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CHAPTER 7

REVISITING SPECIES AND SUBSPECIES OF ISLAND BIRDS FOR A BETTER ASSESSMENT OF BIODIVERSITY

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Abstract.—Outdated and overly lumped alpha taxonomy among the world's island birds has serious consequences for scientific research and conservation. The underestimation of biodiversity on islands obscures their role as speciation laboratories, distorts sampling in genetic studies, biases research planning, leads to neglect of endangered island species mistakenly classified as subspecies, and reduces potentially valuable information that might be gathered by recreational birders. Suggestions such as abandoning the biological species concept and the subspecies category in favor of the phylogenetic species concept create new problems and disrupt widely understood terminology. I review avian taxonomic history in the Hawaiian Islands, speciation patterns in Pacific island pigeons and doves, and patterns of variation in the widespread Polynesian Starling (*Aplonis tabuensis*) to demonstrate that the biological species concept, if applied with consideration of potential isolating mechanisms, vagility, and degree of geographic isolation, along with the judicious use of subspecies, produces hypotheses of island biodiversity that meet research and conservation needs. I suggest a thought process for evaluating biological species limits in island birds that is less subjective and more repeatable than previous methods, and use the Fiji Shrikebill (*Clytorhynchus vitiensis*) as a working example. A review of taxonomic history in the Bridled White-eye (*Zosterops conspicillatus*) complex in Micronesia shows that while genetic data are useful for testing hypotheses of species limits based on other data, alone they are insufficient for the purpose and should not be considered essential in species revisions.

Key words: biological species concept, island birds, isolating mechanisms, speciation, subspecies, taxonomy.

Revisitar las Especies y Subespecies de Aves de Islas para una Mejor Evaluación de la Biodiversidad

Resumen.—La taxonomía alfa desactualizada y exageradamente agrupada de las aves isleñas del mundo tiene serias consecuencias para la investigación científica y la conservación. La subestimación de la biodiversidad de las islas oscurece su papel como laboratorios de especiación, distorsiona los muestreos en los estudios genéticos, sesga el planeamiento de las investigaciones, lleva a desatender especies isleñas amenazadas clasificadas erróneamente como subespecies y reduce la cantidad de información potencialmente valiosa que puede ser recolectada por los observadores de aves. Las sugerencias como el abandono del concepto biológico de especie y de la categoría de subespecie a favor del concepto filogenético de especie crean nuevos problemas y alteran la terminología ampliamente utilizada. Revisé la historia taxonómica de las aves de las Islas de Hawái, los patrones de especiación en las palomas de las islas del Pacífico y los patrones de variación en la especie ampliamente distribuida *Aplonis tabuensis* para demostrar que el concepto biológico de especie, si se aplica considerando los mecanismos potenciales de aislamiento, la capacidad de dispersión y el grado de

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aislamiento geográfico, junto con el uso juicioso del concepto de subespecie, genera hipótesis sobre la biodiversidad de islas que contemplan las necesidades de investigación y conservación. Sugiero un proceso razonado para evaluar los limites biológicos de las especies en las aves isleñas que es menos subjetivo y más repetible que los métodos anteriores, y empleo a la especie *Clytorhynchus vitiensis* como un ejemplo de trabajo. Una revisión de la historia taxonómica en el complejo de *Zosterops conspicillatus* en Micronesia muestra que mientras los datos genéticos son útiles para evaluar hipótesis de los límites entre especies basados en otros datos, por separado son insuficientes para este propósito y no deben ser considerados esenciales en las revisiones de las especies.

WE WHO STUDY the world's island birds are burdened with an outdated and overlumped taxonomy that has serious consequences for the assessment and conservation of biodiversity (Collar 2005). Many island endemics that would qualify as biological species by modern standards remain subsumed in what might be called "megaspecies" that reflect the biases of mid-20th-century taxonomy (Collar 1997, 2005; Pratt and Pratt 2001; Chikara 2002; Rheindt and Hutchinson 2007). Despite our increasing knowledge of these birds, most species limits among most island taxa have not been reassessed in the light of new information. A taxonomy that would not pass muster by modern standards remains entrenched, and efforts to alter it often meet resistance. This problem has serious consequences for both science and conservation. Using a series of examples, I discuss the history of species-level taxonomy among island birds and the special nature of allopatry on islands, and suggest a revised methodology for evaluating biological species and subspecies limits among oceanic island birds. I also make a plea for authors and editors not to denigrate species revisions that are based solely on phenotypic characters.

THE PROBLEM AS ILLUSTRATED BY MICRONESIAN FLYCATCHERS (*MYIAGRA*)

In his influential field guide *Birds of the Southwest Pacific*, Mayr (1945) lumped four previously recognized species of flycatchers in Micronesia (*Myiagra erythrops*, from Palau; *M. freycineti*, from Guam; *M. oceanica*, from Chuuk; and *M. pluto*, from Pohnpei) as subspecies of *M. oceanica*, but he observed that they were "so distinct that they might also be considered 4 different species" (Mayr 1945:296). Mayr had no knowledge of these birds in life, and he presented no evidence that they form a monophyletic group, let alone one species. Baker (1951) noted differences in overall size, color, and bill size but accepted Mayr's one-species taxonomy uncritically and thus set the pattern for decades.

