

Taxonomy *is* important in conservation: a preliminary reassessment of Philippine species-level bird taxonomy

A. TOWNSEND PETERSON

Summary

Alpha taxonomy involves delineation of the basic unit of biology: the species. The concepts by which we define species, however, have been controversial, with several alternatives competing at present, some creating fewer and some more species units, depending on interpretation of species limits. Although it is tempting to assume that species concepts would have little interaction with the geographic foci of species richness and endemism — and some have so argued — this assumption does not withstand careful analysis. In this paper, I develop a first-pass assessment of Philippine bird taxonomy under an alternative species concept, and compare the results with the traditional biological species concept lists. Differences between the two lists were dramatic, but not just in numbers of species; rather, new, previously unrecognized or previously underappreciated foci of endemism were noted. A thorough understanding of the taxonomic basis of species lists is therefore critical to conservation planning.

Introduction

Recent taxonomic studies have pointed out conservation implications of their results for several parts of the world (Boon *et al.* 2000; Lovette *et al.* 1999; Ortíz-Pulido *et al.* 2002): new viewpoints on species limits led to new priorities for conservation action, mainly via recognition of ‘new’ (although not necessarily undescribed) species-level taxa. What is more, recent reviews have indicated broader-scale effects of taxonomic treatments on conservation priorities, in that taxonomic viewpoints underlying suites of species used as bases for conservation priority-setting affect the results of those priority-setting exercises, often dramatically (Danielson and Treadaway 2004; Hazevoet 1996; Meijaard and Nijman 2003; Peterson and Navarro-Sigüenza 1999, 2000a; Sangster 2000). Hence, the picture appears clear: efforts to prioritize areas for conservation action based on biodiversity considerations should take into account the taxonomic viewpoint underlying the ‘authority list’ of species involved, otherwise unforeseen and unwanted biases resulting from inconsistencies among taxa may creep into the results.

Nonetheless, biodiversity considerations such as species’ distributions continue to be used in numerous current conservation priority-setting exercises (Amori and Gippoliti 2001; Balmford 2003; Bibby *et al.* 1992; Bonn *et al.* 2002; Brooks *et al.* 2001; Brooks and Thompson 2001; Cowling *et al.* 2003; Mittermeier *et al.* 1998; Seymour *et al.* 2001), and even mention — much less careful consideration — of taxonomic considerations is rare. What is more, the early commentary of Hazevoet (1996)

arguing for the need for careful attention to species concepts in developing conservation assessments received strong rebuttal from the conservation 'establishment' (Collar 1996), suggesting that the message has not been appreciated broadly. Finally, a recent paper (Fjeldså 2003) carried the provocative title "How much does taxonomy matter?" and arrived at the conclusion that 'species concepts' did not affect the conservation priorities resulting from detailed analysis.

In this paper, my aim is to address this question yet again. In my previous analyses along these lines (Navarro-Sigüenza and Peterson 2004; Peterson 1998; Peterson and Navarro-Sigüenza 1999, 2000b), colleagues and I have focused on the example of the birds of Mexico. However, the Mexican example is but a single region, and is representative only of continental avifaunas. As a consequence, I have now taken first steps towards development of a second regional example of an alternative species concept taxonomy — the Philippine avifauna — that provides a new view from the standpoint of insular and archipelagic avifaunas. Although the formal taxonomic and nomenclatural issues are only beginning to be addressed, I have nonetheless attempted to identify discrete species units based on at least a preliminary review of essentially all the Philippine avifauna. Perhaps more importantly, in parallel with the 'before' (biological species concept) and 'after' (evolutionary species concept) of the Mexican studies (Escalante-Pliego *et al.* 1993; Peterson and Navarro-Sigüenza 1999), this new review can be compared directly with results of a previous compendium developed under a biological species taxonomy (Peterson *et al.* 2000) to see how alternative species concepts will function in insular regions (Philippines) as compared with continental regions (Mexico).

Philippine birds

A recent summary of the Philippine avifauna (Dickinson *et al.* 1991) indicated the presence of 556 biological species, of which about 395 breed in the country and 169 are endemic (Peterson *et al.* 2000). However, many of these species vary dramatically from island to island. These differentiated forms are frequently described as subspecies of biological species, and as such may be confused with other ('minor') subspecies that are not genuinely distinct. The resulting confusions between genuinely distinct forms and forms that are only subtly distinct (or not distinct!) lead to neglect of the distinct forms in conservation planning (Peterson *et al.* 2000).

Several recent studies have re-evaluated species limits in Philippine birds, and have led to the recognition of additional species taxa (Collar *et al.* 1999; Kennedy *et al.* 1997, 2001). As in other regions (Navarro-Sigüenza *et al.* 2002, 2003), however, much more alpha taxonomic work is necessary to achieve a genuinely comparative treatment of species limits, both in reassessing species limits under the biological species concept and in outlining species limits under alternative concepts. In this paper, I offer a first-pass summary of such species that show discrete among-population phenotypic variation. This list will eventually evolve into a full alternative taxonomy for the Philippine avifauna under the evolutionary species concept (Wiley 1978), a concept operationally similar to the phylogenetic species concept (at least in applications to birds) but that presents several distinct advantages, reviewed elsewhere (Navarro-Sigüenza and Peterson 2004).

Methods

Specimens of almost all named taxa of Philippine birds (Dickinson *et al.* 1991) were inspected in most major systematic collections from the Philippines, as well as in several smaller collections: Field Museum of Natural History, American Museum of Natural History, British Museum (Natural History), Academy of Natural Sciences of Philadelphia, Yale Peabody Museum, Museum of Vertebrate Zoology, University of Kansas Natural History Museum, Museum Mensch und Natur (Munich) and the Naturmuseum Senckenberg (Frankfurt).

For each taxon, I compared skin specimens of males and females from each named population. Wherever feasible, I also made comparisons among potentially distinct populations within named populations (e.g. among mountain ranges within Mindanao, among islands inhabited by the same subspecies) to detect any potentially unnamed distinct populations. Differences sought included variation in coloration, size or shape.

To be considered for inclusion in my lists, I used the following criteria: (1) Differences among populations had to be discrete, permitting easy separation of essentially 100% of individuals of that age/sex class from the two populations. (2) Whenever possible, differences were confirmed based on independent series of specimens housed at other scientific collections to avoid problems with specimen conservation or treatment (Peterson and Navarro-Sigüenza 2000a). As discussed elsewhere (Navarro-Sigüenza and Peterson 2004), this operational approach can be taken as a first pass towards a taxonomic treatment under the evolutionary species concept, and certainly would qualify as a phylogenetic species concept treatment as well. Results are summarized in terms of present-day endemism, and in terms of endemism at the level of Pleistocene islands, that is, the larger and more inclusive units that remained separated by sea channels at the Last Glacial Maximum (Heaney 1991; Peterson and Heaney 1993).

