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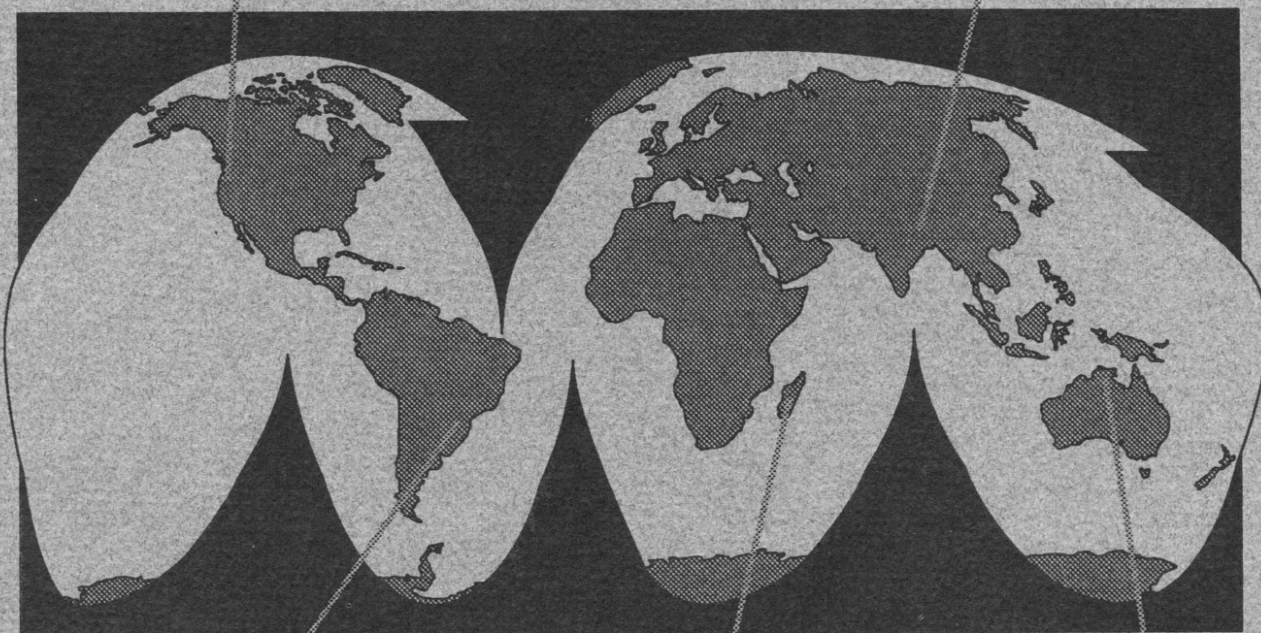
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Owls of Old Forests of the World

Bruce G. Marcot



Cover

The cover illustrates a few selected species of owls found in old forests of the world. Clockwise from upper left: in conifer forests of North America is the Northern Spotted Owl (*Strix accidentalis caurina*); in dense evergreen forests of Southeast Asia is the Bay Owl (*Phodilus badius*); in rain forests of Australia is the Rufous Owl (*Ninox rufa*); in dense evergreen rain forests of Madagascar is the Soumagne's Owl (*Tyto soumagnei*); and in Neotropical lowland forests of South America is the White-Chinned or Tawny-browed Owl (*Pulsatrix koeniswaldiana*).

Author

BRUCE G. MARCOT is a wildlife ecologist, Ecological Framework for Management Research Development, and Application Program, Pacific Northwest Research Station, P.O. Box 3890, Portland, OR 97208-3890

Abstract

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A review of literature on habitat associations of owls of the world revealed that about 83 species of owls among 18 genera are known or suspected to be closely associated with old forests. Old forest is defined as old-growth or undisturbed forests, typically with dense canopies. The 83 owl species include 70 tropical and 13 temperate forms. Specific habitat associations have been studied for only 12 species (7 tropical and 5 temperate), whereas about 71 species (63 tropical and 8 temperate) remain mostly unstudied. Some 26 species (31 percent of all owls known or suspected to be associated with old forests in the tropics) are entirely or mostly restricted to tropical islands. Threats to old-forest owls, particularly the island forms, include conversion of old upland forests, use of pesticides, loss of riparian gallery forests, and loss of trees with cavities for nests or roosts. Conservation of old-forest owls should include (1) studies and inventories of habitat associations, particularly for little-studied tropical and insular species; (2) protection of specific, existing temperate and tropical old-forest tracts; and (3) studies to determine if reforestation and vegetation manipulation can restore or maintain habitat conditions. An appendix describes vocalizations of all species of *Strix* and the related genus *Ciccaba*.

Keywords: Owls, old growth, old-growth forest, late-successional forests, spotted owl, owl calls, owl conservation, tropical forests, literature review.

Summary

To better understand the broader context of conservation strategies developed for the Northern Spotted Owl in the Pacific Northwest of the United States, this paper reviews the status and management of owls associated with old, closed-canopy, or undisturbed temperate and tropical forests throughout the world.

A total of 83 extant owl species are associated with old forests. Twelve of these species (seven tropical or subtropical and five temperate) are fairly well known to be closely associated mostly with dense, old, or undisturbed forests. Examples include Soumagne's Owl of dense, evergreen rain forests of Madagascar; the Bay Owl of Himalayan forests; the Northern Spotted Owl of the Pacific Northwest, and its cousin the Himalayan Wood Owl of eastern Himalayas oak and conifer forests; and the Crested Owl of dense forests of the Neotropics (figs. 22, 23). The remaining 71 species (63 tropical and 8 temperate) are associated with, and may be dependent on, old forests but are essentially unstudied.

Basic inventories and ecological studies of habitat associations of many of these 83 species are needed. Priority should be given for species in isolated, insular, or increasingly fragmented environments (for example, Celebes Barn Owl and Giant Scops Owl) whose primary old-forest habitat is threatened and in decline, as it is with many of the tropical species (for example, Scully's Wood Owl and Fulvous Owl; see figs. 12, 13).

Nearly a third of the 83 species occur on islands or peninsulas, and the remainder are found in continental settings. The island forms are often at relatively higher risk of population decline and extinction. At least six owl species recently extinct likely were associated with old forests; five of these occurred on islands.

The greatest threat to owls of old forests is the direct loss of their habitats. One example is the loss in recent decades of old, dense, interior forest habitat of wet evergreen and moist deciduous forests in the Indo-Malayan area, which has caused declines in populations of Brown Wood Owls and Bay Owls. Other threats, particularly to island forms, include conversion of older upland secondary forests, use of pesticides, loss of riparian gallery forests, loss of trees with cavities for nests or roosts, and tourism and other human disturbance.

No scientific studies have demonstrated to date that forestry can be used to restore old-forest habitats and associated owl populations. In the Pacific Northwest, however, silvicultural studies are underway to test how well old-forest components, such as large live trees, large snags and down logs, and dense and diverse vegetation structures, can be maintained intentionally or induced by direct stand manipulation. One phase of these studies involves testing behavioral and population responses by the Northern Spotted Owl in National Forests. Restoration projects elsewhere, as in Costa Rica and India, might help identify useful silvicultural methods to recover local populations and habitats of old-forest owls, but much work still is needed.

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Introduction

The Northern Spotted Owl (*Strix occidentalis caurina*) has been the center of recent controversies over conservation of ancient forests in the Pacific Northwest of the United States. Globally, however, it is not the only owl species associated with old-forest habitats. This paper reviews species of owls associated with old temperate and tropical forests throughout the world.

Although other authors (for example, Clark and others 1987) have summarized occurrence of some owl species by general forest types, none has done so for old forests and with a global perspective. This report discusses owl species closely associated with old, dense, or undisturbed forests, particularly species with populations or habitats declining in abundance or distribution. I generally follow taxonomies presented in Everett (1977), Clark and others (1978), Amadon and Bull (1988), and Voous (1988). Scientific names of all old-forest owls are listed in table 1. Scientific names of selected subspecies and species are included in the text for clarity or for species not closely associated with old forests.

I do not discuss all species of owls found in forested habitats. I list species associated with dense, old-forest conditions in two categories: (1) species whose associations with such forests have been documented by primary scientific autecological studies, and (2) those without studies but with anecdotal accounts suggesting close association. I also denote species (1) whose ranges primarily occur in tropical latitudes ("tropical") and (2) those mostly in temperate latitudes or in high-elevation temperate forest habitats in tropical latitudes ("temperate"). As a point of comparison, I also discuss some species that seem to inhabit other forest conditions successfully and that can coexist in human-altered landscapes. I hope that this review will lead to a broader understanding and better informed decisions on managing old-forest habitats, such as those for the Northern Spotted Owl in the Western United States.

Owls of Old Forests of the World

It is not unusual for forest-dwelling wildlife species to exhibit specific affinities and adaptations for old- or undisturbed-forest environments. In many ways, much of the wildlife of the world evolved in association with vegetation and environments unaltered by human presence. This is also true with owls. Some owls have persisted in spite of persecution by humans, such as the Great Horned Owl (*Bubo virginianus*), or have successfully adapted to use of buildings and human habitations, such as the Barn Owl (*Tyto alba*). Others, including the Eurasian Eagle-Owl (*Bubo bubo*), have been extirpated throughout much of their previous range (Clark 1987, Clark and others 1978, Fremming 1987; see fig. 26) but have persisted in areas of rather sparse human presence. Such persistence indicates the extent to which some owl species can tolerate additional habitat change. Many owl species have retained their close affinities with the old forests in which they likely evolved (table 1) and have suffered great declines because of habitat alteration.

Ecologies of most owl species are little known. Habitats, particularly of forest owl species, seldom are described in details of forest age, structure, flora, or degree of disturbance. Thus, in this report, "old forest" refers to various conditions, particularly (1) closed-canopy forests (which often denotes undisturbed, mature or old-growth forests); and (2) forested stands and landscapes little disturbed by human activities, especially timber harvests, human settlements, agriculture, and human-caused fires.

Table 1-Owls primarily associated with old tropical or temperate forests^a

Species	Tropical ^b	Temperate ^b	Range, habitat
<i>Tyto</i> , Barn Owls and relatives:			
Celebes Barn Owl (<i>T. rosenbergii</i>)	?		Celebes rain forest
Sooty Owl (<i>T. tenebricosa</i>)-	?		Australia
Lesser Sooty Owl (<i>T. multipunctata</i>) (recently listed as separate species)	?		Northeast Queensland
Soumagne's Owl (<i>T. soumagnei</i>)	x		Madagascar dense evergreen rain forest
Sula Island Barn Owl (<i>T. nigrobrunnea</i>)	?		Indonesia
Minahassa Barn Owl (<i>T. inexpectata</i>)	?		Indonesia
<i>T. pollens</i> (extinct)	(?)		Bahamas pine barrens
<i>Phodilus</i> , Bay Owls:			
Bay Owl (<i>P. badius</i>)	x		Himalayas dense evergreen forest
Prigogine's Owl or African bay owl (<i>P. prigoginei</i>)	?		Congo montane forest
<i>Otus</i> , Scops Owls:			
Spotted Scops Owl (<i>O. spilocephalus spilocephalus</i>)-		?	Southeast Asia evergreen forest
Javan Scops Owl (<i>O. s. angelinae</i>) ^c	?		Java mountain forests
White-Fronted Scops Owl (<i>O. sagittatus</i>)	?		Malaysia lowland and foothill forest
Reddish Scops Owl (<i>O. rufescens</i>)	?		Southeast Asia dense low-elevation forest
Giant Scops Owl (<i>O. gurneyi</i>) (sometimes <i>Mimizuku gurneyi</i>)	?		Philippines lowland rain forest
Tawny-Bellied Screech Owl (<i>O. watsonii</i>)	?		Amazonia rain forest
Puerto Rican Screech Owl (<i>O. nudipes</i>)	?		Puerto Rico
Flores Scops Owl (<i>O. alfredi</i>)	?		Lesser Sundas mountain woods
Rajah's Scops Owl (<i>O. brookii</i>)	?		Sumatra
Lesser Sunda Scops Owl (<i>O. silvicolus</i>)	?		Lesser Sundas coastal forest
Sandy Scops Owl (<i>O. icterorhynchus</i>)	?		African Gold Coast forest
Sokoke Scops Owl (<i>O. ireneae</i>)	?		East Kenya coastal forest
Mentaur Scops Owl (<i>O. umbra</i>)	?		Southwest Pacific coastal forest
Cuban Screech Owl (<i>O. lawrencii</i>)	?		Cuba forest
Santa Barbara or Bearded Screech Owl (<i>O. barbarus</i>)	?		Mexico
Black-Capped Screech Owl (<i>O. atricapillus</i>)	?		South America subtropical rain forest
Rufescent Screech Owl (<i>O. ingens</i>)	?		South America subtropical forest
Cinnamon Screech Owl (<i>O. petersoni</i>)	?		Peru and Ecuador high-cloud forest
Cloud-Forest Screech Owl (<i>O. marshalli</i>)	?		Peru high-elevation cloud forest
Colombian Screech Owl (<i>O. colombianus</i>)	?		Colombia high-elevation mountain forest
Bare-Shanked Screech Owl (<i>O. clarkii</i>)	?		Central America highland forest
White-Throated Screech Owl (<i>O. albogularis</i>)		?	Northern Andes highland cloud forest
Roborate Screech Owl (<i>O. roboratus</i>)		?	Peru Andes highland forest
Seychelles Scops Owl (<i>O. insularis</i>)	?		Mahe in Seychelles
São Thomé Scops Owl (<i>O. hartlaubi</i>)	?		São Thomé island
Lan Yu Scops Owl (<i>O. elegans botelensis</i>)	?		Taiwan forests
Pacific Screech Owl (<i>O. cooperi</i>)	?		Neotropics deciduous and evergreen forest
Anjouan Island Scops Owl (<i>O. rutilus capnodes</i>) (recently extinct)	(?)		Anjouan Island forests?
Mauritius Scops Owl (<i>O. commersoni</i>) (recently extinct)	(?)		Mauritius Island forests?
<i>Bubo</i> , Eagle-Owls:			
Forest Eagle-Owl (<i>B. nipalensis</i>)	x		India Himalayas dense submontane forest
Shelley's Eagle-Owl (<i>B. shelleyi</i>)	?		Africa tropical and subtropical forest
Akun Eagle-Owl (<i>B. leucostictus</i>)	?		Africa tropical and subtropical forest
Fraser's Eagle-Owl (<i>B. poensis</i>)	?		Africa tropical and subtropical forest
Barred or Malay Eagle-Owl (<i>B. sumatranus</i>)	?		Greater Sundas forests
Milky or Verreaux's Eagle-Owl (<i>B. lacteus</i>)	?		Sub-Saharan Africa dense riverine forest
Philippine Eagle-Owl (<i>B. philippensis</i>)	?		Philippine Islands tropical rain forest
Nduk Eagle-Owl (<i>B. vosseleri</i>)	?		Tanzania Usambara Mountain forests
Leguat's Owl (<i>B. leguati</i>) (recently extinct)	(?)		Leguat forests

Table 1-Owls primarily associated with old tropical or temperate forests^a (continued)

Species	Tropical ^b	Temperate ^b	Range, habitat
<i>Strix</i> , Wood Owls:			
Northern Spotted Owl (<i>S. occidentalis caurina</i>)		x	Western North America old-growth conifers
California Spotted Owl (<i>S. occidentalis occidentalis</i>)		x	California mixed- and old-growth conifers
Himalayan Wood Owl (<i>S. aluco nivicola</i>)		x	Eastern Himalayas oak and conifer forest
Scully's Wood Owl (<i>S. aluco biddulphi</i>)		?	Kashmir
Brown Wood Owl (<i>S. leptogrammica</i>)	x		Indo-Malaysia hill and submontane jungles
Fulvous Owl (<i>S. fulvescens</i>)	?		Neotropics cloud and mountain forest
Malay Wood Owl (<i>S. orientalis</i>)	?		Malaysia forests
Spotted Wood Owl (<i>S. seloputo</i>)	?		Malaysia forests
Rufous-Legged Owl (<i>S. rufipes</i>)	?		South America dense tropical forest
Rusty-Backed Owl (<i>S. hylophila</i>)	?		South America dense tropical forest
Mauritius Owl (<i>S. sauzieri</i>) (recently extinct)	(?)		Mauritius forests?
<i>Ciccaba</i> , Mottled Owls:			
Black-and-White Owl (<i>C. nigrolineata</i>)	x		Neotropics lowland evergreen forest
Black-Banded Owl (<i>C. huhula</i>)	?		Amazon Basin lowland tropical forest
Rufous-Banded Owl (<i>C. albitarsis</i>)		?	Andes humid temperate forest
African Wood Owl (<i>C. woodfordii sokokensis</i>)	?		Sub-Sahara Africa lowland and mountain forest
Crested Owls and relatives (<i>Lophotrix</i> spp.):			
Crested Owl (<i>L. cristata</i>)	x		Neotropical dense forest
Maned Owl or Akun Scops Owl (<i>L. lettii</i>) (sometimes <i>Jubula lettii</i>)	?		West Africa tropical forest
Fish Owls (<i>Ketupa</i> spp.):			
Blakiston's Fish Owl (<i>K. blakistoni</i>)		x	Southeast Asia riverine forest
Tawny Fish Owl (<i>K. flavipes</i>)		?	Southeast Asia riverine forest
Fishing Owls (<i>Scotopelia</i> spp.):			
Pel's Fishing Owl (<i>S. peli</i>)	?		Africa gallery and tropical rain forest
Rufous Fishing Owl (<i>S. ussheri</i>)	?		Africa gallery and tropical rain forest
Vermiculated Fishing Owl (<i>S. bouvieri</i>)	?		Africa gallery and tropical rain forest
Spectacled Owl and relatives (<i>Pulsatrix</i> spp.):			
Spectacled Owl (<i>P. perspicillata</i>)	?		Neotropical lowland forest
White-Chinned or Tawny-Browed Owl (<i>P. koeniswaldiana</i>)	?		Neotropical lowland forest
Rusty-Barred or Band-Bellied Owl (<i>P. melanota</i>)	?		Neotropical lowland forest
Pygmy-Owls (<i>Glaucidium</i> spp.):			
Red-Chested Owlet (<i>G. tephronotum</i>)	?		West Africa rain forest
Chestnut-Backed Owlet (<i>G. sjostedti</i>)	?		West central Africa lowland rain forest
Andean Pygmy-Owl (<i>G. jardinii</i>)		?	Andes wet dense montane forest
Albertine Owlet (<i>G. albertinum</i>)	?		Zaire
Cuckoo Owl (<i>G. cuculoides</i>)		?	Himalayan forests
Eared Owls (<i>Asio</i> spp.):			
Abyssinian Long-Eared Owl (<i>A. abyssinicus</i>)	?		East Africa
Madagascar Long-Eared Owl (<i>A. madagascariensis</i>)	?		Eastern Madagascar humid forests
Long-Whiskered Owlet (<i>Xenoglaux loweryi</i>)	x		Peru Andes upper subtropical cloud forest
Papuan Hawk Owl (<i>Uroglaux dimorpha</i>)	x		New Guinea

Table 1-Owls primarily associated with old tropical or temperate forests^a (continued)

Species	Tropical ^b	Temperate ^b	Range, habitat
Hawk Owls (<i>Ninox</i> spp.):			
Rufous Owl (<i>N. rufa</i>)	?		Australia
Ochre-Bellied Hawk Owl (<i>N. perversa</i>)	?		Celebes deep virgin forests
Andaman Hawk Owl (<i>N. affinis</i>)	?		East Indies forests
Philippine Hawk Owl (<i>N. philippensis</i>)	?		Philippines forests
Indonesian Hawk Owl (<i>N. squamipila</i>)	?		Southeast Asian island forests
Brown Owl (<i>N. theomacha</i>)	?		New Guinea lowland rain forest
Fearful Owl (<i>Nesasio solomonensis</i>)	?		Solomon Island lowland primary forest
Tengmalm's or Boreal Owl (<i>Aegolius funereus</i>)	x		Holarctic conifer forest
Forest Spotted Owlet (<i>Athene blewitti</i>) (recently extinct?)	(?)		Central India deciduous forest
Total living species, (x) known to be primarily associated with old forests (12 total)	7	5	
(?) suspected to be primarily associated with old forests (71 total):	63	8	
Total (83 spp. ^d)	70	13 ^e	

^a Many additional owl species are not listed here that also occur in old forests but not necessarily as primarily selected habitat. See text for citations.

