Old-growth forests: their ecological characteristics and value to forest-dependent vertebrate fauna of south-east Australia

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ABSTRACT

Old-growth forests of south-east Australia are characterized by high numbers of large live trees, stags and large logs on the ground and in streams. These features dominate the forest structure and in large part determine composition (including flora and fauna) and function (energy flow and nutrient cycling). The management of south-east Australia's old-growth forests has entered a critical phase. They will continue to decline in area and be fragmented due to demand for timber products. The long-term implications for wildlife dependent on resources found most abundantly within old-growth forests is uncertain. Flexible management strategies are required to curb the trend towards fragmentation and to ensure the continued viability of forest age-classes that are many times older than those planned for under the proposed timber harvesting rotation periods. A proposed scheme of Regional Systems of Retained Habitat, including present and future old-growth forest, offers a means of maintaining viable old-growth ecosystems.

INTRODUCTION

The structure and composition of Australia's forests are changing rapidly mainly because of the strategies being used to extract timber from State forests.

Such strategies have reduced the prevalence of the "old-growth forests" considered crucial to the survival of many species of wildlife. Yet no detailed inventory of the extent and disposition of "old-growth forests" is available; indeed, there is not even a description of the ecological characteristics of "old-growth forests" in Australia.

Here I describe the ecological characteristics of old-growth forests in south-east Australia and the importance of these characteristics to the wildlife that finds optimal habitat within such forests. I then propose management strategies that provide alternatives to current practices which are progressively fragmenting remaining old-growth forests and their associated wildlife populations. I have drawn heavily on the ideas of Franklin et al. (1981, 1986), Franklin and Spies (1984), and Thomas et al. (1988) because I believe the ecological characteristics they describe for the old-growth forests of the USA are broadly applicable in south-east Australia.

I use the term "old-growth forest" rather than the term "ecologically mature forest" (sensu Conservation Strategy for Victoria, 1987) because "old-growth forest" is the more widely accepted. But what is an "old-growth forest"?

DEFINITIONS OF OLD-GROWTH FOREST

Ecologists recognize three stages of forest development: young, mature, and old (Franklin et al. 1981, 1986). Foresters recognize these same stages as immature, mature and overmature. This is not to say that the two sets of terms correlate precisely. Foresters consider stands to be mature when their average yearly increase in volume reaches a maximum (Franklin et al. 1986; Thomas et al. 1988). Ecologists consider stands of Eucalyptus spp. to be mature at an age when trees begin to form hollows suitable as dens and nest-sites for arboreal marsupials and reptiles, forest bats and certain forest birds. But the age at which trees develop hollows suitable for wildlife will depend on several ecological characteristics typical of the forest or stand of trees. Such characteristics of old-growth forests will develop over different lengths of time, depending on such features as site conditions and the forest's history (Franklin et. al. 1981, 1986; Franklin and Spies 1984; Harris 1984).

Thomas *et al.* (1988) have suggested that old-growth should be defined ecologically based on (1) composition of plant and animal species; (2) vegetative structure, including sizes and densities of living and dead trees (standing and fallen), and the number and nature of canopy layers; and (3) minimum size (area) of stands as related to specific ecological functions, particularly those affecting wildlife and fish habitat.

A broader working definition suggested by Nyberg *et al.* (1987), in an attempt to encompass a variety of old-growth forest types in the USA, is "a stand well past the age of maximum growth, frequently showing a great horizontal and vertical diversity of structure and plant species composition, and possessing one or more features not seen in younger forests, such as snags, down woody material or arboreal lichens."

The general thrust of the definition by Nyberg *et al.* (1987) probably presents a broad picture of old-growth in south-east Australian forests, but the definition lacks the detail necessary for mapping and management of old-growth forests.

I consider that some of the more important characteristics of "old-growth forest" include:

1. Vertical diversity produced by a deep, multi-layered canopy often resulting from the presence of more than one tree age-class and/or dominant and sub-dominant members of the major age-classes.

2. Individual live trees (present at a basal area comprising at least 50% of the total stand basal area) that are either old (well past the phase of maximum exponential growth, e.g., 150 years) or have become large (>1.0 m dbh).

3. Stags and logs of large dimensions (>0.5 m diameter and >6 m length) present in significant numbers (e.g., 4/ha for stags and 10/ha for logs).