Results

In all, 108 of the 556 or so bird species known to occur in the Philippines were found to constitute examples of discrete interpopulation differentiation (see summary in Appendix). These examples ranged from differences between Philippine populations and populations further to the south and west (e.g. Buff-banded Rail *Gallirallus philippensis*, Barred Rail *G. torquatus*, Slaty-legged Crake *Rallina eurizonoides*) in Indonesia and South-East Asia to taxa representing complexes of many distinct forms. These latter complexes included, for example, Tarric Hornbill *Penelopides panini*, Greater Flameback *Chrysocolaptes lucidus* and Philippine Hanging Parrot *Loriculus philippensis*, each of which appears divisible into five distinct forms, and Island Thrush *Turdus poliocephalus*, which appears divisible into seven distinct forms, including three on Mindanao alone. These populations, in each case, are clearly distinguishable, separation among well-prepared specimens of appropriate age/sex classes being essentially 100%.

Geographic divisions among the 'new' distinct forms (Figure 1) generally follow divisions among islands that existed and were maintained through periods of lower sea level in the Pleistocene (Heaney *et al.* 2002; Peterson and Heaney 1993).

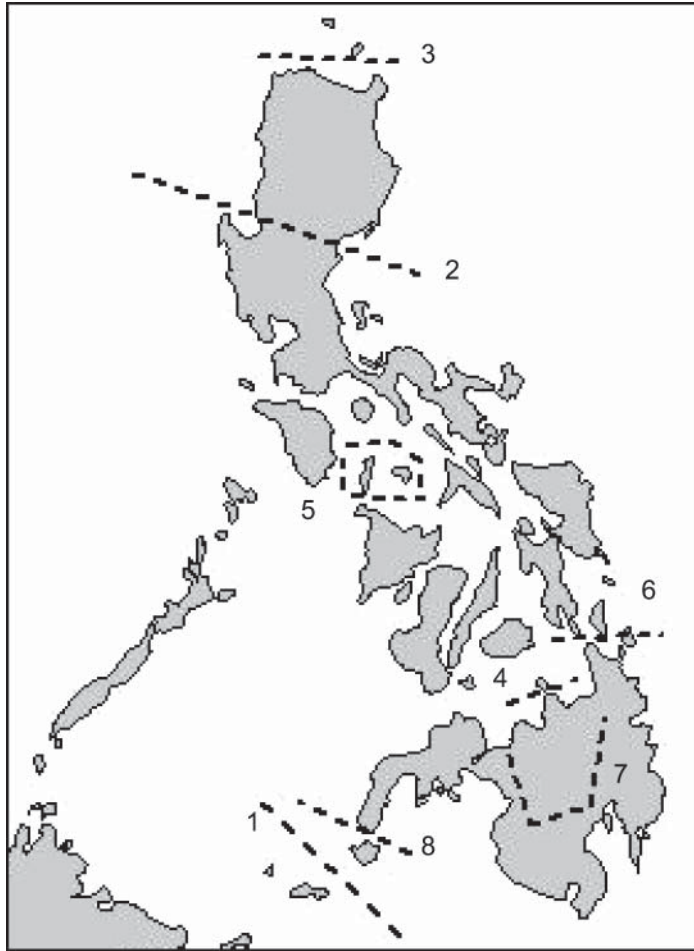


Figure 1. Summary of sets of coincident boundaries found among the differentiated populations summarized herein. Apart from well-known breaks between Pleistocene islands, the following additional zones of turnover of species were noted: (1) the Sulu Archipelago versus the remainder of the Philippines; (2) northern versus southern Luzon; (3) the Batanes and Babuyan islands versus the remainder of the Philippines; (4) Camiguin Sur versus Mindanao; (5) Tablas, Romblon and Sibuyan versus the remainder of the Philippines; (6) northern islands versus southern islands within Greater Mindanao; (7) subdivisions within Mindanao proper; and (8) Basilan versus Mindanao.

Pleistocene islands showing greater differentiation of bird populations than has been appreciated in present taxonomic treatments included, in particular, the Sulu Archipelago (e.g. forms of Dark-eared Brown Dove *Phapitreron cinereiceps*, *Loriculus philippensis*, White-bellied Woodpecker *Dryocopus javensis* and Brown Tit Babbler *Macronous striaticeps*); the Batanes and Babuyan islands (e.g. forms of Black-chinned Fruit Dove *Ptilinopus leclancheri*, Brown Cuckoo Dove *Macropygia phasianella* and Yellow-bellied Whistler *Pachycephala philippinensis*); Tablas, Romblon and/or Sibuyan (e.g. forms of Philippine Hawk Owl *Ninox philippensis*, Streak-breasted

Bulbul *Hypsipetes siquijorensis*, Spangled Drongo *Dicrurus hottentottus*); and tiny Camiguin Sur (e.g. forms of *Loriculus philippensis*, Golden-green White-eye *Zosterops nigrorum* and Yellowish Bulbul *Hypsipetes everetti*) (Table 1; Figure 1).

Differentiation among present-day islands within single Pleistocene islands was observed principally in Greater Mindanao (Table 1; Figure 1). (1) Populations of the northern islands (e.g. Samar, Leyte, Bohol) differed from those of Mindanao proper (e.g. *Penelopides panini*, *Dryocopus javensis*, *Chrysocolaptes lucidus*); and (2) Basilan populations were distinct from those of Mindanao and islands to the north (e.g. Philippine Fairy Bluebird *Irena cyanogaster*, *Zosterops everetti*). Additional examples of within-island differentiation were observed within both Luzon (e.g. *Turdus*

Table 1. Summary of biological species concept (BSC) and evolutionary species concept (ESC) perspectives on distribution of bird species endemic to single islands and single Pleistocene islands in the Philippine archipelago.

Island	Single Pleistocene island endemics			Single island endemics		
	BSC	ESC	% increase	BSC	ESC	% increase
<i>Greater Mindanao</i>	31	73	235.5	15	30	200.0
Mindanao	30	65	216.7	15	27	180.0
Samar	11	37	336.4	0	0	–
Leyte	11	37	336.4	0	0	–
Bohol	7	32	457.1	0	1	+
Basilan	10	33	330.0	0	2	+
<i>Greater Luzon</i>	19	44	231.6	1	24	184.6
Luzon	19	44	231.6	13	24	184.6
<i>Greater Negros</i>	9	23	255.6	8	11	137.5
Negros	6	20	333.3	5	8	160.0
Panay	2	11	550.0	1	1	100.0
Cebu	2	9	450.0	2	2	100.0
<i>Greater Palawan</i>	16	25	156.3	8	12	150.0
<i>Greater Sulu</i>	3	12	400.0	2	4	200.0
<i>Greater Romblon</i>	0	3	+	0	0	–
Romblon	0	2	+	0	0	–
Tablas	0	3	+	0	1	+
<i>Mindoro</i>	5	11	220.0	5	10	200.0
<i>Siquijor</i>	0	1	+	0	1	+
<i>Agutayan Group</i>	0	1	+	0	1	+
<i>Batan and Babuyan Groups</i>	0	4	+	0	1	+
<i>Camiguin Sur</i>	0	3	+	0	3	+

BSC figures are simplified from a previous paper on the subject (Peterson *et al.* 2000), based on a previous monographic treatment (Dickinson *et al.* 1991); ESC figures are drawn from a first-pass summary of individual cases listed in the Appendix.