In *A Field Guide to the Birds of Hawaii and the Tropical Pacific*, Pratt et al. (1987), drawing on considerable field experience in the region, reversed Mayr's (1945) equivocal lumping and recognized the original four species, which exhibit color variation as broad as that of the entire genus (Burn 2006) and also differ strikingly in size, voice, and, to a lesser extent, habitat. These four inhabit the four high islands found along an east–west (Pohnpei–Palau) axis. With interisland distances ranging from 765 km (Pohnpei-Chuuk) to 1,912 km (Chuuk-Palau), the chance that any of these now highly sedentary birds will ever encounter each other in the wild is almost nil, despite the fact that their ancestors must have crossed large water gaps. Except for Guam, which lies north of the main axis, the Micronesian high islands are closer to potential colonization sources in northern Melanesia than to each other, so origins from different ancestral species for the four forms seem at least as likely as interisland dispersal by a common ancestor. The four-species classification has been used for decades within the region (Pyle and Engbring 1985, Pratt et al. 1987, Wiles 2005), probably because it makes sense to those who know the birds in the field, and it is also followed in some major world check-lists (Sibley and Monroe 1990, Clements 2000, Gill and Wright 2006).

However, in the authoritative *Handbook of Birds of the World*, Gregory (2006) reverted to Mayr's (1945) taxonomy and Burn (2006) depicted three of the nominal subspecies as far more similar than they really are (*M. freycineti* was by then extinct and not included, further distorting the view presented). The third edition of the Howard and Moore checklist (Dickinson 2003) also considered these disparate birds conspecific. Dickinson (2003) stated that those involved in preparing the checklist were unaware of a detailed review of the taxonomy, despite citing Pratt et al. (1987). The original decision to lump these species (Mayr 1945) was based on their occurrence in the same region and the author's preference for polytypic species, not on any review of evidence for conspecificity. The obvious potential isolating

mechanisms among these birds should justify restoration of the original four species, but over-lumped taxonomy in island avifaunas remains exasperatingly entrenched (Rheindt and Hutchinson 2007). Examples of polytypic bird species in need of revision can be found throughout the tropical Pacific and include, but are not limited to, *Ptilinopus porphyraceus, Todiramphus chloris, T. cinnamomina, Coracina tenuirostris, Pachycephala pectoralis, Clytorhynchus vitiensis, Chasiempis sand-wichensis, Myiagra azureocapilla, Rhipidura rufifrons, R. spilodera, Cettia ruficapilla, Turdus poliocephalus, Aplonis tabuensis, Myzomela cardinalis, Foulehaio carunculata, Gymnomyza viridis, Zosterops cinereus,* and *Erythrura cyaneovirens.*

Resistance to changes in species limits reflects (1) a widespread belief among non-systematists that species-level taxonomy is irrelevant, (2) an understandable desire for list stability (Sangster 2000), and increasingly (3) the reluctance of editors to publish revisions that do not include genetic data (even though such data may be irrelevant at the species level, as I discuss below). The failure to recognize that many island subspecies are actually species has several unfortunate consequences that are far more serious than simply misleading illustrators or inconveniencing list-makers.

Repercussions of Ranking Species as Subspecies

From a scientific perspective, the most damage occurs when authors of theoretical studies wrongly assume that published species lists for taxonomically long-neglected island regions are essentially equivalent to those of well-studied ones. Underestimation of species-level diversity on islands obscures their important role as speciation laboratories and their importance in the preservation of biodiversity. Modern DNA studies, especially those that require complete taxon sampling, are especially vulnerable to overlumped taxonomy because they may include only one representative of an overlumped polytypic species and assume, falsely, that including others would not change the result. Especially egregious is the conflation of data from subspecies that later turn out to be separate species. For example, Amerson et al. (1982) combined data from the two forms of *Aplonis tabuensis* in American Samoa that, as discussed below, are probably different species, in which case the statistics become meaningless. Research planning may also suffer from

underestimation of species-level biodiversity. For example, Fiji's four largest islands are relatively close together but have distinctive avifaunas. The three islands that have endemic species (Viti Levu, Taveuni, and Kadavu) receive most of the attention of both professional and amateur observers. Vanua Levu, the second largest, whose endemics are all currently ranked as subspecies, is relatively poorly known and visited much less often. Incredibly, I have heard several biologists say that the loss of Guam's entire avifauna (as documented by Savidge 1987) is less regrettable because most of the island's endemics were subspecies.

Unfortunately, given our uncertainties about species limits among island forms, the species category also holds an iconic status among conservationists (Sangster 2000), recreational birders (Pratt 1990), and the general public. Many authors (e.g., Collar et al. 1994, Hazevoet 1996, Myers et al. 2000) have decried the fact that nongovernmental organizations such as World Wildlife Fund and BirdLife International often focus only on endangered species and ignore even highly distinctive endangered subspecies that might turn out to be species. Recreational birders also rely on existing species lists, whether the limits are well constructed or not. These dedicated amateurs are often our only source of new information on remote island endemics, yet they routinely ignore distinctive island subspecies, despite advice to seek out those that are potential splits (Pratt 1990). Popular writers such as Cokinos (2000) usually concern themselves only with species, even when subspecific examples may be equally important and instructive for conservation. The Newfoundland Red Crossbill (*Loxia curvirostra percna*) was driven to extinction by the ill-advised introduction of Red Squirrels (*Tamiasciurus hudsonicus*) to the island (Benkman 1989, 1993b; Parchman and Benkman 2002), but its demise was largely unnoticed at the time because it was only a subspecies. Now that the Newfoundland bird appears to have been an endemic island species (Benkman 1993b), its lessons will perhaps be better appreciated.

Concepts, Species, and Subspecies

Hazevoet (1996) suggested that species chauvinism actually promotes extinction of island endemics, and he advocated abandoning the biological species concept in favor of the phylogenetic species concept because the latter would reclassify nearly all island subspecies as species.