Therefore "old-growth forests" are characterized by their structural diversity, which also provides the greatest contrasts between intensively-managed timber stands and unmanaged forests, including old-growth forests (Franklin and Spies 1984). Such structural diversity depends on the presence of (1) large live trees, (2) large standing dead trees (stags), (3) large logs on land and (4) large logs in streams (Franklin and Spies 1984). Each of these characteristics affects the composition of the flora and fauna and the cycling of energy and nutrients (Franklin *et al.* 1981).

STRUCTURAL CHARACTERISTICS OF OLD-GROWTH FORESTS

Live Old-growth Trees

Each old-growth tree is shaped by its response to site conditions, competition with nearby trees, the effects of past fires, storms, diseases, insect attack and drought, and its own genetic heritage (Franklin *et al.* 1981).

The resources that may limit certain forest-dependent fauna in forests dominated by trees of younger age-classes abound in forests dominated by old-growth trees. Of prime importance is the availability of tree hollows of various sizes and depths required by hollow-dependent species.

Australia has many species of obligate hollow-nesters: 11% of Australia's land birds are obligate hollow-nesters, compared with 6% of Southern Africa's, and 4% of Northern America's (Saunders *et al.* 1982). Thirty-nine per cent of the birds and mammals recorded in the tall, wet sclerophyll forests of central Victoria use tree hollows, and 24% depend on those hollows for nesting or roosting or both (Ambrose 1979). Australia lacks primary excavators, such as the woodpeckers of USA, and the fauna relies on hollows formed over a longer time by agents such as termites and fungus (Saunders *et al.* 1982). The high value of old-growth trees stems from their provision of hollows of various sizes. Smaller hollow-nesting species such as White-throated Treecreeper *Climacteris leucophaea*, Brown Antechinus *Antechinus stuartii*, Eastern Pygmy-possum *Cercartetus nanus* will occupy small hollows with small entrances (Ambrose 1982; Menkhorst 1984), but species such as Sooty Owl *Tyto tenebricosa* (Schodde and Mason 1980), Yellow-tailed Black-cockatoo *Calyptorhynchus funereus* (Forshaw 1969), maternity colonies of some forest bats (Lunney *et al.* 1988), and family groups of Yellow-bellied Gliders *Petaurus australis* (Henry and Craig 1984) require larger and deeper hollows present only in the eucalypts generally older than 200 years of age (Mackowski 1984; Smith and Lindenmayer 1988; Inions *et al.* 1989; Lindenmayer 1989; Lindenmayer *et al.* 1990a).

If either or both the age distribution and the size distribution of large, live dominant trees and smaller sub-dominant trees is uneven (typical of multi-aged old-growth in Victoria) the result is what Harris (1984) terms a rough canopy surface. Such a canopy surface increases the interchange of gases, the amount of dew drip caught by leaves and branches, and the interception of rain and snow (Harris 1984). This rough canopy provides a greater range of habitats for invertebrates required by canopy foraging insectivorous birds such as the Satin Flycatcher *Myiagra cyanoleuca,* Black-faced Monarch *Monarcha melanopsis,* White-bellied Cuckoo-shrike *Coracina papuensis* and Cicadabird *C. tenuirostris.*

Standing Dead Trees (Stags)

Another characteristic of old-growth forests is stags which contribute, as do live old-growth trees, a valuable nesting resource for hollow-dependent fauna (Smith and Lindenmayer 1988; Lindenmayer *et al.* 1990a,b,c); basking sites for heliothermic reptiles (Brown and Nelson, unpubl. data); perching sites for a variety of forest birds, including raptors (Thomas 1979; Maser *et al.* 1988); a deadwood medium for arthropods and therefore an increased foodbase for insectivorous birds (Harris 1984). Stags also create openings in the canopy and allow light to hit the ground. The light often leads to the establishment of otherwise suppressed vegetation which contributes to overall diversity or patchiness in the habitat available within the old-growth stand. The role of stags in the cycling of nutrients may be similar to that played by large logs (Franklin *et al.* 1981).

The dynamics of stag formation and the progression of stags through various stages have been studied in the USA (Cline *et al.* 1980) and in the ash forests of Victoria's Central Highlands (Smith and Lindenmayer 1988; Lindenmayer 1989; Lindenmayer *et al.* 1990c). These studies include classification of the stages of tree development and include a time sequence in decomposition and disintegration of a dead tree. Each stage has a changed value for wildlife such as arboreal mammals (Smith and Lindenmayer 1988; Lindenmayer *et al.* 1990c).

