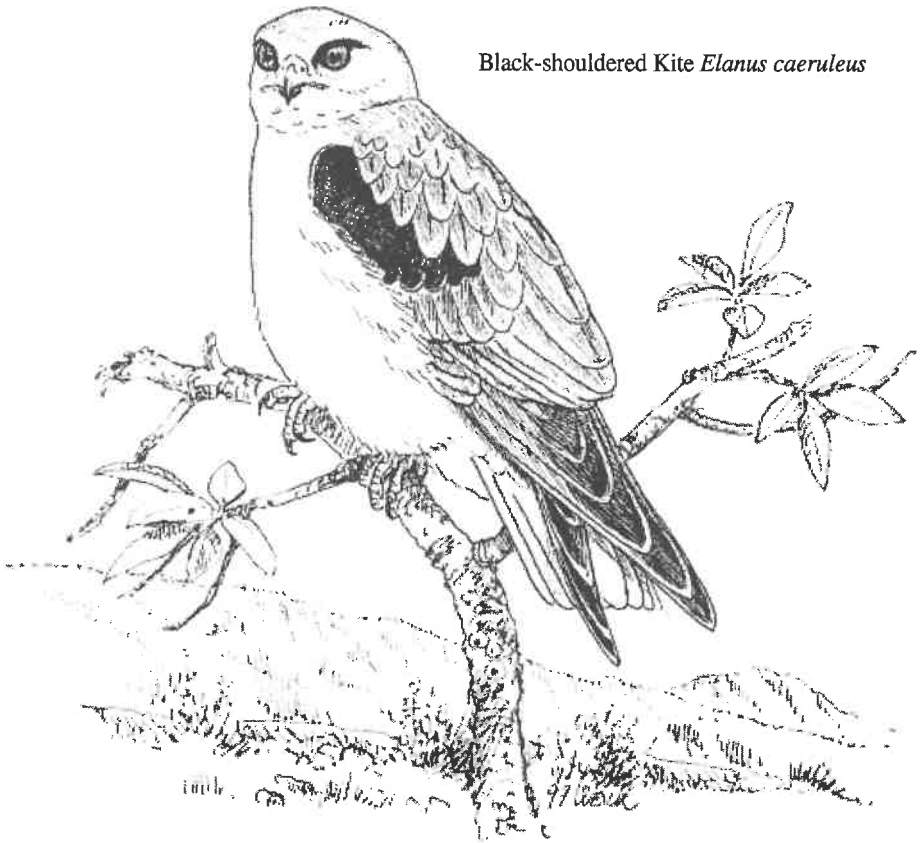


Part 9

Islands and Raptors

Black-shouldered Kite *Elanus caeruleus*



Conveners:

Clayton M. White & Luis Felipe Oliveira

Biodiversity, Island Raptors and Species Concepts

Clayton M. White and Lloyd F. Kiff

ABSTRACT

The biological species concept (BSC), which emphasizes reproductive isolation, and the phylogenetic species concept (PSC), based on unique combinations of characters, yield different numbers of raptor species. Based on the former approach, only taxa that are morphologically diagnosable are designated as species or subspecies, but new molecular techniques may reveal the existence of taxa ("putative" and "cryptic" species) unrecognizable by traditional morphological characters. Additionally, there are population groups, termed "evolutionarily significant units" (ESU's), which are on their own evolutionary trajectory, are usually identifiable by molecular characteristics, and often considered the same as phylogenetic species. In the extreme, many subspecies of the BSC are simply elevated to the species level of the PSC (Cracraft 1992). The taxonomic level at which conservation efforts are concentrated may have profound financial and logistical ramifications. A preliminary analysis reveals that 22% of 477 biological species (Sibley & Monroe 1990), at least 30% of a conservative estimate of about 592 phylogenetic species, occur on islands with about 28% and 44%, respectively, being insular endemics.

Regardless of the taxonomic approach, populations of island raptors usually have unique gene pools. In a biogeographic sense, islands may be any disjunct block of habitat, ranging from mountaintops and other isolated mainland habitats to bodies of land surrounded by water, but only the latter are considered here. According to the treatment of Sibley and Monroe (1990), a BSC-based list, there are 238 species of Accipitridae, 64 Falconidae, 17 Tytonidae and 159 Strigidae. A large proportion occur on islands (excluding Australia), as follows: Accipitridae; 45% (18% endemic), Falconidae; 41% (17%), Tytonidae; 83% (53%), and Strigidae; 48% (26%). A high percentage occur only on single islands or clusters of small islands. Of raptor species designated as threatened by the IUCN (Baillie & Groombridge 1996), 58% of Accipitridae are on islands, as are 50% of Falconidae, 80% of Tytonidae, and 67% of Strigidae. Of near-threatened, islands have 38% of listed Accipitridae, 14% of Falconidae, 100% of Tytonidae, and 21% of Strigidae. Examples of the importance of islands to overall raptor species diversity and problems of determining species status (BSC vs. PSC) of insular taxa on islands are provided by *Tyto* owls, owls of the genus *Otus* from SE Asia, Indonesia and Philippines, the serpent-eagle genus *Spilornis* in SE Asia and Indonesia, and the goshawks *Accipiter novaehollandiae* that range from Australia through Indonesia.

INTRODUCTION

Currently, one of the major concerns in conservation biology is the preservation of unique genetic combinations in the effort to maintain biodiversity (Vogler & DeSalle 1994, Barrowclough & Flesness 1996). From the standpoint of preserving biodiversity, the maintenance of unique island taxa is a critical conservation concern, since they tend to be evolutionarily isolated groups possessing the vulnerabilities peculiar to restricted-range species (King 1985, Long *et al.* 1996). Indeed, beginning with Darwin himself, it has long been understood that, as a result of isolation, islands tend to be unique places occupied by endemic and novel taxa; such a radiation or modification has often been called the "insular syndrome" (Masetti & Mazza 1996). Regrettably, the majority of documented avian extinctions have occurred on islands (Diamond 1984, Olson & James 1982), owing mostly to their often small populations, coupled with the effects of introduced biota and new forms of predation.

In the process of defining biodiversity and taxonomic boundaries, there is no present consensus on which of several major concepts should be followed (National Research Council 1995, Sites & Crandall 1997, Woodruff 1989). Some suggest that the diversity is best expressed at the species level (see discussion in Whittemore 1993), others argue that the polytypic subspecies concept better expresses that diversity, and still others contend that conservation efforts should be focused at taxonomic levels below the subspecies (National Research Council 1995). From a conservation standpoint relative to raptors, the choice of taxonomic concepts becomes important in trying to define the number of "species," especially when dealing with island-dependent or endemic taxa, because higher conservation priorities are accorded to species than to subspecies or populations (Collar *et al.* 1994, Haig 1998).

Traditionally, the most widely used species definition, and still the basis for most contemporary species lists and conservation laws, is the **biological species concept (BSC)**, the limits of which are set by isolation that requires geographic sympatry to test reproduction compatibility (Mayr 1969). However, many workers now advance the **phylogenetic species concept (PSC)**, which defines species as unique combinations of characters, whether morphometric or molecular (Zink & McKittrick 1995, Haffer 1997). The PSC accommodates the existence of "cryptic" and "putative" species, taxa that may have virtually imperceptible morphological differences, but which may be readily separated by molecular techniques (Davis & Nixon 1992). Further, the PSC is said to give a better description of the spatial patterns of biodiversity and produces units required by conservation biology (Zink 1997). Most island raptor subspecies as defined by the BSC possess unique combinations of characters; thus, they are generally elevated to the species level using the PSC.

