b) showed that the Lāna'i and O'ahu 'akialoas were actually closer to the Kaua'i 'Akialoa in bill length, and lumped all forms again. The AOU (1983), however, maintained Amadon's (1950) split. Pratt et al. (1987: 302) reviewed the situation and pointed out that if two species are recognized, the line of separation had to go between Lāna'i and Hawai'i with resultant nomenclatural changes. They suggested the names Lesser 'Akialoa (*H. obscurus*) for the Hawai'i bird and Greater 'Akialoa (*H. ellisianus*) for the other three forms; the AOU (1997) eventually adopted this two-species classification.

But the situation is complicated by recent paleontological data. James and Olson (1991) described a second species of 'akialoa, *H. upupirostris,* from Kaua'i and O'ahu that was sympatric with the historically known forms. Additionally Olson and James (1995) reported two sympatric prehistoric 'akialoas from Maui and a larger species sympatric with the Lesser 'Akialoa on Hawai'i, all as yet undescribed. Because the relationships of these forms are unresolved, Olson and James (1991, 1995) recommend recognition of all described forms as species: Hawai'i 'Akialoa (*Akialoa = Hemignathus obscura*), Maui Nui 'Akialoa (*A. lanaiensis*), O'ahu 'Akialoa (*A. ellisiana*), Kaua'i 'Akialoa (*A. stejnegeri*), and Hoopoe-billed 'Akialoa (*A. upupirostris*). Interestingly, plumage variation among the historically known forms is of the same degree as that in several other groups or pairs of species (e.g., 'amakihis, Hawaiian solitaires, O'ahu and Maui 'alauahios) and is nonclinal (for illustrations of all forms, see Pratt in

press). This case, perhaps more than any other, shows the folly of the old "if in doubt, lump" dictum. Obviously, 'akialoas cannot all be conspecific no matter what their interrelationships turn out to be. Presumably, the five species delimited by Olson and James (1995) can be considered phylogenetic as well as biological.

NUKUPU'US

The three island forms of Nukupu'u and the 'Akiapōlā'au comprise another group of honeycreepers with long, hooked bills. Each was described in the 1800s as a separate species: *Hemignathus lucidus* from O'ahu, *H. hanapepe* from Kaua'i, *H. affinis* from Maui, and *H. wilsoni* from Hawai'i. Bryan and Greenway (1944) combined all four, but Amadon (1950) separated the 'Akiapōlā'au because of its unique straight, rather than decurved, lower mandible. This taxonomy was supported by Olson and James' (1994) morphological studies and discovery of a specimen of Nukupu'u supposedly from Hawai'i (Olson and James 1994), indicating possible sympatry. Thus the Nukupu'u and 'Akiapōlā'au cannot even constitute a superspecies. Since Amadon's (1950) work, systematists have ignored the nukupu'u complex, and the AOU (1983) considered the Kaua'i and Maui forms as subspecies of *H. lucidus.* With all three taxa extinct or nearly so, their classification must depend on careful study of the fewer than 100 specimens scattered among a dozen museums from Honolulu to Berlin. Ongoing studies by T. K. Pratt and J. K. Lepson (pers. comm.) reveal that measurements and coloration consistently, and in some cases strikingly, distinguish the three nukupu'us from each other. The PSC would certainly consider them three species, but it is likely that by the criteria of the BSC the same outcome would be reached. Fleischer et al. (1998) identified the nukupu'us as a good test case for seeking a match between genetic divergence and sequence of colonizing new islands as they emerge down the Hawaiian chain.