Pleistocene islands are listed in italics, and component islands (if any) for which data were available are listed beneath each Pleistocene island. Plus signs (+) indicate an increase from zero and minus signs (–) indicate no change from zero.

poliocephalus, Lemon-throated Leaf Warbler *Phylloscopus cebuensis* and Green Imperial Pigeon *Ducula aenea*) and Mindanao (e.g. Mindanao Wattled Broadbill *Eurylaimus steerei*, *Turdus poliocephalus*, Purple-throated Sunbird *Nectarinia sperata*).

Discussion

Philippine bird taxonomy

One important impediment encountered in the course of this study was the paucity of bird specimens from parts of the Philippines. Although important and extensive series were assembled in decades past, particularly by D. S. Rabor and colleagues, these series frequently include few or no representatives of key taxa, such as *Dicrurus hottentottus* from Tablas or *Turdus poliocephalus* from Sibuyan. Not only are new collections needed for further progress in establishing species limits based on phenotypic characters, but modern series including associated tapes of vocalizations and frozen tissue material are critical to permitting more in-depth study. Such incomplete representation prevented this broad survey from resulting in a complete, checked and verified list including final decisions regarding synonymy and priority. Hence, targeted new collections are key to progress with understanding Philippine bird taxonomy.

The existence of heretofore unrecognized distinct populations within currently recognized species taxa is, of course, quite common (Escalante-Pliego and Peterson 1992; Navarro-Sigüenza *et al.* 2001; Pitman and Jehl 1998; Thompson 1991; Zink 1994). Indeed, recent studies in the Philippines have also indicated that avian diversity is greater than appreciated under current taxonomic treatments, showing the existence of distinct, species-level taxa (Kennedy *et al.* 1997, 2001). Detailed studies of mammal species have indicated even more impressive increases in numbers of distinct forms in the country (Heaney 2002; Heaney and Mallari 2002; Heaney *et al.* 2002; Peterson and Heaney 1993). Clearly, though, the often-partial treatments offered in this paper beg the need for distribution-wide reassessments rather than treatments of Philippine populations only.

The degree to which the forms identified herein should be considered as valid species taxa is a considerably more difficult question; clearly, though, full appreciation of avian diversity will depend on reassessment of species limits within currently recognized bird species (Peterson 1998). The Philippines provide a particularly difficult challenge, as these differentiated forms are almost universally disjunct in nature. Disjunct differentiated populations have represented a serious challenge for the biological species concept from its first applications (Mayr 1942). Although the forms listed below would clearly qualify as species taxa under the phylogenetic (Davis and Nixon 1992; De Queiroz and Donoghue 1988; McKittrick and Zink 1988) or evolutionary (Wiley 1978) species concepts, their consideration as species under the biological species concept will depend on the evolving reinterpretation of that concept that has characterized recent taxonomic treatments, such as the American Ornithologists' Union's check-list of North American birds (AOU 1983, 1998).

The hope in development of the lists presented herein is that they will aid in spurring development of a truly comparable species taxonomy for the Philippine

avifauna. If this taxonomy is to be developed under alternative species concepts, then the distinct populations listed herein would all qualify as candidate species taxa, and unresolved issues would be largely nomenclatural in nature. If, on the other hand, the taxonomy is to be developed under the biological species concept, continuing the excellent start provided by previous summaries (Dickinson *et al.* 1991), then the principal challenge will be that of making *parallel* decisions across taxa. For instance, the *Penelopides* hornbills have been treated recently as one (Dickinson *et al.* 1991), four (Kemp 1988) or five (Sibley and Monroe 1990) species under the biological species concept, with no particular stability in the decision. Decisions regarding *other* disjunct differentiated populations of these and other complexes and their representatives elsewhere in South-East Asia will have to follow parallel criteria in setting new species limits in order to achieve a genuinely comparable species taxonomy for the country's avifauna.

Taxonomy and conservation priorities

Returning to Ejelds s's (2003) provocative question, in the analyses presented herein, the answer is clear: taxonomy *does* matter. First, different regions are emphasized more or less under the alternative species concept (here ESC, for evolutionary species concept) as opposed to the biological species concept (BSC) viewpoints: for example, Greater Palawan was seen to hold 56% more single-Pleistocene-island species under the ESC than under the BSC, whereas the Greater Sulu Islands increased in single-Pleistocene-island species richness by 400%. These differences appear to be related to the relative isolation of particular islands in relation to neighbouring islands, although causes are not completely clear.

Second, the ESC identifies several other Pleistocene island groups as having endemic species when few or none were known or prioritized previously. The Greater Sulu Islands (although their unity through the Pleistocene is somewhat uncertain) rose in single-Pleistocene-island species richness from three to 12 species; Greater Romblon was seen to hold three ESC species when it previously was known to hold none, and similarly for the Batanes and Babuyan islands (four species now appreciated), Camiguin Sur (three species now appreciated) and the Cagayan Group and Siquijor (one species each now appreciated). These islands or island groups were previously unappreciated or underappreciated as conservation priorities, and are now 'visible' as holding endemic species.

Finally, and perhaps most interesting, in three cases, the ESC lists have permitted further appreciation (Mallari *et al.* 2001; Stattersfield *et al.* 1999) of centres of speciation and differentiation *within* Pleistocene islands: (1) differentiation of populations (even in species of lowland forests) between northern and southern Luzon, (2) differentiation of populations in the northern islands of Greater Mindanao (Samar, Leyte, Bohol) from those of Mindanao, and (3) differentiation of populations *within* Mindanao (in addition to a few already known; Kennedy *et al.* 1997). Many of the broad-brush-stroke patterns had, of course, been appreciated by even the earliest workers in the region (Dickerson 1928). Although a previous prioritization of Philippine regions on the basis of bird diversity (Stattersfield *et al.* 1999) suggested that elevation of many subspecific taxa to species status would not affect areas of

endemism identified, this paper and others (Peterson and Navarro-Sigüenza 1999) indicate the contrary. Consideration of endemic subspecies as units of conservation action (Mallari *et al.* 2001) would be misleading as well, as many subspecies reviewed in this effort were *not* distinct, thus once again clouding the picture. Put simply, new conservation priorities were revealed or known areas of importance were emphasized thanks to an alternative species taxonomy.