Peterson (2006) suggested that adoption of the phylogenetic species concept would not only increase the number of species but would reveal such information as previously overlooked centers of endemism. Although I agree that many endemic island species are being neglected because of faulty taxonomy and that current classifications obscure important information, I also agree with Collar (1997:133) that we should "not allow frustration with the misapplication of one concept to result in complete dependence on another." Sangster (2000) suggested that the problem was not a faulty species concept, but rather the fact that avian taxonomy is not as well documented as non-systematists seem to believe. Also, the subspecies concept is quite useful for showing varying levels of differentiation among an array of allopatric populations. Adoption of the phylogenetic species concept would produce a degree of taxonomic inflation that would be just as problematic for conservationists (Collar 1996, Sangster 2000, Pratt and Pratt 2001, Isaac et al. 2004) as current practice under the biological species concept. Noteworthy is that Hazevoet's (1995) phylogenetic reclassification of birds of the Cape Verde Islands was rejected by BirdLife International (Collar 1996).

The biological species concept is fundamentally operational rather than typological or evolutionary in its application. It is not based on degrees of difference, whether morphological, behavioral, or genetic, but rather on how such differences affect (or, in the case of allopatric forms, might affect) the ability of two forms to interbreed. In other words, the criterion is whether the differences are, or are likely to be, isolating mechanisms (I use this widely understood term despite Mallet's [1995] objections). The biological species concept has always had difficulty with allopatric, but obviously related, populations because operational tests are usually unavailable. Mayr (1969) suggested comparisons with related sympatric species pairs as a way of evaluating degrees of difference in allopatric forms, a method Rheindt and Hutchinson (2007) called the "yardstick approach" and used effectively to evaluate some Moluccan birds. Unfortunately, that method is often unavailable. Johnson et al. (1999) suggested a modification of the biological species concept that considers some aspects of the phylogenetic species concept such as diagnosability and genealogy, and stressed the importance of what they termed "independent evolutionary trajectories." Helbig et al. (2002)

provided practical guidelines that supported, more or less, Johnson et al.'s (1999) proposals, but they focused on continental species, or continental species with island populations, rather than on archipelagic taxa with multiple allopatric populations that differ in varying degrees. For these, Helbig et al.'s (2002) guidelines need some modification because, as Steadman (2006:415) stated, "oceanic islands . . . and continental islands or continents . . . have some fundamental differences in geologic development, evolutionary histories, and barriers to colonization." The following examples will show, as did Pratt and Pratt (2001), how an updated application of the biological species concept to island taxa, including effective use of subspecies, can accomplish Hazevoet's (1996) desired goals and more accurately represent the biodiversity of island birds without undermining a long-established and widely understood species definition and without overwhelming endangered species lists with trivially differentiated nominal species. I do not advocate adjusting taxonomy to accommodate attitudes that value species over subspecies, nor do I advocate treating species and subspecies equally when it comes to preserving biodiversity in a world with priorities to set, but we should strive to recognize all biological species as such because their survival may depend on it.

The Hawaiian Islands: A Well-studied Example

The Hawaiian avifauna is particularly instructive in this context (Pratt and Pratt 2001) because it is arguably the most thoroughly studied archipelagic fauna, and our knowledge of it is enlightened by both a rich subfossil record (Olson and James 1982, 1991; James and Olson 1991; Burney et al. 2001) and an ever-growing body of genetic data (Fleischer and McIntosh 2001; Fleischer et al. 1998, 2008) with some studies that combine both lines of evidence (Fleischer et al. 2001, Paxinos et al. 2002). Amadon's (1950) classification, which exhibits the overuse of polytypic species typical for its era, was the standard for many decades. Beginning in the 1980s, most of Amadon's polytypic species were dismantled (Pratt and Pratt 2001) on the basis of new behavioral, ecological, and morphological (Pratt 1982, 1989, 1992), as well as paleontological (Olson and James 1995) and genetic (Tarr and Fleischer 1994, Fleischer et al. 2007), information. As a result, his 25 passerine species

comprising 56 named forms have become 51 biological species with only 5 forms remaining as subspecies (as reviewed by Pratt and Pratt 2001). Not counted in this tally are three intra-island subspecies of *Chasiempis sandwichensis* (Pratt 1980) of which Amadon was unaware. If, as ongoing genetic studies (R. C. Fleischer pers. comm.) suggest, all three subspecies of *Loxops coccineus* are elevated to species rank as Pratt (2005) suggested might happen, only three subspecies will remain among Hawaiian passerines. Encouraging is the fact that DNA studies have, to date, corroborated species limits based on phenotypic characters in every case, although they have revealed some strikingly misleading examples of convergence at generic (Reding et al. 2008) or higher (Fleischer et al. 2008) levels. As numerous authors have noted, populations on islands are more strongly isolated than allopatric mainland populations (Phillimore and Owens 2006, Steadman 2006) and the severely restricted gene flow can drive rapid speciation (Moyle et al. 2009). We should expect island birds to exhibit a greater ratio of species to subspecies than continental avifaunas. Even though the Hawaiian example is the extreme, it suggests that Mayr's (1942b, 1969) clearly articulated when-in-doubt-lump precept is the wrong approach when applied to islands. Indeed, as Pratt and Pratt (2001:69) stated, the opposite bias "is more likely to result in a species list that will stand up to independent corroboration." Interestingly, by proper use of the biological species concept, Hawaiian species limits are now nearly the same whether we use the biological or the phylogenetic species concept (Pratt and Pratt 2001), but that will not likely be the case in less isolated archipelagoes.