^b x = primarily associated with old forests; ? = reportedly associated with old forests, but little is known of their ecology; (?) = recently extinct.

^c Considered as a separate species, Javan Scops Owl (*Otus angelinae*), by Hume and Boyer (1991) and Amadon and Brown (1988).

^d Includes listing of 2 subspecies of *Otus spilocephalus* under both tropical and temperate categories but only one listing of *Strix occidentalis* under temperate category.

^e Includes listing of 2 subspecies of *Strix aluco* under both known and suspected categories.

In this report, I discuss the various old forests in which owls are found, the threats to the survival of forest habitats and owl populations, the need to conserve and restore owl populations and their old-forest habitats, and the roles owls have played in human cultures. All these topics need to be studied and considered in conservation plans if we are to provide successfully for continued existence of owls associated with old forests of the world.

Owls of the Genus *Tyto*

Most species of *Tyto*, including the Barn Owl, inhabit grassy or open habitats. A few little-known species, however, occupy deeply forested environments.

Celebes Barn Owl-This species inhabits rain forests of Celebes (Everett 1977). Hume and Boyer (1991) noted that it occurs in rain forests of several of the Sulawesi (Celebes) islands but that it also is associated with lowland habitats now eroded by deforestation. Little is known of its ecology.

Sooty Owl and Lesser Sooty Owl-Another little-studied *Tyto*, the Sooty Owl occupies dense forests of eastern Australia and New Guinea (Clark and others 1978, Everett 1977, Pizzey 1980, Prestt and Wagstaffe 1973; also see fig: 59). Like the Celebes Barn Owl, its ecology is also little known. Cayley (1975) noted that the Sooty Owl occurs as isolated pairs in heavy mountain forests. Pizzey (1980:205) denoted habitat of the Sooty Owl as "dense tropical, subtropical and temperate rain-forests and fern-gullies."

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Old Conifer Forests of North America



1. Ancient forest of western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*), Olympic National Park, western Olympic Peninsula, Washington. Such stands are habitat for the Northern Spotted Owl (*Strix occidentalis caurina*) but in recent years also have been invaded by the Barred Owl (*Strix varia*). The Barred Owl is fast becoming coexistent with, and in many cases replacing, the less aggressive Spotted Owl.



2. Fragmentation of western hemlock forests in southeast Alaska, Tongass National Forest, from timber harvesting (clearcutting). Such harvesting locally opens forest canopies and eliminates habitat for Boreal (Tengmalm's) Owls (*Aegolius funereus*) and other species.



3. Selective cutting of western hemlock forests in southeast Alaska. If such cutting does not greatly reduce canopy closure or nesting substrate (including snags and cavity-bearing trees), then it may be compatible with conserving habitat for some of the old-forest owl species. Studies are needed, however, to assess the response of each species.

Hume and Boyer (1991) and Amadon and Bull (1988) list the Lesser Sooty Owl, previously considered a subspecies of the Sooty Owl, as a separate species. Hume and Boyer note that both species inhabit patches of rain forest and wet eucalyptus forests containing old trees with hollow trunks suitable for nesting and roosting, and that the Lesser Sooty Owl favors extensive tracts of rain forests. Both owls have recently taken to roadsides and clearings as foraging habitat, however.

Soumagne's Owl-Soumagne's Owl is found only in large, dense, evergreen forests of northeastern Madagascar. It has been sighted only in 1929 and 1973 (Clark and others 1978). Its precise habitat requirements are unknown. Hume and Boyer (1991) called this species Madagascar Grass Owl. They suggest that the loss of forest cover on Madagascar and the conversion of forests to plantations of introduced eucalyptus and other trees unsuitable for this species have contributed to its decline and present scarcity.

Owls of the Genus *Pholidus*

The genus *Phodilus* shares the family Tytonidae with the well-known Barn Owl and Grass Owls. Although the Barn Owl is known for-indeed, even named for-its tolerance and affinities for human-built structures and habitations, *Phodilus* is less well known and is associated only with deep forests of Indonesia. A second species recently has been discovered in Africa.

Bay Owl-The seldom-seen Bay Owl is small with short ear tufts, fully feathered legs, a compressed bill, and rather short wings for hunting in deep forests of the Himalayas (figs. 55, 56). Natural history of Bay Owls is little known (Marshall 1966).

Ali (1962) noted that one subspecies, the Sikkim Bay Owl (*P. badius saturatus*), is a rare resident of dense foothill forests in Himalayan valleys of Nepal and Sikkim, India (fig. 35). It is confined to dense evergreen forest in the submontane tracts and foothills locally up to about 1500 m (Ali and Ripley 1983). King and others (1975) note habitat associations of this subspecies as forest and second growth. They define "second growth" as new plants growing where the original plants have been removed, as in the rank growth following deforestation. All other sources, however, describe habitat of Bay Owls as dense, old, and undisturbed forests.

Little is known of Sikkim Bay Owls. Ali and Ripley (1983) provide the following descriptions. Sikkim Bay Owls are strictly nocturnal and seldom seen. In daytime they roost in cavities and hollows in tree trunks. The nest is in an unlined hollow in a tree trunk or rotten stump about 2 to 5 m high. The same nest site is used every year and is littered with casts and pellets. At night, Sikkim Bay Owls hunt by launching from perches to fly through dense understory stands of young trees after its prey of small mammals, birds, lizards, frogs, and beetles and other large insects.

The Burmese subspecies *P. b. badius* occurs in evergreen and pine forests and feeds chiefly on mammals and birds. It frequents pools and riparian areas along rivers and also takes some fish. In higher elevations, it is confined to evergreen forests (Smythies 1984). The Ceylon subspecies (*P. b. assimilis*), endemic to Sri Lanka, is a little-known, scarce resident of forests below 1200 m in both the wet and hill zones (Ali and Ripley 1983). The Peninsular Bay Owl (*P. b. ripleyi*), a rare resident of central and southern India, occurs in dense wet evergreen forests (Ali and Ripley 1983; also see fig. 38).

Prigogine's Owl or African Bay Owl-Everett (1977) and Clark and others (1978) briefly note the discovery of Prigogine's Owl, a single specimen of which was discovered in 1951 northwest of Lake Tanganyika of the eastern Congo. It seems to inhabit montane forests (fig. 29)-Hume and Boyer (1991) speculate that it survives inside the threatened forests of Zaire-but essentially is unknown.

Old Hardwood Forests of North America



4. Emory oak woodland (*Quercus emoryi*) at Madera Canyon, southern Arizona. The upland forests here also contain silverleaf oak (*Q. hypoleucoides*), Arizona sycamore (*Plantanus wrightii*), alligator juniper (*Juniperus deppeana*), and Chihuahuana pine (*Pinus leiophylla* var. *chihuahuana*); and Fremont cottonwood (*Populus fremontii*) along riparian areas. Flammulated Owls (*Otus flammeolus*), as well as Western Screech-owls (*O. kennicottii*), Whiskered Owls (*O. trichopsis*), and Mexican Spotted Owls (*Strix occidentalis lucida*), inhabit the canyon forests.



5. Blue oak woodland (*Quercus douglasii*) along the interior foothills to the Sierra Nevada mountains, Central Valley, California. Such woodlands are used by some individual California Spotted Owls (*Strix occidentalis occidentalis*) which migrate seasonally from higher mixed conifer forests. Blue oak woodlands often also contain digger pine (*Pinus sabiniana*) and are threatened with removal from increasing urban construction.

Owls of the Genus *Otus*

Taxonomy of *Otus* species, particularly of the Neotropics, Middle East, and South-east Asia, is somewhat uncertain. Clark and others (1978) list 32 species, Everett (1977) lists 34, Hume and Boyer (1991) list 41, and Marshall and King (1988) list 52, worldwide.

Following are descriptions of eight species of *Otus* facultatively associated with old forests, although a few subspecies seem to be obligate associates. Lesser known, more habitat-specific old-forest obligates are then listed beyond.

Mountain Scops Owl (*O. spilocephalus*)-Found throughout the mountains of Southeast Asia, the Mountain Scops Owl inhabits various evergreen forest types. These types include oak, rhododendron, pine, and deodar forests of the Himalayas at 600 to 2700 m (de Schauensee 1984); and both cool, evergreen, broad-leaved and mossy elfin forests of the Sumatra and Borneo highlands (Voous 1988). King and others (1975) note that the species occurs in both evergreen and second-growth forests.

One subspecies of the Mountain Scops Owl, the Spotted Scops Owl, is found up to 2600 m (All 1977) and is confined to hill-oak, pine, and deodar forests (All 1949; also see fig. 38). Its daytime perch is in tree cavities (All 1977). Nests in the Himalayas have been found in abandoned woodpecker or barbet cavities (Voous 1988). Another subspecies, the Javan race *O. s. angelinae*, occurs in mountain rain forests and is considered by some as a separate species (Amadon and Bull 1988, Hume and Boyer 1991).

Oriental Scops Owl (*O. sunia*)-The Oriental Scops Owl *O. s. stectinattus* is probably the Old World ancestor of the Flammulated Owl.¹ In Southeast Asia, the Oriental Scops Owl occurs in tropical evergreen and deciduous forests in lowlands and hills, up to 2300 m in oak and pine forests in the Himalayan foothills (Roberts and King 1986). In Myanmar (Burma), this species also is found in hill cultivations, gardens of rural villages, and teak forests (Voous 1988). Although it probably is not dependent on old, undisturbed forest habitats, it is found in open or primeval deciduous and mixed-riparian forests (Knystautas and Sibnev 1987, Pukinsky 1977) and in broad-leaved forests up to 1500 m in Honshu, Japan (Voous 1988).

Daytime roosts are high in a tree in dense foliage. It feeds in glades and along forest edges and in open, parklike woods, taking prey from the forest floor as well as from the tree canopy and has been observed nesting in the big sacred trees surrounding temples and shrines (Voous 1988).

Collared Scops Owl (*O. bakkamoena*)-This Indo-Malayan species is found in tropical rain forests, tropical winter-dry forests, savannah, temperate, and marginally boreal climatic zones. It inhabits evergreen and deciduous tropical and subtropical, humid and arid forests, as well as forest edges and wooded areas near cultivations and villages (Ali 1977, 1979; Hume and Boyer 1991; Voous 1988). Collared Scops Owls are found in dipterocarp, oak, pine, and deodar forests in the Himalayan foothills up to 2400 m (Ali 1977, Ali and Ripley 1969); in subtropical and temperate mixed-deciduous forests in China (Voous 1988); in primeval broad-leaved forests with elms, ashes, and grassy openings in the Russian Far East (Knystautas and Sibnev 1987, Nechaev 1971); and in river valleys and hills near edges of coniferous taiga of birch and poplar in Siberia (Voous 1988). Although the species is associated with many forest types, some of them old growth, it also has acclimated to nest boxes and human-altered landscapes (Voous 1988).

Flammulated Owl (*O. flammeolus*)-This western North American species inhabits a diversity of conifer and mixed-conifer-hardwood forest types (for example, fig. 4), including pine, Douglas-fir, and true firs (Bull and others 1990, Goggans 1986, Marcot and Hill 1980, Reynolds and Linkhart 1987), with affinities to mature and old-growth forests (Howle and Ritcey 1987, Reynolds and Linkhart 1987). The species, however, does not seem to be an obligate associate of old-growth forests. Nests are typically in abandoned woodpecker cavities in dead trees and less commonly in natural cavities of dead or live trees, including oaks (for example, Marcot and Hill 1980). The diet consists of arthropods and lepidopterans. Reynolds and Linkhart (1987) report that the affinity of Flammulated Owls for old yellow pine forests in Colorado is because such forests afford nest cavities, adequate stand structure for roosts, and availability of arthropod prey. In Colorado, where on rare occasions Flammulated Owls will nest in pinyon-juniper woodland, the diet includes moths (see footnote 1).

¹ Personal communication. Jon Winter, 5331 El Mercado Parkway, Santa Rosa, CA 95401.

Vermiculated Screech Owl (*O. guatemalae*)-This species is found in Central America and western South America in dense, tall, and continuous broad-leaved forests, from tropical deciduous and thorn forests in lowlands and foothills up into oak woodland; and also in evergreen upper elevation tropical rain forests in southern Mexico (Marshall 1967, 1978; Peterson and Chalif 1973; Voous 1988; also see fig. 11). Clark and others (1978) note that it is found in open forests and plantations. Hilty and Brown (1986) list its habitat as understory to lower midlevels of humid forest and second-growth forests in lower elevations. It also inhabits temperate oak woodlands of Mexico and tropical cloud forests of Central and South America (Stiles and Skutch 1989, Voous 1988; see fig. 19). The Vermiculated Screech Owl is a facultative but not obligate inhabitant of older native forests.

Other species of *Otus* facultatively associated with old forests include the Western Screech Owl (*O. kennicotti*), Eastern Screech Owl (*O. asio*), and Whiskered Screech Owl (*O. trichopsis*) (see Marshall 1967, 1978). Each of these species is found in North America in various conifer, mixed-conifer and hardwood, and pure hardwood forests, at times near human habitations (for example, see fig 4). Each is found not only in old undisturbed forests but also in various other types of broken woodlands (personal observation) and sometimes in nonwooded areas, in the case of the Western Screech Owl.²

A listing of other, little-studied *Otus* species of dense tropical forests (Clark and others 1978, Everett 1977, Hilty and Brown 1986, Hume and Boyer 1991, King and others 1975) is formidable (table 1):

- White-Fronted Scops Owl, occurring in Malaysian lowland and foothill forests
- The rare Reddish Scops Owl of Southeast Asian dense lowland and hill forests (Hekstra 1973)
- Giant Scops Owl, sometimes placed in the monospecific *Mimizuku* (Amadon and Brown 1988, Clark and others 1978, Hume and Boyer 1991), endemic to lowland rain forests of the Philippines
- Tawny-Bellied Screech Owl of Amazonian rain forests (fig. 17)
- The endangered Puerto Rican Screech Owl of submontane woodland and tropical forests of Puerto Rico and Virgin Islands (see figs. 6-10)
- Flores Scops Owl of mountain woods in the Flores Islands of the Lesser Sundas
- Rajah's Scops Owl of lowland forests of Sumatra and Borneo
- Lesser Sunda Scops Owl of coastal forests in Flores and Sumbawa Islands of the Lesser Sundas, although Hume and Boyer (1991) note that it lives close to human settlements and seems adaptable to several habitats
- Sandy Scops Owl of forests of the African Gold Coast from Ghana to East Congo
- Sokoke Scops Owl of coastal forests of East Kenya, Africa

² Personal communication. Carl Marti, Department of Zoology, Weber State College, Ogden, UT 84408.

- Mentaure Scops Owl, found in coastal forests of the Simaur and Engano Islands of the southwest Pacific
- Cuban Screech Owl, sometimes placed in the monotypic genus *Gymnoglaux*, which inhabits forests of limestone country of Cuba (see figs. 6-9)
- Santa Barbara or Bearded Screech Owl, found in mountain woodlands from 1350 to 1850 m in Mexico and Guatemala (fig. 11)
- Black-Capped Screech Owl of subtropical rain forests in eastern South America, including Paraguay, southeast Brazil, and northeast Argentina
- Rufescent Screech Owl, found in subtropical humid cloud forests of western South America from Bolivia to Venezuela (figs. 18, 19)
- Three closely related species listed by flume and Boyer (1991): Cinnamon Screech Owl of Peruvian and Ecuadorian high-elevation cloud forests, Cloud Forest Screech Owl of high cloud forests of Peru (figs. 50, 51), and Colombian Screech Owl of Colombian high-elevation mountain forests (figs. 18, 19)
- Bare-shanked Screech Owl of highland forests from 1300 to 2330 m in Costa Rica and Panama (fig. 15; although Hilty and Brown 1986 list habitat as including forest, woodland borders, and tree-lined fence rows)
- White-Throated Screech Owl of subtropical to temperate forests in the Andes and other mountains above 2100 m, found in western South America from Venezuela to Bolivia (fig. 18; although Hilty and Brown 1986 also list highland forest borders, open woodland, and semiopen areas with scattered trees as habitat for this species)
- Roborate Screech Owl, found in Andean forests at about 3000 m in western Peru (fig. 18), although flume and Boyer (1991) list its habitat as scrub and high open woodland
- Seychelles Scops Owl, rare in remote, high valley cloud forests, but possibly increasing as secondary forests mature; once considered an island race of the Madagascar Scops Owl (flume and Boyer 1991)
- São Thomé Scops Owl, found in forests on São Thomé island off western Africa and possibly a well-marked race of the common Scops Owl (flume and Boyer 1991)
- Lan Yu Scops Owl of Taiwan forests
- Pacific Screech Owl, which frequents deciduous and evergreen forests of the Neotropics (Marshall 1967; personal observation; fig. 17), although flume and Boyer (1991) list its habitat as low scrub and coastal mangrove. Solis and Manley³ report the species in a building compound in a private reserve of primary dry tropical forest in northwestern Costa Rica.

³Personal communication. David Solis and Patricia Manley, USDA Forest Service, Pacific Southwest Regional Office, Fish and Wildlife Unit, 630 Sansome Street, San Francisco, CA 94111.

Owls of the Genus *Bubo*

Members of *Bubo* include some of the most aggressive hunters in the owl world. The following species seem to associate primarily with old or dense forests.

Forest Eagle-Owl-The Forest Eagle-Owl is well named, as it is a fierce hunter of primarily densely forested areas. Habitat of several subspecies closely associated with old forests have been described as follows.

The rare Forest Eagle-Owl *B. nipalensis nipalensis* occurs in dense tropical forests of Sikkim, India, up to about 2100 m, more normally to about 900 to 1200 m (Ali 1962, Ali and Ripley 1983; also see fig. 35). It frequents submontane forest tracts of the lower Himalayas, occurring in dense evergreen and moist deciduous forests in tropical valleys, terai and duars (wet perennial grasslands along the Himalayan foothills), and sholas (dense riparian gallery forests) (Ali 1977, Ali and Ripley 1983). Mostly nocturnal, the Forest Eagle-Owl roosts diurnally on densely foliated tree boughs in deep forests or sholas (Ali 1949) and occasionally hunts during the daytime. At dusk, it moves to the edge of clearings and streams but “is essentially a forest dweller and does most of its hunting within the forest” (Ali and Ripley 1983:248). Its nest typically consists of “a hollow in an ancient tree or a deserted stick-nest of an eagle” (Ali and Ripley 1983:248), although it also lays eggs on bare soil in a cave or in a fissure on a rock scarp (Ali 1949, Ali and Ripley 1983).

Smythies (1984) reports that *Huhua nipalensis* (= *Bubo nipalensis*) frequents forests and their outskirts in the Himalayas of Myanmar. In Sri Lanka, the endemic Ceylon Forest Eagle-Owl (*B. n. blighi*) also inhabits deep tropical forests (Ali and Ripley 1983). The only reported nest was a “collection of debris in the hollow formed by the junction of large boughs” about 6 m high in a big tree by a stream in dense forest at about 600 m (Ali and Ripley 1983:249).

Other, less well-known species of *Bubo* associated with old or dense, mostly tropical forests (Clark and others 1978, Everett 1977, Fogden 1973, Hume and Boyer 1991, King and others 1975, Voous 1988), include the following:

- Shelley’s Eagle-Owl, Akun Eagle-Owl, and Fraser’s Eagle-Owl of African tropical and subtropical forests (fig. 28)
- Barred or Malay Eagle-Owl of mountain rain forests in the Greater Sundas
- Milky or Verreaux’s Eagle-Owl of dense riverine forests of sub-Saharan Africa (Newman 1991; also see figs. 30, 31), although Hume and Boyer (1991) describe its habitat as including dry woodland, introduced conifers and eucalyptus, and brushveld
- Philippine Eagle-Owl of tropical rain forests of the Philippine Islands

Owls of the Genus *Strix*

Commonly referred to as “wood owls,” species of the genus *Strix* are found throughout the Northern Hemisphere. Wood owls occur mostly in temperate to subboreal forests, although a few specialists are found in subtropical to tropical environments. Extant members of *Strix* likely are derived from a more circumpolar stock that was north temperate or subboreal, some offshoots of which radiated into narrower geographic areas and evolved close affinities with specific climatic environments and vegetation conditions. Examples of such radiations include the split of Tawny Owl and Ural Owl in Europe and Asia and the Barred Owl and Spotted Owl in North America. Of these two pairs, the Tawny and Barred Owls attained a more southerly distribution and evolved a greater tolerance to disturbed temperate forests and to a wider range of vegetation conditions and climates than did their Ural and Spotted Owl counterparts.

