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## Systematics

## SYSTEMATICS—INTRODUCTION

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Unreachable to amphibians, reptiles, and most land mammals, the Hawaiian Archipelago has been colonized naturally only by the most vagile of vertebrates. The native terrestrial vertebrates of the islands consist entirely of birds and a couple of species of bats. Indeed, the islands are so remote from other complex terrestrial ecosystems that even birds have difficulty establishing themselves. The native birds that dwell as year-round residents in Hawai'i's terrestrial and wetland habitats can be traced to as few as 20 colonizing species (James 1991).

These successful colonists speciated and evolved in the islands to give rise to an avifauna with over 100 resident species. Sadly, many extraordinary species are extinct and known only through fossil remains. The fossil species include large flightless waterfowl, flightless woodland ibises, many flightless rails, a variety of raptors, three or four large crows, and diverse species of Hawaiian honeycreepers or drepanidines (Olson and James 1991, James and Olson 1991). Despite these losses, a host of remarkable endemic species survived in the islands long enough to be studied and appreciated by ornithologists. Most of the survivors are passerine forest birds, including many species in the adaptive radiation of drepanidines. Besides passerines, the only birds that escaped early extinction are a hawk, an owl that is probably a recent colonist, the Hawaiian Goose (*Branta sandvicensis*), and a variety of smaller waterbirds (including some that had moved into terrestrial habitats).

The Hawaiian Islands are one of the world's hottest of hot spots for the extinction of birds. Twenty-four endemic species of birds have become extinct there since 1778, and another eight are either recently extinct or imminently threatened (these figures vary slightly according to the taxonomy followed; Pratt 1994). In addition, the thirty-five fossil species that have been described and approximately twenty that are currently waiting to be described are thought to have disappeared mainly in the prehistoric period of human settlement (Olson and James 1991, James and Olson 1991). The causes of the decline and extinction of so many birds include habitat degradation and loss, introduced pathogens such as avian malaria and poxvirus, and introduced predators such as the small Indian mongoose (*Herpestes auropunctatus*).

Hawai'i's avifauna has garnered considerable

attention from ecologists and evolutionary biologists. The extreme geographic isolation of the resident birds, the clear-cut barriers to dispersal within the archipelago (water gaps between islands), and the roughly linear progression of island ages (the islands to the northwest being older than those to the southeast), provide a relatively simple setting where the processes that underlie modern biogeographic patterns may be relatively accessible to inference. Classic papers on Hawaiian birds have addressed such topics as the allopatric model of speciation (Amadon 1950), character displacement (Bock 1970), dynamic equilibrium theory in island biogeography (Juvik and Aустring 1979), and the processes underlying macroevolutionary change (Amadon 1950, Bock 1970, 1979). The basic information relied upon in these studies is the systematics and distribution of Hawai'i's endemic birds.

Formal study of the systematics and distribution of Hawai'i's birds began in the late eighteenth century, when the specimens collected on Captain James Cook's third voyage (in 1778–1779) reached England. The century that followed saw the steady addition of new species from Hawai'i, as subsequent voyages returned to western ports with specimens, and later, various foreigners took up residence in the islands and made their own collections (Olson and James 1991, 1994a). The lure of discovery finally inspired a period of intense exploration of the islands aimed specifically at collecting and describing the native birds and other endemic organisms. Between 1887 and 1902, the islands' birds were thoroughly sampled by Scott Wilson, R. C. L. Perkins, and especially by Lord Walter Rothschild's collectors Henry Palmer, G. C. Munro, and E. Wolstenholme, followed shortly by H. W. Henshaw (Olson and James 1994a). These efforts lead to three comprehensive publications (Rothschild 1893–1900, Wilson and Evans 1890–1899, Henshaw 1902a, and Perkins 1903).

Decades after this age of exploration and discovery, papers on the systematics and evolution of Hawaiian birds began to appear with regularity again. Miller (1937) studied anatomical adaptations for terrestriality in the Hawaiian Goose, while most other authors focused on the adaptive radiation of drepanidines (e.g., Amadon (1950) on eclectic systematics and speciation, Richards and Bock (1973) on functional anatomy, Raikow (1977) on myology, Sibley and

Ahlfquist (1982) on DNA-DNA hybridization, Johnson et al. (1989) on protein electrophoresis, Tarr and Fleischer (1993, 1995) on mitochondrial DNA). Also, beginning in the 1970s, fossil birds were being found in Hawai'i with surprising frequency (e.g., Olson and Wetmore 1976, Olson and James 1982b, 1984, James et al. 1987, Olson and James 1991, James and Olson 1991).

As the papers in this volume attest, more effort is now focused on the systematics of Hawaiian birds than at any time since the 1890s. This coincides with a renaissance in phylogenetic research, spurred by advances in methods of analysis and by the technological revolution in molecular genetics. Hawaiian birds attract extra attention because of the urgency of studying species threatened with extinction, and the need to place the new fossil species in an evolutionary context.

The most active program in molecular genetics of Hawaiian birds is that of Robert C. Fleischer and his collaborators. A long-term goal of this program is to study the evolutionary genetics of each endemic lineage of Hawaiian birds. Fortunately, even the extinct fossil lineages can be studied, through amplification and sequencing of DNA fragments from fossil bones (Cooper et al. 1996, Paxinos 1998, Sorenson et al. 1999). By including appropriate outgroups and assuming a molecular clock based in part on earlier Hawaiian drepanidine research (Fleischer et al. 1998), Fleischer and McIntosh (*this volume*) are able to estimate the length of time that each lineage has been present in the islands. Their paper offers a glimpse of the types of questions we can answer with molecular genetics that we could only speculate about before, and also hints at the large number of molecular genetic studies of Hawaiian birds that are currently in progress.