However, it is an increasingly widely held notion that it is the population and not the species that is the ultimate currency of biodiversity (Crozier 1997). Various authors (e.g., Whitney *et al.* 1995) have made a persuasive case for the conservation of unique, isolated taxa, whether the "taxon" is currently judged to be a valid subspecies or not. How, then, does one define the unit of greatest evolutionary or conservation significance (Ryder 1986)? In recently assessing the effectiveness of the United States Endangered Species Act a committee of biologists proposed that an "evolutionary unit" (we prefer the earlier, but similar term "evolutionarily significant unit," or ESU) "is a group of organisms that represents a segment of biological diversity that shares evolutionary lineage and contains the potential for a unique evolutionary future," and they noted that each of these units is distinct from all other equivalent units in morphological, behavioural, biochemical, and/or physiological attributes (National Research Council 1995). This essentially follows the **evolutionary species concept (ESC)**, as described by Wiley (1981).

Definition of what is significant and how one makes such determinations remains complex, somewhat arbitrary, and accompanied by its own suite of characteristics and problems (Fleischer 1998). It is beyond the scope and intent of this paper to attempt to reconcile competing species definitions. However, we tend to agree with ESU adherents (e.g., O'Hara 1993) who argue that the evolutionary process is simply too dynamic to describe within the fixed boundaries of the BSC or PSC, or, as the National Research Council committee noted, "Speciation is a dynamic process with many factors involved, and science cannot delineate what nature itself does not." It is the maintenance

of biodiversity and not so much the "species" that is of conservation importance.

Our goal is to review some of the issues of raptors on islands, discuss something of their biodiversity, and call attention to their distribution. "Islands," in a biogeographic sense, include a wide variety of geographical features ranging from lakes and isolated mountains, surrounded by dissimilar or inhospitable habitat (see Vuilleumier 1970), to land islands surrounded by water, all of which produce genetic isolation. Among the numerous examples of raptor taxa on habitat "islands" are the Red-chested Owlet *Glaucidium tephronotum elgonense*, which is confined to Mt. Elgon in Kenya, and Long-whiskered Owlet *Xenoglaux loweryi* known only from cloud forests around 1900 m elevation in central Peru (O'Neill & Graves 1977).

For the purpose of this paper, however, only land islands surrounded by water will be considered. Such islands may earlier have been connected to a continental land mass and contain continental rock or fragments of continents (a variety of islands such as Fiji and the Seychelles), or, in various fashions, may have arisen from ocean floors and are called oceanic islands. (Williamson 1981). Many of the former islands, especially in the seas between peninsular India and the greater Australian regions, approximate oceanic islands in the processes that produced their biological patterns and contents (Gorman 1979, Williamson 1981). Good accounts of tropical island raptors and their current status are found in Bildstein *et al.* (1998), Virani and Watson (1998), Thiollay (1998) and van Balen (1998).

MATERIAL AND METHODS

We have attempted to assess the differences in island raptor biodiversity as measured by the numbers of "species/taxa" according to the BSC, and PSC concepts (Table 1). Lacking detailed analyses of character data sets of the 580 raptor taxa considered here, our judgement is based on (1) morphological and (where available) molecular criteria and their relation to known distribution and the degree of isolation from other bird taxa, (2) our combined knowledge and experience in raptor taxonomy and raptor ecology, and (3) implications by others that can be used to estimate numbers of PSC species.

Table 1. Comparison of projected number of "species" within the families of raptors based on the biological species concept (BSC) and phylogenetic species concept (PSC). First number is for total species, second number for island endemics, and third number is percentage of total that are insular endemics. Numbers of BSC species were taken from Sibley and Monroe (1990). See text for the basis and rationale underlying PSC totals. These are given as a range of estimated numbers with the lower one representing the most conservative PSC approach and the higher figure representing the number of "stocks" or ESU's embedded within the PSC and often considered to equate with it. Percents rounded to the nearest whole number. Note increasing importance of islands as the number of taxa increases from BSC to PSC treatments.

<i>Families</i>	<i>BSC</i>			<i>PSC</i>		
Accipitridae	239	45	19 %	288 - 405	80 - 179	28 - 44 %
Falconidae	63	9	14 %	84 - 115	19 - 43	23 - 37 %
Tytonidae	17	9	53 %	21 - 55	13 - 41	62 - 75 %
Strigidae	158	42	27 %	198 - 276	63 - 130	32 - 47 %
TOTALS (MEANS)	477	105	(28%)	(721	284	44%)

In general, we have followed the treatment of Sibley and Monroe (1990) for our estimates of the numbers of biological species and their generic designations. Because of its contemporary widespread adoption, their list was also followed for the most part by del Hoyo (1994). Our few departures from strict adherence to the Sibley and Monroe list were based mostly on supplementary information in Amadon and Bull (1988). The approximate number of raptor species recognized under the BSC is

rather straightforward and relatively little changed during the last half of this century, although there remain perennial subjective judgements about reproductive compatibility among many allopatric taxa.

Peters (1940), Mayr and Cottrell (1979), and Howard and Moore (1991) contain valuable information on raptor subspecies names and ranges. The latter reference was especially useful for determining the ranges of insular subspecies. Our determinations of what constitutes a phylogenetic species are largely subjective, but are based on degree of morphological differences, degree of geographic isolation, or a combination of both when one or the other is somewhat weak or questionable. In actual practice, we have mostly elevated well-marked subspecies under the BSC concept to phylogenetic species rank where specific taxonomic or molecular studies were lacking. This is not entirely satisfactory, since some avian subspecies may have been described on the basis of genetically insignificant plumage or other variations (Barrowclough & Flesness 1996). Ideally, species designated under the PSC should require cladistic or molecular analyses (Zink 1997, Haffer 1997), but such data are not yet available for most raptor taxa.

ESU's are best defined by the disjunctness of populations as usually identified by molecular data, regardless of where presumed taxonomic boundaries may be set by the other two systems. We recognize the diagnosis of them as important to issues in conservation especially if one considers them more equivalent to the "stocks" in wildlife biology, as have others (see Fleischer 1998). To be conservative, however, we will for the purpose of this paper, be content to view ESU's as synonymous with taxonomic units of the PSC in accordance with the argument of Barrowclough and Flesness (1996) and will not consider them further. In the following discussion, we use the term "taxon" (*pl.* taxa) to refer to a taxonomic entity, including genera, species or subspecies, as traditionally described, but not for unnamed ESU's.

For our analysis, Australia is not considered an island, as is often customary. For perspective, it is only about 16% smaller than the continental United States, or 35% larger than the size of continental Europe, and its conservation problems and types of endemic taxa more resemble those of larger continental land masses than islands. The largest islands incorporated into our analyses are those of New Guinea (over 85% smaller than the U.S.), Borneo, and Madagascar.

Traditional geographical regions (Neill 1969, Müller 1981) are used with a few modifications, i.e., some of our categories are a mixture of parts or all of two or more traditional regions. The regions include: **Nearctic** (North America north of the Mexican Plateau), **Neotropical** (South and Middle America south of the Mexican Plateau, except for most associated islands), **Caribbean** (islands in the Caribbean between North and South America), **Eurasia or Palearctic** (Europe and Asia, except Japan, Sakhalin, and associated islands), **Holarctic** (Palearctic and Nearctic combined), **Afrotropical** (Africa south of the Sahara and Madagascar, but not including other associated islands), **South Asia** (Pakistan east through India to Burma [Myanmar], but not Sri Lanka), **Indian Ocean** (islands from Madagascar east to Andaman and Nicobar Islands including Sri Lanka), **Indomalayan** (Thailand east to Philippine Islands and Indonesia), **Wallacea** (eastern Indomalayan area from Wallace's Line lying west of Sulawesi and between Bali and Lombok east to Lydekker's Line, i.e., to the east of the Moluccas and Lesser Sundas; see Coates and Bishop (1997)), **Australasia** (from the Moluccas in the centre of Wallacea eastward to Fiji and New Caledonia and Australia), **Australopapuan** (Australia, New Guinea, New Zealand and islands between New Zealand and New Guinea; generally used term for a region that is essentially a subset of Australasia but takes in New Zealand), **Pacific Ocean** (remaining islands in that ocean), and **Atlantic Ocean** (remaining islands in that ocean).