The wood owls, true to their namesake, are strongly affiliated with and adapted to forest habitats. There they find cover, prey, and nesting substrates to meet their life needs. Their brownish cryptic coloration, broad wing shape, and maneuverable manner of flight and foraging all suggest life within wooded environments. Despite their worldwide distribution, members of the genus *Strix* and the related subtropical and tropical genus *Ciccaba* (see below) have many common vocalization patterns (see appendix A).

Spotted Owl-A denizen of western North America, the Northern Spotted Owl (*S. occidentalis* *caurina*) is known to consistently select old-growth and mature stands of conifer forests (appendix F in

Thomas and others 1990; also see fig. 1, this report). Northern Spotted Owls typically nest in large cavities in trees and less often on mistletoe clumps and abandoned raptor nests in the understory of tree canopies (Forsman 1980). Day roosts of this mostly nocturnal species are in older forest stands with dense overhead foliage and diverse understory vegetation (Thomas and others 1990).

The California Spotted Owl (*S. o. occidentalis*) is found throughout Sierran forests of mixed-age and mixed-species composition (also see fig. 5), but Verner and others’ (1992:9) analysis demonstrated that it selects very large, old trees for nest sites and forests having medium-sized and larger trees and high canopy closure. Thus, it can be considered here as closely associated with old-forest conditions. The Mexican race (*S. o. lucida*) of the Southwest United States and northwest Mexico is found in copses of hardwoods, along forested washes, and in more extensive mixed forests of pine, perhaps representing an ecotype of the species locally adapted to shady, moist microhabitats (fig. 4).

Because of rising polemics over conflicting use of its old-growth habitat, the Spotted Owl is probably one of the best known species of owls in the Western United States. In recent years, dozens of scientists and several hundred biologists have been engaged in research, inventory, and monitoring studies of the species in young and old forests on private and public lands.

Old Forest Species of *Strix*

Northern Spotted Owl	<i>S. occidentalis caurina</i>
Himalayan Wood Owl	<i>S. aluco nivicola</i>
Scully’s Wood Owl	<i>S. aluco biddulphi</i>
Brown Wood Owl	<i>S. leptogrammica</i>
Fulvous Owl	<i>S. fulvescens</i>
Malay Wood Owl	<i>S. orientalis</i>
Spotted Wood Owl	<i>S. seloputo</i>
Rufous-Legged Owl	<i>S. rufipes</i>
Rusty-Backed Owl	<i>S. hylophia</i>

Old Forests of the Caribbean



6. Old-growth forest of Caribbean pine (*Pinus caribbeanensis*), central Andros Island, Bahamas. These forests probably once held the meter-tall, flightless *Tyto pollens*. Similar forests on Cuba still provide habitat for the rare Cuban Screech Owl (*Otus lawrencii*).



8. Most of the old-growth Caribbean pine forests of Andros Island, Bahamas, had been harvested and converted to crop fields or, as shown here, second-growth pine plantations. The plantations are cut by individual tree or small group selection and provide forest cover. It is unknown, however, if such silvicultural methods would suffice to retain habitat for Cuban Screech Owls on Cuba or other old-forest owls of the Caribbean and the Greater and Lesser Antilles.



7. Much of the old tropical forest of the Caribbean has been converted to second-growth scrub and human habitations. Here, the old Caribbean pine forests of the Bahamas have been cleared for industrial agriculture. Similar conversions have occurred in the tropics worldwide, reducing available habitat to many island-dwelling species of old-forest birds.



9. The original old forests of the shores of the Caribbean islands (above) have been largely invaded by introduced species such as Australian pine (*Casuarina equisetifolia*), reducing or eliminating habitat for owls more closely associated with native pines and hardwoods.

10. Dense, tropical second-growth scrub of St. John, U.S. Virgin Islands (left). The old tropical forests were eradicated mostly during the latter half of the 19th century. Then sugar mills dominated the Lesser Antilles. The Puerto Rican Screech Owl (*Otus nudipes*) has become a scarce inhabitant found only on Puerto Rico and the Virgin Islands, its habitat greatly reduced from felling of the old tropical forests.

Barred Owl (*S. varia*)-The Barred Owl occurs throughout North America in various forest ages, types, and conditions, ranging from dense Douglas-fir forests of the Pacific Northwest to lowland basswood groves and isolated hammocks of mahogany and broad-leaved hardwoods of southern Florida (personal observation). The species is not an old-forest obligate. Its recent movement into the Pacific Northwest of North America (Taylor and Forsman 1976), including into both young, managed forests and extensive tracts of old-growth conifer forests, has led, however, to direct territorial conflict with the Spotted Owl (Hamer 1985, Johnson 1992). It apparently has recently moved west across British Columbia, south into the Pacific Northwest, and now into California. This movement might have resulted from widespread logging of old forests over the second half of the 20th century, as such activities often remove large snags and live trees with hollows affording nest sites (Bosakowski and others 1987). This hypothesis is untested, however.

In a few cases, Barred Owls have hybridized with Northern Spotted Owls and even produced apparently fertile offspring.⁴ This is not surprising, however, as many closely related species of birds have been observed to hybridize (Ehrlich and others 1988:501ff), including the Tawny and Ural Owls in Europe (Scherzinger 1983). To date, observations of interactions and interbreeding between Barred and Spotted Owls definitively indicate neither long-term genetic swamping of either species (particularly the threatened Spotted Owl) nor competitive exclusion of entire Spotted Owl populations by the Barred Owl. The outcome of the Barred Owl's range extensions on long-term viability of Spotted Owl populations has yet to be determined and deserves further study.

Great Gray Owl (*S. nebulosa*)-The circumpolar Great Gray Owl is found in old mature subalpine forests of spruce, fir, and pine; mixed-hardwood forests in east Asia; and taiga and boreal muskegs and bogs (Hilden and Solonen 1987, Hume and Boyle 1991, Spreyer 1987, Voous 1988; see figs. 2, 3). It also is found in fairly open subboreal forests of North America.⁵ In Sweden, it inhabits northern conifer forests and is tied closely to vole cycles (Mikkola 1983). In winter, it ventures into agricultural fields and along forest edges and openings for foraging on small rodents, sometimes close to human habitations (but see fig. 26). Although found in mature subboreal forests, the Great Gray Owl probably is not an old-forest obligate per se. In fact, in northeastern Oregon, it reached greatest nonbreeding densities in heavily logged areas (Bull and Henjum 1990, Bull and others 1988). De Schauensee (1984), however, notes its habitat in China as dense coniferous forests, and Hume and Boyle (1991) wrote that in Europe and Asia it occupies mature; lichen-covered spruce, fir, and pine, often mixed with larch and poplar, and sometimes birch woodlands.

⁴ Personal communication. Eric Forsman, USDA Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331.

⁵ Personal communication. Evelyn Bull, USDA Forest Service, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850.

Great Gray Owls nest mostly in abandoned raptor nests, particularly those of Northern Goshawks (*Accipiter gentilis*), and also in mistletoe platforms in eastern Oregon (Bull and others 1987). They do not use tree cavities, but in Idaho and California, this species nests in the tops of broken-off snags in areas where raptor nests are scarce (Winter 1986; see endnote 5). Their use of raptor nests and mistletoe clumps accounts for their presence in boreal forests that otherwise lack snags of adequate size and number.

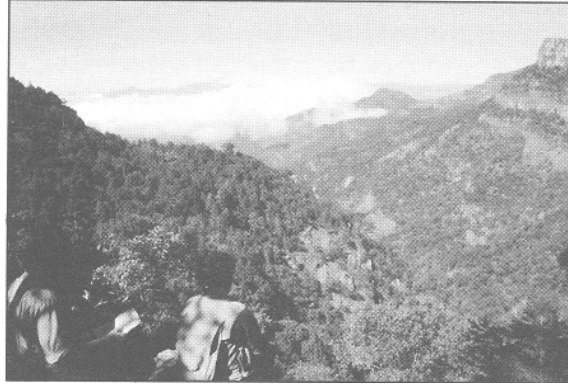
Tawny Owl (*S. aluco*)-The well-studied Tawny Owl is found widespread throughout mixed woodlands, especially deciduous forests (Perrins 1987), of Europe and Asia (Mikkola 1987). It normally nests in tree cavities. In Europe, it has acclimated to the use of nest boxes and occurs in various forest conditions, including old dense forest, upland spruce forests (Petty 1983), and relatively young forest plantations (Southern 1970, Voous 1988).

Two subspecies of the Tawny Owl seem associated primarily with dense, undisturbed forest conditions. The Himalayan Wood Owl (*S. a. nivicola*) is resident in the eastern Himalayas between 1200 and 4250 m in rocky wooded ravines in oak and conifer forests (Ali 1977; also see fig. 35). It lays its eggs in the hollow of an ancient tree or in the fissure of a rock cliff without any proper nest (Ali 1949). Scully's Wood Owl (*S. a. biddulphi*) is found in wooded ravines in Kashmir and the north-west Himalayas up to about 3350 m (Ali 1949; also see fig. 35), although its habitat associations are less well known than those of the Himalayan Wood Owl.

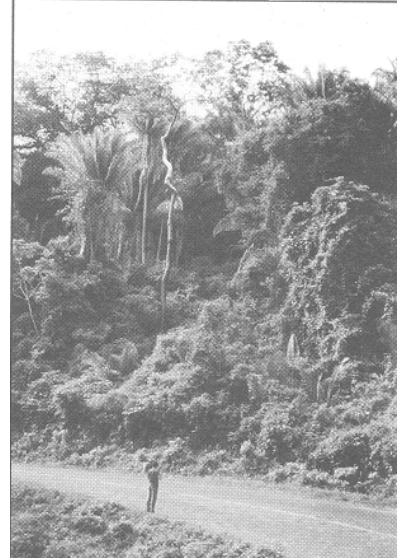
Ural Owl (*S. uralensis*)-This northern owl of the Old World inhabits tall and open taiga forests of spruce, fir, and pine, as well as forest glades, bogs, and hardwood riverine taiga forests, upper elevation fir forests, and lowland forests in eastern Asia and Japan to 5000 m (de Schauensee 1984; Lahti 1972; Lundberg and Westman 1984; Mikkola 1983, 1987; Voous 1988). Hume and Boyle (1991) characterize habitat of Ural Owls as remote, undisturbed forests far from human communities. They note that the species is drawn to old-conifer forest or mixed woodland with clearings (although in Finland it has begun to use forest bogs of spruce and birch and damp heathland with scattered trees) and that it now nests in buildings and nest boxes (see fig. 26). Ural Owls nest in natural tree cavities and in abandoned raptor nests. Mikkola (1983) notes that, in the southern parts of its range, Ural Owls usually breed in montane forests including beech woods, but elsewhere they prefer dense mixed forests and conifer forests (personal observation; fig. 40). He reports Ural Owls nesting in cavities in stumps of a pine or a spruce tree in natural forests, but more recently they have taken to various nesting sites, including tree stumps, holes in trees, twig nests, nest boxes, buildings, rock faces, and even flat ground. Thus, the Ural Owl may not necessarily be closely associated only with old forests but also may be able to use other habitats in at least a portion of its wide range.

Most of the literature sources note the occurrence of Ural Owls in dense forests. Scherzinger (1987), however, speculates that Ural Owls depend on open areas and cannot live in dense woods, and that recent management policies in Scandinavian national parks to regrow old, virgin woodlands from large clearcuts might reduce prey densities and habitat suitability for this species. Similarly, Mikkola (1983) suggests that, although Ural Owls breed in large conifer woods, they prefer the more open sections and forest edges for hunting, and thus that large clearings of felled trees are attractive. This conjecture has not been tested scientifically.

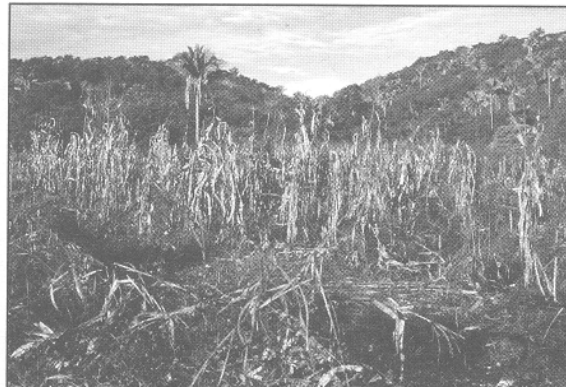
Old Forests of Mexico and Central America



11. Diverse Neotropical forests are found in creep canyons or *barrancas* of the Sierra Madre Occidental of western and southern Mexico. Here reside species associated with dense, undisturbed forests, including Stygian Owl (*Asio stygius*), Vermiculated Screech Owl (*Otus guatemalae*), and Santa Barbara or Bearded Screech Owl (*O. barbarus*).



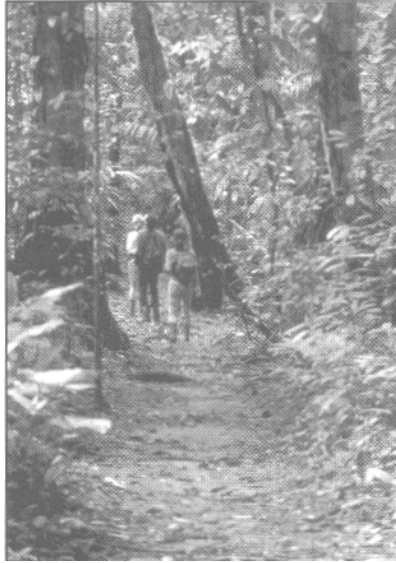
12. Upper Sanguita Jungle of San Blas, western Mexico. These increasingly scarce old tropical forests of Mexico occur from the west coast through Chiapas and Campeche of southeast Mexico. They contain old-forest owls such as mottled owl (*Ciccaba virgata*) in western Mexico, and Fulvous Owl (*Strix fulvescens*) and Stygian Owl in south Mexico and Central America. In the higher cloud forests of southern Mexico and Central America also occurs the Unspotted Saw-Whet Owl (*Aegolius ridgwayi*).



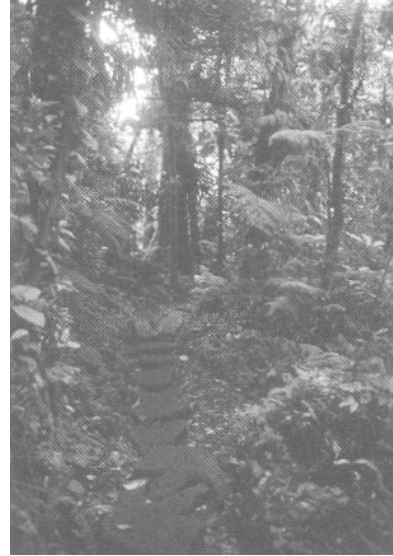
13. Many of the tropical forests of southern Mexico and Central America have been cut, burned, and converted to agricultural fields or pastureland. Often the soil is thin and provides at best only a few years of production, such as this corn field converted from west coast tropical forest in Nayarit, western Mexico.

Hume and Boyle (1991) list David's Wood Owl (*S. davidi*) as a separate species, although many authorities consider it to be a strongly marked race of the Ural Owl (viz., *S. uralensis davidi*). David's Wood Owl occurs in mountain forests of western Szechwan, China, and is rare and probably endangered.

Brown Wood Owl-This Indo-Malayan species (*S. leptogrammica*) inhabits deep tropical forests and dense hill jungles, from subtropical submontane forests up to oak-rhododendron forests in the Himalayas, and lowland primary rain forests in Sunda (Hume and Boyer 1991, Voous 1988; also see figs. 53, 54). The species avoids contact with humans and with cultivations (Voous 1988) and seems to closely associate with dense old forests.



14. Caribbean slope rain forest of La Selva, Costa Rica. Found in these old forests are Black-and-White Owl (*Ciccaba nigrolineata*) and Crested Owl (*Lophotrix cristata*).



15. Upper montane cloud forest, Monteverde, Costa Rica. These dense tropical old forests provide habitat for mottled owl and Bare-Shanked Screech Owl (*Otus clarkii*).



16. Typical fate of tropical forests of Central America: clearing for pastureland and fuelwood gathering. Under such land use, little if any suitable habitat remains for the native old-forest owls. Cordillera de Talamanca, Costa Rica.

Ali (1962) reports that on subspecies, the Himalayan Brown Wood Owl (*S. I. newarensis*), is a resident of forests of Sikkim, India, up to about 4000 m. It occurs in deep forests, particularly for daytime roosts (Ali 1977). A very shy bird, it is disturbed easily on the roost. Much of its breeding biology is unknown, although its nest has been reported as consisting of “a few sticks and feathers in the hollow of a forking tree-trunk, on a shelf in a cliff-face, or shallow scrape in the bare ground at the foot of a rock or large tree in some shady ravine” (Ali and Ripley 1983:256).

The central and south Indian race *S. I. indranee* occurs in deep sholas (dense, moist forest groves) (Ali 1962; personal observation). It resides in dense evergreen and moist-deciduous forests in mountains of the southern Indian peninsula (Ali and Ripley 1983; also see figs. 37, 38). Smythies (1984) reports that, in Myanmar, *S. indranee* (= *S. I. indranee*) occurs in the higher hills, keeping to deep forests during the daytime, but may venture to glades and more open parts of the forest in the evening (also personal observation). Throughout Myanmar, the subspecies occurs in “well-wooded localities” up to nearly 2000 m (Smythies 1984:314).

Mottled Wood Owl (*S. ocellata*)-This species is not to be confused with the Mottled Owl (*Ciccaba virgata*) of the New World tropics (see below), which in some accounts (for example, see Stiles and Skutch 1989) bears the same common name. *Strix ocellata* is found throughout much of the Indian subcontinent. It keeps to lightly wooded plains and frequents mango topes and groves of tamarind and banyan on village outskirts and in areas of cultivation (Ali 1979; personal observation). One race, the Northern Mottled Wood Owl, lives in mangos and groves of ancient, densely foliated banyans and tamarinds, often beside land close to villages (Hume and Boyer 1991). Mottled Wood Owls seem more tolerant of human habitation and agricultural landscapes than do their sympatric cousins the Brown Wood Owls.

Fulvous or Guatemala Barred Owl-This species is closely related to the Barred Owl and occurs from south Mexico through Central America in cloud forest and pine-oak mountain zones (Peterson and Chalif 1973; also see figs. 18, 19). Hume and Boyer (1991) describe its habitat as humid upper tropical and temperate pine-oak forest.

Several other species of *Strix* are associated with forest habitats, although virtually nothing is known of their ecologies. Two Southeast Asian species are the Malay Wood Owl and the Spotted Wood Owl. These two species are combined in some taxonomies. They inhabit forests, but Clark and others (1978) and Hume and Boyer (1991) also note that they are found in second growth, town parks, orchards, open country with scattered woodland, and paddyfields. In South America, the Rufous-Legged Owl is a little-known species associated with dense tropical forests, and the Rusty-Backed Owl (also called Rusty-Barred Owl or Brazilian Owl) is found in forests from southeast Brazil to northern Argentina (Clark and others 1978, Hume and Boyer 1991).

Owls of the Genus *Ciccaba*

The circumtropical species of *Ciccaba* resemble those of *Strix* and, indeed, are sometimes listed in that genus. They are the southerly forms of the wood owls and constitute a diverse assemblage of species found throughout many tropical forest types and elevations.

Mottled Owl (*C. virgata*)-The Mottled Owl widely inhabits dense Neotropical forests from humid lowlands (fig. 12) to montane cloud forests, as well as semideciduous and tropical dry forest (Voous 1988), humid forest borders and tall second growth (Hilty and Brown 1986), and heavily timbered areas (Everett 1977; see figs. 46, 47). Stiles and Skutch (1989) and Peterson and Chalif (1973) note that Mottled Owls occur in semiopen, old second growth and in coffee plantations with shade trees. Hume and Boyer (1991) describe habitat for this species as tropical forest, plantations, and open woods. Thus, the species is not an old-forest obligate. Mottled Owls

roost in low thickets by day, and in Costa Rica they also roost in subcanopies of montane cloud forests (personal observation; fig. 15). Nothing, however, is reported on their ecological adaptations to specific tropical forest conditions.