The value of genetics and systematics to conservation of endangered species is exemplified by Judith Rhymer's contribution on the endangered Hawaiian Duck (*Anas wyvilliana*) and Laysan Duck (*Anas laysanensis*). Using a battery of molecular genetic techniques, Rhymer addresses several pressing questions that will affect the management plans for these two species. First, she shows that the Hawaiian and Laysan Ducks have separate evolutionary histories and certainly merit species rather than subspecies status. She also cites anecdotal evidence that Laysan Ducks rarely hybridize in captivity. Combined with her previous collaborative research showing that the former range of the Laysan Duck included the main Hawaiian islands (Cooper et al. 1996), this lays the groundwork for possible reintroduction of the Laysan Duck

in the main islands. Rhymer also develops molecular markers that can be used to monitor the extent of hybridization between Hawaiian Ducks and introduced Mallards. Such hybridization threatens the survival of Hawaiian Ducks on O'ahu but, so far, not on Kaua'i. The information and genetic tools provided by Rhymer will be indispensable in formulating management plans for these rare species.

Phylogenetic analysis can also contribute to conservation planning by providing a way to assess the phylogenetic "distinctiveness" of threatened species. The number of threatened species is disproportionate to the funding that is available to help them, forcing managers to make hard decisions about which species to focus upon. One objective of such decisions is to preserve evolutionary diversity. It is consequently useful to know to what degree a particular threatened species differs from its surviving relatives. The study by Fleischer et al. in this volume assesses the evolutionary relationships and phylogenetic distinctiveness of an endangered drepanidine, the Po'ouli (*Melanprosops phaeosoma*), using genetic and osteological data. Both datasets place the Po'ouli within the clade of drepanidines. However, an index of distinctiveness applied to both datasets also indicates that the Po'ouli is very different from other living drepanidines, both genetically and morphologically. Fleischer et al. conclude that saving the Po'ouli from imminent extinction would be well worth the effort from this perspective.

Douglas Pratt, who contributes a cladistic analysis of the drepanidine radiation based on eclectic phenotypic characters, recommends that no changes be made to his taxonomy in the light of molecular genetic data, which he regards as preliminary, inconsistent, and in the case of mitochondrial DNA sequences, perhaps giving a false signal due to hybridization (although there are no confirmed hybrids among the drepanidines). Where his results conflict with my dissertation research on drepanidine osteology (James 1998), he describes my work as perhaps based on superficial resemblances and illustrative of the weaknesses of "single character or single-complex analyses." My results are remarkably congruent with Raikow's (1977) early cladistic analysis of myology and external anatomy, but Pratt also considers Raikow's character analysis to be vague where it conflicts with his own results. I can only urge readers to consult the original sources and form their own opinions.

Two corrections should be made here, however. Pratt (p. 88, this volume) implies that my tree topologies bring together unrelated species with similar bill shapes in the red-and-black plumaged group and the green plumaged group.

Actually, my analysis (James 1998) recognized the red-and-black birds as a clade, including the full range of bill morphologies from “finch-like” to long and sickled. None of the green birds with parallel bill morphologies joined this clade. Also, whereas Pratt states that James and Olson (1991) previously suggested lumping *Loxioides* and *Chloridops*, we actually wrote that future research may justify merging *Loxioides* with *Telespiza*.

The contribution on species concepts by Pratt and Pratt is very much in the tradition of Pratt's dissertation (Pratt 1979), an eclectic assessment of alpha taxonomy with emphasis on vocalizations, plumages, and behavior as potential isolating mechanisms. Many allopatric populations of island birds were long ago demoted to subspecies by Ernst Mayr and others who embraced his biological species concept. For example, in his dissertation, which was supervised by Mayr, Amadon (1950) applied the biological species concept to the drepanidines and came up with many fewer species than were recognized by the late 19<sup>th</sup> century authorities (see Pratt 1979). However, Pratt and Pratt argue that Amadon and Mayr often erred in applying their own species concept, or simply lacked information that would have kept them from lumping. Properly applied, they feel that the biological species concept would elevate most of Amadon's allopatric subspecies to full species status. Although they stress potential isolating mechanisms in their evaluations, their way of applying the biological and phylogenetic species concepts result in very similar taxonomic lists. While the debate over

species concepts continues, non-taxonomists can take comfort in knowing that, with the growth of knowledge about Hawaiian birds, the choice of species concept now appears to have little effect on the species-level taxa that are recognized.

This is an exciting time for evolutionary and biogeographic studies of Hawai'i's avifauna. The abundance of fossils enables us to study morphological change through time, calculate rates of species turnover and extinction using data with real time depth, and gain insight into the former ranges and habitat preferences of endangered species. With ancient DNA we can identify fossil species, place them on phylogenetic trees, and even study their population genetics over long stretches of time. Because the genetic divergences between isolated island populations cannot be older than the islands themselves, multiple local calibrations of the minimum rates of DNA sequence change are possible in Hawai'i. Putting aside differences of opinion on whether genetic or phenotypic data are best for phylogenetic analysis (see Pratt, *this volume*, and Fleischer and McIntosh, *this volume*), phylogenetic hypotheses can be strengthened and insights into character evolution can be gained through comparison of data and results from these two types of studies. The confluence of knowledge from these various sources is leading to a much improved picture of change in Hawai'i's avifauna through time. The growth of information from genetics, phylogenetics, and paleontology is contributing not only to basic knowledge, but in important ways to conservation management as well.