Large stags are a characteristic of old-growth but they are not unique to forests of that age-class. Young-growth forests developing after wildfire have high densities of stags from the original stand which remain standing for various lengths of time (Franklin *et al.* 1981; Smith and Lindenmayer 1988; Lindenmayer *et al.* 1990c). An example of such young-growth forests is found in the montane-ash forests of Victoria's Central Highlands. High densities of stags resulted from the catastrophic wildfire in 1939 when huge areas of Mountain and Alpine ash trees were killed. Today these stags provide crucial nesting resources for arboreal mammals and other hollow-dependent species. The stag's rapid rate of fall is the biggest single threat to Leadbeater's Possum *Gymnobelideus leadbeateri* because there are few alternative nesting sites within the predominantly 50 year old ash regrowth resulting from the fire (Smith and Lindenmayer 1988; Lindenmayer 1989; Lindenmayer *et al.* 1990a,c). Remaining areas of old-growth forest in the Central Highlands are crucial refuge areas for Leadbeater's Possum and other hollow-dependent species (Lindenmayer *et al.* 1990a,c).

Logs on the Forest Floor

Logs, an often overlooked component of old-growth stands (Franklin *et al.* 1981), are important in the cycling of nutrients, particularly carbon and nitrogen, as well as creating and maintaining structural diversity and heterogeneity in the ground-layer of forest communities. Logs decompose slowly and there-fore provide a continuity of potential habitat from one forest generation to another (Maser *et al.* 1979). Ashton (1986) described Mountain Ash *Eucalyptus regnans* logs that had been 75 to 80 years on the forest floor as "still intact". Nevertheless logs can be classified according to their stage of disintegration (Franklin *et al.* 1981). At an early stage of decomposition the logs' moisture content tends to increase and the logs subsequently retain significant quantities of water (Sollins *et al.* 1987). This phemonenon may be important in the provision of potential habitat for wildlife and as sites for nitrogen fixation by bacteria (Franklin *et al.* 1981).

Micro-organisms, invertebrates, vertebrates and higher plants use logs for shelter, feeding, reproduction, basking, nesting and as sites for lookout (Maser and Trappe 1984). Logs may be important habitat for many reptiles, may provide travel routes for small mammals, may be a concentrated source of invertebrates, and may offer nest protection for ground-nesting birds (Harris 1984). The logs' high moisture content makes them particularly important as habitat for amphibians (Franklin *et al.* 1981) and may make them important as refuge areas during fires. Fruiting bodies of hypogeous mycorrhizal fungi are produced in

association with tree roots often in rotten wood of decomposing logs and stumps. These sporocarps provide nutrients and energy to insects and mammals (Maser *et al.* 1979). One south-east Australian mammal, the Long-footed Potoroo *Potorous longipes*, appears almost totally reliant on this food resource (Scotts and Seebeck 1989).

Logs may also serve as sites for reproduction of trees. In the Douglas-fir forests of USA a fallen tree oriented along the contour of a slope is filled, on the upside, with humus and debris that may act as a site for seedling germination (Franklin *et al.* 1981). The rotting log may also be a site where seeds germinate. This "nurse-log" phenomenon is widespread in forest types of north-west USA, and may be important in south-east Australian old-growth forests.

Logs in Streams

Large items of organic debris and logs greatly influence the physical and biological characteristics of streams "by forming pools and protected backwater areas, providing nutrients and substrate for biological activity, dissipating energy of flowing water, and trapping sediment" (Sedell *et al.* 1988).

Logs seem to be predominant debris in streams in south-east Australian old-growth forests and their importance in the ecology of aquatic ecosystems needs to be studied. In many Victorian streams logs do provide shelter, orientation, spawning sites, and increased substrate diversity (Koehn and O'Connor 1990).