The Importance of Geography

The Hawaiian Islands are so remote that successful colonists are immediately isolated from their source populations. In other parts of the tropical Pacific, distance from a mainland or island source plays an important role in the degree of differentiation possible, with remote populations likely to become species while those closer to colonization sources may only differentiate to the level of subspecies because of episodic or continuing gene flow. The avifaunas of Micronesia and Polynesia have many large polytypic species whose component taxa occupy islands in more than one archipelago scattered over vast expanses of ocean (e.g., the aforementioned Micronesian

Flycatcher). These species can exhibit many levels of differentiation among several allopatric populations. Amadon and Short (1976) introduced the term "megasubspecies" in an effort to improve the description of such variation, but only a few recent studies (e.g., Mayr and Diamond 2001) have used it extensively, and subspecies on oceanic islands are still too often regarded as essentially equivalent within a species (Phillimore and Owens 2006, Phillimore et al. 2008), especially by non-systematists.

For Helbig et al. (2002), all allopatry was essentially the same regardless of distances involved, but the dynamics of island biogeography clearly modify evolutionary trajectories. Uniformity across a large oceanic region can indicate a recent expansion and colonization, or ongoing gene flow, or a combination of the two. Deciding the role of each of these processes can be difficult, but environmental, behavioral, geographic, historical, and paleontological information can provide inferences. Evaluating the degree of isolation of a population involves the interplay of vagility and distance, and such judgments are subjective because vagility cannot be measured precisely and birds differ widely even within taxa. Paradoxically, selection against dispersal begins immediately upon successful colonization (Carlquist 1974, Moyle et al. 2009), producing the seeming contradiction that although rails (Rallidae) are highly vagile colonizers of even the most remote islands, most endemic island rails are flightless (Steadman 2006). Pigeons and doves (Columbidae) are excellent island colonizers, distributed throughout Polynesia and Micronesia to some of the most remote islands (Pratt et al. 1987, Steadman 2006). Because columbids live on both atolls and high islands, they can take advantage of intervening stepping stones that many land birds cannot. Both the Pacific Imperial Pigeon (*Ducula pacifica*) and Micronesian Imperial Pigeon (*D. oceanica*) apparently move across large water gaps frequently enough to prevent genetic differentiation across vast regions. One observer in Fiji (V. Masibalavu pers. comm.) reports seeing pigeons flying seaward from Viti Levu in large numbers after passage of a particularly devastating typhoon that destroyed the fruit crop. Perhaps dispersal after such storms drives regional genetic homogenization and slows population differentiation in large pigeons. Archeological evidence indicates that *D. pacifica* is a post-human arrival in Tonga and the Cook Islands (Steadman 2006), perhaps because

it was able to colonize only after anthropogenic extinction of other *Ducula* spp., so its lack of geographic variation results from both high vagility and recency of dispersal. Pacific fruit doves (*Ptilinopus* spp.) appear to be somewhat less vagile because their species limits tend to coincide roughly with archipelagoes rather than regions, but the most remote forms, such as the Henderson Island Fruit Dove (*P. insularis*) and Rapa Fruit Dove (*P. huttoni*), are distinctive single-island endemics (Pratt et al. 1987). Clearly, geographic remoteness plays a role in speciation, even in highly vagile birds.

Archipelagoes sometimes sample variation in a way that resembles a series of snapshots taken along a cline. Perplexingly, a trend across an island chain may result from an environmental gradient, as in a true cline, but without any continuing interisland gene flow. Cline-like archipelagic variation is infrequent (none of the former polytypic species in Hawaii resembled fragmented clines). Geographic variation in the Polynesian Starling resembles a fragmented cline in some characters but not in others (Mayr 1942a). This small starling is distributed on high islands from the Santa Cruz group (eastern Solomons) eastward through Fiji to Samoa and Tonga. Western populations have brown eyes, eastern ones yellow, with the shift occurring within Fiji, where some populations have both eye colors. Overall coloration varies from mostly brown in the west to mostly gray in the east, but several populations break the flow of this trend. The prominence of pale shaft streaks on the breast feathers also varies, as does overall size, but with no discernible directional trends. One of the largest and most prominently streaked forms is *A. t. tutuilae* on Tutuila, American Samoa. Immediately to the east, on the isolated Manu'a Islands, *A. t. manuae* represents the end of the line for the species. It is much smaller and darker than *tutuilae*, lacks breast streaks altogether, and has pale feather edges that impart a scaly look unique in the complex. Such sudden shifts in characters between neighboring forms, especially if one is a geographic outlier, may signal the existence of previously unappreciated species.

Reevaluating Species and Subspecies among Island Birds

Collar (2006a, b; 2007b) used a numerical scoring system for phenotypic characters to determine species limits, similar to Rheindt and Hutchinson's

(2007) "yardstick approach," apparently trying to accomplish the same goals I am advocating here (splitting of distinctive allopatric subspecies) and bring some objectivity to the process. I agree with Peterson and Moyle (2008) that Collar's method is essentially a phylogenetic species approach used in a biological species context. Furthermore, Collar has failed to factor in such things as the role of characters as potential isolating mechanisms and the degree of geographic isolation. Peterson and Moyle (2008) also decried the amount of subjectivity in what is supposed to be an objective process. But Collar (2008) rightly pointed out that all species-limit judgments that involve allopatric forms are, at some level, subjective. The model I offer is an attempt to add geographic and biological dimensions to the process and reduce the inevitable subjectivity so that the decisions reached will be repeatable by other disinterested scientists, but setting biological species limits among allopatric taxa can never be a mindless or mechanical exercise under the biological species concept.