Black-and-White Owl-Sometimes considered a subspecies of the Black-Banded Owl (Stiles and Skutch 1989, Voous 1988), the Black-and-White Owl is found in or near tall, humid, lowland forests (Peterson and Chalif 1973; personal observation; figs. 14, 17, 22, 23), in evergreen or gallery forests in arid areas, or sometimes in tall mangroves (Stiles and Skutch 1989). Hilty and Brown (1986) list habitats as humid forest, forest borders, tall second growth, and clearings with trees, sometimes near habitations. Strictly nocturnal, it roosts in thickets by day and often hunts along forest edges and clearings of damp woods by night.

Two other species of *Ciccaba* associated with forests in South America include the Black-Banded Owl found in primary lowland tropical forests in the Amazon Basin (personal observation; fig. 17) and the rare Rufous-Banded Owl of humid mountain forests in the Andes mountains (fig. 18). Little is known of the ecologies of these two species. Everett (1977) suggested that the Black-Banded Owl is showing signs of adapting to human presence by its regular occurrence in banana and coffee plantations, and Hilty and Brown (1986) noted its habitat as including humid forests, forest borders, and trees in clearings. Hume and Boyer (1991) denote habitat of the Rufous-Banded Owl as humid temperate cloud forests of the northern Andes, but that in Venezuela it is observed in forest openings. They also suggested, however, that accommodation to human presence is secondary and that removal of rain forest for monocultures and ranch land almost certainly poses a threat to the species (figs. 20, 21).

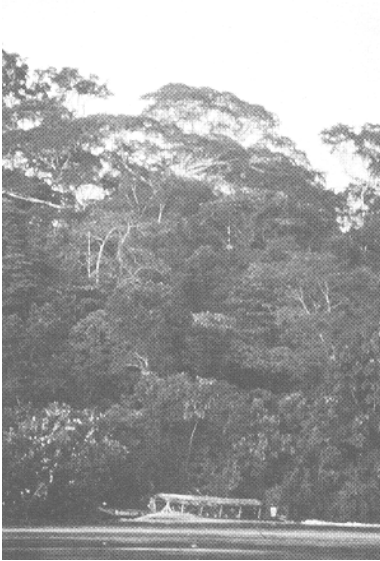
The African Wood Owl, the only Old World member of *Ciccaba*, is widespread south of the Sahara in evergreen and riparian forests and moist mountain forests (Clark and others 1978; also see fig. 30). This species prefers forest but only the edges of denser rain forest tracts, and it survives well in plantations and riparian forests (Hume and Boyer 1991, Newman 1991). Newman (1991) noted that day roosts are in large trees. Of the five recognized races, *C. woodfordii sokokensis* is an endangered, local, endemic form found only in the Sokoke Forest, Kenya. Whether its endangered status is due to surrounding deforestation and reduction in its habitat is unknown; it has not yet been studied.

Other Little-Known Forest Owls

In addition to the above genera, several other little-studied owl species also are associated with old, dense, or undisturbed forests, mostly in the tropics. Little is known of their specific habitat associations, particularly with forests of various ages, tree densities, degrees of fragmentation, and disturbance histories. These owls are listed below by genus.

- **Lophotrix**-Crested Owl of dense Neotropical humid lowland forests (Stiles and Skutch 1989; personal observation; figs. 22, 23) and tall second-growth and woodland patches (Hilty and Brown 1986); and the Maned Owl of tropical forests in west Africa (Everett 1977; but listed in the genus *Jubula* by Hume and Boyer 1991).

Old Forests of South America



17. Riverine rain forests of the Upper Amazon Basin, Rio Napo, Ecuador. Such forests are becoming much more fragmented as they are cleared by settlers for agricultural development. These highly diverse forests contain lowland interior species such as BlackBanded Owl (*Ciccaba huhula*), Blackand-White Owl (*C. nigrilineata*), TawnyBellied Screech Owl (*Otus watsonii*), Pacific Screech Owl (*O. cooperi*), Spectacled Owl (*Pulsatrix perspicillata*), and the little-known Rusty-Barred or Band-Bellied Owl (*P. melanota*).



18. Peru and Ecuador high cloud forests. These old forests contain a high diversity of screech owls, including Cinnamon (*Otus personi*), CloudForest (*O. marshalli*), Colombian (*O. colombianus*), White-Throated (*O. albogularis*), Rufescent (*O. ingens*), and Roborate (*O. roborates*) Screech Owls. Also found in some of these old cloud forests are Fulvous Owl (*Strix fulvescens*), Long-Whiskered Owllet (*Xenoglaux loweryi*), Rufous-Banded Owl (*Ciccaba albitarsis*), and Andean Pygmy-Owl (*Glaucidium jardinii*).



19. Patches of *Polylepis* woodland occur amidst the paramo grasslands in the high Andean passes west of Quito, Ecuador, here at nearly 4300 m elevation. Such cloud forests may provide habitat for the highland screech owls and other species. One inhabitant is the Buff-Fronted Owl (*Aegolius harrisii*), which is a very rare and little known denizen of semiopen areas with old trees, to the edge of paramo in Colombia and Ecuador.



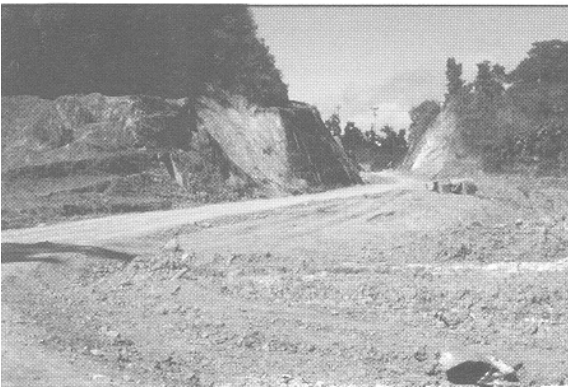
20. Highland forests of the Andes have been largely cleared for crops fields and human habitations. Interior valley south of Otavalo, Ecuador, approximately 2700 m elevation.



21. Most of the forest cover in the Andes consists of plantations of introduced species, such as pines and, as shown here, *Eucalyptus*. Along Pan-American Highway, central Ecuador.



22. Lowland Pacific slope tropical Forests. As with most other tropical forests of the world, these forests have been reduced by clearing and their old forest characteristics have been compromised by selective cutting of the larger trees. This forest occurs at approximately 600 m elevation in Ecuador northeast of the tiny village of Mindo and is one of the most extensive remaining lowland Pacific slope tropical forests, although it too is being cleared (foreground). Owls of the lowland tropical forests of the Pacific slope include Crested Owl, Spectacled Owl, and Black-and-White Owl.



24. Ever-growing human densities in South America Amazonia and lowland coastal areas result in tropical forests lost to new highway corridors and settlements.



23. Dense tropical forest of the lowland Pacific slope, Rio Palenque Forest Reserve, Ecuador.



25. Large old specimen of fig (*Ficus* sp.) in western Mexico symbolizes both the plight and promise of tropical forest conservation for owls of old forests of the world. In India and parts of Asia, old-growth *Ficus* trees are revered for their sacred qualities and remain uncut, thereby also preserving old woodlands for wildlife.

- ***Ketupa* and *Scotopelia***-Many of the fish owls of dense Asian and African riparian gallery forests (Ali 1962, Ali and Ripley 1983, Everett 1977, Newman 1991; personal observation), particularly Blakiston's Fish Owl and Tawny Fish Owl of Southeast Asian dense primary riverine forests (fig. 42); and Pel's Fishing Owl, Rufous Fishing Owl, and Vermiculated Fishing Owl of African gallery and tropical rain forests (fig. 30).
- ***Pulsatrix***-Spectacled Owl and White-Chinned or Tawny-Browed Owl of Neotropical lowland forests (figs. 17, 22, 23); and Rusty-Barred or Band-Bellied Owl of remote Andean highland forests and humid lowland forests (Everett 1977, Hilty and Brown 1986, Hume and Boyer 1991, Stiles and Skutch 1989; personal observation; figs. 17, 18, 48, 49).
- ***Glaucidium***-Some of the pygmy-owls of more northerly temperate and taiga forests, as well as others of tropical forests, associated with mature forest conditions (Stiles and Skutch 1989, Voous 1988; personal observation). Hume and Boyer (1991) denote habitat for the Northern Pygmy-Owl (*G. gnoma*) as open and mature coniferous or mixed forest in western North and Central America. Other references (also personal observation), however, suggest a more catholic use of various forests and woodlands. The species might be undergoing a long-term decline in density, although this is unstudied. Most pygmy-owls seem adapted to open forests with clearings and can tolerate plantations and human disturbances of their forest habitats. Some members of this genus are associated with old or dense primary forest conditions: the little-known Red-Chested Owlet and Chestnut-Backed Owlet of primary tropical rain forests of west Africa (Clark and others 1978); the Andean Pygmy-Owl, considered by some as a race of the Northern Pygmy-Owl, found in wet, dense, montane forests of the Andes (fig. 18); the Albertine Owlet, rare in forests of eastern Zaire and Rwanda and threatened by logging and forest clearance for agriculture (fig. 34); and the Cuckoo Owl found in Himalayan forests and rain forests of Southeast Asia (Hume and Boyer 1991).
- ***Asio***-*Asio* species occur variously in dense forest, broken woodland, and open country. Taxonomies differ as to number of species. Hume and Boyle (1991) note that the Abyssinian Long-Eared Owl inhabits mountain heaths and interior highland cedar forests of east Africa and Zaire (fig. 33), and the Madagascar Long-Eared Owl survives in the restricted and vanishing humid forests of eastern Madagascar.
- ***Xenoglaux***-Long-Whiskered Owlet, an owl genus discovered in 1976 in upper subtropical cloud forests of Peru and dense old growth of the eastern slopes of the Andes (Clark and others 1978, Hume and Boyer 1991; also see fig. 18).
- ***Uroglaux***-Papuan Hawk Owl of dense, hot tropical forests of New Guinea and Japan.

Old Forests of Europe



26. Most of the old forests of Europe have been harvested and inhabited for centuries. Populations of Eurasian Eagle-Owls (*Bubo bubo*), Ural Owls (*Strix uralensis*), Great Gray Owls (*S. nebulosa*), and Eurasian Pygmy-Owls (*Glaucidium passerinum passerinum*) have declined or become extirpated throughout much of the European landscape but persist in scattered woodland reserves and parks. The viability of their mostly isolated populations is unknown.



27. Many decades of intensive silviculture in the Black Forest of southwest Germany have resulted in even-aged forests of simple structure, which provide poor habitat for the native old-forest owls.

- **Ninox**-At least six species of hawk owls might be associated with old, dense forest conditions (Clark and others 1978, Everett 1977, Hume and Boyer 1991): Rufous Owl (fig. 61), a secondary cavity-nester (Cayley 1975), occurring in thick woodlands and rain forests of Australia (figs. 59, 60) and New Guinea (Pizzey 1980); the little-known Ochre-Bellied Hawk Owl found in deep virgin forests of Sulawesi, Celebes (Harrison 1973; also see figs. 57-58); Philippine Hawk Owl of Philippine forests; Andaman Hawk Owl found in forests of Andaman and Nicobar Islands of the East Indies; Indonesian Hawk Owl of scattered island forests in Southeast Asia; and Brown Owl of New Guinea lowland forests. Four other species narrowly endemic to islands of the New Guinea area and likely to be closely associated with old forests are Admiralty Islands Hawk Owl (*N. meeki*), New Ireland Hawk Owl (*N. solomonis*), New Britain Hawk Owl (*N. odiosa*), and Solomon Islands Hawk Owl (*N. jacquinoti*). These four species might also inhabit lowland tropical forests, but their ecologies are unknown (Hume and Boyer 1991).

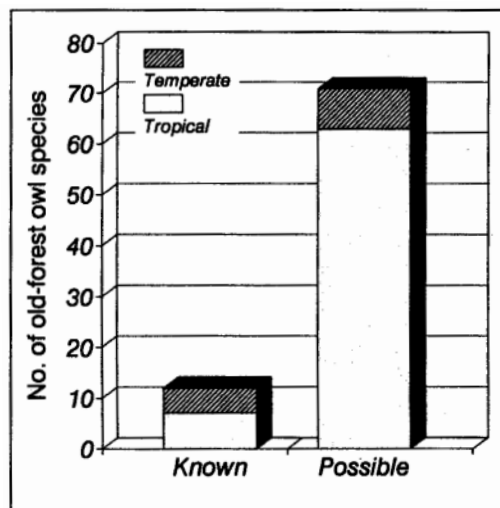


Figure A-Number of known and possible old-forest owl species in temperate and tropical settings.

- **Nesasio**-The rare Fearful Owl occurs in lowland primary forest only on three of the Solomon Islands in Australasia, and little is known of its ecology (Everett 1977).
- **Aegolius**-All four species of this genus are adapted to forest conditions, although it is unclear if they all typically associate with old forests per se. One species, Tengmalm's or Boreal Owl, is associated with old Holarctic conifer forests (Everett 1977, Ryder and others 1987, Whelton 1989; see figs. 2-3). Mikkola (1983) notes that, in Europe, the favored breeding habitat of Tengmalm's Owl is dense coniferous forest of the taiga belt. The species has a specific preference for spruce but also occurs in mixed forests of pine, birch, and poplar. Farther south in Europe, it also uses subalpine conifer forests and, in Germany, pine forests on lower mountain slopes and similar forests on the plains.

Members of other owl genera, notably *Athene*, *Micrathene*, *Nyctea*, *Pseudoscops*, *Rhinoptynx*, *Sceloglaux*, and *Surnia*, seem better adapted to various conditions, including open grassland, savannah, park woodlands, and broken forests, and thus are not treated here.

Implications for Old-Forest Management

Summary of Owls in Old Forests

Twelve extant owl species are fairly well known to be associated mostly with dense, old, or undisturbed forests (table 1, fig. A). These 12 species include 7 tropical or subtropical forms: Soumagne's Owl, Bay Owl (which also inhabits high-elevation temperate forest habitats in low northern latitudes), Forest Eagle-Owl, Brown Wood Owl, Black-and-White Owl, Crested Owl, and Papuan Hawk Owl; and 5 temperate forms: Northern and California Spotted Owls, Himalayan Wood Owl, Blakiston's Fish Owl, Long-Whiskered Owlet, and Boreal Owl (fig. B). Because so few temperate owl species are known to be associated primarily with old forests, controversies over the conservation of old-growth temperate coniferous forests for the Northern Spotted Owl are a rather unique case.

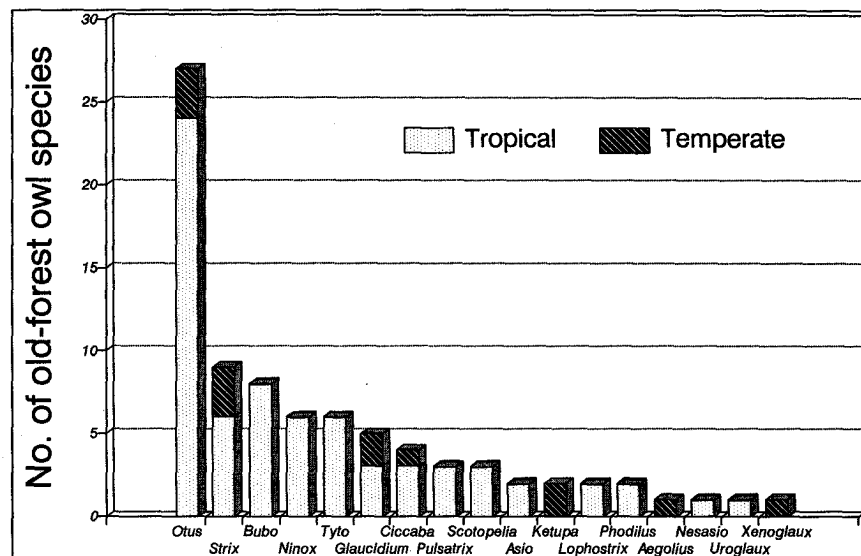


Figure B-Number of old-forest owl species in temperate and tropical settings, by genus.

Another 71 extant forms-63 tropical and 8 temperate-are known to be associated with forests and also might be dependent on dense, old, or undisturbed forests (marked with “?” in table 1; also see fig. A), but not enough is known of their ecologies to make definitive designations. These 71 forms include 5 species of *Tyto*, 7 species of *Otus*, 7 species of *Bubo*, 6 species of *Strix*, 6 species of *Ninox*, and the rest distributed over 9 other genera (fig. B). Several other species, such as the Great Gray Owl, Flammulated Owl, and Ural Owl, also are found in dense, old, or undisturbed forests but not as their sole or primary habitats, and thus are not included in these tallies.

My listing of 71 species unconfirmed as old-forest obligates underscores our overall poor inventory base and scientific knowledge, particularly in tropical environments. To aid their conservation, these species should be assumed to be associated primarily with old forests until further information becomes available. Basic inventories of the presence and distribution of all species with either known or unconfirmed associations with old forests should be conducted, and nest stands should be protected.

In addition, ecological studies of habitat associations also should be pursued. For the set of unconfirmed old-forest associates, greater priority should be given for species (1) in isolated, insular, or increasingly fragmented environments, as with Celebes Barn Owl, Giant Scops Owl, Fearful Owl, and others; or (2) whose primary habitat is threatened and in decline, as with many of the tropical species including Scully’s Wood Owl, Fulvous Owl, Malay Wood Owl, Spotted Wood Owl, Rusty-Barred Owl, and others.

See bookmarks to continue

Extinct and Endangered Owls of Old Forests

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Extinct owls-Clark and others (1978) list nine owl species that became extinct during historic time. Among these, the Anjouan Island Scops Owl, Mauritius Scops Owl, Leguat's Owl, and Mauritius Owl likely inhabited native forests. Their populations probably declined from deforestation of their island environments.

At least two additional species can be added to this list. *Tyto pollens* was a flightless, 1-m-tall congener of barn owls that likely occurred in old-growth Caribbean pine (*Pinus caribaea*) barrens of Andros Island, Bahamas, in association with early human settlers (see figs.

6-9). It probably gave rise to local lore of chickcharnies, a mischievous leprechaunlike, nocturnal imp said to have three toes and the ability to turn its head all the way around. If disturbed, chickcharnies would impart terrible misfortune. It is possible that territorial defense behaviors of a meter-tall *Tyto* could give rise to such legends.

The Forest Spotted Owlet of central India is known from less than a dozen specimens and has not been reported since 1914 (Ali and Ripley 1983). It was associated with dense or mature deciduous forests, particularly moist-deciduous jungle and groves of wild mango near streams, in the Satpura Range of Maharashtra and Madhya Pradesh States (Ali and Ripley 1983; also see fig. 36). These forests have become heavily modified during the 20th century by clear-felling and conversion to coppice, by planting of even-aged stands of teak (*Tectona grandis*), and from intensive human intrusions to extract other forest products (Marcot and others 1991; also see fig. 36). Although members of *Otus* and *Glaucidium* still inhabit these teak forests (personal observation), the Forest Spotted Owlet has not been reported recently.

Endangered owls-Clark and others (1978) also listed nine endangered owl species or subspecies, some of which may be associated with old native forest. Such species might include Lan Yu Scops Owl of Taiwan, and Nduk Eagle-Owl, a local endemic of Usambara Mountains, Tanzania (fig. 29). Little is known, however, of the ecology of either species. In addition, Hume and Boyer (1991) list the Sula Islands Barn Owl as known from only one specimen and possibly extinct. This species might have inhabited older native forests, but nothing is known of its habitat associations and status. They also list the Minahassa Barn Owl as a rare or endangered species in northern Sulawesi where rich tropical rain forests abound, but nothing is known of the ecology of the species.