'ALAUAHIOS

These small warblerlike birds of the genus *Paroreomyza* are confined to the central islands of O'ahu and the Maui Nui complex. Despite extreme interisland color variation that ranged from brilliant scarlet to dull gray, Amadon (1950) considered the four named forms of *Paroreomyza* conspecific with the two species of *Oreomystis* from Kaua'i and Hawai'i. Certainly, the inclusion of the brilliant scarlet Kākāwahie (*P. flammea*) of Moloka'i, with yellow and green birds from O'ahu, Maui, and Lāna'i, should have been a red flag indicating the existence of more than one species. But Amadon

(1950:166) stated that "variation from yellow to red is obviously accomplished readily and need not be considered as necessarily indicating specific difference." Lumping the Moloka'i, Lāna'i, and Maui forms meant that their striking differences had to have evolved since the breakup of Maui Nui, a period we now know to have been as little as 10,000 years. In fairness, we should point out that such geological information was unavailable in the period in which Amadon (1950) worked. Pratt (1979) hypothesized that the fact that the Kākāwahie was the largest *Paroreomyza* and had the heaviest bill, and the Maui/Lāna'i form was the smallest with the smallest bill suggested character displacement during a period of sympatry on Maui Nui. Olson and James (1982b) found paleontological evidence of such sympatry and agreed that *Paroreomyza* had to comprise more than one species. The other two Maui Nui forms, known historically from Lāna'i (*montana*) and Maui (*newtoni*), are very similar, differing only in that the Lāna'i birds are slightly brighter dorsally. No one since Bryan and Greenway (1944) has ever suggested that they are other than a single biological species, the Maui 'Alauahio (*P. montana*), but whether they qualify as phylogenetic species is problematical. The slight but consistent color differences they exhibit, rather than evolving in 10,000 years, may represent fragments of a former interisland cline, such as that shown by 'elepaios on Hawai'i (Pratt 1980), in which paler birds inhabited the lower and drier parts of Maui Nui and darker ones the rain forests of Haleakalā. The relatively few specimens from west Maui do appear somewhat intermediate in dorsal coloration. Questions such as at what point the fragments of a former cline become phylogenetic species show that the PSC is not free of subjective judgments (Collar 1997, Snow 1997). The O'ahu 'Alauahio (*P. maculata*), now possibly extinct, was considered conspecific with the Maui/Lāna'i bird by Olson and James (1982b), but later (James and Olson 1991) they joined other authors in separating it. Its bill is intermediate between those of *P. flammea* and *P. montana* but the coloration of both males and females is clearly different and diagnostic (Pratt et al. 1987).

'ĀKEPA

Representatives of the drepanidine "crossbills" (*Loxops*) were known from Kaua'i, O'ahu, Maui, and Hawai'i, with a distinct taxon on each island. Most forms are small birds with yellow or gray bills, the males red or orange-yellow, the females gray-green, and neither sex with any bold black patterning or other markings. The Kaua'i form is so distinctive that it

was at first placed in its own genus *Chrysomitridops* (Wilson 1890). It is larger, with a proportionally larger blue bill. Both sexes are patterned in yellow and green with a prominent dark mask and pale forehead, although males are brighter than females. Bryan and Greenway (1944) recognized two species of *Loxops*: *L. caeruleirostris* ('Akeke'e) for the Kaua'i form, and *L. coccineus* ('Ākepa) for the O'ahu, Maui, and Hawai'i forms. Despite the striking plumage differences, which he did not consider great, Amadon (1950) believed it "by no means improbable that they all would interbreed freely were their ranges to overlap" and considered them all conspecific. Pratt (1979) showed that the plumage and bill differences were paralleled by others in vocalizations, but his recommendation of a return to Bryan and Greenway's classification was not adopted by Berger (1981). Thus the AOU (1983) maintained Amadon's single species of 'Akepa. Further research by Pratt (1989) and others (summarized by Lepson and Freed 1997, Lepson and Pratt 1997) revealed fundamental differences in nest construction and ecology. As a result, the AOU (1991) finally recognized the 'Akeke'e as a separate species. This is yet another case in which plumage differences predicted potential isolating mechanisms in other aspects of the birds' biology.

The status of the three named forms of 'Ākepa is less clear because the O'ahu form (*wolstenholmei*) is extinct and known from only a few specimens, and the Maui one (*ochracea*) is very rare if not extinct and was never common in historical times. Males of each form can be distinguished with near 100% accuracy on coloration alone, but females are more difficult to identify visually. Whether the color differences are sufficient isolating mechanisms, in the absence of other data, for recognition of O'ahu and Maui 'ākepas as biological species is moot (Pratt 1989), and their status as phylogenetic species is likewise unclear. Perhaps biochemical data, as yet unavailable, will reveal clearer differences.