COMPOSITION OF SOUTH-EAST AUSTRALIA'S OLD-GROWTH FORESTS

That the faunal composition of old-growth forests differs from that of young forests is evident when the resident fauna of young, regenerating forest is compared to that of old-growth forest of the same type. The responses of mammals and birds to the successional changes in plant communities after a disturbance to a stand, for example, clearfelling in south-east Australian forests, have been well documented (Loyn 1980, 1985a; Recher *et al.* 1980; Kavanagh *et al.* 1985; Smith 1985a,b; Macfarlane 1988). Associated with the structural diversity of old-growth forest is an abundance of sites for nests and dens and an abundance of foraging substrates; such an abundance makes this habitat crucial for a distinctive group of forest vertebrates dependent on certain specialized resources. Such vertebrates are specialized species referred to as "forest-dependent" (Kikkawa 1968, 1974; Tyndale-Biscoe and Calaby 1975). Their specialized resource requirements and their often large home ranges and sometimes complex social organizations make them susceptible to the loss of resources brought about by intensive forest management (Recher *et al.* 1987). Their susceptibility is exacerbated by on-going fragmentation of old-growth forests, the overall lowering of forest age-classes and loss of "interior" forest habitat (Franklin and Forman 1987). These species differ from "generalist" species which occur in a broad variety of forest types and within a broad range of successional stages which coincide with the development of a stand of a particular type of forest (Gilmore 1990). Often the forest-dependent species are found only in wetter forest habitats (Kikkawa 1968, 1974) where resources are provided by particular age-classes of trees, namely the older age-classes on stands on sites of high nutrient status (Braithwaite *et al.* 1989; Gilmore 1990).

Tyndale-Biscoe and Calaby (1975) and Australian Biological Research Group (in Fergusen 1985) have identified those mammal and bird species of eucalypt forests that they regarded as sensitive to intensive forest management. Loyn (1985a), Howe (1986) and Recher *et al.* (1987) have identified several bird species whose numbers are largest within mature or old-growth forests of south-east and eastern Australia. A summary of these findings and a list of species that find optimum habitat in old-growth forest of different types are provided in Table 1.

The specialized resources required by these forest-dependent species includes food such as insects, foliage and nectar from particular plant species and substrates (Kavanagh 1984; Loyn 1980, 1985a; Pahl 1987; Braithwaite *et al.* 1989); home sites such as hollow trees and logs (Davey 1984; Henry 1984; Henry and Craig 1984; Mackowski 1984; Smith 1984; Lunney 1987; Lunney *et al.* 1988; Smith and Lindenmayer 1988; Lindenmayer 1989; Lindenmayer *et al.* 1990b); basking sites on large logs, stumps and stags (Brown and Nelson, unpubl. data).

Whether some species of vertebrate depend on old-growth for survival is unresolved and should be a prime focus for future research. There is even less data on the relationship between invertebrate species

Table 1. Vertebrate animals that find optimum habitat for foraging (F) or nesting (N) or both (FN) in old-growth Eucalyptus forests of southeastern Australia. Nomenclature used: Menkhorst (1987) for mammals; Royal Australasian Ornithologists Union (1978) for birds; Cogger (1986) for reptiles and amphibians.

Group	Common Name	Scientific Name	
Mammals	Tiger Quoll	*Dasyurus maculatus*	FN
	Tuan	*Phascogale tapoatafa*	N
	Yellow-bellied Glider	*Petaurus australis*	N
	Squirrel Glider	*Petaurus norfolcensis*	N
	Greater Glider	*Petauroides volans*	N
	Great Pipistrelle	*Falsistrellus tasmaniensis*	N
	Other forest bats		N
Birds	Glossy Black-Cockatoo	*Calyptorhynchus lathami*	N
	Yellow-tailed Black-Cockatoo	*Calyptorhynchus funereus*	N
	Gang-gang Cockatoo	*Callocephalon fimbriatum*	N
	Australian King-parrot	*Alisterus scapularis*	N
	Superb Parrot	*Polytelis swainsonii*	N
	Regent Parrot	*Polytelis anthopeplus*	N
	Powerful Owl	*Ninox strenua*	N
	Sooty Owl	*Tyto tenebricosa*	N
	Leaden Flycatcher	*Myiagra rubecula*	F
	Satin Flycatcher	*Myiagra cyanoleuca*	F
	Cicadabird	*Coracina tenuirostris*	F
	Varied Sitella	*Daphoenositta chrysoptera*	F
	Red-browed Treecreeper	*Climacteris erythrops*	FN
	Mistletoebird	*Dicaeum hirundinaceum*	F
	Lewin's Honeyeater	*Meliphaga lewinii*	F
	Regent Honeyeater	*Xanthomyza phrygia*	F
	Crescent Honeyeater	*Phylidonyris pyrrhoptera*	F
Reptiles	Diamond Python	*Morelia spilota spilota*	FN
	Carpet Python	*Morelia spilota variegata*	FN
	Tree Goanna	*Varanus varius*	FN
	Spencer's Skink	*Pseudemoia spenceri*	F
Amphibians	Southern Barred Frog	*Mixophyes balbus*	F
	Spotted Tree Frog	*Litoria spenceri*	F

and old-growth forests. Because old-growth has occupied vast areas for a long time complex ecological relationships involving many wildlife species and other organisms have probably evolved in old-growth forests (Forman and Godron 1986; Franklin and Forman 1987).