Old-Forests Owls in Continental and Island Settings

Of all 83 extant owl species of old forests (table 1), almost a third-26 species (31 percent)-occur only on islands or peninsulas (for example, Malay Peninsula), and the remainder are found in continental settings (fig. C). This proportion of island forms is greater than that of all owls of the world regardless of habitat association: only about one-fourth (26 percent) of the 155 owl species worldwide in all habitats are found on islands or peninsulas. In general, species occurring only on islands typically are at much greater risk than are species found in continental settings, because small population dynamics increase the risk of local extinctions (Gilpin and Soule 1986). Add to this the loss of old-forest habitats and direct exploitation,

Owls of Old Forests of the World Recently extinct species

Andros Island Barn Owl	<i>Tyto pollens</i>
Anjouan Island Scops Owl	<i>Otus rutilus capnodes</i>
Mauritius Scops Owl	<i>Otus commersoni</i>
Leguat's Owl	<i>Bubo leguati</i>
Mauritius Owl	<i>Strix sauzieri</i>
Forest Spotted Owlet	<i>Athene blewitti</i>

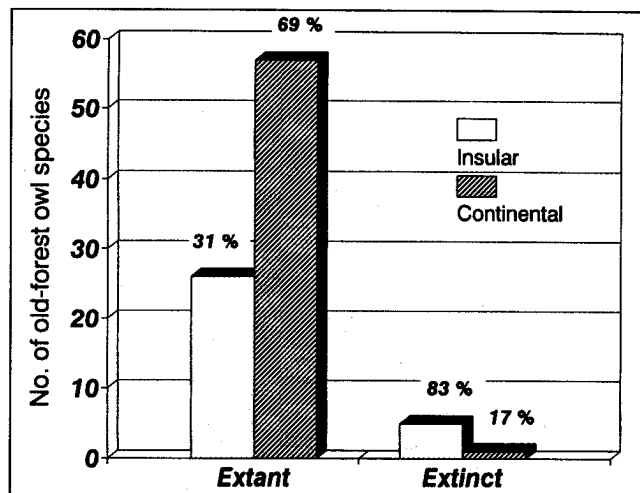


Figure C-Number of extant and recently extinct old-forest owl species in insular and continental settings.

and the threat of extinction to associated owl species greatly increases. Further, of the six extinct species of owls likely associated with old forests (discussed above), five (83 percent) were island forms (fig. C). Clearly, island living adds substantial risk to viability.

If habitats and populations are left undisturbed, many populations not already depressed to moribund levels may survive. For example, Walter (1990) cites the case of the Socorro Island Red-Tailed Hawk (*Buteo jamaicensis socorroensis*) persisting in isolation in small local numbers (20 5 pairs) because it has been undisturbed. Although this hawk is more of a generalist in habitat and diet than many old-forest owls, it nonetheless is illustrative of how small-island populations can persist with local protection of habitats and resources. Few, if any, such studies have been made, however, of population persistence of old-forest owls on islands.

Threats to Owls of Old Forests

Most owls live outside reserves and their fortunes are largely dictated by the activities of landowners, foresters, farmers, and planners.

Mikkola (1983:311)

The greatest threat to owls of old forests is the direct loss of their habitats. Old forests are logged throughout the world for wood and other forest products, thereby resulting in their conversion to young forests or nonforest conditions. Many old forest have been converted to pasture and croplands, human habitations, and other uses (Wilson and Peter 1988).

There are few forest conservation reserves established for owls per se throughout the world. In Europe, as of 1981, only one reserve had been designed for birds of prey at Sabed, near the town of Tirgu Mures in Romania (Mikkola 1983). This reserve provides habitat for Long-Eared (*Asio otus*), Scops (*Otus scops*), Little (*Athene noctua*), and Tawny Owls.

Threats to Owls of Old Forests

- Loss of habitat
- Insular settings
- Pesticides
- Disturbance
- Persecution
- Collection

Old Forests of Africa



28. Tropical and subtropical forests of southern Africa contain Shelley's Eagle-Owl (*Bubo shelleyi*), Akun Eagle-Owl (*B. leucostictus*), and Fraser's Eagle-Owl (*B. poensis*). Shown here is Lake Manyara National Park, central Tanzania, in a rift valley at an elevation of 945 m. Old tropical forest in foreground, savannah with acacia trees behind; baobob tree legacies on hillsides. (Photo courtesy of David Hays)



29. Mountain forests northwest of Lake Tanganyika and possibly within Zaire provide habitat for the rare Prigogine's Owl (*Phodilus prigoginei*). Such habitat appears as these semideciduous forests occurring near the rim of Ngorongoro Crater, Tanzania, at 2440 to 2740 m elevation. In the Usambara Mountains of Tanzania this type of forest provides habitat for the locally endemic Nduk Eagle-Owl (*Bubo vosseleri*). (Photo courtesy of David Hays)



30. Dense riverine tropical forests of sub-Saharan Africa provide habitat for the scarce Milky or Verreaux's Eagle-Owl (*Bubo lacteus*) and the more widespread African Wood Owl (*Ciccaba woodfordii sokokensis*). Such tropical gallery forests also contain several species of fishing owls, including Pel's (*Scotopelia peli*), Rufous (*S. ussheri*), and Vermiculated (*S. bouvieri*) Fishing Owls. Riparian forest of Serengeti National Park, Tanzania along the Grumeti River. (Photo courtesy of David Hays)



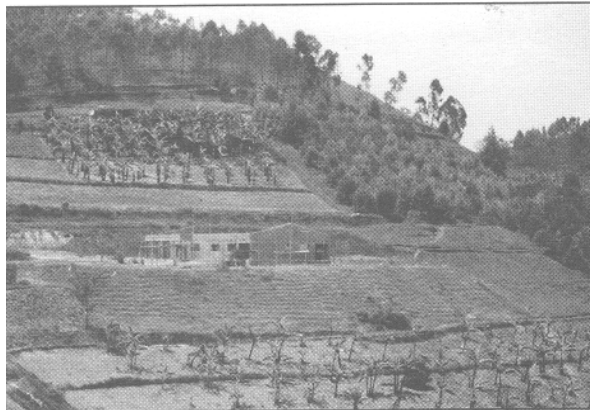
31. This mature riparian forest along the Seronera River in Serengeti National Park, Tanzania, at approximately 1525 m elevation, provides roosting habitat for the Milky or Verreaux's Eagle-Owl. (Photo courtesy of David Hays)



32. The hagenia forests of Virunga Mountains, Rwanda, 2440 to 3050 m elevation, are the home of the mountain gorilla and eagle-owls. (Photo courtesy of David Hays)



33. In Zaire, mountain heath and cedar forests are habitat for the Abyssinian Long-Eared Owl (*Asio abyssinicus*). Photo taken in Aberedere National Park, central Kenya, at approximately 3050 m elevation. (Photo courtesy of David Hays)



34. Deforestation in Rwanda includes terracing hillsides for row crops and eucalyptus plantations (upper right). (Photo courtesy of David Hays)

In the Pacific Northwest, some of the last remaining old-growth conifer forests on federally administered public lands are being designated as ancient forest reserves, in part for protection of the Northern Spotted Owl. Current polemics over use and conservation of these ancient forests, however, are unique only in the degree of popularity of the issues and the specific kinds of forests involved. The general issues are timeworn when compared to the fate of many other owl species associated with old forests throughout the world. Examples of such issues, listed by genus, follow.

Tyto-Soumagne's Owl likely is endangered from destruction of its tropical evergreen forest habitat on Madagascar. This species is included in appendix I of the 1977 CITES Resolutions and in the IUCN Red Data Book of 1968 and updates thereto (Clark and others 1978). Conversion of humid rain forests on Madagascar likely is causing declines of this little-known species (Hume and Boyle 1991).

Phodilus-The Bay Owl is vulnerable to loss of its evergreen conifer and hardwood forests in the Himalayan foothills, where logging and cutting of trees has accelerated in recent decades from increases in human populations. Over the past century, much of its habitat in wet evergreen tropical forests of south India and Sri Lanka has been converted to cropland or even-aged forest or coconut plantations, which has heavily fragmented remaining habitat into small isolated parcels (personal observation; figs. 38, 39). Bay Owls (and a host of other associated primary and secondary cavity-using species) might be particularly vulnerable to loss of large cavity-bearing trees in these areas. The related African Bay Owl might still occur in threatened forests of Zaire (fig. 33), but its response to commercial use of these forests is unknown.

Otus-Forest habitat of the Mountain Scops Owl is "constantly under threat of destruction" (Voous 1988:32). The Puerto Rican Screech Owl is one of the most endangered species of *Otus* because of the progressive felling of its forest habitat (Everett 1977; and see fig. 10).

On the other hand, Voous (1988) speculates that Flammulated Owls have benefited from the spread of open, arid ponderosa pine (*Pinus ponderosa*) forests in the Western United States from human-caused forest fires. Potential threats to the Flammulated Owl, an insectivore, also might include reduction of large flying insect populations from pesticide use (Voous 1988) and loss of dead trees with woodpecker cavities for nest sites (Goggans 1986, Marcot and Hill 1980). Similar loss of cavity trees in the Himalayas (personal observation) might adversely affect populations of the related Spotted Scops Owl, one subspecies of the Mountain Scops Owl.

Pesticides also might have had adverse effects on populations of the European Scops Owl (*Otus scops*) (Voous 1988). Although this species likely has benefitted from its association with human-altered landscapes of Europe (figs. 26, 27) and is not an old-forest obligate, environmental pollution has caused population declines in the Middle East (Voous 1988). Understanding reasons for population declines of the European Scops Owl might aid in understanding other, less well-known congeners associated with old native forests. It is unclear how its populations might be affected by the current environmental crisis induced by the 1991 Iraqi war, especially pollution of the atmosphere from hundreds of burning oil wells and other battle-related fires. Other populations of the European Scops Owl have decreased because of conversion of woodlands to vineyards in the Rhone valley of Switzerland and the loss of trees with hollows (Arlettaz 1987, Voous 1988).

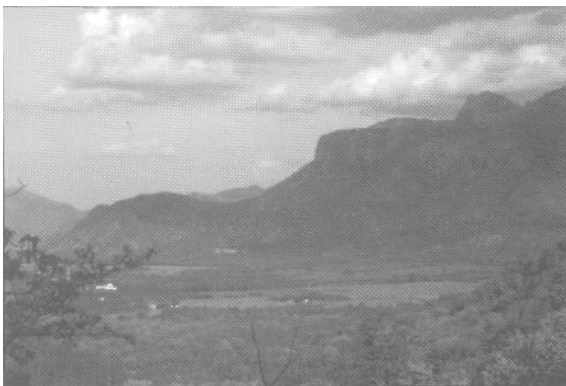
Old Forests of the Indian Subcontinent



35. The old forests of deodar (*Cedrus deodara*), blue pine or kail (*Pinus wallichiana*), and chir pine (*P. roxburghii*) of the Himalayas of India, Nepal, Tibet, and Bhutan, have provided habitat for the Bay Owl (*Phodilus badius*), Forest Eagle-Owl (*Bubo nipalensis*), Himalayan Wood Owl (*Strix aluco nivicola*), and Scully's Wood Owl (*S. aluco biddulphi*). However, severe overuse, including terracing, lopping of trees, fires, and deforestation, has eliminated forest habitats and resulted in great erosion and slope failures in many areas.



37. A remnant "preservation plot" of tropical moist deciduous forest in Kerala, southwest India, containing teak (*Tectona grandis*) and *Lagerstroemia lanceolata* in the overstory and *Randia dumetorum* and *Wrightia tinctoria* in the understory. Such forests provide habitat for Brown Wood Owls (*Strix leptogrammica*), one of the Asian cousins of North America's Spotted Owl



36. Much of the older, dry deciduous forests of India has been removed for agricultural production. Some have been replaced by plantations of sal (*Shorea robusta*) in the north and teak (*Tectona grandis*) or exotic species such as eucalyptus (*Eucalyptus globulus*) in the center and south. Forest reserves and wildlife sanctuaries protect remnants of the original dry deciduous forests. This forest reserve occurs in Melghat Tiger Reserve, Satpura Hills, Madhya Pradesh and Maharashtra of the High Deccan Plateau of central India. It is the last known forest habitat of the Forest Spotted Owlet (*Athene blewetii*), not seen since 1914.



38. A tropical wet evergreen rain forest in Tamil Nadu, south India (left). These amazingly diverse forests are characterized by Dipterocarp trees (for example, *Dipterocarpus grandiflorus*, *D. pilosus*, *D. kerrii*, *D. gracilis*, and others). Shown here is the scarce giant evergreen forest of the Western Ghats, containing trees of the families Clusiaceae, Anacardiaceae, Sapotaceae, Meliaceae, and Lauraceae. These forests host Brown Wood awls, Brown Fish Owls (*Bubo Zeylonensis*), and, in Southeast Asia, Spotted Scops Owls (*Otus spilocephalus spilocephalus*).

39. The lowland moist evergreen and wet evergreen tropical forests of south central and Southeast Asia have largely been converted to agriculture and other land uses. Some of these forests in upper elevations have been preserved in recently formed forest and wildlife reserves. Their small size and scattered distribution, however, do not guarantee the long-term viability of associated old-forest owls, including Forest Eagle-Owls, Brown Wood Owls, and Brown Fish Owls.

Loss and conversion of old forests also might adversely affect many other subtropical and tropical species of *Otus*, including the Oriental Scops Owl, which is dependent on such habitats. Clearing of primary lowland rain forests in Malaysia, Sumatra, Java, Borneo, and the Philippines likely is threatening the Rufous Scops Owl, but nothing is known of how it might respond to increasing fragmentation of its primary forest habitat and to growth of secondary forest (flume and Boyer 1991). Although the species is not currently endangered, loss of its habitat should be of concern. Collared Scops Owls and Pacific Screech Owls, on the other hand, might be more able to persist in human-altered landscapes and various forested landscapes in the absence of old forests per se.

Ancient Mayan corn crop rotations and agricultural practices likely led to declines in amount of undisturbed forest vegetation in Mexico and Central

America (Terborgh 1989). This may have had adverse effects on the Whiskered Screech Owl in the Neotropics (Voous 1988). More recent and widespread conversions of forest cover to human habitations and croplands in Mexico likely have caused greater population declines. The species still remains locally abundant, however, in areas of denser forest cover.

Actions Needed

- Inventories
- Studies of habitat associations
 - Tropical and insular settings
- Protect existing key old forests tracts
 - Temperate and tropical
- Study reforestation and vegetation manipulation

Populations of the Vermiculated Screech Owl also have declined because of destruction of its New World tropical forests in Mexico, which have all but been cleared and converted to cropland and secondary scrub forest (Voous 1988; see figs. 12 and 13). Voous (1988:78) notes that “local, geographically marginal populations in Mexico and South America have already disappeared as a result of habitat destruction, and some of these probably extinct populations have recently been described as new subspecies in an attempt to call attention to their former existence (Hekstra 1982).”

The Sokoke Scops Owl, discovered in 1965 by S. Dillon Ripley in the remnants of the Sokoke Forest on the Kenyan coast, is threatened by loss of its forest habitat and by specimen collectors (Everett 1977). Between 1956 and 1966, its forest habitat was halved to 350 km². Further deforestation poses a threat to the remaining population, as only one reserve of 40 km² has been established (flume and Boyer 1991). Its population has been estimated at 1,300-1,500 pairs and is considered endangered (Clark and others 1978). Its plight was highlighted in 1966 in the IUCN Red Data Book.

Continued clearing of tropical mountain forests in Sumatra, Java, and Borneo may be an increasing threat to the Rajah's Scops Owl (flume and Boyle 1991). In Mahe, Seychelles, new forest harvest methods have led to reduction of upper valley forests, habitat of the Seychelles Scops Owl. Apparently, the only habitat preserved for this species occurs in Morne Seychellois National Park. Eventual clearing of highland forests likely will separate the remaining individuals into one small, isolated population in the park.

In Brazil, loss of lowland dry deciduous tropical forest likely is reducing habitat available to Black-Capped Screech Owls.

The Giant Scops Owl also is threatened by loss of its forest habitat in the Philippines (Clark and others 1978, Everett 1977). Although not a forest bird, the Palau Scops Owl (*O. podarginus*) likewise is vanishing because its primary, lowland mangrove swamp habitat is “fast disappearing” from the Palau islands of Micronesia (Everett 1977:147).

Bubo-The Forest Eagle-Owl depends for its survival on the continued existence of the “much endangered” tropical south Asian lowland and hill forests (Voous 1988:108). Other, less well-known Asian and African congeners, including the Akun Eagle-Owl and Philippine Eagle-Owl, also might be adversely affected by removal, modification, and fragmentation of their tropical forest habitats (Hume and Boyle 1991). Mikkola (1983:311) reports that the Eagle-Owl has been persecuted heavily by humans and “may well fade from the European avifauna if they are not strictly protected.” In fact, Eagle-Owls were on a list of “vermin” in France until the early 1960s, and as a result, their range and numbers declined markedly (Mikkola 1983). Captive breeding programs are underway in Sweden, Germany, and England and are needed in Norway (Mikkola 1983).

Ecological Studies Needed

- In insular or fragmented environments (Celebes Barn Owl, Giant Scops Owl, etc.)
- In habitats threatened or in decline
 - Many tropical species (Scully’s Wood Owl, Fulvous Owl, Malay Wood Owl, Spotted Wood Owl, Rusty-barred Owl, others)

Strix-The Northern Spotted Owl has become the cause celebre for conservation of old-growth forests of the Western United States. Its numbers and distribution have doubtless declined from extensive clearcutting of ancient forests, thereby prompting a new wave of alternative forestry practices to be considered for use on commercial forest lands. Barred and Great Gray Owls have evolved greater tolerance for broken and open forest conditions and do not seem to be in similar peril. In particular, the Great Gray Owl might never have been very abundant in extensive dense forests as they usually forage in more open habitats (see footnote 5).

In Eurasia, the Ural Owl likely has suffered declines from widespread conversion of its northern forests to agriculture or human habitations. The species apparently is taking to other substrates for nesting, however. Mikkola (1983) notes that in former times, breeding habitat was old-conifer or mixed forest far from human habitation, but in the last 25 years this has become more varied. Ural Owls still favor damp heath forest but now also regularly nest in dry heath forests and spruce bogs, with additional breeding records in pine bogs and herb-rich forests. Mikkola (1983:171) concludes that “such adaptability will favor it in the future.”

Because of its tolerance to young forest conditions and its small territory size among *Strix* species, the Tawny Owl has persisted in woodlands of Europe. Little is known, however, of the status of two Asian subspecies, the Himalayan Wood Owl and Scully’s Wood Owl. As with the northern subspecies of the Spotted Owl, these subspecies of the Tawny Owl seem more dependent on dense or older forests of the mountains. Loss of ancient trees as nest and roost substrates in the Himalayas from burgeoning human populations very likely are adversely affecting the populations of the owls.



40. Broadleaf hardwood and conifer forests of Far East Russia supply habitat for Ural Owls, Eurasian (or Northern) Eagle-Owl, and Brown Hawk-Owl (*Ninox scutulata*). This forest is found in central Ussuriland south of Khabarovsk. The higher elevation larch and pine forests of Ussuriland support the more northern Holarctic species including Great Gray Owl, Eurasian Pygmy-Owl, and Boreal (Tengmalm's) Owl.



41. Forest reserves or *zapovedniki* help conserve old-forest habitats in the Ussuriland region of Far East Russia. Bolshe-Khekhtsivsky Zapovednik just south of Khabarovsk. Forests here consist of many locally endemic plants including large cork trees (*Phellodendron amurense*), two species of linden (*Tilia mandshurica* and *T. amurensis*), Korean pine (*Pinus koraiensis*), Manchurian walnut (*Juglans mandshurica*), Manchurian ash (*Fraxinus mandshurica*), and the ancient, relict Mongolian oak (*Quercus mongolica*).



42. Undeveloped broad flood-plain forests of Far East Russia, eastern China, and Korea contain the rare Blakiston's Fish Owl (*Ketupa blakistorni*). Upper Bikin River Basin, Ussuriland, Far East Russia.

Little is known also of the population status of the Brown Wood Owl. This species is a close associate of interiors of dense old forests in the Indo-Malaysian area. Like its Tawny Owl relatives, likely it has suffered declines in recent decades. Its evergreen, moist deciduous, subtropical submontane, and lowland rain forest habitats have been reduced greatly. Altering and fragmenting its selected habitats, as with the conversion of wet evergreen forests to teak plantations in south India (fig. 39) and Sri Lanka, may pose an even greater threat to the Brown Wood Owl than to the Tawny Owl, which may be more tolerant of forest edges and openings.