'APAPANES

The 'Apapane (*Himatione sanguinea*) is found in montane forests throughout the main Hawaiian Islands with no geographic variation. A now extinct related form on low, unforested Laysan was long regarded as a subspecies, but Olson and James (1982b, 1991) regarded it as a species (*H. freethi*) without comment. Schlanger and Gillett (1976) had considered the Laysan Honeycreeper a relict of the days when Laysan was a high island, but Olson and Ziegler (1995) believed it to be a colonizer from the main islands that has speciated on Laysan. With distinctive coloration (orangish rather than bright

crimson body feathering, dingy pale brown rather than white undertail coverts), a shorter bill, and distinctive cranial osteology, it is unquestionably a species under the PSC. Olson and Ziegler (1995) split it on the basis of unspecified osteological differences. Overlooked in most discussions are several obvious potential isolating mechanisms of the Laysan Honeycreeper: distinctive song and song phenology (Rothschild 1893–1900); different feeding behavior (including often walking on the ground to forage among flowers; Fisher 1903); different nest placement and structure (Schauinsland 1899, Bailey 1956); and, most obviously, totally different habitat. A previously unreported anatomical difference, noticed by H. Douglas Pratt in preparing illustrations (Pratt in press) is that the Laysan bird has differently shaped tips to its primaries, lacking or possessing in very reduced form the truncation that produces the 'Apapane's wing noise. It now appears highly unlikely that these birds, adapted to two different worlds, could successfully interbreed, much less do so freely. Although Fancy and Ralph (1997) considered it a subspecies, future authors, including Pratt (in press), will likely split it, bringing the BSC and PSC into agreement on 'apapanes.

SUMMARY

A wealth of new morphological, behavioral, ecological, and genetic data have dramatically changed the systematics and taxonomy of Hawaiian birds. For example, a comparison of Amadon's (1950) classification of Hawaiian honeycreepers with the one we outline above shows that for 40 named taxa, the number of biological species (if all that have been proposed are accepted) swells from 23 to between 34 and 38, the final figure depending upon the classification of 'ākepas and nukupu'us. Correspondingly, the number of taxa designated as subspecies has dwindled from 17 to 6 or as few as 2! These two poorly differentiated taxa (Maui Nui 'amakihi and Lāna'i 'alauahio) amount to small pickings indeed over which to debate the BSC versus PSC. The status of the 25 undifferentiated, and therefore unnamed, island populations ('Ō'ū [*Psittirostra psittacea*], 'Apapane, and 'I'iwi on six islands, the three Maui Nui 'amakihis, and 'Ākohekohe [*Palmeria dolei*] on Moloka'i and Maui) does not change. Likewise, the 19 named populations of songbirds that are not honeycreepers have increased from 10 to 15 species, with one subspecies sunk, one in dispute, and one subspecies of Hawai'i 'Elepaio intergrading clinally with the nominate race, and another isolated but with limited and, as yet, little understood secondary contact.

Why is interisland endemism at the species level so striking in Hawai'i? The answer lies partly in the geographical setting: the Hawaiian Archipelago comprises moderately large islands with relatively few offshore islets and atolls inhabitable by landbirds. Distances between main island groups average 58 km, a formidable crossing for most sedentary songbirds. Birds newly colonizing one island from another could become quickly isolated genetically by weight of numbers. Because the pool of potential immigrants on neighboring islands is much smaller than would be the case if the source area were a continent or much larger island, conspecifics would arrive infrequently, and in low numbers they would enter a resident population numbering in the hundreds of thousands at least. Thus, adaptation to local conditions would proceed almost immediately without significant genetic input from ancestral populations, and evolution of endemic forms could proceed rapidly (Freed et al. 1987a).