For the purposes of our analysis we have either retained some genera separate or combined them as described below. In this choice we used what we deemed to be the most persuasive evidence, a procedure that is unavoidably subjective. Thus, we include *Asturina* (2-5 species) with *Buteo* (del Hoyo 1994), place *Ketupa* (4-5 species) with *Bubo* (Amadon & Bull 1988), unite *Ciccaba* (4 species) with *Strix*, and maintain *Speotyto* separated from *Athene* (Sibley & Monroe 1990). It is likely that the curious monotypic island endemic genus *Mimizuku* (Giant Scops-owl) should be included with *Otus* (Miranda *et al.* 1997), although we have maintained it as a separate genus as did Miranda *et al.* (1997).

Putative species are taxa that may be allocated to one species but, based on other criteria, could be a valid species in their own right. An example is shown by the disagreement over whether the so-called Harlan's Hawk *Buteo harlani*, represented by dark-coloured populations in interior Alaska and the Yukon, should be treated as a distinct species, or as a geographic race of the Red-tailed Hawk *Buteo jamaicensis harlani*. A similar question exists over whether the pale falcons of central Asia and North Africa are a separate species, the so-called "Barbary" Falcon *Falco peregrinoides*, or merely geographic races of the Peregrine Falcon *Falco peregrinus*, i.e., *F. p. peregrinoides* and *F. p. babylonicus*, or divided in some other manner (see Wink *et al.* this vol.).

One of many examples of unresolved taxonomic questions among raptors is provided by the goshawk on Christmas Island in the Indian Ocean. That taxon, given the trinomial *natalis*, is currently allocated as a subspecies of the Australasian Goshawk *Accipiter fasciatus*, but some authorities regard it as a subspecies (?) in the Variable Goshawk *Accipiter novaehollandiae* complex, and others as a full species in its own right. Regardless of the taxonomic treatment, *natalis* possesses distinct morphological traits; thus, at the least, it appears to be an ESU with a unique gene pool, evolutionary history, and evolutionary future. Many similar examples exist throughout the Falconiformes and Strigiformes.

Cryptic species are similar and defined as those taxa that appear, or are suspected, to be a species in their own right, but for which sufficient data or analyses have not been acquired to confirm their status. This is the situation with the *Tyto* owl on the Galapagos Islands, which is currently regarded as a subspecies, *Tyto alba punctatissima*, of the cosmopolitan Barn Owl complex. The term "species group" has been used similarly to indicate taxa lumped by some as one species, but separated as valid species by others, as shown in insular Indian Ocean "superspecies" of the Madagascar Scops-Owl *Otus rutilus*, with the Malagasy representative nominate *rutilus*, and two "groups," Pemba Scops-Owl *O.[r.] pembaensis* and Adjouan Scops-Owl *O. [r.] capnodes* (Sibley & Monroe 1993). As we proceed through the discussion it will be evident that some of the taxa considered probably properly fall into the category termed "megasubspecies", that is, defined as a subspecies (or cluster of subspecies) known or judged to be approaching species status; many were originally described as full species (Stresemann & Amadon 1979, Amadon & Short 1976, 1992) and some may be restored to full species, even under the BSC, in the future.

RESULTS

The concepts:

It is of perhaps coincidental interest that the numbers of island-dependent Falconiformes and Strigiformes are about equal based on the BSC. About 220 taxa of Falconiformes and 225 taxa of Strigiformes are island-dependent; of these we regard 51-53 and 52-53, respectively, as full species. The island endemic "species" are also about equal between hawks and owls with 54 and 51 respectively (Table 1). It is also clear in Table 1 that the numbers of island endemics increase, in some cases slightly more than double, if one uses the PSC rather than the BSC. In most of the cursory analyses done on a variety of groups of birds, the number of species overall with the PSC increases by a factor of about 2.5 over the number of species with the BSC (R. Zink pers. comm.). The important information in Table 1 is that the percentage of island endemics increases as the focus becomes finer and the resulting populations viewed in some taxonomic fashion are smaller. It should be remembered that: 1). There is not full agreement among workers as to which of the island taxa or populations are full species in their own right so the number is tentative, and 2). Our assessment of the numbers of species with the PSC are not based on rigorous analyses and there is a range of values depending on the inclusion of the ESU's within the larger units.

In nearly each case for the larger genera included in our analysis, the numbers given by Amadon and Bull (1988) were fewer, usually only by one or two but as many as five in the case of *Otus*, since their list is BSC-based. The number of named taxa may change as knowledge increases, but also in part based on the penchant by investigators to lump or split.

As shown in Table 2 the number of taxa listed by the IUCN (based on the BSC) as threatened is nearly equal between Falconiformes and Strigiformes, although more of the Strigiformes occur on islands, but not significantly so ($\chi^2 = 0.52$). There are, however, nearly three times more Falconiformes than Strigiformes listed as near-threatened (significant difference, $\chi^2 = 29$, $p < 0.001$) with about the same differential on islands ($p < 0.01$). The differences may simply reflect our poorer knowledge of Strigiformes; thus, fewer species have been assigned to that category.

Table 2. Distribution of taxa considered by the IUCN to be in the threatened and near-threatened category for Falconiformes and Strigiformes. The threatened category includes: CE = critically endangered, E = endangered, V = vulnerable.

Locations	Number Threatened Taxa (percent of IUCN listed total ¹)						Near-threatened	
	Falconiformes			Strigiformes			Falconi-	Strigi-
	CE	E	V	CE	E	V	formes	formes
Mainlands	2 (6)	2 (6)	10 (32)	1 (4)	2 (8)	6 (23)	31 (70)	9 (60)
Australia	----	1 (3)	2 (6)	----	----	1 (4)	----	1 (7)
Islands								
Atlantic Ocean	----	----	----	----	----	----	----	1 (7)
Indian Ocean	2 (6)	1 (3)	1 (3)	3 (12)	1 (4)	----	4 (9)	3 (30)
Indo-malayan	1 (3)	1 (3)	4 (13)	1 (4)	1 (4)	7 (27)	2 (5)	1 (7)
Australo-papuan	----	----	2 (6)	----	1 (4)	3 (12)	5 (11)	----
Pacific Ocean	----	1 (3)	1 (3)	----	----	----	2 (5)	----
Caribbean	----	1 (3)	----	----	----	----	----	----

¹ Percent rounded to next nearest 0.5% so totals may not equal 100%.

Several genera, owing partly to their primarily tropical distribution (see Bildstein *et al.* 1998), contain more island endemics and more putative or cryptic species than genera with a more temperate distribution (Table 3). To recognize each of these forms taxonomically, especially using the BSC, may simply be an exercise in oversplitting. Most are insular taxa.

Because of the trends in the interpretation of molecular data we would predict that some unique island taxa will be raised to the species level. We especially expect this to occur in populations on certain islands where other species of birds have differentiated enough to be allocated species rank. Some of these taxa and the islands where they might be expected to differentiate are shown in Table 4. With the use of molecular techniques differences in the level of magnitude of change found in other well recognized species are being uncovered. For example, Wink *et al.* (1998), using cytochrome b evidence, argued that the Merlins of North America are a separate species from those of Eurasia and that the Red-necked Falcons of Africa are separate from two groups in India. Based on DNA findings, Norman *et al.* (1998) concluded that the species complex of *Ninox squamipila* is comprised of three separate species; treatments based on traditional morphological characters had considered it to be a single species (Peters 1940, Schodde & Mason 1997).

Table 3. Ten genera and their taxa (BSC) with particularly rich island endemic representation (Part A) compared with 5 genera and their taxa (Part B) with rather poor island representation. Putative or cryptic species are taxa (frequently termed subspecies) that may be differentiated at the species level but still taxonomically hidden within another described taxon (see text). The majority of putative or cryptic forms not described or formally named species are island-dependent endemic taxa. Only one of the putative species in Part B is an island endemic. Number of named species taken from Sibley and Monroe (1990) but may be oversplit.