So why did Fjeldså (2003) arrive at such a different conclusion from that found here and in other such analyses (Peterson and Navarro-Sigüenza 1999)? Either the African system on which his analyses were based is qualitatively different from Mexico and the Philippines, or his analyses are somehow biased against such a conclusion. As regards the former, I see no reason why Africa should not also prove to be a rich store of ESC species taxa, with its complex biogeography and long-appreciated intricacies of bird taxonomy. Indeed, given the greater attention to alpha-systematics of the birds of the Neotropics over the past half-century than to those of the Afrotropics, I suspect that even more BSC species will prove to constitute ‘complexes’ in need of revision and splitting, and that these changes will have geographic biases that will affect conservation priorities.

Rather, I believe that the explanation for these differences lies in Fjeldså’s (2003) methodology. His ‘alternative’ species list was based on taxonomic splits suggested in the literature since the excellent atlases of speciation in the African birds (Hall and Moreau 1970; Snow 1978), and not on a comprehensive (if preliminary) reanalysis as my colleagues and I have developed in our examples. I suspect that the African ‘reanalysis’ was simply not sensitive enough, and probably omitted numerous key centres of repeated differentiation and speciation, at least under alternative species concepts.

Conclusions

A recent study (Danielson and Treadaway 2004) of Philippine butterfly species distributions under different species concepts arrived at the same conclusions as I have here. Their conclusions could easily be those of this paper: ‘We demonstrate that a better resolved species level classification could reveal numerous “new” priority areas. In tropical island and mountain regions where the distinctiveness of butterfly subspecies is high, significant evolutionary units may be lost unless fine-scale conservation planning pays attention to well-defined subspecies.’

Put quite simply, taxonomy does matter in establishing conservation priorities. A recent review of species limits and criteria used in describing bird species (Watson 2005) pointed out the impressive degree to which bird species are defined by ornithological taxonomists based on ‘field marks’, in marked contrast to those characters used by other vertebrate zoologists. This focus on identifiable species has clearly simplified the view of bird diversity, but runs the risk of obscuring important, independent evolutionary lineages. Taxonomy is taxonomy, and can always be fixed, but conservation is particularly unforgiving — once a species or lineage is lost, it is lost forever. Workers in bird conservation should therefore pay close attention to the taxonomic basis of the species lists on which they base their conservation assessments.

Appendix. Summary of Philippine bird species within which among-population heterogeneity was detected via inspection of a series of natural history museum specimens. When divisions involve populations that would have micro-scale distributions (e.g. part of a large island, or total restriction to a single small island) the 'microendemics' column is checked. Note that a full synonymy is not provided owing to the preliminary nature of the summary, and given the woefully small samples and unavailability of many of the key taxa.

Taxon	Microendemics	Comments
<i>Aviceda jerdoni</i>		Philippine populations with whitish chest (not brown as in SE Asian forms) and white base colour to throat (not buff)
<i>Spilornis holospilus</i>		Palawan populations with white-spotted breast, but lightly barred on upper chest; populations from the rest of the Philippines with entire underparts spotted white
<i>Accipiter virgatus</i>		Philippine population with solid brown wash on chest (not barred)
<i>Accipiter trivirgatus</i>		Populations in Borneo and Palawan have chest white with long brown streaks, whereas populations from the rest of the Philippines have chest almost solid brown
<i>Microhierax erythrogenys</i>		Populations from Greater Luzon, Mindoro and Negros have small body size; populations from Greater Mindanao are large (Bohol populations are a possible exception)
<i>Gallirallus philippensis</i>		Philippine populations smaller in body size than other populations; possible difference in back colour
<i>Gallirallus torquatus</i>		Philippine populations have brown chest band not present in other populations
<i>Rallina eurizonoides</i>		Philippine populations have cinnamon throat (not white)
<i>Porzana cinerea</i>		Philippine populations larger in body size
<i>Amaurornis olivacea</i>		Philippine populations larger in body size (not small) and with darker plumage overall
<i>Porphyrio porphyrio</i>		Philippine populations with brown (not blue) midback, belly blue as chest grading into it (not purple, distinct from chest)
<i>Himantopus himantopus</i>		Two distinct wintering populations (<i>himantopus</i> , <i>leucocephalus</i>) present (one with white nape, the other with nape white with a black patch)
<i>Phapitreron amethystina</i>		Populations from Greater Luzon and Greater Mindanao have underparts dusky olive-brown; populations from Negros have underparts blue-grey and faintly streaked
<i>Phapitreron cinereiceps</i>	X	Populations from Tawitawi distinct from those of Mindanao and Basilan in head coloration
<i>Ptilinopus merrilli</i>	X	Populations from Cagayan, Isabella and Quirinon provinces, Luzon have a purple-red crown patch; populations from the rest of Luzon and associated islands lack the crown patch
<i>Ptilinopus leclancheri</i>	X	Populations from Batan, Calayan, Camiguin Norte of large body size; populations from the rest of the Philippines of small size
<i>Ducula aenea</i>	X	Populations from northern Luzon have a purple crescent on hindneck, not present in other populations

Taxon	Microendemics	Comments
<i>Macropygia phasianella</i>	X	Populations from Batan, Lanyu (Taiwan), Itbayat and Calayan are of large size and are purplish-brown overall; populations from rest of Philippines are smaller and are brown overall
<i>Prioniturus discurus</i>		Populations from Luzon, Negros and Mindoro with blue forehead; populations from Greater Mindanao with forehead green
<i>Prioniturus montanus</i>	X	Populations from northern Luzon with red nuchal patch; populations from rest of Philippines lack patch
<i>Loriculus philippensis</i>	X	Populations from the Sulus differ from all others in having bill and legs black; populations from most of the Philippines have crown and nape green, forehead orange and an orange breast patch; populations from Camiguin Sur lack the orange breast patch (Tello <i>et al.</i> pers. comm.); populations from Greater Mindanao lack the orange forehead; populations from Negros have crown golden and nape green
<i>Chrysococcyx xanthorhynchus</i>		Philippine populations have rusty wash on throat and upper breast lacking in other populations
<i>Eudynamys scolopacea</i>	X	Populations from Calayan and Fuga may be larger in body size, and with different coloration of female, as compared with populations from the rest of the Philippines
<i>Centropus viridis</i>		Populations in Mindoro have blackish wings; wings rusty in rest of Philippines
<i>Ninox philippensis</i>	X	Complex variation in coloration of crown and back: solid dull brown in much of the Philippines, barred or spotted on Greater Mindanao, barred in the small islands in the central Philippines (e.g. Tablas, Romblon) and lightly barred (and belly barred on buff base colour) on Mindoro
<i>Strix seloputo</i>		Philippine populations with brown bars on buff (not white) below, small (not large) white spots on crown and back
<i>Hemiprocne comata</i>		Philippine populations with large body size as compared with other populations
<i>Alcedo cyanopectus</i>		Populations of Greater Luzon and nearby islands (Masbate, Sibuyan, Ticao) and Mindoro with yellow bill and extensive blue-green on belly; populations from Cebu, Negros and Panay with bill black, and blue-green on belly restricted
<i>Halcyon capensis</i>		Philippine populations in general differ from other populations in having the cap orange (not grey); populations from Palawan have underparts medium orange, whereas those of the rest of the Philippines have underparts light orange
<i>Halcyon smyrnensis</i>		Philippine populations have white on throat restricted (not extending to lower breast)
<i>Halcyon winchelli</i>		Populations of most of the Philippines have buff underparts and slender bill; populations of the Sulus have white underparts and stout bill
<i>Atenoides lindsayi</i>		Populations of Greater Luzon have back and breast green and white throat in female; populations of Negros have back and breast black and buff throat in female