Grant (1994) found that Hawaiian native finches exhibit less variability in bill measurements than Galápagos finches and attributed the difference to greater specialization in feeding habits, greater genetic distance among species, and near absence of hybridization. All of these comparisons relate to the very different geologic history of Hawai'i (Fleischer et al. 1998) as compared to the Galápagos, a tighter cluster of islands of relatively much younger age (Grant 1986). Species saturation was achieved in both archipelagos primarily by adaptive radiation of descendants of very few successful transoceanic colonizations (Diamond 1977, Juvik and Austring 1979), but levels of differentiation fit each unique situation. Because Hawaiian bird populations become genetically isolated virtually from the start, they can quickly evolve differences in plumage and voice, both of which are effective isolating mechanisms. Thus they soon become both biological and phylogenetic species, with only a brief period of intermediacy. The most straightforward case of this has been proposed by Fleischer et al. (1998), who provide genetic data indicating that the four 'amakihis originated from interisland colonizations that followed shortly after emergence of new islands in a conveyor-belt fashion as the archipelago moved across a mid-ocean "hot spot."

Nevertheless, interisland colonizations in Hawai'i obviously proceeded in both directions to produce the species-rich faunas of each island as well as the several examples of intra-archipelagic double invasions (*Myadestes* on Kaua'i, *Paroreomyza* on Maui Nui, 'akialoas on several islands, etc.). Also, some Hawaiian birds are widespread in the islands with no detectable interisland variation. The three Maui Nui 'amakih-

is and the two populations of 'Ākohekohe are fragments that were panmictic during recent periods of lower sea level, but other undifferentiated populations belong to species that disperse widely with relatively frequent intra- and inter-island movements. Despite huge historical populations and the widest geographic range possible, two of those, the 'Apapane and 'I'iwi, are among the least genetically diverse of honeycreepers (Tarr and Fleischer 1995, Jarvi et al. *this volume*). Both may have suffered recent severe genetic bottlenecks then expanded their populations and ranges, and the recently extinct 'Ō'ū, which has not been investigated genetically, probably exhibited the same pattern. Absence of interisland variability in five species of Hawaiian waterfowl reflects large scale interisland movements and reproductively cohesive populations, as confirmed by banding studies (Engilis and Pratt 1993). The fact that far-ranging species move in both directions shows that not all speciation in Hawai'i has resulted from Fleischer et al.'s (1998) conveyor belt. Virtually all oceanic island avifaunas, though always depauperate in number of species as compared to continental areas, have very high levels of endemism (Stattersfield et al. 1998). Isolated, geologically old archipelagos with large interisland distances, such as the Marianas, Carolines, Tuamotus, Marquesas, and many others, can be expected to exhibit species-level endemism comparable to that of Hawai'i as their avifaunas are re-examined for the presence of potential isolating mechanisms.

Reflecting upon the history of avian systematics and taxonomy in Hawai'i, we repeatedly see that coloration, long regarded as relatively insignificant in determining species limits, may be the first and most reliable indicator. Consistent, unique vocalizations or discretely different bill size or shape also virtually always correspond to interspecific boundaries. In every case in which species limits determined on these bases have been tested by biochemical or paleontological data, decisions based on an enlightened use of traditional phenotypic investigations have been upheld. Far from being single characters that identify species, appearance and vocalizations predict where other more subtle isolating mechanisms exist. Because the Hawaiian Islands could well be regarded as the quintessential oceanic archipelago, the lesson is clear: island birds that look or sound different are very unlikely to be conspecific. Allopatric populations that have only average rather than diagnostic differences are little diverged genetically and can be recognized as subspecies. The old prejudice that similar allopatric populations should be classed as subspecies until proven otherwise has not

withstood the test of actual practice on oceanic islands, and the underlying assumptions that produced it must now be questioned or discarded, at least for insular taxa. Properly applied to island endemics, the BSC produces species limits comparable to those of the PSC, and further allows for the recognition of subspecies, a category the PSC would essentially eliminate (Snow 1997, Zink 1997). Because the taxonomy of island birds elsewhere in the tropical Pacific is still based largely on studies done in the first half of the century, we can anticipate a major increase in the number of biological species recognized in the region when the data are re-evaluated with the insights gained from the Hawaiian experience. However, we caution future workers not to follow their predecessors in making taxonomic changes based solely on inference.