PART A

*Island Endemics as % of Species and % of Total Taxa*³

<i>Genera</i>	<i>No. Traditionally Named Species</i>		<i>No. Additional Putative or Cryptic Species</i>	
	<i>Total Taxa</i> ¹	<i>Species</i> ²	<i>Species</i>	<i>Total Taxa</i>
<i>Aviceda</i> (Cuckoo Hawks)	5/31	0	20 %	61 %
<i>Pernis</i> (Honey Buzzards)	3/9	8	33 %	55 %
<i>Spilornis</i> (Serpent Eagles)	5/26	7	80 %	81 %
<i>Accipiter</i> (Goshawks/Sparrowhawks)	48/142	9	46 %	63 %
<i>Spizaetus</i> (Hawk Eagles)	13/23	0	8 %	43 %
<i>Falco</i> (Falcons)	37/108	5	19%	26%
<i>Tyto</i> (Barn/Grass Owls)	12/64	2	50 %	55 %
<i>Otus</i> (Scops Owls)	56/224	7? ⁴	43%	74 % ⁵
<i>Ninox</i> (Southern Hawk Owls)	19/73	3?	74 %	74 %
<i>Asio</i> (Long/Short Eared Owls)	7/29	0	14 %	41 %

1. Includes monotypic species in addition to polytypic ones in the total number of taxa.

2. Category indicates that some named subspecies are allocated by some taxonomists to independent species; taxonomy and systematics not clear with new molecular data changing the number on a regular basis..

3. Rounded to the nearest 0.5 %.

4. *Otus* is difficult. In addition to the putative species at least 10 insular taxa and 5 continental taxa treated by Sibley and Monroe (1990) as full species have been considered subspecies of other taxa.

5. Of the taxa , 46 % are in the New World of which only 5 % are island endemics

PART B

<i>Buteo</i> (True Buzzards) ⁶	26/73	3 ? ⁶	15 %	25 %
<i>Aquila</i> (True [booted] Eagles) ⁷	12/19	?	8 %	11 %
<i>Bubo</i> (Eagle Owls) ⁸	18/27 ⁸	1 + ?	6 %	14 %
<i>Strix</i> (Wood Owls) ⁹	18/65	2 ± ?	0 %	26 %
<i>Glaucidium</i> (Pygmy Owls)	20/66	3 ± ?	5 %	15 %

6. Between 2-5 species are sometimes placed in the genus *Asturina* rather than *Buteo* as here (see Amadon & Bull 1988 and Sibley & Monroe 1990). As recently as 1998, the species *poecilochrous* and *polyosoma* were said to be conspecific (Farquhar 1998).

7. Opinions differ on the species limits in the *A. rapax/nipalensis* and *A. heliaca/adelberti* complexes.

8. Herein the genus *Ketupa* (Fish Owls) are included in *Bubo* (see Sibley and Monroe 1990).

9. The Neotropical genus *Ciccaba* (Neotropical Wood Owls) is included in *Strix* (see Sibley and Monroe 1990)

While there is not general agreement even among molecular workers themselves, as to what level of molecular divergence might suggest the species level, we can use an example from among passerines where the average sequence divergence (D) values between subspecies is 0.0058 and between species 0.174 (Barrowclough 1980). Boyce (1989) found that the divergence (D) value between a sample of North American and Argentine American Kestrels *Falco sparverius* was 0.144, suggesting differentiation at the species level, and at least six other populations of kestrels seemingly have equivalent levels of genetic divergence. Whether to regard these various taxa as species or subspecies under the BSC remains problematical, but they presumably qualify as phylogenetic species. The different populations of Merlins, Red-necked Falcons and American Kestrels mentioned here are certainly on their own evolutionary trajectories.

Table 4. Traditional taxa (BSC), often geographically widespread, that occur on certain islands but not differentiated enough on those islands to be given separate binomial or trinomial names. The islands on which they occur are islands where other raptor taxa (as well as many birds) have differentiated sufficiently to be given *nomen*. As shown below in the second column, many of the taxa listed are not prone to differentiation while others are, and probably have done so on the islands listed (see text for discussion). Where a trinomial name is in parenthesis the islands involved refer only to that subspecies.

Taxon No.	Taxa / No.	Island Endemics	
		Total Named Geographic Area	Islands Occupied But Taxa Not Differentiated
<i>Pandion haliaetus</i> subsp.	6 / 0	Indomalayan, Pacific Ocean	some in Indomalayan but also
<i>Machaeerhamphus alcinus</i>	3 / 1	Australopapuan	w Caledonia and Tasmania
<i>Milvus migrans</i>	9 / 3	Indomalayan	Sumatra, Borneo
<i>Milvus milvus</i>	2 / 1	Indomalayan, Australopapuan	several, but mainly New Guinea
<i>Haliaeetus indus</i>	4 / 1	Eurasia	Canary Islands
<i>Ichthyophaga humilis</i>	2 / 0	Indomalayan, Indian Ocean	mainly Sri Lanka, New Guinea
<i>Spilornis cheela (malayensis)</i>	20 / 15	Indomalayan	Sulawesi
<i>Butastur liventer</i>	1 / 0	Indomalayan	North Borneo
<i>Butastur indicus</i>	1 / 0	Indomalayan	Java, Sula Islands
<i>Circus spilonotus</i>	2 / 1	Indomalayan	Japan, Philippine Islands
<i>Circus approximans</i>	1 / 0	Australopapuan, Pacific Ocean	Philippine Islands, Borneo
<i>Circus buffoni</i>	1 / 0	Neotropical	various, including New Zealand
<i>Accipiter badius</i>	6 / 0	Africa, Asia	Trinidad
<i>Accipiter novaehollandiae</i>	23 / 22	Indomalayan, Australopapuan	Sri Lanka, Taiwan
<i>Accipiter fasciatus</i>	12 / 10	Indomalayan, Australopapuan	Tasmania
<i>Accipiter virgata (besra)</i>	8 / 6	Asia, Indian Ocean	Tasmania
<i>Accipiter cirrhocephalus</i>	4 / 2	Australopapuan	Sri Lanka, Andaman Islands
<i>Leucopternis albicollis</i>	4 / 0	Neotropical	Tasmania
<i>Buteogallus urubitinga</i>	2 / 0	Neotropical	Trinidad
<i>Buteo polyosoma</i>	2 / 0	Neotropical	Trinidad
			Falkland (Malvinas) Islands

Table 4. continued

<i>Buteo jamaicensis</i>	14 / 4	Nearctic, Neotropical	Bahamas
<i>Ictinaetus malayensis</i>	2 / 0	S. Asia, Indomalayan	Sri Lanka,
<i>Hieraetus kienerii</i>	2 / 0	S. Asia, Indomalayan	several, mainly Sri Lanka, Sulawesi
<i>Spizaetus cirrhatus</i>	6 / 4	S. Asia, Indomalayan	Several, mainly Borneo, Java
<i>Spizaetus nanus</i>	2 / 1	Indomalayan	Several, mainly Sumatra
<i>Spizaetus alboniger</i>	1 / 0	Indomalayan	Borneo
<i>Polyborus plancus</i>	4 / 2	Nearctic, Neotropical	Cuba, Falkland (Malvinas) Islands
<i>Microhierax fringillarius</i>	1 / 0	S. Asia, Indomalayan	Sumatra
<i>Falco tinnunculus</i> subsp.	11 / 4	Pacific Ocean, Indian Ocean	Socotra, Philippines
<i>Falco cenchroides</i>	2 / 1	Australopapuan	Tasmania
<i>Falco severus</i>	1 / 0	S. Asia east to Australopapuan	New Guinea
<i>Falco longipennis</i>	3 / 0	Australopapuan	Tasmania
<i>Tyto alba</i> subsp	35 / 20	Indian Ocean to Australopapuan	several, Sri Lanka, Solomon Islands
<i>Tyto capensis</i>	10 / 4	Africa, Asia to Australopapuan	Lesser Sundas
<i>Phodilus badius</i>	5 / 3	S. Asia, Indomalayan	Java, Borneo
<i>Otus scops</i>	9 / 4	Eurasia, Indomalayan	Taiwan
<i>Otus bakkamoena</i>	7 / 0	Eurasia, S. Asia	Sri Lanka
<i>Otus lempiji</i> subsp	13 / 8	Asia, Indomalayan	Sakhalin, Sumatra
<i>Bubo virginianus (heterocnemis)</i>	20 / 0	Nearctic, Neotropical	Newfoundland
<i>Bubo bubo (tenuipes)</i>	20 / 1	Eurasia	Kurile Islands, Hokkaido
<i>Bubo sumatrana</i>	2 / 1	Indomalayan	Sumatra
<i>Bubo ketupu</i>	4 / 2	S. Asia, Indomalayan	Java-Borneo
<i>Strix seloputo</i>	3 / 2	S. Asia, Indomalayan	Java
<i>Strix uralensis</i>	11 / 4	Eurasia	Hokkaido
<i>Speotyto cunicularia</i>	19 / 2	Nearctic, Neotropical	Bahamas
<i>Ninox scutulata</i>	11 / 4	Asia to Indomalayan	Sri Lanka, Sumatra