Taxon	Microendemics	Comments
<i>Merops viridis</i>		Philippine populations with throat light green (not sky blue)
<i>Penelopides panini</i>		Complex variation in bill pattern; also, rufous tail band is restricted (Greater Luzon) versus broad (remaining populations) and dark (Mindoro) versus light (remaining populations) in colour; populations from the Visayas are of large body size (remaining populations small); rump is black, except for in the Visayas, Bohol, Leyte and Samar (where it is beige); belly is cream, except for in the Visayas (rusty); hence, distinct populations are found on Greater Luzon, Greater Mindanao, Visayas and Mindoro
<i>Aceros leucocephalus</i>		Populations of Greater Negros with upper breast dark rufous; populations of Mindanao, Dinagat and apparently Camiguin Sur with upper breast light cream
<i>Buceros hydrocorax</i>		Populations of Greater Luzon with bill red (not yellow with red at base, as in populations of Greater Mindanao)
<i>Megalaima haemacephala</i>		Populations of Greater Mindanao, Greater Luzon and Mindoro with throat yellow; populations of Cebu, Negros and Guimaras with red throat
<i>Dinopium javanense</i>	X	Populations of Palawan and Culion with reduced black on face and underparts reduced, and with buff-grey patch in middle of chest, as compared with several populations farther west
<i>Mulleripicus funebris</i>		Populations of Luzon blackish; those of Greater Mindanao medium grey
<i>Dryocopus javensis</i>	X	Populations of the Sulus with black bib, throat lightly speckled with white, and of small body size; populations of Bohol, Leyte, Samar and Panaon with entire bib speckled white, and of small body size; populations of Luzon, Mindanao, Basilan, the Visayas and Mindoro with bib black, throat broadly speckled white, and of large body size
<i>Dendrocopos maculatus</i>	X	Complex variation among four sets of populations: those of the Sulus have back solid brown, some white in midback, tail dusky brown without spots, throat white, two brown moustaches, caudal border brown, breast yellow and brown streaked; populations of Greater Luzon and Mindoro have dark grey overall, breast streaked, spots on throat reduced, back strongly black and white, tail mostly black; populations of Greater Mindanao have black overall, throat and upper breast spotted, belly streaked, back strongly black and white, tail mostly white or grey; and populations of the Visayas have dark grey overall, throat with two thick streaks on sides, streaking on breast reduced, back mostly dark grey, tail mostly blackish
<i>Chrysocolaptes lucidus</i>		Complex variation among five sets of populations: populations of Greater Luzon have the back mostly red, buffy face, and diffusely barred belly; populations of Mindanao and Basilan have the back tinged red, face buffy and belly scalloped black; populations of Bohol, Leyte, Panaon and Samar have the back solid red, face

Taxon	Microendemics	Comments
		buffy tinged red and belly scalloped black; populations of Greater Palawan have the back light green, face buffy tinged with red and the belly strongly barred; and populations of Guimaras, Negros, Panay, Masbate and Ticao have the back mostly red, face yellow and belly clear yellow
<i>Eurylaimus steerii</i>	X	Populations of Basilan and the Zamboanga Peninsula of Mindanao have a bright yellow patch in the white on the wing; remaining populations lack yellow
<i>Pitta erythrogaster</i>		Variation in coloration of breast is complex in this species, but coloration in Philippine populations (including Palawan) is unique
<i>Pitta sordida</i>		Black belly patch is prominent (not reduced) in Philippine populations
<i>Coracina striata</i>		Populations of Greater Luzon have male solid grey and female with grey throat and barred belly; populations of Greater Palawan are similar but overall light grey in colour; populations of the Visayas and Greater Mindanao have both sexes barred (male with grey throat); and populations of Mindoro, Tablas and Libagao have both sexes solid grey
<i>Lalage melanoleuca</i>		Populations of Greater Luzon and Mindoro have female underparts white barred with light grey; populations of Greater Mindanao have female underparts medium grey barred with white
<i>Pericrocotus flammeus</i>		Complex variation and few specimens, but Philippine populations show distinct combinations of plumage characters
<i>Pycnonotus plumosus</i>		Philippine (Greater Palawan) populations have primaries medium grey-olive (not green)
<i>Hypsipetes philippinus</i>		Populations of Mindoro and Semirara have the throat grey-olive; remaining populations have throat warm rusty colour
<i>Hypsipetes siquijorensis</i>	X	Populations of Romblon and Tablas have olive streaks on breast and crown grey tinged blackish; populations of Siquijor have olive breast streaking reduced and crown black
<i>Hypsipetes everetti</i>	X	Populations of Camiguin Sur have the throat and upper breast green strongly washed with dark cinnamon; populations from Greater Mindanao have the throat and upper breast light cinnamon
<i>Dicrurus balicassius</i>		Populations of Greater Luzon and Mindoro have belly black; populations of Visayas (Bantayan, Cebu, Guimaras, Masbate, Negros, Panay, Ticao) have belly white
<i>Dicrurus hottentottus</i>	X	Complex variation that requires more specimen material to elucidate; unique specimen from Tablas has tail elongated and splayed laterally, quite different from remaining populations
<i>Oriolus xanthonotus</i>		Populations of Greater Palawan have bib dark grey (not black)
<i>Oriolus steerii</i>		Populations of Greater Mindanao and the Visayas with lores black, underparts with grey bib and belly white striped black; populations of Greater Luzon have lores white and underparts yellow striped with grey