I recommend a thought process wherein any oceanic island bird population is considered a species (or allospecies) if (1) at least one age or sex class is distinct from sister taxa in at least one qualitatively discrete phenotypic character (populations that differ only quantitatively are more likely to be subspecies unless measurements show no overlap or proportions are very different, as in one population having a proportionally larger bill, in which case other criteria come into play); and (2) the population is so isolated geographically that present or future gene flow between it and another related population is nearly impossible (i.e., the likelihood of phylogenetic reticulation is extremely low); and (3) it possesses one or more obvious potential isolating mechanism; or, if not strongly isolated geographically, it possesses two or more functionally independent potential isolating mechanisms (i.e., a plumage difference plus a vocal or morphological difference).

This thought process is not operationally different from Mayr's (1942b) earliest suggestions, but it differs philosophically by placing the burden of proof on the lumper rather than the splitter. Mayr's (1969) comparison method is a valuable tool, although underused in the past, for determining whether a difference is likely a potential isolating mechanism, but when no closely related sympatric species pairs exist, that technique cannot be applied. However, one can use such an approach with more distantly related species to

infer the kinds of isolating mechanisms likely to operate in a given taxon. For example, the kinds of isolating mechanisms that separate species of nocturnal burrow-nesting petrels are likely to be very different from those among diurnal forest passerines. In practice, Mayr and his followers rarely considered potential isolating mechanisms among island taxa, perhaps because, at the time, these birds were not well known biologically. The most frequently observed potential isolating mechanisms among terrestrial island birds are differences in appearance, vocal differences, morphological differences, differences in breeding biology, other behavioral differences, and ecological differences.

Differences in appearance.—Though often denigrated by earlier taxonomists (e.g., Amadon 1950), color differences in plumage and soft tissues remain the most obvious and predictive indicator of species limits in island birds (Pratt and Pratt 2001). So far, genetic studies have shown that remote island birds that look different to humans in the field usually are different species. Appearance also includes the presence or degree of sexual dimorphism (Pratt 1989, 1992), variation in maturational stages (i.e., distinctive juvenal or immature plumages), or variation in molt timing or sequence (Banks and Laybourne 1977), all of which can indicate species boundaries.

Vocal differences.—As with coloration, birds that sound different to humans, in song or call notes, often are different species. Darwin's finches are a good example of birds that are not highly variable in color but distinguish themselves with different songs (Grant and Grant 2008). Slabbekoorn and Smith (2002) have shown that song can play a prominent role in speciation even in birds whose songs are not innate, but vocal differences are less significant among birds that learn their songs (e.g., oscine passerines) than among those that inherit them. Island birds have been in the forefront of historical playback studies among birds that look similar but sound different (e.g., Lanyon 1967, Pratt 1982), but note that such experiments do not address the important issue of female choice. Recent studies of crossbills (Snowberg and Benkman 2007, Edelaar 2008, Benkman et al. 2009) suggest that call notes as well as songs can serve as isolating mechanisms.

Morphological differences.—Variation in bill shape and relative size may indicate differences in diet and foraging behavior (Benkman 1989; Pratt 1992, 2005; Smith and Benkman 2007) that

are potential isolating mechanisms. The Hispaniolan Crossbill (*Loxia megaplaga*) was recently split almost entirely on the basis of differences in bill size and shape that indicated distinctive food sources (Benkman 1994), and such differences were the first clue that the Kauai Amakihi was a separate species (Pratt et al. 1987, Tarr and Fleischer 1995). Such different physical attributes may also produce differences in appearance (above).

Differences in breeding biology.—Even if two birds can form an initial pair-bond, they will not breed successfully if their nesting habits are incompatible. Important considerations include nest composition and location, different laying and hatching schedules, and differences in roles of the sexes. Nest placement (terminal leaf clump vs. cavity), along with vocal and visual potential isolating mechanisms, were important in splitting the Akekee (*Loxops caeruleirostris*) from the Akepa (*L. coccineus*; Pratt 1989).

Other behavioral differences.—These can be anything from the numerous well-documented examples of differing mating displays to differential response to predators (mobbing vs. hiding; Pratt 1992) and variation in flocking behavior (Smith et al. 1999).

Ecological differences.—These can be such obvious things as differing habitats or differential response to disturbance, as in the case of white-eyes (*Zosterops* spp.) on Saipan and Rota in the Mariana Islands (Fancy and Snetsinger 2001) or the Elepaio (*Chasiempis sandwichensis*) on Kauai and Oahu (VanderWerf et al. 1997, VanderWerf 1998).