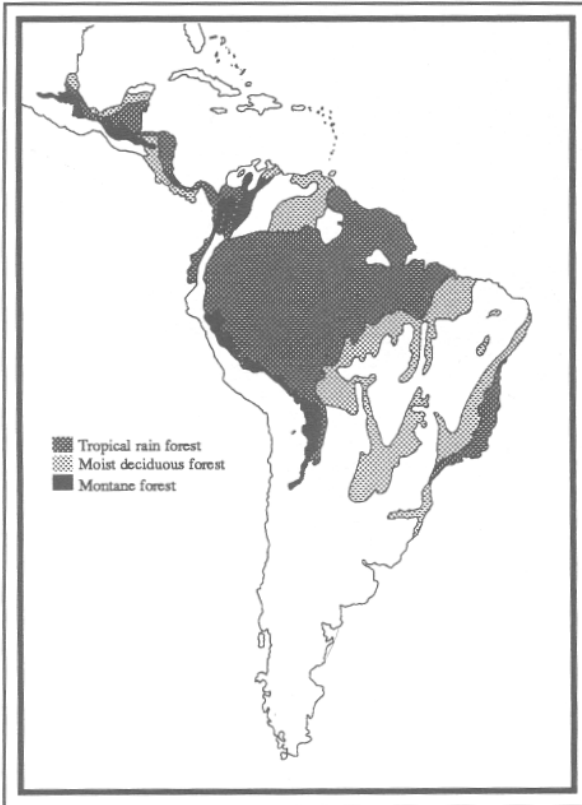
43. Across the border from the Russian Far East is Heilongjiang Province, northeast China, where lowland forests have long since given way to rice paddies, agricultural fields, and pasturelands. Old-forest owls of the Far East are essentially extirpated throughout most of eastern China under the enormous and growing human population pressures for land use.



45. Eastern China has seen great episodes of deforestation. Its rich, loess-covered agricultural fields are subject to tremendous wind erosion and gulying, further reducing suitability for growth of forests. Restoration of native forests is virtually unheard of and most forest cover consists of plantations of three or fewer tree species where dozens once stood. Few if any old-forest owls have survived these changes.

Partly sympatric with the Brown Wood Owl is the Mottled Wood Owl, which is more tolerant of human-altered landscapes and may not be as affected by loss and conversion of old-forest habitats. Recently, measures have been taken to protect wet evergreen forest stands in Kerela and Tamil Nadu states in south India, such as with the creation of Indira Ghandi Wildlife Preserve. These are major positive steps that will aid in conserving habitat for Brown Wood Owls, Mottled Wood Owls, and their old-forest associates (for example, Uniyal and Surendrnathan Asari 1988).

Examples of Forest Distributions and Owl Ranges Central and South America



46. Distribution of South American tropical rain forest, moist deciduous forest, and montane forest.



48. Range (above) of Band-Bellied Owl (*Pulsatrix melanota*) coincides with lowland tropical forests east of the Andes.



49. Band-Bellied Owl (left).



47. Range of Mottled Owl (*Ciccaba virgata*). Note coincidence with distribution of tropical forests.



50. Range of Cloud-Forest Screech Owl (*Otus marshalli*) in Andean cloud forests of Peru. An example of a locally endemic species with narrow distribution.



51. Cloud-Forest Screech Owl.

A more subtle potential threat to the Brown Wood Owl and associates may be the intensive use of forests by humans for forest products other than commercial timber. In Southeast Asia, such forest products and uses include gathering of bamboo, canes, resins, and bidi leaves; collection of deer antlers; falling of hazard trees; selection cutting of trees for poles and construction; lopping of tree limbs for livestock fodder; and grazing livestock. Such use, if conducted in moderation, should pose no threat to the owls or their habitats. Unconstrained use, however, results in forests of substantially sparser canopy and ground cover and lower overall plant and animal diversity (personal observation). This use is apt to adversely affect resident owl populations by reducing forest cover and availability of trees with nest cavities. Such potential effects on owl populations need further study.

Little is known of the population status of Fulvous Owls in the Neotropics. It can be surmised that cutting of their associated pine-oak and cloud-forest habitats has detrimental effects on population sizes of this and other related owl species of the New and Old World tropics, including the Malay Wood Owl, Spotted Wood Owl, and Rufous-Legged Owl.

Ciccaba-The Mottled Owl does not seem threatened as long as tropical forests remain protected in sundry parks and reserves, such as the cloud forests of Monteverde Biological Preserve in Costa Rica (fig. 15). Little is known of the population status of other tropical members of *Ciccaba*, although it can be surmised that reduction of tropical gallery and evergreen forests has adversely affected Black-and-White and Black-Banded Owls in the lowlands and perhaps also Rufous-Banded Owls in the Andean highlands.

Other genera-The Blakiston's Fish Owl is threatened with the removal of the taiga forests on which it depends in Japan and the Russian Far East (Voous 1988; personal observation). The Japanese race *Ketupa b. blakistoni* of Hokkaido and Kunashire Island numbered 50 birds in 1984 (Hume and Boyle 1991) and is endangered from loss of its dense, primary forest habitat (Clark and others 1978). In the Russian Far East, its primary habitat is mixed old-growth forests of broadleaved and conifer trees; most of these forests have been logged and the species persists only in small, isolated populations in broad, mostly undisturbed valleys of the Amur, Bikin, Khor, and a few other major rivers of the region. Likely, it is mostly extirpated in northeast China because of conversion of vast native forests to agriculture, pasture, or forest plantations (personal observation; figs. 43-45). Other threats to its persistence include increasing human populations, selective harvesting of its nest trees, and disturbance from tourists, although it seems to be taking to use of nest boxes in Hokkaido (Hume and Boyle 1991).

The Eurasian Pygmy-Owl (*Glaucidium p. passerinum*) had disappeared from the Black Forest mountains of Germany because of intensive timber management activities, including parcelling of the spruce-fir forests and clearcutting of old-growth forest stands (Konig 1981; see figs. 26, 27). More recently, the species has been at least partially restored with the use of nest boxes (Voous 1988). The Albertine Owlet likely is endangered because of logging and clearing of the Nyungwe Forest in Rwanda and mining in the Itombwe Mountains of central Africa (Hume and Boyle 1991). Zaire and Rwanda have planned, but not yet implemented, some conservation measures. Other species, including Papuan Hawk Owl, Ochre-Bellied Hawk Owl,

Indonesian Hawk Owl, Stygian Owl (*Asio stygius*; see fig. 11), and Madagascar Long-Eared Owl, also increasingly might be threatened from reductions in their tropical forest habitats.

Certainly, there are many other threats to forest owl species of the world, including disturbance by photographers, birders, and tourists, as with Eagle-Owls in Britain and Great Gray Owls in California; use of pesticides; poisoning, shooting, and electrocution; and collecting of eggs and specimens. Another major cause of habitat loss is reduction of riparian forests from drainage of wetlands, streams, and lakes. This probably has reduced numbers and distributions of Eagle-Owls and Brown Fish Owls throughout Europe and the Mediterranean region, particularly in Israel (Mikkola 1983) and India (personal observation).

Restoration of Old Forests

Cleared old native forests rarely are returned to original or near-original condition. I am aware of no scientific study that has demonstrated unequivocal success in intentionally restoring an owl species or other wildlife associated with ancient forest conditions through use of reforestation or other specific forest management practices. Several projects underway deserve special mention and support, however.

In temperate conifer forests, environmental concerns for loss of old-forest habitats are fostering a new era of forest management techniques. In part, such techniques are aimed at maintaining and restoring at least some older forest conditions on public commercial timber lands of the Pacific Northwest (for example, Franklin and others 1986, Klinka and others 1990). Silvicultural prescriptions are being written to demonstrate and test how well old-forest components, such as large live trees, large snags and down dogs, and dense and diverse vegetation structures, can intentionally be maintained or induced by direct stand manipulation. One phase of these studies involves testing behavioral and population response by the Northern Spotted Owl on National Forests. Indeed, one conservation strategy for managing habitat for Northern Spotted Owls on Federal forest lands (Thomas and others 1990) calls for developing and testing such silvicultural techniques as an integral part of the long-term success of the strategy. Such new forestry tactics are best applied in a careful scientific program of hypothesis testing to evaluate effects on forest stand structure and composition, production of desired commodities, and particularly long-term response by owl populations. In using an approach of this type, existing scarce and declining old forests should be protected at least in the interim (Johnson and others 1991).

Restoration of wetlands and associated riparian gallery forests in Europe and Asia could aid in recovery of associated owl species. Brown Fish Owls, Eagle-Owls, and the host of other fishing owl species would benefit.

Several owl species primarily associated with old forests also show some use of mixed-age or older secondary forests. These species include the Tawny-Bellied Screech Owl, Fraser's Eagle-Owl, and perhaps the Spotted Owl in limited parts of its range. Manipulation experiments to test the response of these species to carefully applied silvicultural prescriptions might help identify new methods for conserving their habitats and allowing some degree of use of forest commodities. Such experiments should be conducted, however, as strict scientific and statistical studies, as aberrant case observations can easily lead to overestimating the degree of adaptability of these species.

In tropical forest systems, restoration projects are being proposed or implemented to help bring back old-forest conditions. Among these is the restoration of dry deciduous tropical forests in the Guanacaste region of northwestern Costa Rica (Jantzen 1988). Success of this project might benefit species of *Ciccaba*, *Otus*, and other tropical genera and concomitantly would provide for sustained use by humans for farming and livestock grazing. In the Western Ghats mountains of southern India, silvicultural monitoring projects are aimed at restoring some of the highly modified and fragmented wet evergreen forests from converted teak plantations (fig. 37). The restoration also might help recover Forest Eagle-Owls and Brown Wood Owls in these areas (personal observation). Many other tests of effects of forest openings, patch cuts, and canopy gaps in Brazilian Amazonia (Lovejoy and others 1986) and Caribbean slope rain forests of Costa Rica (for example, Denslow and others 1990) are being explored as well. Results of these and other studies can be used to identify forest management activities that can restore or maintain old-forest owl species even in the presence of human use of forests.

Nest Boxes Are Not a Long-Term Solution

Many forest owl species benefit from nest boxes or artificial nest platforms, including Tawny (Southern 1970), Barred (Johnson 1987), Great Gray (Bull and others 1987), Flammulated (Hasenyager and others 1979), Striated Scops (*O. brucei*; Voous 1988), European Scops (Arlettaz 1987, Barthos 1957, Kadochnikov 1963, Randik 1959), and Collared Scops (Pukinsky 1977) Owls. Mikkola (1983) also lists the Hawk (*Surnia ulula*), Tengmalm's, and Little Owls as readily using nest boxes.

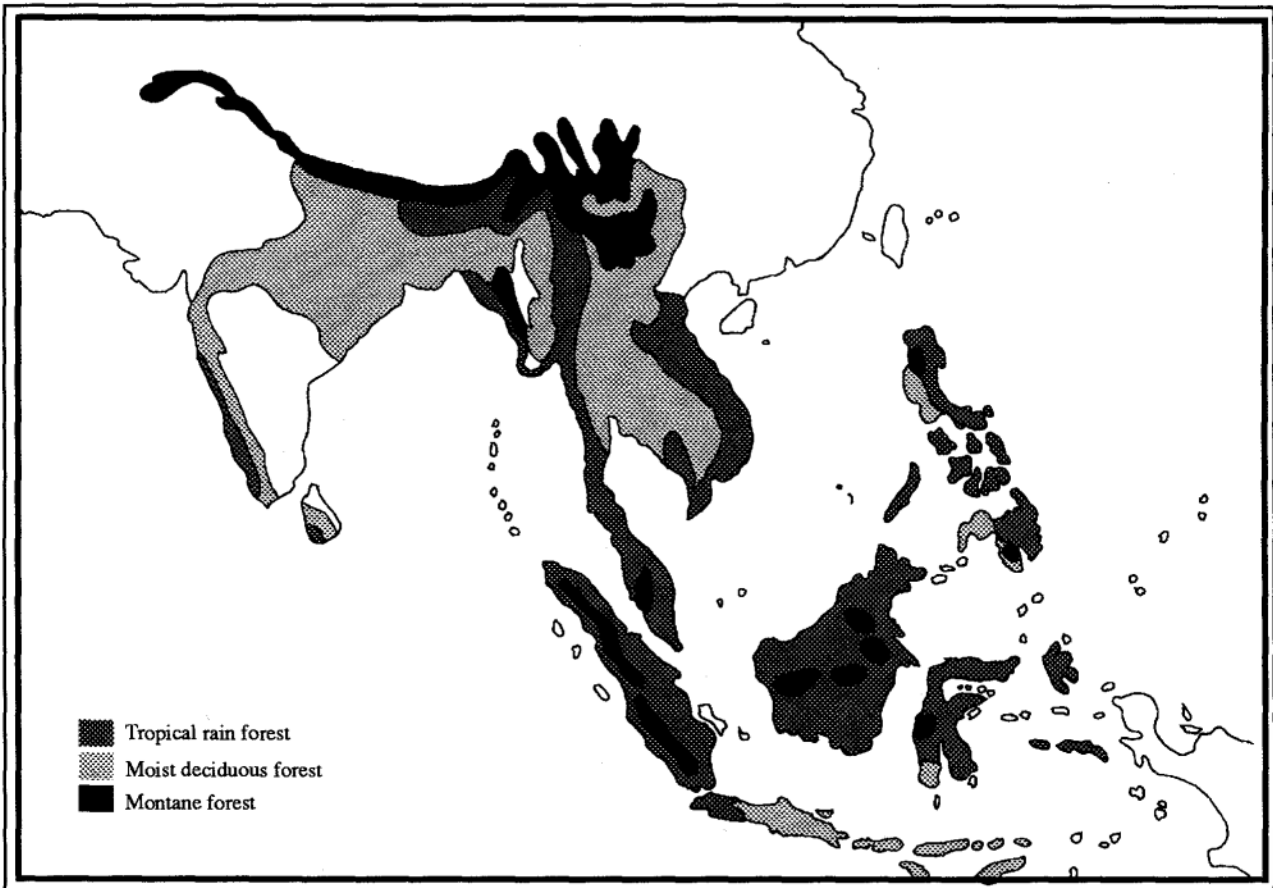
By far, however, most of these species are notably more generalist in the ages and kinds of forests they inhabit than are their old-forest congeners discussed in this report. Similar nest-box programs for owl species more closely associated with old forests, such as for Brown Wood Owls and Northern Spotted Owls, likely would not meet all their life needs found in old forests, including availability of prey and thermal and predation cover. Possibly for this reason, the Northern Pygmy-Owl has not taken to nest boxes as has its European congener the Eurasian Pygmy-Owl (Voous 1988), and the Northern Spotted Owl has been induced to use nest boxes or artificial nesting platforms only in isolated cases.⁶ The removal and prevention of old rotting wood in European forests by modern forestry programs is detrimental to breeding successes of Hawk, Tawny, Ural, Tengmalm's, and Pygmy Owls, who use natural fissures and tree cavities as nest sites (Mikkola 1983). In Sweden and Finland, however, many nest boxes have aided in increasing local numbers of Ural Owls. If instituted for old-forest owls, nest-box programs should first be conducted to scientifically test hypotheses of behavioral and long-term population responses rather than as a full-fledged management program (Marcot and Gardetto 1980).

Interpreting Habitat Associations

Studies of the Northern Spotted Owl have described clearly its selected habitat as mature and old-growth conifer forests (Thomas and others 1990). Nevertheless, many people interested in the commercial values of its preferred habitat cite occurrence of the subspecies in second- and young-growth forests as evidence of its "adaptability" (for example, Craig 1986). Studies have revealed that such atypical associations occur for only a small portion of the subspecies, if at all (atypical associations with young forests also are reported with other old-forest owl species).

⁶ Personal communication. Jeffery Mattison, Six Rivers National Forest, Fish and Wildlife Unit, 1330 Bayshore Way, Eureka, CA 95501.

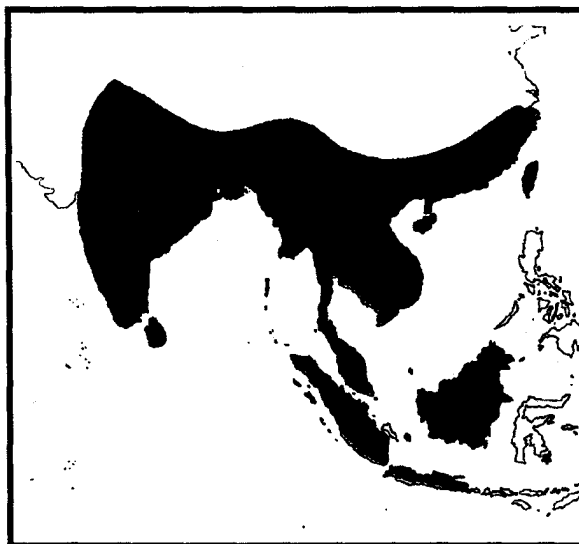
Examples of Forest Distributions and Owl Ranges Southeast Asia

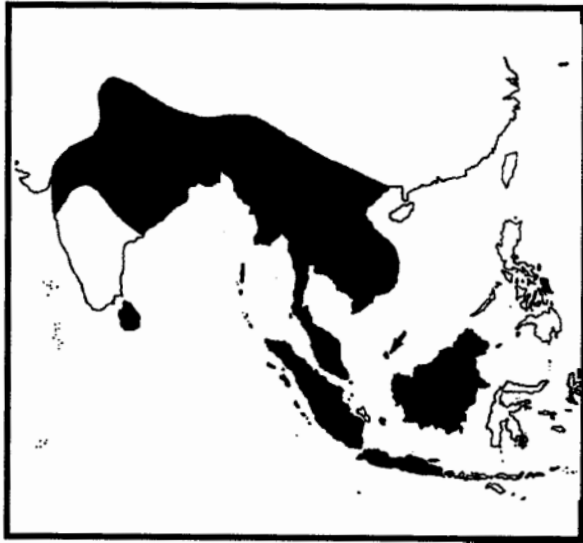


52. Distribution of rain forests of the Indo-Malaysian region.

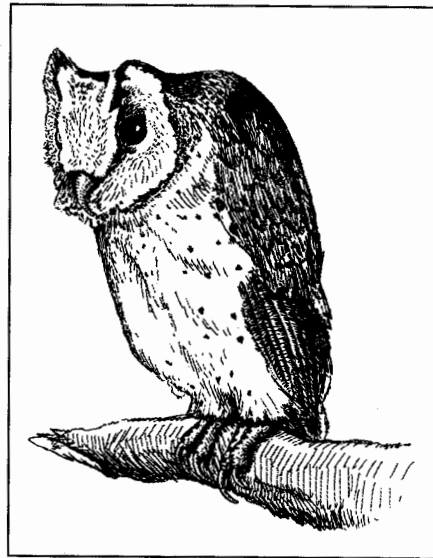
53. Range of Brown Wood Owl (*Strix leptogrammica*) in Southeast Asia. Note general coincidence with distribution of tropical rain forests.

54. Brown Wood Owl (far right).

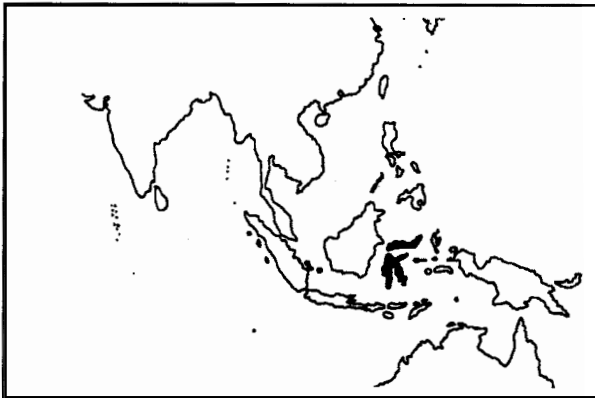




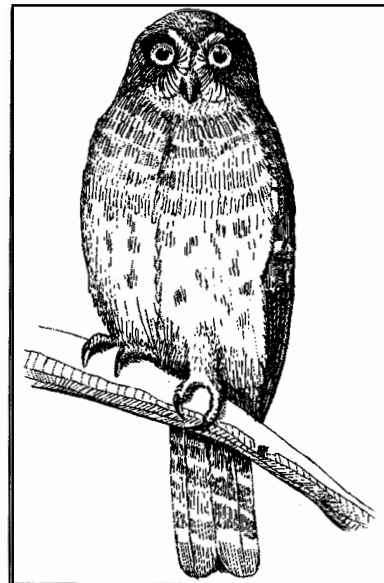
55. Range of Bay Owl (*Phodilus badius*) in Southeast Asia.