Taxon	Microendemics	Comments
<i>Irena cyanogaster</i>	X	Populations of Basilan duller and less glossy overall
<i>Corvus enca</i>		Philippine populations of small body size
<i>Parus elegans</i>		Populations of Greater Mindanao have cream-yellow wing spots; remaining populations with white spots
<i>Sitta frontalis</i>		Populations of Greater Luzon and Greater Negros with nape light lilac and belly brown; populations of Greater Palawan with nape blue and belly brown; populations of Greater Mindanao with nape light lilac and belly washed violet; no Philippine populations present the white throat of mainland populations
<i>Rhabdornis mystacalis</i>		Populations of Greater Mindanao with a short bill; remaining populations with long bills
<i>Rhabdornis inornatus</i>		Populations of Greater Mindanao with light grey on throat restricted and dull streaking; populations of Negros have throat more broadly light grey and streaking pronounced
<i>Napothera rabori</i>	X	Populations of southern Luzon with throat white; populations of northern Luzon with throat dark
<i>Stachyris plateni</i>		Populations of Mindanao with crown and throat rusty, forming a distinct bib; populations of Leyte and Samar with crown and throat grey-olive, with an indistinct caudal border
<i>Stachyris nigrocapitata</i>		Populations of Luzon with throat all-over rusty over yellow; populations of Leyte, Samar and Bohol with throat yellow and rusty moustaches
<i>Macronous gularis</i>		Philippine populations with throat cream-yellow and breast with indistinct throat streaks (not yellow with distinct stripes)
<i>Macronous striaticeps</i>	X	Populations of Greater Mindanao with crown black and streaked boldly with white; populations of the Sulus with crown brown streaked lightly with white
<i>Brachypteryx montana</i>	X	Philippine populations have some blue in females (not brown); females of populations of Luzon, Negros and Mindoro with blue-black body and brown head; females of populations of Mt Malindang have females overall dark blue (almost as male); remaining populations of Mindanao require inspection
<i>Copsychus luzoniensis</i>		Populations of Greater Luzon have white spots in wing and rump rusty; populations of the Visayas have wing without white and rump black
<i>Turdus poliocephalus</i>	X	Complex variation: populations of Luzon with male black and dark brown bib, and female overall grey-brown (northern Luzon) or blackish (southern Luzon, also Sibuyan); populations of Negros have both sexes all-over dusky grey-brown; populations of Mindoro have both sexes with a grey hood, brick belly and white ventral midline; populations of Mt Malindang (Mindanao) have both sexes medium brown, with a grey bib and white belly; populations of Mt Kitanglad (Mindanao) have both sexes blackish, with grey bib, brown flanks and white belly; and populations of the rest of Mindanao have both sexes all-over dark grey-brown, with a medium grey-brown bib

Taxon	Microendemics	Comments
<i>Phylloscopus cebuensis</i>	X	Populations of northern and central Luzon have reduced lemon yellow on throat and almost no yellow under tail; populations of southern Luzon, Cebu and Negros have ample lemon yellow in both areas
<i>Phylloscopus trivirgatus</i>	X	Populations of Mt Kitanglad (Mindanao) have belly whitish-yellow tinged green and back dull olive green; remaining populations have belly lemon yellow tinged green and back bright olive green
<i>Megalurus timoriensis</i>		Philippine populations are large with large bills
<i>Orthotomus castaneiceps</i>		Populations of Greater Mindanao have brown on crown restricted to lores (rest grey), belly black with white stripes, and small size; populations of Luzon have crown brown, throat black, belly black with white stripes, and large size; populations of the Visayas have crown brown, throat with black strips, belly white, and large size
<i>Orthotomus cucullatus</i>		All Philippine populations have heavy bills as compared with other populations; populations of Luzon have crown brown, nuchal area and cheeks grey, throat white; populations of Mindanao have entire head brown, including throat
<i>Cisticola exilis</i>		Philippine populations have cinnamon crown (not striped), browner underparts
<i>Eumyias panayensis</i>		Philippine populations differ from remaining populations in several respects; populations of Luzon and Mindoro have a black mask and white belly; populations of Mindanao have black only on the lores and belly tinged orange; populations of Negros and Panay have black only on the lores and belly white
<i>Ficedula hyperythra</i>		Philippine populations have white in crown restricted to the eyeline (not forehead)
<i>Cyanoptila cyanomelana</i>		Two migratory populations occur in the Philippines: one (<i>cyanomelana</i>) with throat and breast black and warm blue back, and the other (<i>cumatilis</i>) with throat and breast dark grey and back dull light blue
<i>Culicicapa helianthea</i>		Philippine populations of small body size
<i>Rhipidura cyaniceps</i>		Populations of Greater Luzon and Tablas have belly cinnamon; populations of the rest of the Visayas have belly white
<i>Rhipidura javanica</i>		Philippine populations of large body size
<i>Terpsiphone atrocaudata</i>		Philippine populations have belly black, back black, and white restricted to near vent
<i>Pachycephala grisola</i>		Philippine (Palawan) populations have breast washed grey (not olive-buff)
<i>Pachycephala philippinensis</i>	X	Populations of Calayan very different from remainder of populations: chest light olive (not bright yellow washed with olive), belly light creamy yellow (not bright yellow)
<i>Lanius schach</i>		Philippine populations have black crown and nape (not mask only) sharply (not graded) defined from grey back
<i>Sarcops calvus</i>	X	Populations of the Sulus have back light grey; remaining populations have back black

Taxon	Microendemics	Comments
<i>Nectarinia sperata</i>		Populations of much of the Philippines have upper back orange red and breast red; populations of northern Luzon have upper back black and breast orange-red; populations of central Mindanao have upper back shining purple and breast red; populations of southern Mindanao, Basilan and the Sulus have upper back orange-red and breast yellow
<i>Nectarinia jugularis</i>		Philippine birds have crown dull grey (not iridescent blue); populations of Palawan have yellow breast tinged with orange; remaining populations have breast yellow
<i>Aethopyga flagrans</i>		Populations of Luzon have bill large, throat orange, belly dull yellow and upper back green; populations of Guimaras, Panay and Negros have bill small, throat dull orange, belly bright yellow and upper back maroon
<i>Aethopyga pulcherrima</i>		Populations of Greater Luzon have bill large and orange-red chest spot; populations of Greater Mindanao (except Bohol) have bill small and orange-red chest spot; populations of Bohol have bill small and lack chest spot
<i>Aethopyga shelleyi</i>		Complex variation in need of careful study
<i>Aethopyga siparaja</i>		Philippine populations of large body size, with long and strong bill
<i>Arachnothera longirostra</i>		Populations of Greater Mindanao with lower belly yellow and short bill; populations of Palawan with lower belly dirty white and bill long
<i>Prionochilus olivaceus</i>		Populations of Greater Mindanao with sides of throat grey and bill small; populations of Luzon with sides of throat black and bill large
<i>Dicaeum anthonyi</i>		Populations of Luzon and Mindanao differ in coloration of crown, belly and undertail coverts (red versus yellow)
<i>Dicaeum australe</i>		Most Philippine populations have throat grey and breast grey with red spot; populations of Guimaras, Negros and Panay have throat white, and black on breast around red spot
<i>Dicaeum trigonostigma</i>	X	Populations of Greater Luzon, Mindoro and the Visayas with throat and belly orange; populations of Greater Mindanao and Camiguin Sur with throat grey and belly orange; populations of Romblon and Sibuyan with belly yellow or light orange; populations of Sibu have throat almost black and belly orange
<i>Dicaeum hypoleucum</i>	X	Populations of Greater Luzon with belly light olive grey; populations of Greater Mindanao (except southern portion) have back dark brown and belly light grey; populations of the Zamboanga Peninsula, Basilan and the Sulus have back black (slightly iridescent) and belly off-white
<i>Dicaeum pygmaeum</i>		Populations of most of the Philippines with sides of throat medium grey, and back and rump light green; populations of (at least parts of) Mindanao with sides of throat black, and back and rump black
<i>Dicaeum ignipectus</i>		Philippine populations with throat red (not beige) and lacking red chest spot