A WORKING EXAMPLE:
THE FIJI SHRIKEBILL COMPLEX

The Fiji Shrikebill (Monarchidae: *Clytorhynchus vitiensis*; Fig. 1), with a dozen allopatric subspecies, provides a good model for the reassessment of species limits in a large, widely distributed complex (but I do not regard this exercise as an actual revision because the data have not yet been completely analyzed). Shrikebills are skulking denizens of the forest understory that forage for insects in dead vegetation such as leaf clumps, vine tangles, or tree bark (Watling 2001). Their bills are more or less wedge-shaped and laterally compressed, with a slightly upturned look produced by the shape of the lower mandible, and resemble those of Neotropical antshrikes (*Thamnophilus* spp.). Shrikebills are generally solitary, but they join mixed-species foraging flocks on some
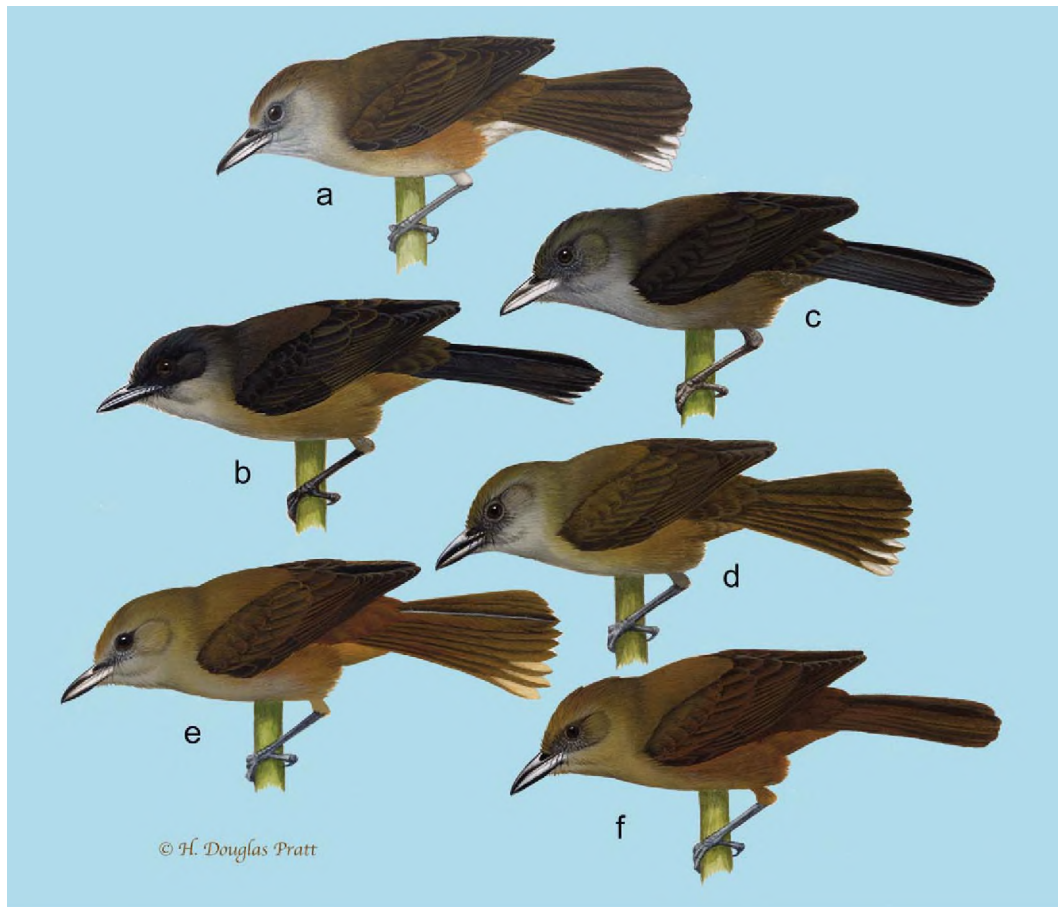
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FIG. 1. Representative geographic variation in the Fiji Shrikebill (*Clytorhynchus vitiensis*) complex: (A) *C. v. fortunae*, Futuna and Alofi; (B) *C. v. powelli*, Manu'a Islands, American Samoa; (C) *C.v. keppeli*, Niuatoputapu, Tonga; (D) *C. v. vitiensis*, Viti Levu, Fiji; (E) *C. v. compressirostris,* Kadavu, Fiji; and (F) *C. v. layardi*, Taveuni, Fiji.

islands (Watling 2001). The Fiji Shrikebill is plain and rather featureless in gray and russet, but intensity and hue vary geographically and, less so, individually. The presence or extent of broad pale tips to the tail feathers and a white stripe along the side of the bill also show geographic variation. The characteristic song is a long, quavering, descending whistle usually described as plaintive or melancholy (Pratt et al. 1987, Watling 2001). Seven subspecies are found among the main islands of Fiji, and three more are found on the neighboring islands of Rotuma (*C. v. wiglesworthi*; ~360 km northwest), Futuna and Alofi (*C.v. fortunae*; ~220 km northeast), and Tonga (*C. v. heinei*; ~250 km southeast). The other two subspecies are isolated outliers: *C. v. keppeli* on the remote northern Tongan islands of Niuatoputapu and Tafahi, >300 km

from the next nearest population; and *C. v. powelli*, ~400 km east of Niuatoputapu on the Manu'a Islands at the far eastern end of the Samoan Archipelago (shrikebills are unknown on the geographically intervening, larger Samoan islands). Within Fiji, many characters vary within and between shrikebill taxa in a bewildering mosaic that makes it "rather difficult to work out subspecies that are well defined and geographically restricted" (Mayr 1933:6). Watling (2001) considered most of the subspecies unidentifiable in the field, and some are connected by intermediate populations (Mayr 1933). The Rotuma and Tonga forms are not strikingly different from most of those in the core range.

On the other hand, at least four forms are megasubspecies with consistently distinctive characters.

Clytorhynchus v. fortunae is the smallest and palest form, with the most prominent and sharply defined white tail tips, unique faint gray streaking in the throat, a nearly white belly, contrasting bright tawny flanks, and a thinner, less wedge-shaped and only slightly compressed bill with a very bold white stripe mostly on the lower mandible. Its song, imitated in the local name *tikilili*, comprises metallic notes (Guyot and Thibault 1987) that are apparently very different from shrikebill songs in Fiji, which could not, in the broadest sense, be called metallic (H. D. Pratt pers. obs.). On Kadavu, the southernmost of Fiji's larger high islands, lives *C.v. compressirostris*, a form with plumage, including the pale tail tips, strongly tinged tawny throughout and a long, thin, and very strongly compressed bill as reflected in its epithet. This distinctive bill shape suggests that this population has rather different feeding habits, but no direct observations of such have been reported. Vocally, *compressirostris* generally resembles other Fijian taxa (H. D. Pratt pers. obs.), but I have not made direct comparisons.