Table 5. Islands or areas and their endemic formerly named taxa from greatest number (top) to lowest. In some cases (especially Madagascar, Sulawesi and New Guinea), the island named also includes smaller satellite or adjacent islands that also have the species. Sulawesi species must also be included in the Wallacea group and thus Wallacea has the greatest number with 20 species although the two entities are listed separately.

Madagascar	15 species	<i>Aviceda madagascariensis</i> <i>Haliaeetus vociferoides</i> <i>Eutriorchis astur</i> <i>Circus maillardi</i> <i>Polyboroides radiatus</i> <i>Accipiter francesii</i> <i>Accipiter madagascariensis</i> <i>Accipiter henstii</i> <i>Buteo brachypterus</i> <i>Falco newtoni</i> <i>Falco zoniventris</i> <i>Tyto soumagnei</i> <i>Otus rutilus</i> <i>Ninox superciliaris</i> <i>Asio madagascariensis</i>
Philippines	including Palawan, 12 species	<i>Spilornis holospilus</i> <i>Pithecophaga jefferyi</i> <i>Spizaetus philippensis</i> <i>Microhierax erythrogenys</i> <i>Otus mirus</i> <i>Otus longicornis</i> <i>Otus megalotis</i> <i>Otus mindorensis</i> <i>Otus fuliginosus</i> <i>Mimizuku gurneyi</i> <i>Bubo philippensis</i> <i>Ninox philippensis</i>
Sulawesi	11 species—see below for remainder of Wallacea	<i>Spilornis rufipectus</i> <i>Accipiter griseiceps</i> <i>Accipiter trinotatus</i> <i>Accipiter nanus</i> <i>Accipiter rhodogaster</i> <i>Spizaetus lanceolatus</i> <i>Tyto inexpectata</i> <i>Tyto rosenbergii</i> <i>Otus manadensis</i> <i>Ninox ochracea</i> <i>Ninox punctulata</i> .
Bismarck Archipelago	9 species * = endemic to New Britain	<i>Henicopernis infuscatus</i> * <i>Accipiter luteoschistaceus</i> * <i>Accipiter princeps</i> * <i>Accipiter brachyurus</i> * <i>Tyto manusi</i> <i>Tyto aurantia</i> * <i>Ninox meeki</i> <i>Ninox variegata</i> <i>Ninox odiosa</i> *
Wallacea	9 species on islands other than Sulawesi where there are 11, thus 20 total for Wallacea	<i>Accipiter henicogrammus</i> <i>Accipiter erythrauchen</i> <i>Tyto nigrobrunnea</i> <i>Tyto sororcula</i> <i>Otus alfredi</i> <i>Otus silvicola</i> <i>Otus</i> sp.

New Guinea	8 species	<i>Ninox rudolphi</i> <i>Ninox squamipila</i> <i>Henicopernis longicauda</i> <i>Accipiter melanochlamys</i> <i>Accipiter poliocephalus</i> <i>Accipiter meyerianus</i> <i>Erythrorhynchus buergeri</i> <i>Harpyopsis novaeguineae</i> <i>Ninox theomacha</i> <i>Uroglauis dimorpha</i>
Caribbean	8 species on various islands * = Cuba, ** = Hispaniola	<i>Chondrohierax</i> spp.* <i>Accipiter gundlachi</i> * <i>Buteo ridgwayi</i> ** <i>Tyto glaucops</i> ** <i>Otus nudipes</i> <i>Otus lawrencii</i> * <i>Glaucidium siju</i> * <i>Pseudoscops grammacus</i>
Pacific Ocean	6 species to include New Caledonia and New Zealand	<i>Accipiter haplochrous</i> <i>Accipiter rufitorques</i> <i>Buteo galapagoensis</i> <i>Buteo solitarius</i> <i>Falco novaezeelandiae</i> <i>Otus podargus</i> .
Solomons	5 species	<i>Haliaeetus sanfordi</i> <i>Accipiter imitator</i> <i>Accipiter albogularis</i> <i>Ninox jacquinoti</i> <i>Nesasio solomonensis</i>
Andaman and Nicobar	4 species	<i>Spilornis minimus</i> <i>Spilornis elgini</i> <i>Spilornis klossi</i> <i>Otus balli</i> <i>Ninox affinis</i>
Indian Ocean other than Andaman and Nicobar	3 species, * = Sri Lanka, see below	<i>Falco punctatus</i> <i>Falco areae</i>
Java	3 species	<i>Glaucidium castanonotus</i> * <i>Spizaetus bartelsi</i> <i>Otus angelinae</i> <i>Glaucidium castanopterum</i>
Sumatra	3 species ¹	<i>Otus umbra</i> <i>Otus enganensis</i> <i>Otus mentawi</i> <i>Otus brookii</i> ²
Borneo	3 species ³	<i>Spilornis kinabaluensis</i> <i>Microhierax latifrons</i> <i>Otus mantanensis</i> ³ <i>Otus brookii</i> ²
Atlantic Ocean	1 species	<i>Otus hartlaub.</i>
Tasmania	1 species	<i>Tyto castanops</i>
Sri Lanka	1 species- also listed separately because somewhat distant from the other islands in the Indian Ocean	<i>Glaucidium castanonotus</i>
Mediterranean	1 species	<i>Falco eleonorae</i>

1. Van Marle and Voous (1988) recognize the Stresemann's Mountain Scops-Owl *Otus stresemanni* as an endemic species thus giving Sumatra four endemics but suggest that it may be a subspecies of the Mountain Scops-Owl *O. spilocephalus*, where it is also placed by Sibley and Monroe (1990).

2. In both Sumatra and Borneo

3. Off coast of N.W. Borneo but counted.

Table 6. Comparison of raptor taxa (species and subspecies, BSC) endemic to islands in the Caribbean and Mediterranean seas. Some small islands and islets, e.g., along eastern coast of Mexico and western coast of Italy, where no endemics occur, are not listed. Islands in the Caribbean are in Part A and those in the Mediterranean in Part B. Abbreviations in Part A are: CU = Cuba and Isle of Pines, HI = Hispaniola, PR = Puerto Rico, JA = Jamaica, BH = Bahamas, LA = Lesser Antilles except Trinidad and Tobago, TT = Trinidad and Tobago, NA = Netherlands Antilles. X = present, – = absent. Percents are rounded to nearest whole number.