Taxon	Microendemics	Comments
<i>Zosterops everetti</i>	X	Most populations with large, thick bill; populations of the Sulus have smaller and more slender bill; populations of Basilan differ in aspects of coloration
<i>Zosterops nigrorum</i>	X	Most populations have bill small, green forehead and lores, belly yellow-green, small body size; populations of Camiguin Sur differ in having bill large; populations of Cagayan differ in having bill large, forehead yellow, large body size; populations of Mindoro have bill small, forehead green, lores yellow, belly yellow-green, and small body size
<i>Zosterops montanus</i>		Most populations (including outside of the Philippines) have belly tinged yellow; populations of northern Luzon have the belly greyish white, with yellow only on crissum
<i>Lophozosterops goodfellowi</i>	X	Populations of Mt Apo and Mt Kitanglad (Mindanao) have crown medium green; populations of Mt Hilong Hilong and Mt Malindang have crown grey
<i>Lonchura punctulata</i>		Philippine populations have scaling on underparts less well defined than other populations
<i>Loxia curvirostra</i>		Philippine populations with small body size and small bills
<i>Pyrrhula leucogenis</i>		Populations of Mindanao with base of mandible black and dusky underparts; populations of Luzon with base of mandible yellow and light underparts

Acknowledgements

I thank the curators and collections staff of the natural history museums listed in the Methods for their kind assistance during my studies at their institutions. Thanks also go to Adolfo Navarro for help with museum studies, and to Ed Dickinson for comments on a draft of the manuscript.

References

- Amori, G. and Gippoliti, S. (2001) Identifying priority ecoregions for rodent conservation at the genus level. *Oryx* 35: 158–165.
- AOU (1983) *Check-list of North American birds*. Sixth edition. Washington, DC: American Ornithologists' Union.
- AOU (1998) *Check-list of North American birds*. Seventh edition. Washington, DC: American Ornithologists' Union.
- Balmford, A. (2003) Conservation planning in the real world: South Africa shows the way. *Trends Ecol. Evol.* 18: 435–438.
- Bibby, C. J., Collar, N. J., Crosby, M. J., Heath, M. F., Imboden, C., Johnson, T. H., Long, A. J., Stattersfield, A. J. and Thirgood, S. J. (1992) *Putting biodiversity on the map: priority areas for global conservation*. Cambridge, U.K.: International Council for Bird Preservation.
- Bonn, A., Rodrigues, A. S. L. and Gaston, K. J. (2002) Threatened and endemic species: are they good indicators of patterns of biodiversity on a national scale? *Ecol. Lett.* 5: 733–741.
- Boon, W., Kearvell, J., Daugherty, C. and Chambers, G. (2000) Molecular systematics of New Zealand *Cyanoramphus* parakeets: conservation of orange-fronted and Forbes' Parakeets. *Bird Conserv. Int.* 10: 211–239.

- Brooks, T. and Thompson, H. S. (2001) Current bird conservation issues in Africa. *Auk* 118: 575–582.
- Brooks, T., Balmford, A., Burgess, N., Hansen, L. A., Moore, J., Rahbek, C., Williams, P., Bennun, L. A., Byaruhanga, A., Kasoma, P., Njoroge, P., Pomeroy, D. and Wondafraash, M. (2001) Conservation priorities for birds and biodiversity: do East African Important Bird Areas represent species diversity in other terrestrial vertebrate groups? *Ostrich Supplement*: 3–2.
- Collar, N. J. (1996) Species concepts and conservation: a response to Hazevoet. *Bird Conserv. Int.* 6: 197–200.
- Collar, N. J., Mallari, N. A. D. and Tabaranza, B. R. (1999) *Threatened birds of the Philippines: the Haribon Foundation/BirdLife International Red Data Book*. Manila, Philippines: Bookmark, Inc.
- Cowling, R. M., Pressey, R. L., Rouget, M. and Lombard, A. T. (2003) A conservation plan for a global biodiversity hotspot: the Cape Floristic Region, South Africa. *Biol. Conserv.* 112: 191–216.
- Danielson, F. and Treadaway, C. G. (2004) Priority conservation areas for butterflies (Lepidoptera: Rhopalocera) in the Philippine islands. *Anim. Conserv.* 7: 79–92.
- Davis, J. I. and Nixon, K. C. (1992) Populations, genetic variation, and the delimitation of phylogenetic species. *Syst. Biol.* 41: 421–435.
- De Queiroz, K. and Donoghue, M. J. (1988) Phylogenetic species concepts and species revisited. *Cladistics* 6: 83–90.
- Dickerson, R. E. (1928) *Distribution of life in the Philippines*. Manila: Bureau of Science.
- Dickinson, E. C., Kennedy, R. S. and Parkes, K. C. (1991) *The birds of the Philippines*. Tring, U.K.: British Ornithologists' Union.
- Escalante-Pliego, P. and Peterson, A. T. (1992) Geographic variation and species limits in Middle American woodnymphs (*Thalurania*). *Wilson Bull.* 104: 205–219.
- Escalante-Pliego, P., Navarro-Sigüenza, A. G. and Peterson, A. T. (1993) A geographic, historical, and ecological analysis of avian diversity in Mexico. Pp. 281–307 in T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa, eds. *Biological diversity of Mexico: origins and distribution*. New York: Oxford University Press.
- Fjeldså, J. (2003) Patterns of endemism in African birds: how much does taxonomy matter? *Ostrich* 74: 30–38.
- Hall, B. P. and Moreau, R. E. (1970) *An atlas of speciation in African passerine birds*. London: Trustees of the British Museum (Natural History).
- Hazevoet, C. J. (1996) Conservation and species lists: taxonomic neglect promotes the extinction of endemic birds, as exemplified by taxa from eastern Atlantic islands. *Bird Conserv. Int.* 6: 181–196.
- Heaney, L. R. (1991) A synopsis of climatic and vegetational change in Southeast Asia. *Climatic Change* 19: 53–61.
- Heaney, L. R. (2002) A decade of research on Philippine mammals: progress and challenges. *Silliman J.* 42: 88–108.
- Heaney, L. R. and Mallari, N. A. D. (2002) A preliminary analysis of current gaps in the protection of threatened Philippine terrestrial mammals. *Sylvatrop: Technical Journal of Philippine Ecosystems and Natural Resources* 10: 28–39.
- Heaney, L. R., Walker, E. K., Tabaranza, B. R. and Ingle, N. (2002) Mammalian diversity in the Philippines: an assessment of the adequacy of current data. *Sylvatrop: Technical Journal of Philippine Ecosystems and Natural Resources* 10: 6–27.
- Kemp, A. C. (1988) The systematics and zoogeography of Oriental and Australasian hornbills (Aves: Bucerotidae). *Bonn. Zool. Beitr.* 39: 315–345.
- Kennedy, R. S., Gonzales, P. C. and Miranda, H. C. J. (1997) New *Aethopyga* sunbirds (Aves: Nectariniidae) from the island of Mindanao, Philippines. *Auk* 114: 1–10.