Two remote outliers are even more distinctive than *fortunae* and *compressirostris*. Both *keppeli* and *powelli* are much darker than the core group of subspecies, *powelli* being nearly black on the crown, and both have very restricted white tail tips, but otherwise they do not closely resemble each other. On Niuatoputapu, *keppeli* is nearly uniform dusky gray, slightly paler below, with a prominent white base to the bill that is the most noticeable field character (M. LeCroy pers. comm.). The bill is as large as those of Fiji/Tonga birds but not strongly wedge-shaped and only slightly compressed laterally. The only behavioral information available comes from field notes made by M. LeCroy (pers. comm.) in 1997. She described a flock of 8–10 birds "calling, whistling, giving a trill and squawking." Such a large conspecific flock has never been reported for any other shrikebill, and the vocalizations seem quite different, although in an unexpected social context, from those in the species' core range. The Samoan *powelli* is more colorful than *keppeli*, with a strong tinge of russet in the flanks and a pale gray throat that contrasts sharply with the very dark crown and cheeks. The bill is black, with only a thin white line along the tomia (H. D. Pratt pers. obs.), and a strikingly different shape compared to the bills of other populations: relatively shorter without the upturned look, resembling the bills of more typical monarch flycatchers.

The different shape suggests distinctive feeding behavior, but comparative studies have not been done. Importantly, the Samoan bird's songs are only vaguely similar to those given by shrikebills in Fiji (H. D. Pratt pers. obs.; details to be published elsewhere).

Under the guidelines proposed here, the Fiji Shrikebill would be broken up into several allospecies. The Samoan Shrikebill (*C. powelli*), Dusky Shrikebill (*C. keppeli*), and Futuna Shrikebill (*C. fortunae*) qualify as species unequivocally, but the case of *C. compressirostris* is not so clear-cut. Its plumage differences approach those seen in other nearby populations, although most individuals would be identifiable on that basis alone, so whether coloration is a potential isolating mechanism in this complex is questionable. Likewise, its vocalizations may not be sufficiently different to be a potential isolating mechanism (they have not been thoroughly analyzed). Its different bill shape is quite striking, however, and suggests ecological differences that might affect the survival of hybrids should it become sympatric with a neighboring subspecies. So it is a borderline case, best regarded as a megasubspecies until we have more data on additional potential isolating mechanisms. The other subspecies in Fiji (including Rotuma, although its isolation suggests the need for further investigation) and Tonga seem clearly to be conspecific, and some probably do not warrant recognition even as subspecies. The small islands in the Lau Archipelago of eastern Fiji are numerous and close together, which suggests that gene flow may be producing a true fragmented cline in that region. As this case demonstrates, while many island species are wrongly classified as subspecies, the category is still valuable in describing diversity on islands.

THE PARAPHYLY DILEMMA

The influence of phylogenetic thinking has recently set back the cause of island species revision. Many taxonomists are reluctant to recognize well-differentiated peripheral isolates of large complexes, even when they are obviously good species, because doing so might render the remaining complex paraphyletic. Such thinking allows the perfect to become the enemy of the good. Funk and Omland (2003) showed that more than one in five currently recognized species are paraphyletic, so avoidance of paraphyly is hardly a reason to obstruct progress. In my opinion, the

fact that we do not yet understand the evolution-
ary patterns within a large complex should not
deter us from recognizing that some peripheral
isolates have clearly diverged to the level of spe-
cies. If that leaves a paraphyletic group, which
Rheindt and Hutchinson (2007) called a "Swiss
cheese lump" because some forms have been
removed from the complex, leaving holes as in
Swiss cheese, it may reflect genuine biological
processes and the fact that we have more work
to do, but at least the island endemics will receive
proper conservation attention in the meantime.

An example of the paraphyly problem is the
Rufous Fantail *Rhipidura* [*rufifrons*] complex (see
front cover), a huge conglomerate with 30 named
forms (Mayr and Moynihan 1946, Schodde and
Mason 1999), mostly on islands but with a few
on continental Australia. Variation in this group
is complex, with many forms that look rather
similar found throughout the range but with very
distinctive ones imbedded within it or on the pe-
riphery. Because two of the rather similar-looking
forms are sympatric in northern Australia, the
complex was split into two species distinguished
mainly on tail shape rather than color pattern, *R.
rufifrons* with 19 subspecies and *R. arafura* with 11
subspecies (Schodde and Mason 1999). The very
distinctive peripheral form *kubaryi* on Pohnpei has
been long recognized by many (Pratt et al. 1987,
Sibley and Monroe 1990, Clements 2000, Wiles
2005) as a separate species. It is the most isolated
of the forms in the *rufifrons* complex (1,625 km
from nearest other member of the group), and the
most distinctive in color. Nevertheless, according
to Boles (2006:231), it is

> sometimes considered a separate species, based
> on geographical isolation, vocalizations, and lack
> of rufous in plumage [i.e., exactly the criteria
> outlined herein]; however, almost certainly de-
> rived from other populations within the *rufifrons*
> cluster, and separation at species level presents
> complications.

Yet in the same publication, he split the much less
distinctive Manus Island form *semirubra* without
comment, apparently solely on the basis of a re-
port that its vocalizations were distinctive! That
form is the nearest neighbor to *R. kubaryi* and lies
between it and other subspecies of *R. rufifrons*
and thus presents all the same complications and
more. Application of the steps outlined above
would alleviate such inconsistencies. In my opin-
ion, recognition of all the strongly differentiated

peripheral isolates (the aforementioned plus
ugiensis [Ugi, Solomon Islands] and *utupuae*
[Santa Cruz Islands]) as allospecies, along with
the split of *rufifrons* and *arafura*, would be the
most informative interim taxonomy for the Rufous
Fantail group.