ECOLOGICAL FUNCTIONS OF OLD-GROWTH FORESTS

The main ecological functions of forest ecosystems include primary production; energy flow; conservation and cycling of nutrients; and regulation of water flow (Franklin *et al.* 1981).

Old-growth forests are productive ecosystems (Franklin *et al.* 1981; Franklin and Spies 1984) but ecologists and foresters generally measure forest productivity in different ways. Franklin and Spies (1984) see this difference as follows: "Ecologists define net primary production as the biomass increment plus mortality, including litterfall, and materials removed by grazing (and browsing). A forester's definition of productivity (wood increment) is, therefore, generally limited to only a portion of the ecologist's net productivity and comments on the low productivity of old-growth forests really refer to the relatively low levels of new wood production."

Total organic matter — living and dead — continues to increase in old-growth forests (Franklin and Spies 1984) mainly because coarse woody debris and particularly large logs accumulate (Franklin *et al.* 1981; Ashton 1986). Such an accumulation of dead matter is an important characteristic of old-growth forests and relates to the cycling of nutrients through a "closed cycle, detrital-based system" (Odum 1971). This system operates through the actions of micro-organisms and other organisms, such as plants,

fungi, and animals that derive nutrients from the micro-organisms (Maser *et al.* 1988). The release of energy and nutrients from dead materials is slow and in old-growth forests nutrients are therefore tightly retained within the system (Fredriksen *et al.* 1975).

The processes involved in the decomposition of large logs, the concentration of nutrients as logs decay, and the role of micro-organisms and large animals in the decomposition and concentration of nutrients have been reviewed by Maser *et al.* (1988). But I must highlight the importance of the process of recycling and fixation of nitrogen by old-growth forest ecosystems.

The balance of nitrogen availability is crucial in forest ecosystems (Adams and Attiwill 1984; Stewart *et al.* 1985; Sollins *et al.* 1987). Large logs in the forests of northwestern USA are sites of nitrogen fixation by free-living bacteria (Cornaby and Waide 1973; Silvester *et al.* 1982). Nitrogen fixation by this method may be relatively slow (1 kg ha^{-1} year^{-1}) in an old-growth Douglas-fir stand in northwestern USA relative to requirements of 40 kg ha^{-1} year^{-1} for the same stand; nevertheless it may be important in the overall nitrogen budget (Sollins *et al.* 1987). The role of large logs in the fixation of nitrogen in Australian forest ecosystems requires investigation, as does the importance of lichens inhabiting the trunks and canopies of the forest trees. In old-growth Douglas-fir forests, cyanophycophilous lichens fix about 10 kg of nitrogen per hectare each year, but are absent during the first 100–150 years of the forest's development (Sollins *et al.* 1987). This time lag may be important when site productivity of forests managed on short rotations is being assessed. In old-growth forests little nitrogen is lost through soil erosion and leaching and so relatively low rates of nitrogen fixation gradually accumulate nitrogen to appreciable amounts (Maser *et al.* 1988).

Large items of organic debris and fallen trees greatly influence the physical and biological characteristics of streams in old-growth forests (Sedell *et al.* 1988). Franklin *et al.* (1981) provided a concise summary of the functional role of logs in streams. This goes as follows: "Coarse woody debris is extremely important to streams in old-growth (coniferous) forests. Debris dams and associated plunge pools and trapped sediments, such as gravel bars, provide a great diversity of habitats for organisms. The resulting stepped stream profiles provide for greater physical and biological stability by dissipating energy otherwise used in cutting channels and moving sediment. Debris dams also slow the routing of other organic inputs, allowing organisms time to more fully process these materials before they are exported downstream. Finally, the woody debris is itself a major source of energy and nutrients for the stream ecosystem". The same principles probably apply to streams in south-east Australian old-growth forests and these may be important for water production and the conservation of aquatic fauna.