- Kennedy, R. S., Fisher, T. H., Harrap, S. C. B., Diesmos, A. C. and Manamtam, A. S. (2001) A new species of woodcock (Aves: Scolopacidae) from the Philippines and a re-evaluation of Asian/Papuan woodcock. *Forktail* 17: 1–12.
- Lovette, I., Bermingham, E. and Ricklefs, R. (1999) Mitochondrial DNA phylogeography and the conservation of endangered Lesser Antillean *Icterus* orioles. *Conserv. Biol.* 13: 1088–1096.
- Mallari, N. A. D., Tabaranza, B. R. and Crosby, M. J. (2001) *Key conservation sites in the Philippines: a Haribon Foundation and BirdLife International Directory of Important Bird Areas*. Manila: Bookmark, Inc.
- Mayr, E. (1942) *Systematics and the origin of species*. New York: Columbia University Press.
- McKittrick, M. C. and Zink, R. M. (1988) Species concepts in Ornithology. *Condor* 90: 1–14.
- Meijaard, E. and Nijman, V. (2003) Primate hotspots on Borneo: predictive value for general biodiversity and the effects of taxonomy. *Conserv. Biol.* 17: 725–732.
- Mittermeier, R. A., Myers, N., Thomsen, J. B. and Fonseca, G. A. B. d. (1998) Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. *Conserv. Biol.* 12: 516–520.
- Navarro-Sigüenza, A. G. and Peterson, A. T. (2004) An alternative species taxonomy of Mexican birds. *Biota Neotropica* 4(2): online journal.
- Navarro-Sigüenza, A. G., Peterson, A. T., López-Medrano, E. and Benítez-Díaz, H. (2001) Species limits in Mesoamerican *Aulacorhynchus* toucanets. *Wilson Bull.* 113: 363–372.
- Navarro-Sigüenza, A. G., Peterson, A. T. and Gordillo-Martínez, A. (2002) A Mexican case study on a centralised database from world natural history museums. *CODATA J.* 1: 45–53.
- Navarro-Sigüenza, A. G., Peterson, A. T. and Gordillo-Martínez, A. (2003) Museums working together: the atlas of the birds of Mexico. *Bull. Brit. Ornithol. Club* 123A: 207–225.
- Ortiz-Pulido, R., Peterson, A. T., Robbins, M. B., Díaz, R., Navarro-Sigüenza, A. G. and Escalona-Segura, G. (2002) The Mexican Sheartail (*Doricha eliza*): morphology, behavior, distribution, and status. *Wilson Bull.* 114: 1–8.
- Peterson, A. T. (1998) New species and new species limits in birds. *Auk* 115: 555–558.
- Peterson, A. T. and Heaney, L. R. (1993) Genetic differentiation in Philippine bats of the genera *Cynopterus* and *Haplonycteris*. *Biol. J. Linn. Soc.* 49: 203–218.
- Peterson, A. T. and Navarro-Sigüenza, A. G. (1999) Alternate species concepts as bases for determining priority conservation areas. *Conserv. Biol.* 13: 427–431.
- Peterson, A. T. and Navarro-Sigüenza, A. G. (2000a) A new taxon in the '*Amazilia viridifrons*' complex of southern Mexico. *Proc. Biol. Soc. Washington* 113: 864–870.
- Peterson, A. T. and Navarro-Sigüenza, A. G. (2000b) Western Mexico: a significant centre of avian endemism and challenge for conservation action. *Cotinga* 14: 42–46.
- Peterson, A. T., Ball, L. G. and Brady, K. M. (2000) Distribution of birds of the Philippines: biogeography and conservation priorities. *Bird Conserv. Int.* 10: 149–167.
- Pitman, R. L. and Jehl, J. L., Jr (1998) Geographic variation and reassessment of species limits in the Masked Boobies of the Eastern Pacific Ocean. *Auk* 110: 155–170.
- Sangster, G. (2000) Taxonomic stability and avian extinctions. *Conserv. Biol.* 14: 579–581.
- Seymour, C. L., De Klerk, H. M., Channing, A. and Crowe, T. M. (2001) The biogeography of the Anura of sub-equatorial Africa and the prioritisation of areas for their conservation. *Biodiv. Conserv.* 10: 2045–2076.
- Sibley, C. G. and Monroe, B. L. J. (1990) *Distribution and taxonomy of birds of the world*. New Haven, CN: Yale University Press.
- Snow, D. W. (1978) *An atlas of speciation in African non-passerine birds*. London: British Museum (Natural History).
- Stattersfield, A. J., Crosby, M. J., Long, A. J. and Wege, D. C. (1999) *Endemic Bird Areas of the world: priorities for global conservation*. Cambridge, U.K.: BirdLife International.
- Thompson, C. W. (1991) Is the painted bunting actually two species? Problems determining species limits between allopatric populations. *Condor* 93: 987–1000.
- Watson, D. M. (2005) Diagnosable versus distinct: evaluating species limits in birds. *BioScience* 55: 60–68.

Wiley, E. O. (1978) The evolutionary species concept reconsidered. *Syst. Zool.* 27: 17–26.

Zink, R. M. (1994) The geography of mitochondrial DNA variation, population structure, hybridization and species limits in the Fox Sparrow (*Passerella iliaca*). *Evolution* 38: 96–111.

A. TOWNSEND PETERSON

Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS 66045, U.S.A.

Received 17 March 2005; revision accepted 5 September 2005