PART A Taxa endemic in Caribbean Islands

	% taxa island endemics / % taxa	CU	HI	PR	JA	BH	LA	TT	NA
<i>Chondroheirax uncinatus</i> ¹	50 / 100	X	–	–	–	–	X	–	–
<i>Rostrhamus sociabilis</i> ²	25 / 100	X	–	–	–	–	–	–	–
<i>Accipiter striatus</i> ³	30 / 100	X	X	X	–	–	–	–	–
<i>Accipiter gundlachi</i>	100 / 100	X	–	–	–	–	–	–	–
<i>Buteogallus anthracinus</i> ⁴	67 / 50	X	–	–	–	–	–	–	–
<i>Buteo ridgwayi</i>	100 / 100	–	X	–	–	–	–	–	–
<i>Buteo platypterus</i> ⁵	83 / 100	X	–	X	–	–	X	X	–
<i>Buteo jamaicensis</i> ⁶	29 / 50	X	X	X	X	–	–	–	–
<i>Falco sparverius</i> ⁷	31 / 80	X	X	X	–	X	X	–	X
<i>Tyto alba</i> ⁸	57 / 25	X	–	–	X	X	X	–	X
<i>Otus nudipes</i>	100 / 100	–	–	X	–	–	–	–	–
<i>Otus lawrencii</i>	100 / 1100	X	–	–	–	–	–	–	–
<i>Speotyto cunicularia</i> ⁹	16 / 66	X	X	–	–	–	–	–	X
<i>Glaucidium siju</i>	100 / 100	X	–	–	–	–	–	–	–
<i>Pulsatrix perspicillata</i> ¹⁰	17 / 100	–	–	–	–	–	–	X	–
<i>Asio stygius</i> ¹¹	33 / 100	X	X	–	–	–	–	–	–
<i>Asio clamator</i> ¹²	33 / 100	–	–	–	–	–	–	X	–
<i>Asio flammeus</i> ¹³	60 / 33	–	X	X	–	–	–	–	–
<i>Pseudoscops grammicus</i>	100 / 100	–	–	–	X	–	–	–	–

1. Population on CU sometimes treated as separate species, the Cuban Kite *Chondrohierax wilsonii*; population on Granada (LA) = *C.h. mirus*

2. CU = *R.s. levis*

3. Populations named *ventralis*, *chionogaster* and *erythronemius*, here considered full species; CU = *A.s. fringilloides*, HI = *striatus*, PR = *venator*.

4. CU = *B.a. gundlachi*

5. CU = *B.p. cubanensis*, PR = *brunescens*, LA and TT = *insulicola*, *rivierei*, and *antillarum*.

6. CU = *B.j. solitudinis*, HI, PR, and JA = *jamaicensis*.

7. CU and BH = *F.s. sparveroides*, HI = *dominicensis*, PR and LA = *caribearum*, NA = *brevipennis*.

8. CU and JA = *T.a. furcata*, BH = *lucayana*, LA = *nigrescens* and *insularis*, NA = *bargei*.

9. Has been placed in the genus *Athene*, CU = *S.c. siguapa*, HI = *noctipetens*, NA = *arubensis*.

10. TT = *P.p. trinitatis*.

11. CU = *A.s. sipuapa*, HI = *noctipetens*.

12. Often in genus *Rhinoptynx*, TT = *A.c. oberi*.

13. HI = *A.f. domingensis*, PR = *portoricensis*.

Table 6, continued PART B. Islands on the Mediterranean Sea. See part A for description of Table content. SY = Sicily, SR = Sardinia, CR = Corsica, CY = Cyprus, GI = Greek Islands (Cyclades, Crete), BA = Balearics, NA = offshore of North Africa.

	Taxa Percent (see Part A)	SY	SR	CR	CY	GI	BR	NA
<i>Accipiter nisus</i> ¹	23 / 50	—	X	X	—	—	—	—
<i>Accipiter gentilis</i> ²	33 / 33	—	X	X	—	—	—	—
<i>Falco eleonorae</i>	100 / 98 ±	X	X	X	X	X	X	X
<i>Tyto alba</i> ³	57 / 10	—	X	X	—	—	—	—
<i>Otus scops</i> ⁴	44 / 50	—	—	—	X	X	—	—
<i>Athene noctua</i> ⁵	7 / 100	—	X	—	—	—	—	—

1. SR, CR = *A.n. wolterstorffi*

2. SR, CR = *A.g. arrigonii*

3. SR, CR = *T.a. ernesti*

4. CR = *O.s. cyprinus*; GI = *O.s. cyclodum*

5. SR = *A.n. sarda*

The data we present for the family Strigidae are admittedly tentative since owls are not as well known taxonomically as Falconiformes. The dynamic nature of strigid taxonomy is illustrated by the recent splitting of the Least Pygmy-owl *Glaucidium minutissimum* into six species (with the naming of a new one and the elevating of subspecies to species level), based on differences in vocalizations thought to isolate the taxa reproductively in zones of present or potential contact (Howell & Robbins 1995). At least three of the taxa, *G. palmarum*, *G. minutissimum*, and *G. sanchezi*, differ only slightly morphologically, but are allopatric and have been regarded as subspecies under the BSC. Aside from the vocalization characters, they may not differ sufficiently to qualify as species under the PSC.

Based on the *Glaucidium* example and the distribution of other isolated strigid taxa, it is possible to predict that among the genus *Otus* the Spotted Scops Owl *O. spilocephalus* may be composed of five species, Eurasian Scops Owl *O. scops* of nine species, Madagascar Scops Owl *O. rutilus* of two species, and Collared Scops Owl *O. lempiji* of six species. If this sort pattern holds true for the entire family, we may have underestimated the number of species of Strigidae based on the PSC concepts by 10-15% and perhaps even as much as 30-40%.

Conversely, we have not shown the numbers of species (BSC) that might be considered conspecific with other species. However, among the Falconiformes a minimum of 30, of which five are island endemics, have been suggested to be conspecific with other taxa. Among the Strigiformes a minimum of 36 have been suggested to be conspecific (Sibley & Monroe 1990) and 12 of these are island endemics. For example, the island-dependent, highly endemic Moluccan Scops-Owl *Otus magicus* complex includes several forms that may properly belong to either the Madagascar Scops-Owl *Otus rutilus* or the Sulawesi Scops-Owl *Otus manadensis* (see Sibley & Monroe 1990, Howard & Moore 1991, Coates & Bishop 1997).

The Islands: Contemporary taxonomy.

As a geographic unit, Wallacea has the most (20) endemic island-dependent species of Falconiformes and Strigiformes combined. This is not significantly different from Madagascar with the next greatest number of endemics ($c^2 = 1.05$). Although Wallacea has 60% more island endemics than the Philippines, both have nearly the same percentage of polytypic species - 35% and 33%, respectively (Dickinson *et al.* 1991, Coates & Bishop 1997) with no significant difference between those that show subspeciation and those that do not ($c^2 = 0.009$). However the Philippines seemingly have higher rates of differentiation among its 7,000+ islands than Wallacea does among 13,500+ islands. The apparent high rate of speciation producing endemic *Otus* owls in the Philippines may reflect taxonomic oversplitting, or simply more thorough study than in Wallacea (Marshall & King

in Amadon & Bull 1988). There may be as high a rate of endemics in equivalent insular situations in other regions, but existing as overlooked cryptic species.

Within the Madagascan fauna we have included the Malagasy Scops-Owl *Otus rutilus*, which occurs not only in the Comoros, but also as an isolated subspecies some 1,300 km away on Pemba Island off the coast of Tanzania; perhaps the latter population is actually a different species (Sibley & Monroe 1993, Langrand 1990). The Madagascar Marsh-Harrier *Circus maillardi* is frequently treated as a subspecies of the very widespread Western Marsh-Harrier *Circus aeruginosus*, as is the Eastern Marsh-Harrier *Circus spilonotus*, which has insular forms on New Guinea, the Philippines, and Borneo (Nieboer 1973).