SPECIES CONCEPTS AND CONSERVATION

Our paper began with, and was largely prompted by, the conflict between the BSC and PSC as debated by Hazevoet (1996) and Collar (1996). Because of the Hawaiian Islands' extremes of location and geologic history, their birds define the issue better than any other isolated insular avifauna. However, the outcome is unexpected: most diagnosable, allopatric taxa can be argued to be biological species on the criteria that they either (1) are not sibling species, or (2) were formerly reproductively isolated in sympatry but now live apart in contracted, relictual ranges, or (3) are genetically and morphologically distinct to a degree similar to related biological species living in sympatry. A few recognizable taxa do not qualify by these criteria, but we question whether these are either truly diagnosable (e.g., Maui 'Amakihi) or evolutionary units (three subspecies of Hawai'i 'Elepaio).

Changing views of biological species limits in Hawai'i has had surprisingly little impact on the course of conservation efforts because the U.S. Endangered Species Act of 1973 does not focus on, nor limit endangered status to, full species only. No named Hawaiian taxon deserving increased protection was omitted from the list because of its designation as a subspecies. Although undiagnosable and unnamed populations were not considered federally, a few were included in an otherwise parallel list of populations protected by the state of Hawai'i. Actual recovery efforts have been less encompassing, however, and reflect the need to engage in triage. Faced with a depressing list of 32 endangered birds, 13 of them on the brink of extinction, state and federal agencies focused their limited per-

sonnel and funding on managing tractable species such as Nēnē (*Branta sandvicensis*), Koloa, Laysan Duck, Newell's Shearwater (*Puffinus auricularis newelli*), and Hawaiian Crow, or 'Alalā. Beginning in the 1980s, recovery efforts began to focus on restoration and protection of habitat, to the benefit of entire bird communities. In the mid-1990s, special programs were initiated for two more endangered birds, the Puaiohi and Po'ouli (*Melamprosops phaeosoma*). The fact that these projects were funded, and not one to restore the Hawai'i 'Amakihi on Moloka'i, shows that even with a program that focuses on populations, conservationists' attentions in Hawai'i as well as worldwide (Collar 1997) are inevitably closely tied to the species concept.

On what few phenotypic or genetic characters should one describe a phylogenetic species? Recent introductions of the endangered Laysan Finch, with subsequent rapid evolution in bill size (Conant 1988a), present proponents of the PSC with some yet-to-be resolved issues. For example, do diagnosable populations that evolved through founder effects and local adaptation in only two decades qualify as phylogenetic species? If not, at what point would they? Further, if introductions result in the creation of populations that are diagnosably distinct (Conant 1988b), and therefore are "new" phylogenetic species, how can this technique contribute to the conservation of the parent population? A related situation is that some introduced birds in Hawai'i, such as House Sparrows (*Passer domesticus,* Johnston and Selander 1964), may already be phenotypically diagnosable. Conservationists are unlikely to regard such introduced populations as endemic phylogenetic species. As Fleischer (1998) has proposed, artificially fragmented populations of endangered species in Hawai'i could become diagnosable at the molecular level through genetic drift and presumably therefore qualify as phylogenetic species. Recovery actions cannot save endangered species when new "species" are created from recently fragmented or introduced populations.

A second problem with the PSC is the possibility that species can appear and then disappear in a reticulate fashion (Zink 1997) because their delimitation does not require genetic isolation. Consider again the example of the 'Elepaio on Mauna Kea. Because its range is almost exactly congruent with that of the endangered Palila (*Loxioides bailleui*), it will be strongly affected by efforts to restore habitat for that species. If plans to connect the upper forests of Mauna Kea (the range of *Chasiempis sandwichensis bryani*) with the rain forests of Hakalau Forest National Wildlife Refuge (where *C. s.*

ridgwayi occurs) succeed, broad contact between two now isolated forms of 'Elepaio, each a potential phylogenic species, could be re-established, resulting in extensive interbreeding. As our Hawaiian examples show, automatic splitting of all populations with diagnosable differences (Cracraft 1997) under the PSC is not as simple in practice as it sounds (Collar 1997) and could undermine the use of such time-honored and successful management techniques as reintroduction and habitat restoration. We agree with Collar (1997) that the PSC would trivialize the species concept and severely stretch limited resources without providing any rational basis for formulating conservation priorities.

