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.

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 Chihuahua pine (Pinus leiophylla var. chihuahuana); and Fremont cottonwood (Populus fremontii along riparian areas. Flammulated Owls (Otus flammeolus), as well as Western Screech-owls (O. keninettii), 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


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. 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 (Vouous 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 (Vouous 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 (Vouous 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; Vouous 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 (Vouous 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 (Vouous 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 (Vouous 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).

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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

2Personal communication. Carl Marti, Department of Zoology, Weber State College, Ogden, UT 84408.
Mentaur 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 Manley\(^3\) report the species in a building compound in a private reserve of primary dry tropical forest in northwestern Costa Rica.

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\(^3\) Personal communication. David Solis and Patricia Manley, USDA Forest Service, Pacific Southwest Regional Office, Fish and Wildlife Unit, 630 Sansome Street, San Francisco, CA 94111.
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 foliaged 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-Sahara 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
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*

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
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<tbody>
<tr>
<td>Northern Spotted Owl</td>
<td><em>S. occidentalis caurina</em></td>
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<tr>
<td>Himalayan Wood Owl</td>
<td><em>S. aluco nivicola</em></td>
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<tr>
<td>Scully’s Wood Owl</td>
<td><em>S. aluco bidulphi</em></td>
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<tr>
<td>Brown Wood Owl</td>
<td><em>S. leptogrammica</em></td>
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<td>Fulvous Owl</td>
<td><em>S. fulvescens</em></td>
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<td>Malay Wood Owl</td>
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<td>Spotted Wood Owl</td>
<td><em>S. seloputo</em></td>
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<tr>
<td>Rufous-Legged Owl</td>
<td><em>S. rufipes</em></td>
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<tr>
<td>Rusty-Backed Owl</td>
<td><em>S. hylophilia</em></td>
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Old Forests of the Caribbean

6. Old-growth forest of Caribbean pine (*Pinus caribbeaensis*), 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*).

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 wins.

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.

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. 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. 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.

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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 northwest 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.
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 Chiapis 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 
orhododendron 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.
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. oscellata*)-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 oscellata* 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 foliaged 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).

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 semopen, 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 (flume 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.

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.

- **Lophostrix**-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. nigrolineata), 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 petersoni), 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 Owlet (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.

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

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

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.
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.

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.
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.