MANAGEMENT OF SOUTH-EAST AUSTRALIA'S OLD-GROWTH FORESTS

The main ecological differences between old-growth forests and intensively managed young-growth forests relate to the structure and ecological functions of old-growth forests, whose characteristics create the diverse range of habitats crucial to forest-dependent fauna.

Another vital difference is that old-growth forests have continued and will continue to decline because of the demand for timber products. The Victorian Government has guaranteed the timber industry access to timber resources in State forests by means of long-term (15-year) licences (Department of Conservation, Forests and Lands 1986). But the government has also pledged protection of remaining "ecologically mature forest" (Conservation Strategy for Victoria 1987).

The situation within the forest estates of the United States is similar. Thomas *et al.* (1988) have said that: "It is certain that there is an ongoing inexorable reduction in old-growth, and that chances of retaining viable populations of plants and animals in a well distributed state over the long term are reduced to some degree with each additional reduction in old-growth."

Probably the most crucial aspect of old-growth harvesting and its impact on forest-dependent fauna is the progression, over the rotation period, towards a highly fragmented landscape (Harris 1984; Franklin and Forman 1987).

Fragmentation of Habitat

Fragmentation includes a loss of "interior" forest habitat as patches of remaining old-growth forests decrease in size and "edge" habitat increases in size (Andren and Angelstam 1988; Robinson 1988; Thomas *et al.* 1988; Yahner 1988). These patches of old-growth may become so small and isolated that

their continued existence is threatened by microclimatic change (Franklin and Forman 1987), and by the lack of connectivity with similar patches (Harris 1984). Ultimately the patches may cease to function as habitat for fauna dependent on old-growth forest (Harris 1984).

The ecological consequences of the strategy of "dispersed coupes" or "checkerboard logging" have been investigated by Franklin and Forman (1987) who modelled the landscape patterns (patch size, edge length, and configuration) created by the use of such a strategy in North America. This same strategy of dispersing logging coupes is the one being used in Victoria's and New South Wales' State forests for which dispersed coupes are being promoted as a beneficial strategy for conservation of forest wildlife (Department of Conservation, Forests and Lands 1989). But recent overseas studies (e.g., Franklin and Forman 1987) indicate that this very strategy may accelerate fragmentation and degeneration of old-growth forest habitats and a decline in associated forest-dependent fauna early during the 80–100 year cutting cycle proposed by the Department of Conservation, Forests and Lands (1989) for the majority of Victoria's State forests, and early during the initial 40 year cutting cycle (Recher et al. 1980) underway in south-east New South Wales' State forests.

The benefits purported to be associated with this strategy include the promotion of edge effects as a benefit to wildlife, largely on the basis of greater species richness near the margins of stands (Hunter 1987). In reality these edge effects are usually of benefit to generalist wildlife species at the expense of forest-interior species (Robinson 1988; Yahner 1988; Gilmore 1990). As Harris (1984) suggested: "the ecological and economic appropriateness of this system (spreading logging coupes) should be re-examined as objectives and techniques change and the fragmentation of the forest landscape continues".

When the future of old-growth forest and the fauna dependent on its structure and function are considered it is important to also consider the context within which present old-growth forests occur and that within which remnants will occur as the current cutting cycles progress (Gilmore 1990). The value of a particular patch of old-growth depends not only on its structural characteristics (content), but also on the matrix within which it occurs (its context) (Harris 1984). One can imagine that a Victorian forest landscape in 80 years' time might consist of a mosaic of forest stands of 40–120 ha ranging in age from zero to 80 years of age. In Victoria the maximum allowable contiguous area logged over three seasons is three coupes of 40 ha each. The early stages of forest development will dominate the landscapes of managed forest (Thomas et al. 1988) and stands of trees older than the rotation age will be rare or absent, except in (i) areas excluded from harvesting because of steep slopes, stream protection, or landscape features; (ii) areas reserved for nature conservation (parks and reserves); (iii) areas dedicated to conserving old-growth forests. But steep and rocky areas excluded from harvesting generally support fewer wildlife than do areas of less severe topography (Lunney and Leary 1988; Lindenmayer 1989; Lindenmayer et al. 1990a) and narrow streamside reserves designed to protect water quality provide little useable habitat for forest-interior species of wildlife (Recher et al. 1987). National Parks and reserves, if not connected to similar areas, will not maintain the distribution of fauna and flora throughout their ranges or the processes of evolutionary development (Recher 1985). Old-growth forest "islands" will be degraded by edge effects and isolation (Harris 1984; Recher et al. 1987; Yahner 1988).