The Role of DNA in Determining Species Limits

Recent genetic studies suggest that the meth-
odology I recommend would hypothesize spe-
cies limits too conservatively, the large number of
resulting splits notwithstanding. The technique
cannot reveal species that have differentiated
genetically to a level usually found in species
but have not differentiated sufficiently in obvi-
ous phenotypic traits such as plumage and voice
(Cibois et al. 2007, Rheindt and Hutchinson 2007,
Phillimore et al. 2008). To date, the few genetic
studies of archipelagic birds have consistently
broken up large polytypic species, often yielding
more species splits than were apparent on phe-
notypic grounds (Freeland and Boag 1999; Cibois
et al. 2004, 2007; Filardi and Moyle 2005; Filardi
and Smith 2005). On the other hand, effective
isolating mechanisms can result from only slight
genetic changes, and thus populations can re-
main close genetically but still be reproductively
isolated as good biological species (Freeland and
Boag 1999, Rheindt and Hutchinson 2007, Grant
and Grant 2008, Moyle et al. 2009). No measure-
ment of genetic distance can determine whether
two populations are species or subspecies under
the biological species concept, although large
distances suggest that speciation has occurred.
How the genes express themselves phenotypi-
cally can drive speciation even in cases of limited
genetic divergence. Genetic evidence is therefore
a "single-edged sword," as characterized by R.
Fleischer (pers. comm.). When DNA reveals huge
genetic differences or branching patterns that are
inconsistent with current taxonomy, we can use it
to modify species limits. But when it reveals only
slight genetic differentiation, we cannot then say
automatically that the taxa in question are con-
specific. Therefore, genetic data should not be
regarded as a deal-breaking essential feature of
species-level revisions.

The "typical" white-eyes (*Zosterops*) of Micro-
nesia provide an example of both the use and
misuse of DNA data for setting species limits.
While dividing them into three groups, Baker

(1951) followed Stresemann (1931) in combining all seven taxa, from the Marianas in the north to Palau in the southwest, to Pohnpei in the east, as the Bridled White-eye (*Z. conspicillatus*). Every high island has its own form, and they vary in plumage almost as much as the genus varies worldwide (Pratt 2008). Not only do they look different, they sound different in both calls and songs, and some forms apparently lack territorial songs (Pratt et al. 1987, H. D. Pratt pers. obs.). As with the "Micronesian Flycatcher," Pratt et al. (1987) began the process of dismantling this conglomeration by splitting it into three species along geographic lines that corresponded to the three groups mentioned by Baker (1951), except that they considered the Rota form *rotensis* conspecific with the other two Mariana Islands taxa (*Z. c. conspicillatus* on Guam and *Z. c. saypani* on Saipan and Tinian). The Rota bird resembles the birds of Palau (*Z. s. semperi*), Chuuk (*Z. s. owstoni*), and Pohnpei (*Z. s. takatsukasai*) in having all-yellow underparts, but it differs from them strikingly in vocalizations and in colors of soft parts. This classification was tested in a pioneering DNA study by Slikas et al. (2000), who largely upheld Pratt et al.'s (1987) species limits. However, on the basis of genetic distance that indicated a divergence time of 2 million years, they suggested that the Rota White-eye be given full species status. They detected a much shorter period of separation (~10,000 years) between *conspicillatus* and *saypani*, which bracket Rota geographically, and considered them conspecific. This arrangement has now been widely accepted (Stattersfield and Capper 2000, Dickinson 2003, van Balen 2008). Though not as different from each other as from the Rota White-eye, the two other Mariana Island forms differ in size, color pattern, and especially in voice to the same degree (using Mayr's comparison approach) as many sympatric white-eye species (Pratt et al. 1987). These differences are, in my opinion and in the context of white-eyes worldwide (van Balen 2008, Moyle et al. 2009), sufficient potential isolating mechanisms to warrant species status for each, inasmuch as white-eyes have been shown to speciate more rapidly than most birds (Moyle et al. 2009). Although not yet widely accepted, a newly described crossbill species may have diverged from its closest relative as recently as 5,000 years ago (Benkman 2007, Benkman et al. 2009). Slikas et al.'s (2000) argument that the Saipan and Guam birds are not different enough genetically to be separate species

misses the point. Biological species have no minimum number for either time of divergence or genetic distance. On the basis of classic Mayrian criteria, these two birds' variety of potential isolating mechanisms can be expected to keep them on their separate evolutionary trajectories, and greater genetic divergence would develop in due course. Sadly, we can never test this hypothesis because the Guam bird is extinct (Savidge 1987).

The Rota White-eye was rare and restricted to habitat remnants on the island's central plateau by the 1970s (Pratt et al. 1979, 1987). Later, it experienced a precipitous population decline (Craig and Taisacan 1994, Fancy and Snetsinger 2001, Amar et al. 2008). In the meantime, BirdLife International, which maintains the world's Red List of endangered birds (Collar et al. 1994), made no mention of it because, as a subspecies, it was not within their purview. Only after publication of Slikas et al.'s (2000) study was the bird included in BirdLife International's listings (Stattersfield and Capper 2000), and it is now regarded as one of the world's most critically endangered birds (Hirschfeld 2008). The Rota White-eye was overlooked primarily because my own team (Pratt et al. 1987) was overly timid in making splits. I will not make that mistake again. Island birds worldwide are poised for a splitting spree, and we should get to it. Time is not on our side.