For New Guinea we include the East and West Papuan Islands, Aru, and islands in the Bay of Geelvink (Beehler *et al.* 1986). Although we have listed here only the three endemic *Accipiter* species (Table 5), there are seven resident species, with three of these more or less centred in Australia. This is rivalled by the Bismarck Archipelago with at least five resident *Accipiter* species, although both regions contain fewer species than Wallacea. The greatest radiation of insular species of *Accipiter* occurs in a region called "Australasia", running from the centre of Wallacea to Fiji and New Caledonia and including Australia, where 17 *Accipiter* species are island residents (see Wattel 1973). It is not surprising that Sulawesi has numerous endemic raptors since it has a generally rich endemic flora and fauna (Whitten *et al.* 1987a). The number of endemics there contrasts remarkably with adjacent Borneo, Java and Sumatra (Table 5), which also have a much poorer endemic fauna overall (Smythies 1960, Whitten *et al.* 1987b, MacKinnon & Phillipps 1993).

It is interesting that at least one additional type of endemic with specific ecological and behavioural traits does not now occur in the Caribbean region (Tables 5 and 6). Walter (1979) commented on the curious lack of a colonial falcon species in the islands of the Caribbean as there is in the Mediterranean islands with the Eleonora's Falcon *Falco eleonorae*. Ecological conditions in the Caribbean, including the biannual stream of migrating passerine species, appear at least superficially similar to those of the Mediterranean. It is possible that early extinctions may have eliminated one or more raptors that filled that role, since ecological changes from European colonization in the last 500 years in the Caribbean have been extensive (Wiley 1986). However, no Caribbean raptor species is known to have become extinct historically, although the Short-eared Owl *Asio flammeus* on Puerto Rico has come close to extinction (Wiley 1986), the Hook-billed Kite *Chondrohierax uncinatus* on Cuba (traditionally considered a subspecies, *C. u. wilsonii*, but recently elevated to full species rank by Raffaele *et al.* 1998) is on the verge of extinction, and the Hook-billed Kite form *C. u. mirus* endemic to Grenada is even more critically endangered.

A comparison of the endemic island taxa in the Caribbean (Voous 1983, French 1991, Raffaele *et al.* 1998) with those in the Mediterranean (Cramp & Simmons 1980, Cramp 1985) clearly shows a significantly greater ($\chi^2 = 6.76$, $p < 0.01$) contemporary number of taxa in the Caribbean than the Mediterranean (Table 6). At the species level, however, the significance level drops ($\chi^2 = 5$, $p < 0.05 > 0.02$). It is curious that only one Mediterranean endemic, the Eleonora's Falcon, occurs on Sicily or its satellite islands; it is also the most widespread.

DISCUSSION

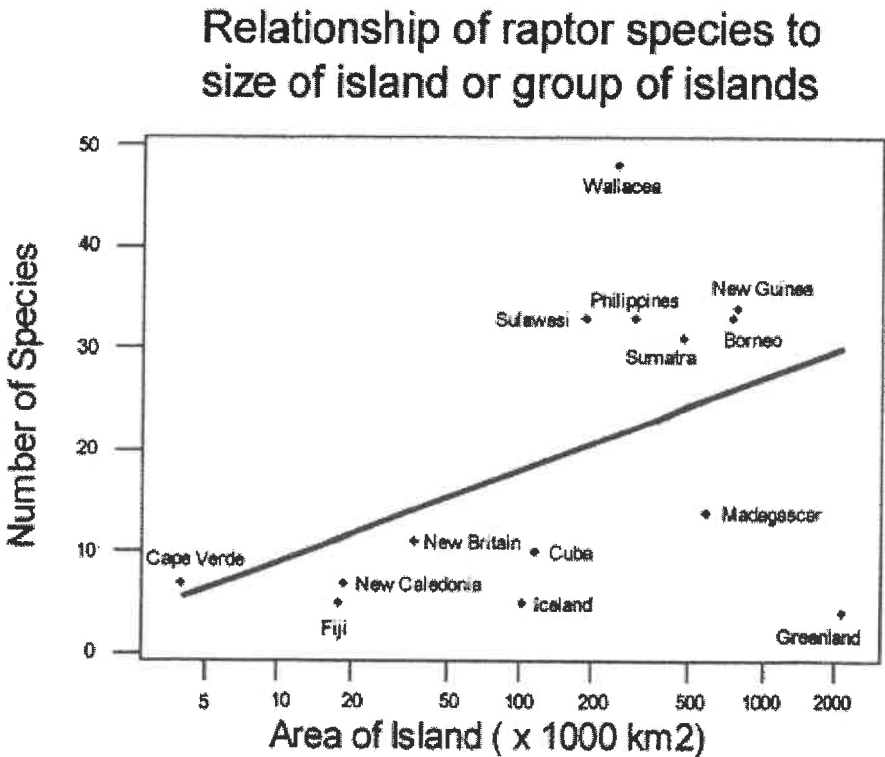
Island Influences on Differentiation

It is well known that some taxa (e.g., *Tyto* and *Otus*) have a marked penchant for colonizing islands and undergoing differentiation at the species or subspecies levels. A major influence on this issue is the exposure to, or opportunity for, isolation on islands. Taxa occurring in areas of abundant islands have the greater exposure to the possibility of isolation. Also, taxa in tropical environments, where there is a greater chance of permanent residency, have more opportunity for the fixation of unique character traits. For all bird species, including the Falconiformes and Strigiformes, it has been shown that there is a significant positive association between the number of island-endemic species and the number of continental species in the family and the number of islands in the vicinity, but this factor only accounts for 50% of the variance ($G=1571$, $P<0.0001$, $df=66$) (McCall *et al.*

1996). This clearly does not explain all the differences seen, since the frequency of gene flow or genetic liability in the taxa is not unusually known. Gene flow, however, cannot be great, or at least is less than the influences and pressure for differentiation.

The degree of island influence on differentiation depends on whether the perspective is at the species or subspecies level. This is illustrated by the comparisons of the Caribbean and Mediterranean sea avifaunas. Since our present knowledge of events in either sea is limited to the relatively short-term historical records and the incomplete fossil record, we cannot know the actual extent of differentiation that has occurred. As a general rule, however, differentiation at the species level (BSC) follows the "island area curve" (MacArthur 1972) as seen in Figure 1. The larger the island the more taxa there are. There are a great many exceptions, however, that may have to do with climate (tropical or arctic as in the case of Greenland), or the age of the island, as examples. Islands long inhabited by humans have usually lost species regardless of their size or degree of isolation. We suspect this may be the case with Madagascar and its fewer than expected species based on island size.

Figure 1. Relationship of raptor species (BSC) to size of some selected islands or group of islands. Generally the relationship follows the "island area curve"(see text) with three important departures. Madagascar is highly depauperate which may be related to vegetational changes since colonization (1,500 years BP). Wallacea represents a group of islands some of which have their own suite of endemics. Greenland is mainly composed of uninhabitable ice, thus for all its size it is an arctic island which typically have fewer species than tropical or temperate islands. The regression is not significant with $P = 0.094$. Without the two outliers of Wallacea and Greenland (see text) the relationship becomes significant at $P = 0.004$.



Striking differences in levels of raptor endemism between adjacent islands is shown between Borneo and Sulawesi, the Philippines and Sulawesi, and New Britain and New Ireland. Borneo has only two endemic raptor species, and none of *Accipiter*; the Philippines has at least 12, but no endemic *Accipiter* species, while Sulawesi has four endemic *Accipiter* species. While the Philippines has five endemic *Otus* species, Sulawesi has but one (see Table 5). Perhaps most unexpected is the low number of endemic raptors on Borneo. New Britain contains 67% of the endemic species, including three of *Accipiter*, in the Bismarck Archipelago, while adjacent New Ireland, although more than 70% smaller, has no completely endemic species, and the only breeding *Accipiter* species there is the widespread Variable Goshawk *Accipiter novaehollandiae*.