Such detrimental effects could be ameliorated by (i) perpetuating existing stands of old-growth forest, (ii) recreating forest ecosystems with old-growth characteristics by long-rotation "islands", and (iii) providing individual features of old-growth forest to be retained within managed stands (Franklin et al. 1984). The same three strategies have previously been proposed for the forests of southeastern Australia by Loyn (1985b). Franklin and Forman (1987) have suggested a reduction in emphasis on dispersing small clear-felling coupes throughout the forest landscape as a way of reducing the effects of intensive management. They favour an approach featuring progressive or clustered coupes from scattered nuclei as a cutting strategy to reduce fragmentation of old-growth, disturbance associated with edges, and number of maintained roads. Another strategy proposed as a way of reducing fragmentation of the remnant habitats is that of retaining or regenerating corridors of habitat for wildlife (Harris 1984; Fahrig and Merriam 1985; Noss 1987).

Consolidating these strategies into a Regional System of Retained Habitat (RSRH) (Bennett 1990) appears to offer the best prospect for the conservation of forest-dependent faunas throughout their present ranges in the face of continued intensive management of State forests.

Regional Systems of Retained Habitat

I suggest that the focus of RSRHs should revolve around the maintenance of viable old-growth forest ecosystems because old-growth forest appears to provide the highest levels of resources essential to many forest-dependent wildlife. The most appropriate way to design an RSRH will be to focus on the conservation of a subset of forest-interior species, because such a subset of wildlife is the most susceptible to changes brought about by intensive forest management (Robinson 1988; Davey and Norton 1990). Generalist wildlife species will probably survive with or without management due to their broad ecological requirements. Yet, generalist species are favoured when edge habitats are created for management of species diversity (Robinson 1988). A more appropriate strategy, in forested land-scapes at least, is to manage for rare, specialized species selected as "habitat indicators". Managing for species most dependent on old-growth, as carried out for the Spotted Owl in USA (Guttierrez and Carey 1985), should help guarantee the continued existence of all species for which old-growth of that forest type provides optimal habitat (Robinson 1988). In southeastern Australia the conserva-tion of the Sooty Owl, Tiger Quoll, or Yellow-bellied Glider, which are three sensitive and specialized forest species, could well ensure the conservation of other species dependent on the same old-growth habitats.

As forecast by the Society of American Foresters (1984), "The ecological complexity of old-growth stands makes it unlikely that forest managers can create functional old-growth through silvicultural manipu-lation of younger-aged second growth forests". The management of viable networks of old-growth forest by means of RSRHs therefore relies, at least initially, on existing old-growth (Thomas *et al.* 1988). However, in some areas old-growth may be insufficient to meet ecological needs. In addition, old-growth will not last forever. Destructive natural events such as wildfire will in all probability convert existing old-growth into younger-aged, unmanaged forest. Such natural events are inevitable in the long term (Harris 1984); there-fore, some younger-aged stands must be allowed to become old-growth stands. Such younger-age stands should be selected to maximize their value to the old-growth network being planned. Where no old-growth forests exist, younger-age stands will assume prime importance as future reservoirs of forest-interior wildlife. Where old-growth forests do exist these younger-age stands may serve as nodes of forest managed on an extremely long rotation; such nodes could be connected by corridors of similarly retained forest to otherwise separated patches of reserved existing old-growth forest (Harris 1984; Recher *et al.* 1987). How large a stand of old-growth forest need be to remain a viable ecosystem unit within the RSRH is a question for future research. The concept of edge is important in this consideration because the width of an edge will vary with forest type, the context of the stand, and the wildlife species being considered. A small reptile's perception of the edge induced by disturbance adjacent to a stand of old-growth forest will be different to that of a wide-ranging species.