Even when, as in the United States, conservation authorities are enlightened about the sometimes arbitrary way that species limits are applied and protect endangered populations of whatever status, alpha taxonomy is still far more than just an academic exercise. Much more is involved in the conservation of island birds than just the decision as to which ones are officially listed as endangered. Often, the only information available on birds of remote islands comes from recreational birders, who seek out endemic species and generally ignore those that are "just subspecies" (see for example Pratt 1990, Wauer 1990a,b). One can argue the rationality of that mindset, but no one can deny that in the eyes of recreational birders, conservationists, and the general public, species status has almost magical properties. It is quite possible that many island species worldwide could become endangered or extinct without anyone noticing because birders ignored forms ornithologists called subspecies. Witness the case of the Island Scrub-jay (*Aphelocoma insularis*) endemic to Santa Cruz Island off California. Few birders were even aware of its existence before it was recognized as a species, but almost immediately afterwards, a small industry developed for the sole purpose of enabling people to see the bird (Atwood and Collins 1997). Had this been an endangered species, we believe the increased population monitoring would have contributed data valuable to the bird's recovery. An example of the latter phenomenon is the case of Bicknell's Thrush (*Catharus bicknelli*). No one voiced concern about its conservation status until it was elevated to species status (Thurston 1998).

Attention from birders may be important even before a bird is listed as endangered. For example, the O'ahu 'Elepaio was rarely sought out except on Christmas Bird Counts because, as a subspecies, it did not score differently with birders. Thus, its sudden population crash in the past two decades (Pratt 1994) went largely unnoticed. Now that it is a candidate for species status

(Conant et al. 1998) as well as for listing as an endangered species (Conant 1995), birders have become more interested (Pratt 1993), and research on the species has resumed (VanderWerf et al. 1997, VanderWerf 1998a). Now, young visitors to Honolulu's Hawai'i Nature Center have their own species of 'Elepaio and 'amakihi on which to focus their local pride and interest. The fact that ecotourists would visit a locality for the sole reason of observing an endemic bird, or that school children take pride in and learn about their local avian specialty, increases public awareness and interest, especially in small countries with limited resources (Wille 1991) in whose hands the fate of many species ultimately lies.

Collar (1997) cited the numerous valuable contributions of recreational birders to taxonomy through their worldwide travel, tape recording, photography, and note taking on breeding biology and general natural history and behavior. Janzen et al. (1993) even refer to birders as "parataxonomists" in recognition of their contributions. We support Collar's (1997) observation that birders are today the ornithologist's most important ally in clarifying species limits and conservation status of birds, and managers of parks and reserves should encourage and facilitate birding rather than discourage it as has all too often been the case in some Hawaiian reserves (Pratt 1993, pers. obs.).

Conservationists and the general public need a rational and observable basis for species recognition. By increasing the number of trivial look-alike "species" to a bewildering and overwhelming degree, adoption of the PSC could destroy scientific credibility with governmental officials and the general public who have little interest in or knowledge of the subtleties of taxonomic philosophy. The BSC makes intuitive sense through its use of observable isolating mechanisms and the subspecies category for intermediate stages, and provides a credible basis for conservation strategies. Although Hazevoet (1996) may be correct that "taxonomic neglect" promotes extinction of island birds, his proposed solution of switching to the PSC will actually increase such neglect by augmenting the taxonomic workload, providing a confused taxonomy for conservation practices (Collar 1997), and recognizing "species" that defy common sense. Besides, his main goal (increasing the number of recognized species on islands) can be accomplished within the BSC without all of the disadvantages of the PSC. Proper application of the BSC, including a long overdue review of the taxonomic status of island taxa worldwide, will do far more for avian conservation than adoption of the phylogenetic species concept.

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