Loss of Diversity on Islands

The IUCN lists six taxa of raptors known to have become extinct since about 1600, and all were island endemics (Baillie & Groombridge 1996). They include a *Falco* sp. (Réunion, Indian Ocean), the Guadalupe Caracara *Polyborus lutosus* (Guadalupe Island, Mexico), an owl *Sauziera* sp. and the Mauritian Owl *Scops commersoni* (Mauritius, Indian Ocean), Rodrigues Little Owl *Athene murivora* (Rodrigues Island, Indian Ocean) and the Laughing Owl *Sceloglaux albifacies* (New Zealand).

While the IUCN category of "threatened" includes the categories "critical," "endangered," and "vulnerable," we think it worthwhile to separate the first two categories from the latter. In the Falconiformes there are 31 taxa listed as threatened, and 11, including nine (82%) island endemics, are in the first two categories. Among the Strigiformes, 26 are listed as threatened and of the nine in the first categories, six (67%) are island endemics. At a lower level of concern are what IUCN terms "near threatened" species, a less precise term, but a category that nevertheless may include taxa requiring conservation action. This category includes 44 species of Falconiformes, of which 13 (30%) are island endemics, while in the Strigiformes, three (12%) of the 25 species are island endemics. Large-sized owls, in fact, the largest known (*Ornimegalonyx*) and a radiation of large-sized insular *Tyto* owls (*T. alba*, *T. noeli*, *T. riveroi*, *T. osstologa* and *T. pollens*) occur in the Quaternary fossil record of the Caribbean (Olson 1985); there was likewise a radiation of raptors, now extinct, in the Mediterranean (Bochenski 1992, Alcover *et al.* 1992). It is not yet clear what impact the long history of human occupancy in the Mediterranean has had on the extinction rates of former endemics there, but Olson and James (1982) have documented the profound effects of man on avian extinctions in Polynesia in recent, but prehistoric times.

The Island Conundrum: Biodiversity and Conservation.

The issue of raptor conservation on islands poses some interesting problems, as with many other groups of insular birds. As previously noted, the tendency, whether administrative, political, or biological, is to devote conservation efforts to birds and other vertebrates at the species level (Collar 1997). However, if we concentrate only on full species, unique genetic combinations and distinctive evolutionary variations stand a chance of being lost. We think this is especially true as consensus on a universally accepted species concept become increasingly unlikely as new technology and different interpretations emerge. This partly reflects generational tensions between adherents of the imperfect traditional species concepts, and molecular researchers, whose search for perfect understanding of raptors' genomes is still subject to the limitations of current analytical techniques. Because of this, certain species of raptors, as identified by future, more sophisticated analyses, will doubtless be lost unknowingly, because of actions taken "too little too late," or because the political climate and geography work against conservation efforts. Increasingly, choices must be made about conservation, as described by Mann and Plummer in their book "Noah's Choice: The future of endangered species" (1995). The complexity of the species definition issue and thus of conservation efforts is demonstrated with several island taxa that are comprised totally, or in part, by island endemics, as is the case among the owls *Tyto*, *Otus*, and *Ninox* and among the diurnal raptors *Accipiter* and *Spilornis*.

At the species level *Tyto alba* is one of the most widespread land birds, having, in the broadest taxonomic sense, an almost cosmopolitan range. With such a widespread species one could argue that the loss of the populations from, say, the Galapagos Islands (currently *T. a. punctatissima*) is not that much of a loss of biodiversity because there are still Barn Owls remaining over large portions of

the earth. However, as previously noted, both this taxon and *T. a. delicatula* of Australia and the Solomon Islands almost certainly constitute phylogenetically independent species (Sibley & Monroe 1990). By any approach other than the BSC, the loss of either of these taxa would, therefore, be a significant conservation event, equivalent to the long-lamented loss of the Guadalupe Caracara *Polyborus butosus*.

Among falconiform genera, *Accipiter* contains the greatest number of species listed by the IUCN in one of the threatened categories. Of the 11 listed, nine are island endemics, namely, the New Britain Sparrowhawk *A. brachyurus* of New Britain Island, Gundlach's Hawk *A. gundlachi* from Cuba, Imitator Sparrowhawk *A. imitator* from the Solomon Islands, Nicobar Sparrowhawk *A. butleri* from the Nicobar Islands, Henst's Goshawk *A. henstii* of Madagascar, Slaty-mantled Sparrowhawk *A. luteschistaceus* of New Britain Island, Madagascar Sparrowhawk *A. madagascariensis* of Madagascar, Small Sparrowhawk *A. nanus* of Sulawesi, and the New Britain Goshawk *A. princeps* of New Britain Island. Part of the problem with this genus is our present lack of taxonomic knowledge. For example, one of the more complex issues with *Accipiter* involves the current makeup of the Variable Goshawk *A. novaehollandiae* complex. As the name suggests, the species is incredibly variable in size and colour, ranging from pure white forms to those with gray barred breasts to those with rufous breast and nuchal collars. Size is variable with mean wing length ranging in males from about 184 mm (an island endemic) to 262 mm in Australia (a 30% difference). The insular Moluccan *griseogularis* complex (213 mm average wing length in males) of three recognized forms with rufous breast and faint barring and rufous nuchal collars may represent a separate species. The yet several smaller insular forms in the Moluccas (represented by *A. hiogaster*) have solid rufous to chestnut breast and lack a collar may be other species. There is no way to use the BSC to test species (reproductive) limits among them, and their status has been mired in controversy among traditional taxonomists. From an empirical standpoint, the PSC supports full species separation.

The serpent eagles, *Spilornis*, are particularly characteristic of islands, and as many as 24 taxa in five species have been recently accorded formal status, with 19 of them being island endemics. The number of species, however, usually varies from two, with eight megasubspecies, to five. Sumatra and her satellite islands are particularly rich in taxa. Within short inter-island distances they have pronounced morphological differences. The form *malayensis* on northern Sumatra is rather dark in colour and large with an average wing length of 364 mm while 125 km westward on Nias Island the form *asturinus* is very pale and small with an average wing of 299 mm. There is clearly no gene flow nor is there a character cline between them. Are these good species? How does one treat them relative to the conservation of species? There are at least two distinct forms on the Nicobar Islands, *kolssi* and *minimus*, both of which are small and similar in colour. Even here, however, the issue is not that simple, and views on their systematic relationship (species or subspecific status) vary from author to author. Pending molecular investigations, the evolution and species limits of this genus is complex, unresolved, and the number of published opinions probably exceeds the number of actual species.

Bock (1995) stated that one concept or one manner of recognizing species is no better than the other when it comes to the issue of conservation, although he recognized the need to conserve unique gene pools. Because of legal, political, financial, and biological considerations, we do not agree that all taxonomic approaches will yield the same conservation result. We would contend that, depending on the level of taxonomic concentration, whether at the traditional BSC level, the PSC, or the fine-grained ESU level, the economic and logistical implications are profound. It is estimated that the cost of the captive breeding and reintroduction programme that brought the Mauritius Kestrel *Falco punctatus* back from near extinction was at least US\$500,000 (W. Burnham, pers. comm.). The expense of rescuing similar endangered raptors will naturally vary widely, depending on such factors as the size of the population, the nature of the conservation problem, and the complexity of the solution. In the future, however, the most important variable of all may be whether we decide to concentrate our conservation resources at the BSC or PSC levels, or whether we will spread them thinner by concentrating on smaller units. In practice, the latter approach may include every disjunct

raptor population on every island of any significant size.

In the foregoing discussion, we have selected a small sample from a very much larger array of possible taxa that could be offered as examples of taxonomic uncertainty. They all indicate the folly in being too definitive -- or too premature -- in judgements on species limits. Without adequate knowledge of taxonomic relationships, there is additional folly in conservation efforts, especially if the goal of the conservation is to preserve genetic diversity. How, then, does one proceed with conservation efforts in politically unstable countries with differing priorities of whether one saves "species" or "evolutionarily significant units," compounded by the problem of taxa with unresolved systematics? Resolution of this conundrum is a challenging task for the future and the preservation of biodiversity. Islands may well present the ultimate test of our commitment and abilities.

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