Another component of the forest RSRH is the management of individual logged stands to maintain some of the attributes of old-growth forest. This component of the RSRH brings management to a finer scale so that the identified structural attributes of old-growth forest, namely large, live old-growth trees, stags and logs, are preserved to some extent on logging coupes. These structural attributes may maintain some continuity of habitat features within these intensively managed stands and possibly encourage re-colonization from unlogged forests. These structural attributes serve not only the important function of providing habitat for wildlife, they are also important in the cycling and conservation of nutrients in forest stands (Franklin *et al.* 1981). Policies and guidelines addressing the retention of large, living trees, stags and logs on coupes are needed. Re-establishment of pre-logging faunal assemblages on logged stands requires that the dynamics of tree ontogeny be taken into account. Not only must existing old-growth trees, stags and logs be retained on logging coupes, but they must also be replaced over time by the retention of younger age-classes of living trees (Lindenmayer 1989; Davey and Norton 1990; Lindenmayer *et al.* 1990a,c). The number of living trees, stags and logs to be retained could depend on the wildlife species reliant on these resources, and on the populations considered desirable to support. The species and the population will vary with forest type.

Linking the components of RSRHs into a viable ecosystem capable of preserving fauna dependent on old-growth is the function of habitat corridors which have been proposed as a management strategy (MacClintock *et al.* 1977) for preserving biotic diversity in managed landscapes.

Habitat Corridors

The concept of habitat corridors for wildlife has been embraced by many researchers including Forman and Godron (1981), Harris (1984), Fahrig and Merriam (1985), Bennett (1987), Noss (1987), and Recher et al. (1987), all of whom have considered wildlife corridors as a way of linking remnant habitats within different landscapes. By so doing these corridors are said to maintain genetic interchange between otherwise isolated populations, increase or maintain immigration rates, provide increased foraging area for wide-ranging species and act as alternative refuges from large-scale disturbances (Noss 1987). Recher et al. (1987) have provided information on use of habitat corridors and suggestions as to the dimensions of corridors required to cater for the needs of fauna such as the Yellow-bellied Glider. Bennett (1990) has reviewed the role played by corridors in linking habitats but much work remains to be done to investigate the applicability of corridor systems in providing the values suggested and in determining the appropriate widths and lengths of corridors in different forest types. To fulfil the role of linking old-growth habitats, wildlife habitat corridors will themselves be ideally composed of old-growth forest. They will need to be wide enough to act as habitat in their own right to facilitate the gradual movement of genetic information across the landscape and so reduce the effects of habitat fragmentation.

When managers and planners undertake the implementation of an RSRH to maintain viable old-growth ecosystems, the dynamic nature of the forest must be considered. Wildlife habitat corridors and long rotation "islands" (see Harris 1984) do not necessarily mean the "locking up" of the resources within them. The planning horizon should be several hundred years or the lifetime of the trees in the forest being logged (A. Gilmore, pers. comm.). If new wildlife habitat corridors and long-rotation "islands" of similar ecological character can be provided as replacements for the initially designated components of the RSRH, there is no reason why these areas cannot be harvested at the appropriate time. But the integrity of the old-growth forest ecosystem must be retained if the aim of its preservation is to be achieved.

Maintaining the Integrity of Old-growth Forests

Thomas et al. (1988) noted that: "Plans for old-growth management must be based on existing management options and knowledge of the ecological system in question." They described three types of essential information: "(i) biological requirements and ecological relationships of associated plants and animals; (ii) amounts, kinds, sizes and arrangements of old-growth environments required to meet general ecological needs and to ensure the continued existence of associated wildlife; and (iii) sizes of old-growth patches required to ensure long-term stability of old-growth as an ecological unit." I suggest that to wait for research to indicate the most appropriate action required is unwarranted. In the past, land managers have not waited to discover the consequences of cutting forests at rates needed to meet demand for timber products. In the USA, harvesting has not been set at scientifically determined rates designed to ensure the maintenance of ecological systems, but largely on considerations such as the traditional timber harvest, the capacity of sawmills, and economic factors (Thomas et al. 1988). The same is equally true in Australia (Norton 1986), and only in recent years have moves been made to lower production to perceived sustainable levels (e.g., Fergusen 1985). Current public demand and government policy present professional biologists with a clear mandate to provide managers such information that will ensure the conservation of viable old-growth forest ecosystems and all their associated and dependent biota. Again quoting Thomas et al. (1988): "The lack of quantitative information about functional attributes of old-growth and habitat association of potentially dependent plants and animals and the rapidly declining old-growth resource indicate that purposely conservative management plans should be developed and implemented."

I suggest that if the management of old-growth forests is to be undertaken seriously then the adoption of strategies that provide minimum areas of habitat to sustain minimum viable populations of old-growth dependent species is inappropriate because if the assessments of minimum requirements are wrong the opportunity to safeguard this ecosystem will be lost.

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