56. Bay Owl.



57. Range of Ochre-Bellied Hawk Owl (*Ninox penrersa*) in tropical rain forests of Celebes.



58. Ochre-Bellied Hawk Owl.

Also, within young forests, Northern Spotted Owls typically are found tightly associated with elements or small patches of old forests (Forsman and others 1977, Thomas and others 1990). The Northern Spotted Owl evolved in association with, and is adapted to, old forests. Populations likely would fare poorly in landscapes with highly fragmented old forests or with purely young-forest conditions (Thomas and others 1990).

Ongoing research is testing these concepts and assessing how well silvicultural manipulations can provide old-forest elements for Spotted Owls and other old-forest associates in commercially managed forest lands (Nyberg and others 1987). Also of particular relevance to management of Spotted Owls

would be an understanding of its old-forest congeners, particularly the Himalayan Wood Owl and Scully's Wood Owl, in their increasingly fragmented and altered mountain forest habitats. Unfortunately, no ecological or demographic studies seem to have been conducted on these populations.

Conservation Activities Needed

- Create old-forest reserves
- Restore old-forest conditions
- Study behavioral and population response
- Restore wetlands, riparian habitats
- Nest boxes . . . ?

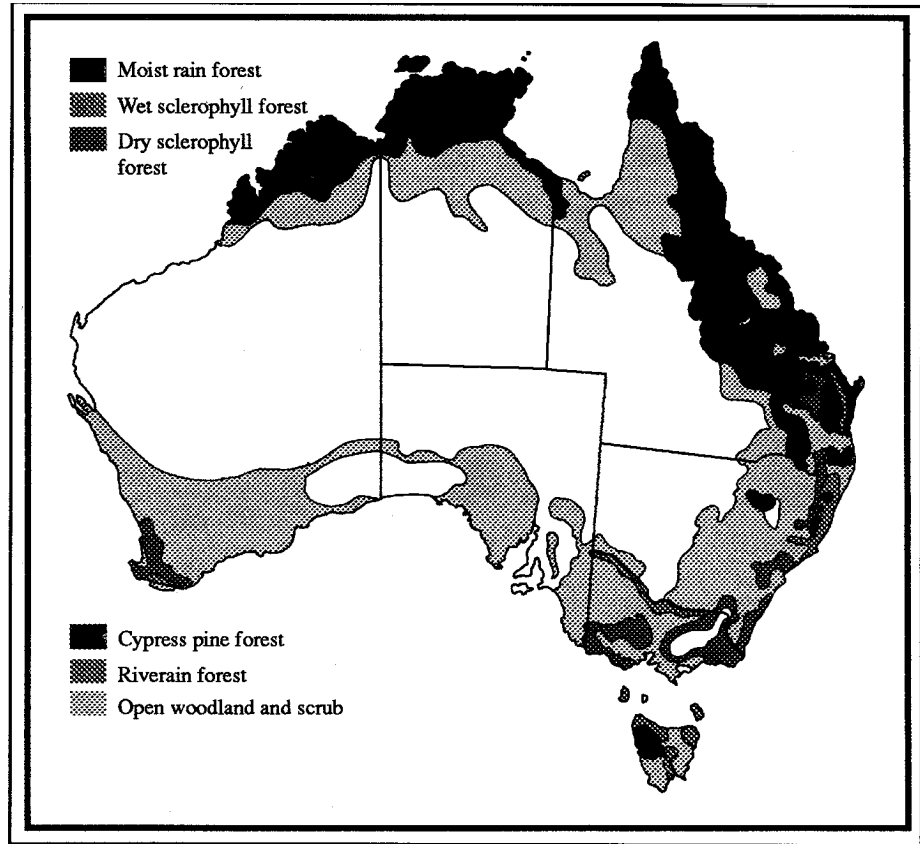
Some species of *Otus*, such as the European Scops Owl, the Striated Scops Owl, and the Collared Scops Owl, seem to do well in cultivated and human-altered habitats. Other congeners, however, such as the Mountain Scops Owl and the Oriental Scops Owl, are associated primarily with old, denser forests and do not tolerate human alteration of landscapes. Similarly, among species of *Strix*, the Barred Owl and Tawny Owl likely are more tolerant of human-altered habitats and concomitant invasions by potential predators and competitors than are other congeners such as the Brown Wood Owl and the Spotted Owl. In the same way, among species of *Bubo*, the Great Horned Owl is more catholic in ages and structures of forests it inhabits than is its Asian cousin, the Forest Eagle-Owl.

It should be no surprise that the various species of a genus complex, such as *Strix* and *Otus*, have evolved to specialize in use of different environments including undisturbed, old forests. Nor should it be a surprise, following this evolutionary history, that no one species of a given genus exhibits the full range of ecological adaptations and habitat associations as seen among all its congeners, just as no one individual of a species exhibits the behavioral variation of all races of the species (Ruggiero and others 1988). Thus, the best way to ensure the continued existence of all species of each genus complex is to provide for the full range of habitat conditions, including old forests, needed by each species.

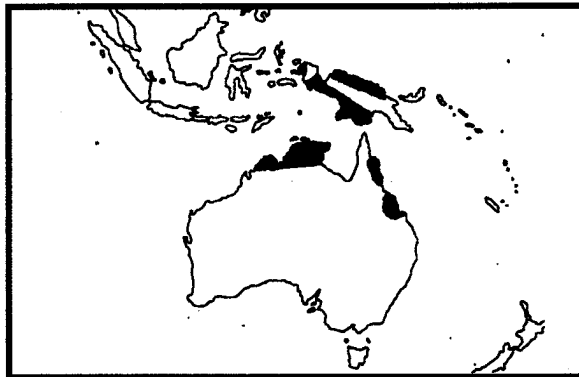
Forest Owls in Human Cultures

Many species of forest owls have played prominent roles in myths and religious beliefs (Holmgren 1988). The plaintive song of the Mountain Scops Owl is known in legends of the mountainous tribes of Myanmar (Smythies 1953, Voous 1988). The Oriental Scops Owl is the subject of folklore in Japan and Korea, its call associated with the mystical treasures of Buddhism (Austin and Kuroda 1953, Voous 1988).

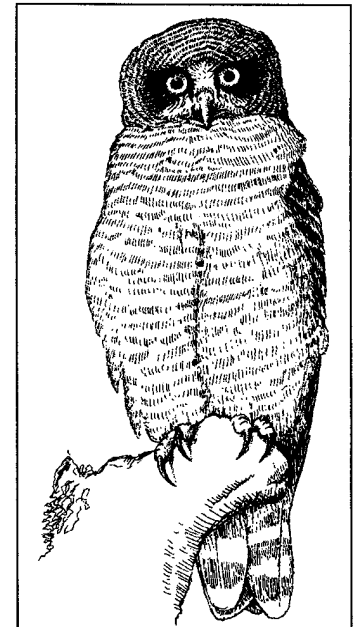
Examples of Forest Distributions and Owl Ranges Australia



59. Distribution of rain forests in Australia.



60. Range of Rufous Owl (*Ninox rufa*) in moist rain forests of northern Australia



61. Rufous Owl (right).

Old-forest owls often are associated with sacred, large trees in riparian gallery forests, near temples, and in cemeteries. In India, the Forest Eagle-Owl plays a major role in many legends and is said to be found calling from Hindu cemeteries that are often the only local bastion of old-growth forests with large hollow trees and snags.⁷ The Brown Wood Owl, Forest Eagle-Owl, and Brown Fish Owl are found in sholas and gallery forests of *Ficus* near waterholes and streams in northern and southern India, sacred areas with mundirs and temples (personal observation; fig. 38). In a sense, then, many of these owl species serve as indicators of the religious value of a forest.

The Collared Scops Owl has survived on Java and Borneo possibly in part because of the ill omen or reverence it represents in legends there (Voous 1988). In China and Korea, these owls are used for medicinal purposes and many have been taken annually for this purpose (Austin 1948, Gore and Won 1971, Voous 1988). For the most part, however, the Collared Scops Owl has adapted well to areas of human habitation.

Ultimately, the Spotted Owl finds itself in similar circles of controversy over forest management as have many other species in other parts of the globe. The fate of Brown Wood Owls in southern India, Sikkim Bay Owls in the Himalayas, and Crested, Black-and-White, and other Neotropical owls in Central and South America similarly are caught in disputes over human use of their selected old-forest habitats. Such controversies include the closure of local forests to commercial timber harvest, national policies in India that have brought hardship to some local tribes and villagers. In response, the Government of India has instituted retraining programs to school the former loggers to become environmental educators and field tour leaders for the growing industry of environmental tourism (Panwar and Rao 1990). Perhaps by similarly incorporating the Spotted Owl once again into the culture of North America through recreational, aesthetic, artistic, scientific, and even ethical interests, it can play a legitimate role in the well being of human societies and thereby continue to persist in some of the least disturbed and oldest temperate forests the world now knows.

Acknowledgments

I thank Evelyn Bull, Carl Marti, David Wilcove, and Jon Winter for helpful technical reviews of the manuscript, and Steven McDonald for a policy review. This paper is dedicated to the many field biologists of Federal and state forest management agencies, universities, research stations, and other private and public organizations whose work is helping to protect owls of old forests throughout the world.

Measure Equivalencies

1 meter (m) = 39.37 inches or 3.28 feet
1 square kilometer (km²) = 0.3861 square mile

⁷ Personal communication. V.B. Sawarkar, Wildlife Institute of India, P.O. New Forest, Dehra Dun 248006, India.

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Appendix A: The Songs of *Strix*

Introduction

The past decade has seen an exponential increase in studies, inventories, and monitoring of Spotted Owls (*Strix occidentalis*) on Federal, state, and even private lands throughout the Western United States and Canada (for example, Allen and others 1989, Fredrickson and others 1990, Simon-Jackson 1989). The USDA Forest Service (1988) has been using protocols for monitoring Northern Spotted Owls (*S. o. caurina*). Such protocols stipulate the use of nocturnal and diurnal calling surveys (Forsman 1983) to locate owls (see also Johnson 1986).

Spotted Owls have a wide variety of songs and calls (Fitton 1991, Forsman and others 1984). Some of these vocalizations have been recorded on audio tape for use in conducting calling response surveys in the field and for training of personnel to recognize owl species (see also Ganey 1990, Laymon 1985, and USDA Forest Service 1988 for studies of Spotted Owl vocalizations and their use in monitoring surveys). In recent years, a small army of field personnel have scoured many types of forests for presence of Spotted Owls by using taped or vocalized calls. What these biologists might not realize is that the Spotted Owl has many cousins throughout the world with rather similar vocalizations. The purpose of this paper is to review the various *Strix* species and their calls. Herein, I compare descriptions of vocalizations from field guides and other sources, many not commonly known by most field-going wildlife biologists. I hope this brief review of vocalizations of 13 species of *Strix*¹ and 5 species of *Ciccaba* (appendix B) will highlight similarities and help foster a greater understanding and appreciation for Spotted Owls and their relatives.

Origin and Purpose of Vocalizations

The evolution of vocalizations by birds, including owls, can be attributed to acoustic properties of their primary habitats, as well as to selective forces of sexual recognition and other intraspecific and interspecific interactions. Specific vocalizations given in particular instances are often the result of mood, pair and breeding status, time of day, age and sex class, and season. Vocalizations generally are given to announce and defend territories for mates or resources or to maintain contact with mates or young (Jellis 1977).

With few exceptions, most species of *Strix* occupy woodland and forested habitats mostly in the Holarctic zoogeographic region. A few species occur in the Neotropical and Oriental zoogeographic regions (Voous 1988). Most *Strix* species are typically monogamous and vocally defend territories for mates or resources. Many vocalizations for territorial defense are loud and forceful, and they consist of various series of several individually recognizable hooting notes. Other vocalizations, projecting a greater state of agitation as when confronting a conspecific at close range, typically include various shrieks, howls, and screams, such as with the Spotted Owl (Forsman and others 1984). Still other sounds include softer calls given by young as food-begging calls, or by females to locate and maintain contact with their young.

Vocalizations of *Strix*

The following accounts describe many of these calls listed by species. Vocalizations for many species are yet undescribed in published material.

I recognize the long-acknowledged difficulty in describing bird sounds with words or phrases (Jellis 1977). Sound spectrograms are vastly superior to words for denoting durations, frequencies, harmonics, and overtones. They are difficult to obtain, however, for as full a set of species as offered in this report and are less mnemonic than are the more subjective descriptions herein.

¹ Fourteen species, if *Strix davidi* is considered separately from *S. uralensis*.

Strix of the Nearctic Region

Spotted Owl (*S. occidentalis*)-Spotted Owls are found throughout western and southwestern North America from southern British Columbia into the mountains of northwestern Mexico. Spotted Owl vocalizations are quite varied, and have been well described by Forsman and others (1984). They include high-pitched hoots, like the barking of a small dog, usually in groups of four, as in **hoo,who-who,whoohoo** (Peterson 1961), the last note drawn out and descending in pitch. These are location calls given by both sexes, with the female's call being slightly higher in pitch.

When more greatly agitated, Spotted Owls also give a call consisting of a rising inflection of **whoo, whoo, hoo, hoo, hoo, hoo-hoot-hoot, hoo-hoot-hoot**, cut off at the end or occasionally terminated with a descending **hoooo**. This call may escalate to a shrill **kre-ick! kre-ick!**, which in turn might escalate to a rising whistle, which rises most abruptly at the end and is cut off sharply, as in **wheee-et!** or **cooo-weep!** This is often given repeatedly and is a contact call, more often given by the female. Other calls include a crowlike bark **khaw khaw khaw**, given by the female. Food-begging calls given by the young or female-young contact calls given by the female generally are heard only at close range and are not commonly encountered during field surveys.

Barred Owl (*S. varia*)-Barred Owls occur throughout southern Canada, the Eastern United States, and into northeastern and central Mexico. Udvardy (1977) described calls as a distinctive, rhythmic series of loud hoots, **who-cooks-for-you, who-cooks-for-you-all** (see also Forrand 1983). The call also has been described as **hoo-hoo-hoo-hoo-hoo-hooaw**, the ending **aw** being characteristic; and other calls include sounds like the barking of a dog (Peterson 1961; personal observation of the author). Still other calls include a hoot that terminates with a diminishing **waahh-ah** that fades away, and a "pleasant duet of the pair with one on a higher tone and twice as fast, and a number of weird chuckles, screams, and assorted haunted-house noises" (Tyler and Phillips 1978:138-139).

Great Gray Owl (*S. nebulosa*)-Great Gray Owls are circumpolar and found in boreal regions of North America, Europe, and Russia (Holarctic distribution). Calls include a series of deep, resonant **whoos** (Udvardy 1977), also described by Peterson (1961) as a deep booming **whoo-hoo-hoo** and deep single **whoos**. The male's territorial call is a regular, deep, booming series **hoo-hoo-hoo**, which can rise gradually in pitch (Hume and Boyer 1991). In Far East Russia, the calls are a loud and muffled **hoo-hoo-hoo** (Flint and others 1984). Perrins (1987:140) reported the voice of the male as "regular, deep growling or booming hoots and **ke-wich** calls" similar to those of the Tawny Owl but deeper.

Mikkola described the primary territorial song given by the male (and sometimes by the female) as a series of up to 8 to 12 regularly spaced ho notes given at a rate of 1.5 notes per second, the series lasting 6-8 seconds, with 33 seconds between series. The most common call of the female is a soft mellow hoot used to communicate with her mate at the nest. Various depictions are **vee-vee**, **nieh-nieh**, and **whoop**. In addition, both sexes give a series of rapid double notes as a defensive or warning cry. The female also gives a loud heronlike squawk or bark at the end of a series of notes ranging from vigorous hooting to high-pitched wails and squeals, as in alarm.

Strix of the Neotropical Region

Fulvous Owl or Guatemala Barred Owl (*S. fulvescens*)-This species occurs in tropical and temperate forests of southern Mexico and northern Central America. The call is described as a four-noted **huho, huhoo**, the combination sometimes repeated twice rapidly (Edwards 1972). Fulvous Owls previously were considered by some to be a race of the Barred Owl (Davis 1972, Eck 1971, Peters 1940). Their calls were described by Peterson and Chalif (1973) as hooting similar to that of the Barred Owl. Indeed, the repeated four-note series sounds similar to the location call of the Barred Owl (see above). Its hooting calls also have been described as similar to those of the Spotted Owl (Dickey and van Rossem 1938, Monroe 1968, Voous 1988).

Rusty-Barred Owl (*S. hylophila*)-This species and the Rufous-Legged Owl are the only *Strix* species in South America. The Rusty-Barred Owl inhabits woodlands of the central part of the continent, and its calls include a rolling **rrrrro**; a rhythmic, descending guttural **gu gu gu gu gu, u, u, u, u**; and a long-drawn **i-u-a** (Hume and Boyer 1991) or ascending and then descending scratchy scream sounding like a frightened human.

Rufous-Legged Owl (*S. rufipes*)-This species is found in southern South America. I could find no reports of its vocalizations. However, the recordings by Hardy and others (1990) include 2-note and 4-note songs, sounding like a scratchy **prrr-prrrrr** (sometimes doubled in the 4-note song), the second note accented and descending in pitch; and the same song with 2 or 3 brief introductory notes and 2 ending notes of the same **prrr** quality added.

Strix of the Palearctic and Oriental Regions

Tawny Owl (*S. aluco*)-Tawny Owls are found throughout Europe and in disjunct populations in the Near East, Far East, and southeastern Asia. Their voice, as reported by Perrins (1987) in Britain and Europe, is quite variable with the male giving a **tu-whit-tu-whoo** and the female responding **ke-wick**; the young give a scratchy persistent **ti-sweep**. In Far East Russia, Flint and others (1984) wrote that the male gives a **hoo-hoo-hoooo**, and the female a **kyouyouyouveeh**. In Southeast Asia, King and others (1975) reported the voice as a high, screeching, sharply accented call of two syllables, **buku**.

Hume and Boyer (1991:139-140) described the call as “a long, pure, or faintly wheezy, hoot, followed by a short pause, then a brief, abrupt hu and a long, resonant, wavering **huhuhuhoooo**.” The contact call is **kewick**, and as followed by a hoot has given rise to the “somewhat inaccurate” depiction as **tu-whit-tuwhoo** (Hume and Boyer 1991). Fledged young have a similar call, but it is a more wheezing, strained, lower, and less explosive **tsi-weep**.

Mikkola (1983) denoted their calls as the most diverse of all European owls, with 10 different basic calls given by breeding adults and 5 calls given by young. The basic call of the male serves for marking territories, during courtship, and when bringing food to the female and young. This call is a long drawn out **hooo**, a pause of 2 to 6 seconds, an abrupt and subdued **hu**, followed at once by a long, resonant **huhuhuhooo**. The females' calls are less clear-phrased, ending with a wailing **wow-wow-hooo**. Other calls include an **oo**-trill given by the male after delivery of prey and as a territorial conflict call; this call also has been described as a loud discordant “caterwauling.” Another call is a hissing trill **co-co-co-co-co-co** given during courtship and territorial fights.

In India, calls of one subspecies, Scully's Wood Owl (*S. a. biddulphi*), have been listed as "a loud **hoohoo..hoo-ho-ho-hoop**, the final **hoo** being somewhat drawn out. There is a pause of about four seconds after the initial **hoo**, and half a second between the second and the rest of the concluding rolling note" (Ali and Ripley 1983: 257; similarly described in China by de Schauensee 1984). Other calls of this subspecies include a loud quack and a soft coo, the latter similar to those of a ring dove or turtle dove (Ali and Ripley 1983:257), and a **khawak** uttered when flying about at night, occasionally when perched (Ali and Ripley 1983:257). Ali and Ripley also noted that Scully's Wood Owls begin calling an hour or so after sunset from some exposed treetop and repeat the call for 10 minutes at a time, with a pair or several birds answering one another. The authors also described calls similar to the above for the Himalayan Wood Owl, *S. aluco nivicola*, including a "loud **hoo..hoo..hoo-ho-ho-hoo**, the final **hoo** drawn out;" and that the call sounds "sometimes merely as a hurried deep low **hu-hoo**" (Ali 1989:62).

The contact call of the Tawny Owl is **kewick** and is given mostly by the female (Mikkola 1983). This is quite similar to the contact calls given by female Spotted Owls. Mikkola (1983) described several other calls of Tawny Owl adults and young.

Ural Owl (*S. uralensis*)-The Ural Owl occurs in middle north temperate latitudes of Europe and Asia: Perrins (1987) reported the Ural Owl's calls as consisting of both hooting and **ke-wick** types, both deeper and more barking than those of the Tawny Owl. Flint and others (1984) noted that the Ural Owl's call in Far East Russia is a barking, high-pitched **hey-hey-hey** or **kaoo-vekk**. Calls in China were reported by de Schauensee (1984) as a long, quavering hoot, and also a barking **khau-khau** and a harsh **ke-wick**. Young Ural Owls give wheezy notes.

Hume and Boyer (1991:146) noted that its call is a double barking hoot, and that pairs might call together. The song is a "simple repetition of hoots, **huow-huow-huow**, the female's version being lower, weaker and harsher in quality." The male also gives a call consisting of **wohu**, a 4-second pause, and then a **wohu-huwohu**, for territorial defense or mate contact. Ural owls also give a loud, sharp **korrwick**, longer and harsher than the **kewick** note of Tawny Owls. Young give food-begging notes.

Hume and Boyer (1991:148) also separate the David's Wood Owl (*S. davidi*), which others consider as a strongly marked race of the Ural Owl. In their account, the David's Wood Owl gives a "long, quavering hoot and barking **khan khau**."

Mikkola (1983) described the courtship song of the male as a deep hooting **wohu...wohu-huwohu**, with a 4-second pause in the middle. Other calls include a barking **huow-huow-huow** given by the male; a single **huu** given by the male in excitement; various calls at the nest given by the female, including barking, gobbling, chuckling, and hissing; and a sharp cry **korrwick**, harsher and longer than similar notes of the Tawny or Great Gray Owls.

Brown Wood Owl (*S. leptogrammica*)-A resident of deep mountain forests in much of the Oriental zoogeographic region, the Brown Wood Owl is poorly studied. The 15 recognized races differ considerably in size and degree of isolation (flume and Boyer 1991). The outer ear structure is less complex than that of other *Strix* species, leading flume and Boyer (1991) to suggest its grouping with *Ciccaba*.

King and others (1975) listed calls as a 1-second series of four deep musical notes, **goke, goke-galoo**, with the first note emphasized and a wide variety of similar calls. In China, the voice was cited by de Schauensee (1984) as a mellow, musical, hollow sounding **tok...tu-hoo**, often repeated, with the **tok** note in undertone. In Sri Lanka, the voice is a sonorous **huhu-hooo** (Henry 1971). Other calls include a “barking **wow wow**, undoubtedly signifying alarm” (Voous 1988:208).

Ali (1962) described the call of the Himalayan Brown Wood Owl (*S. I. newarensis*) as “a deep four-noted hoot, **hoo...hoo-hoo...hoo**.” Other calls include what is probably a conversational note between a pair at dusk—a low, sonorous **koo-krri**, rather like a domestic pigeon—as well as querulous screams and loud snapping of the bill on detection of an intruder near the nest, and when apprehensive (Ali 1962), the calls sometimes being given diurnally (Ali and Ripley 1983). Calls of *S. I. newarensis* also have been described as “a low double hoot **tu-who**” (Ali and Ripley 1983:256).

Smythies (1984: 310, 313) described calls of the Brown Wood Owl, *Strix indranee* (= *S. leptogrammica indranee*) of Burma, as a deep musical call of four syllables, **who-hoo-hoo-hoo**, with the emphasis on the first note, lasting about 1 second; and “diabolical screaming shrieks ...like that of a demented person casting himself over a precipice.” Ali and Ripley (1983:256) described the calls of *S. leptogrammica indranee* as a “mellow, musical, hollow-sounding **tok...tu-hoo** repeated every few seconds,” the initial **tok** (sometimes twice) uttered as a low undertone and audible only at close range (also mentioned in Ali 1989 for *S. I. newarensis*). Birds were described by Ali and Ripley as being particularly vocal during moonlit nights and in the breeding season. Calls include various “weird, eerie shrieks and chuckles, in addition to the loud bill-snapping” (Ali and Ripley 1983:256) denoting aggression (Voous 1988).

Mottled Wood Owl (*S. ocellata*)—The Mottled Wood Owl occurs on the Indian subcontinent. Ali and Ripley (1983:256) described calls of *S. o. ocellata* as “a loud quavering eerie **chuhua-as** uttered regularly as the birds emerge from their daytime retreat, and again before retiring at dawn [and] also from time to time during the night, but not very frequently [see also Ali 1979]. At other [nonbreeding] seasons [calls are] mostly a single mellow, metallic hoot [and] an occasional harsh screech similar to the Barn Owl’s.” King and others (1975) listed the call as a loud, single hoot. In northern India, I have heard it give an eerie descending, quavering whistle, 4 to 5 per minute; a rising, then falling, plaintive vibrato hoot, 20 per minute; and a rather trilled, hooted series **pdd-pddd-pdddd-pdd**.

Hume’s Owl (*S. butleri*)—Hume’s Owls are found mostly in the Middle East. The Hume’s Owl has been considered by some to be a desert offshoot of the temperate Tawny Owl (Voous 1988), but recent studies have not supported this hypothesis (Hume and Boyer 1991). In most accounts it is given separate specific status (Voous 1988). Calls include “an unmistakable clear long-drawn **huu** uttered at intervals, sometimes varied by a tremulous and more throaty hoot as in *Strix aluco*,” and variants (Ali and Ripley 1983:255).

Descriptions by Hume and Boyer (1991:135) include the following. The call has been reported to resemble that of the Tawny Owl and consists of a single long even note that lacks the quavering typical of Tawny Owls. The call also has been described as a “hoot followed by two shorter, double notes-**hoooo huhu huhu.**” Another call, given in agitation, is **hu-hu-hu-hu-hu-hu-hu**, which lasts for 2 to 3 seconds. Two birds have been heard calling in duet. In southern Israel, calls include a series of 12, sometimes 13, notes, given at dusk, the notes increasing slightly in speed and noticeably in volume. The final note in the series was lower and cut short and call series “had a deep, slightly booming but rather muffled quality-**bu bu bu bu bu bu bu BU BU BU BU b**”-and was unlike calls of the Tawny Owl.

Mikkola (1983) described calls of the Hume’s Owl as **hoooo-huhu-huhu** and **whoo-who-who**, a longish hoot followed by two short double hoots. The birds also give an excited and agitated **hu-hu-hu-hu-hu-hu-hu** lasting 2 to 3 seconds when another bird is nearby or in response to taped calls.

Malay Wood Owl (*S. orientalis*)--The Malay Wood Owl occurs in southeast Asia. Smythies (1984) described the calls of *S. orientalis orientalis* as commencing with a rolling **hoo-hoo-hoo** and ending with a prolonged and deep drawn **hoooo**.

Spotted Wood Owl (*S. seloputo*)--The Spotted Wood Owl is found in subtropical and tropical parts of Southeast Asia. In some accounts, it is listed as a subspecies of the Malay Wood Owl. King and others (1975) listed the Spotted Wood Owl in Southeast Asia as *S. seloputo (orientalis)*, whose varied calls include a deep rolling **hoo-hoo-hoo** ending with a prolonged deep **hooo**. Hume and Boyer (1991:137) noted that its calls include a “series of low, musical notes that end with a longer, deeper hoot.”

Ciccaba: Tropical Cousins

Although some authors (Norberg 1977, Voous 1964, 1988) have assigned the mostly tropical wood owls of *Ciccaba* to the genus *Strix*, in this account I retain the separate genera designations, following American Ornithologists’ Union (AOU) (1983).

Mottled Owl (*C. virgata*)--Mottled Owls occur in the New World tropics in Central and South America. Their most common call is “2-3 successively louder grunts, low and guttural, then 2 sharp downslurred hoots, the first louder: **huh-huh; WHOO’, WHOO;**” and “sometimes a single hoot, or 1-3 grunts alone” (Stiles and Skutch 1989: 195). Hume and Boyer (1991) described other calls as a rising, whistling screech. Stiles and Skutch (1989:195) defined it as “a long-drawn-out catlike screech usually heard shortly after dusk or before dawn.” Peterson and Chalif (1973) described the calls as “harsh and mournful **waaa-a’-oooo**, increasing then decreasing in pitch and volume; a **boo, boo-ab, boo-ab, boo-ab, boo-ab, boo-ab**; a descending modulated hoot; and a semi-whistled screech and a gruff growl” (Peterson and Chalif 1973). Hilty and Brown (1986:231) described the most common call in Colombia as “a very deep, resonant **whooou**, usually in pairs or triplets or sometimes 5-6 in a row,” and that vocalizations also include, rarely, a catlike scream. Davis (1972) described the most frequently heard calls as a 2-second series of five hoots cut off, as in hut, the first two hoots spaced half a second apart and the others given at increasingly shorter intervals. In Mexico, I have heard a Mottled Owl give a 10-second series of short but notes, first increasing, then decreasing, in pitch. Edwards (1972:91) described the call as “a slow series of four or five, low-pitched, burred notes, descending in pitch, **hroot, hroot, hroot, hroot, hroot.**”

Voous (1988) noted that Mottled Owls commonly interact vocally and territorially. Their territorial song is “invariably described as a series of deep, often guttural and slightly modulated hoots rendered as **bru bru** and **bu bu bu** (Panama; Wetmore 1968), **keeooweeyo** or **cowooawoo** (Panama, Ridgely 1981), or **whoo-oo** (Venezuela; de Schauensee and Phelps 1978), all of the same character and quality as the call of the Spotted Owl (Miller 1963)” (Voous 1988:203). Other calls of both juveniles and adults include a long, drawn out, whistled screech, and a call sounding like a child crying (Voous 1988). Immatures call with a catlike wail, louder and higher pitched than the previously mentioned call and lasting about 1 second (Davis 1972).

Gerhardt (1991) reported five different vocalizations, including a three- to six-note “hoot” given frequently by males and infrequently by females, the males in response to taped calls and across home range boundaries. Females called at a higher pitch than did the males. Another call given by adult females is used to solicit food from the male, particularly near the nest, and is a “cat-like yowl” (Gerhardt 1991:23). A third call is the food-begging call of juvenile mottled owls: a very soft “high-pitched rattling hiss.” A fourth call is a growl given by adults during capture or when nest trees were climbed. Another call is a peeping of the very young nestlings.

Black-and-White Owl (*C. nigrolineata*)—Sometimes considered a subspecies of *C. huhula* of South America (see below), this species is found from lowland, mostly swampy forests in Central America and northwestern South America (Voous 1988). Its call differs across its range (flume and Boyer 1991). Its most common call is a “low grunt followed by a gruff, strident hoot: huh, **HOOoo**; these sometimes followed by 2 lower, softer, faster hoots, **huh, HOOoo hoo-hoo**, a 4-note call with pattern the reverse of that of Mottled Owls.”

Young birds give an ascending, breathy shriek (Stiles and Skutch 1989:195). In La Selva, Costa Rica, they give a low-pitched hooted series **hu-hu-HU-HU-hu-hu**, the middle two notes higher in pitch and volume than the other notes (personal observation). Peterson and Chalif (1973) described calls as a loud, drawn out catlike **whee-u-u-u**, and a resonant, low-pitched **whoo, whoo, whoo**. Edwards (1972:91) described the voice as an “extended, slightly rasping, mewing sound.” flume and Boyer (1991:131) described the calls as “loud and high-pitched, like a long **who-ah**”; in Panama, the call is a “long nasal **oo-weh** with a marked upward inflection, rather quieter than the similar call of the Mottled Owl.”

Another more explosive, sharp sound is often repeated, sounding in Panama like a deep, resonant and deliberate **whoof, whoof, whoof**; in Colombia, gives a strained, rising and falling catlike scream, and a deeply resonant **hu, hu, hu hoo-ah**, and a series of 9 to 14 **hoo-ah** notes with an occasional single deep boo (flume and Boyer 1991). In Colombia, according to Hilty and Brown (1986:230-231), the species has two very different calls: “a high-pitched dry scream, rising, then falling, catlike, and strained as though only air is expelled (Hilty); and a deep, resonant, deliberate **hu, hu, hu, hoo-ah** (last phrase slurred) with variations.” This last call also has been described as “a series of 9-14 slow **hu-wah’s** and a single, loud, deep **boo** at intervals” (P. Schwartz in Hilty and Brown 1986:231).

Black-Banded Owl (*C. huhula*)-Black-Banded Owls generally are scarce inhabitants of rain forests and plantations in northern and central South America. Its voice is well described as a “rising cat-like scream followed by a loud hoot, **whoeeruh, hoo**”, and also as a “deep, resonant **hu hu hu HOOOO**” (Hume and Boyer 1991:132). Hilty and Brown (1896:231, and P. Schwartz cited therein) described the voice as “an ascending catlike scream, whoeeruh followed after a short pause by a loud **booo**; also a deliberate, deep, resonant **hu, hu, hu, HOOO**, with variations.” The emphasized syllable is particularly forceful (personal observation in Upper Amazon Basin, Ecuador). Hume and Boyer (1991) and Hilty and Brown (1986) both noted that at times its voice is identical to that of the Black-and-White Owl, and that they commonly respond to one another’s calls.

Rufous-Banded Owl (*C. albitarsis*)-This species occurs in Andean mountain forests of South America. The species is said to greatly resemble the Fulvous Owl (Kelso 1940) and is either an offshoot of the more northerly *Strix* or, less likely, is a relict of a tropical form from which *Strix* arose (Voous 1988). In Colombia, it is reported to give a deliberate pattern of deep, resonant notes, as in **hu, hu-hu-hu, HOOOa**, repeated every 8 to 11 seconds (Hume and Boyer 1991). Hilty and Brown (1986:231, and P. Schwartz cited therein) described it as “a deep, deliberate, resonant **hu, hu-hu-hu, HOOOa**, repeated at 8-11 second intervals.” They also noted that in Colombia, the main song of the Rufous-Banded Owl is similar to those of the Black-Banded and Black-and-White Owls, but that it differs in cadence; the Rufous-Banded Owl’s song includes a pause after the first note, the next three notes are quicker, and the final note is more prolonged and more strongly given. Local names of the Rufous-Banded Owl in Venezuela, including Borococo and Surrucuco, resemble the calls (Hume and Boyer 1991).

African Wood Owl (*C. woodfordii*)-African Wood Owls (sometimes *Strix woodfordii*, Newman 1991) are widespread and common in forests and open woodlands of sub-Saharan Africa and the only *Ciccaba* found outside the Neotropics. Descriptions of calls were given by Hume and Boyer (1991:133) as follows. Calls are sometimes given in late afternoon from the top of the forest canopy. Both sexes give a series of rapid hoots; the female’s are higher pitched. Calls begin “loudly and evenly but fade away into an uneven rhythm-**whu-whu-whu whu-uh uh-uh-uh.**” The female also gives a high wheeow which is answered by a low hoot from a nearby male. The pair also will call together in a coordinated duet or in a series of overlapping hoots. Newman (1991:216) described calls of males as “a rapid **HU-hu, hu-HU-hu-hu, hu-hu,**” with females responding with a higher-pitched “hoo.”

Discussion

Although vocalizations of every species of *Strix* and *Ciccaba* have not been studied, several similarities are evident from reports cited herein. Vocalizations of most *Strix* species include location calls. These calls typically consist of a series of four or more hooted notes such as given by Spotted, Barred, Great Gray, Brown Wood, Himalayan Brown Wood, and Fulvous Owls. Other similarities among *Strix* species include various screeched, wailed, or barking calls such as given by Spotted, Barred, Tawny, Ural, and Brown Wood Owls. Still other species give extended wavering notes or single loud hoots, as with Hume’s and Mottled Wood Owls. Malay Wood and Spotted Wood Owls give a long rolling series of hoots. *Ciccaba* vocalizations include four- or five-note location type calls and variations on rolling and downward-slurred notes, similar in description to those of their *Strix* relatives.

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Degree of similarity in vocalizations can be one piece of evidence for degree of evolutionary relatedness. For example, in forests of the Pacific Northwest United States, hybrids of Spotted and Barred Owls (nicknamed “sparred owls”) have been observed giving vocalizations intermediate between the two species.¹ It has been only in recent years that the two species have become sympatric with the Barred Owl invading the range of the Spotted Owl’s (Boxall and Stepney 1982, Hamer 1985, Taylor and Forsman 1976). In Europe, Tawny and Ural Owls, a similar pair of closely related species, have hybridized in captivity (Scherzinger 1983, Voous 1988), with the fertile hybrids having a similar but “more varied vocabulary” than either parent. Also, van der Weyden (1972) demonstrated the close relatedness between the Tawny Owl and the Afrotropical Wood Owl (*Ciccaba woodfordii*, sometimes placed in *Strix*, as with Voous 1988) based on similarity of vocalizations of owls in Morocco and Senegal, West Africa. Understanding degree of relatedness among owl species might help in developing management guidelines by interpreting habitat requirements and evolutionary history of closely related species.

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Appendix B:
Species and
Selected Subspecies

Species and selected subspecies mentioned in the appendix text

Genus *Strix*.

Strix of the Nearctic Region

Spotted Owl (*S. occidentalis*)

Northern Spotted Owl (*S. o. caurina*) Barred Owl (*S. varia*)

Great Gray Owl (*S. nebulosa*)

Strix of the Neotropical Region

Fulvous or Guatemala Barred Owl (*S. fulvescens*)

Rusty-Barred Owl (*S. hylophila*)

Rufous-Legged Owl (*S. rufipes*)

Strix of the Palearctic and Oriental Regions

Tawny Owl (*S. aluco*)

Scully's Wood Owl (*S. a. biddulphi*)

Himalayan Wood Owl (*S. a. nivicola*)

Ural Owl (*S. uralensis*)

David's Wood Owl (*S. u. davidi*) (sometimes considered as the separate species *S. davidi*)

Brown Wood Owl (*S. leptogrammica*)

Himalayan Brown Wood Owl (*S. I. newarensis*)

Brown Wood Owl (Burma) (*S. I. indranee*)

Mottled Wood Owl (*S. ocellata*)

Mottled Wood Owl (India) (*S. o. ocellata*)

Hume's Owl (*S. butlers*)

Malay Wood Owl (*S. orientalis*)

Malay Wood Owl (*S. o. orientalis*)

Spotted Wood Owl (*S. seloputo (orientalis)*) (often combined with Malay Wood Owl)

Genus *Ciccaba*:

Ciccaba of the Neotropical Region

Mottled Wood Owl (*C. virgata*)

Black-and-White Owl (*C. nigrolineata*) (sometimes considered a subspecies of *C. huhula*)

Black-Banded Owl (*C. huhula*)

Rufous-Banded Owl (*C. albitarsis*)

Ciccaba of the Palearctic Region

African Wood Owl (*C. woodfordii*)

Marcot, Bruce G. 1995. Owls of old forests of the world. Gen. Tech. Rep. PNWGTR-343. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 64 p.

A review of literature on habitat associations of owls of the world revealed that about 83 species of owls among 18 genera are known or suspected to be closely associated with old forests. Old forest is defined as old-growth or undisturbed forests, typically with dense canopies. The 83 owl species include 70 tropical and 13 temperate forms. Specific habitat associations have been studied for only 12 species (7 tropical and 5 temperate), whereas about 71 species (63 tropical and 8 temperate) remain mostly unstudied. Some 26 species (31 percent of all owls known or suspected to be associated with old forests in the tropics) are entirely or mostly restricted to tropical islands. Threats to old-forest owls, particularly the island forms, include conversion of old upland forests, use of pesticides, loss of riparian gallery forests, and loss of trees with cavities for nests or roosts. Conservation of old-forest owls should include (1) studies and inventories of habitat associations, particularly for little-studied tropical and insular species; (2) protection of specific, existing temperate and tropical old-forest tracts; and (3) studies to determine if reforestation and vegetation manipulation can restore or maintain habitat conditions. An appendix describes vocalizations of all species of *Strix* and the related genus *Ciccaba*.

Keywords: Owls, old growth, old-growth forest, late-successional forests, spotted owl, owl calls, owl conservation, tropical forests, literature review.

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Pacific Northwest research Station
333 S.W. First Avenue
P.O. Box 3390
Portland, Oregon 97208-3390

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Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
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