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MISTLETOE—A KEYSTONE RESOURCE IN FORESTS AND WOODLANDS WORLDWIDE

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■ **Abstract** Mistletoes are a diverse group of parasitic plants with a worldwide distribution. The hemiparasitic growth form is critical to understanding their biology, buffering variation in resource availability that constrains the distribution and growth of most plants. This is manifested in many aspects of mistletoe life history, including extended phenologies, abundant and high-quality fruits and nectar, and few chemical or structural defenses. Most mistletoe species rely on animals for both pollination and fruit dispersal, and this leads to a broad range of mistletoe-animal interactions. In this review, I summarize research on mistletoe biology and synthesize results from studies of mistletoe-animal interactions. I consolidate records of mistletoe-vertebrate interactions, incorporating species from 97 vertebrate families recorded as consuming mistletoe and from 50 using mistletoe as nesting sites. There is widespread support for regarding mistletoe as a keystone resource, and all quantitative data are consistent with mistletoe functioning as a determinant of alpha diversity. Manipulative experiments are highlighted as a key priority, and six explicit predictions are provided to guide future experimental research.

> *The facts which kept me longest scientifically orthodox are those of adaptation—the pollen-masses in Asclepias—the misseltoe, with its pollen carried by insects and seed by Birds—the woodpecker, with its feet and tail, beak and tongue, to climb the tree and secure insects. To talk of climate or Lamarckian habit producing such adaptation to other organic beings is futile. This difficulty, I believe I have surmounted.*
>
> From a letter to Asa Gray by Charles Darwin, 1857.

INTRODUCTION AND SCOPE

Interactions between mistletoes and animals have long been noted and were used by Darwin as early exemplars of evolutionary adaptation (Burkhardt & Smith 1990, p. 445). Linné is credited as the first to describe mistletoe life history (Landell 1998), noting that thrushes ate the berries and expelled the sticky seeds upon

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subsequent perches. Pliny recorded similar observations some 1600 years earlier (Pliny & Rackham 1960). Indeed, most species of mistletoe are dispersed by animals, chiefly birds (Calder 1983, Hawksworth 1983, Kuijt 1969, Reid 1986, Reid 1991, Snow & Snow 1988); and this close relationship has been treated as a model system in the study of fruit dispersal generally (Howe & Estabrook 1977, Howe & Smallwood 1982, Herrera 1985a,b, McKey 1975, Snow 1971, Wheelwright 1988). The various reviews of avian use of mistletoe are limited either to particular regions—India (Davidar 1978, 1985), North America (Hawksworth & Geils 1996, Stoner 1932), Australia (Reid 1986, Turner 1991), Latin America (Restrepo 1987, Sargent 1994, Skutch 1980)—or concerned solely with frugivory (Reid 1991, Snow & Snow 1988). As Darwin noted (see Burkhardt & Smith 1990), mistletoes are also pollinated by animals (mainly birds and insects; Davidar 1985, Ford et al. 1979, Penfield et al. 1976, Reid 1986, Whittaker 1984), but this aspect of their life history has received markedly less attention than fruit dispersal. Indeed, the majority of records of mistletoe-animal interactions have been incidental; a wealth of anecdotal information is contained in species-specific accounts, autecological studies, and works of natural history. Drawing on these highly dispersed data is challenging, and although similar compendia exist for other plant groups (e.g., lichens, Sharnoff & Rosentreter 1998; palms, Zona & Henderson 1989), the breadth of mistletoe-animal interactions worldwide has not been documented nor fully appreciated.

I begin with an introduction to mistletoes, summarize diversity and distribution patterns, and combine these accounts with information about life history, phenology, pollination, and dispersal syndromes. Drawing on the extensive autecological and natural history literature, I then consolidate known interactions between mistletoe and vertebrates worldwide. I propose that mistletoes function as keystone resources in forests and woodlands of many regions, providing important resources for a broad range of taxa and determining local diversities in these habitats. After evaluating this hypothesis with available data, I identify gaps in our knowledge and make explicit predictions to guide future research.

Incorporating all mistletoe-animal interactions, however, would greatly exceed the scope of this review. Therefore, I restrict my focus to vertebrates, although I recognize that this does not correspond with the breadth of known interactions. Many insects pollinate mistletoes (primarily in the Coleoptera, Diptera, Hymenoptera, and Lepidoptera; Hawksworth & Wiens 1996, Whittaker 1984); more than 200 insect species are documented pollinating a single mistletoe species (Penfield et al. 1976). Many species within the Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Orthoptera, and Thysanoptera feed on mistletoe, and all orders contain mistletoe-obligate species (de Baar 1985, Hawksworth & Wiens 1996, Mushtaque & Baloch 1979, Whittaker 1984). Other than lists of species known to associate with mistletoes, there has been relatively little research on mistletoe-insect interactions (Whittaker 1984) and no comparative or synthetic studies. Indeed, compared with that on vertebrates, the literature is far from complete and any review of the subject would be premature. Mistletoe-vertebrate interactions clearly are only a partial indication of the role mistletoes play in forested ecosystems, and understanding the extent and nature of mistletoe-insect interactions represents a major challenge for future research.

MISTLETOE—AN OVERVIEW

Composition and Distribution

Mistletoes are a polyphyletic group of flowering plants comprising over 1300 species from a broad range of habitats across all continents except Antarctica (Calder 1983, Calder & Bernhardt 1983, Kuijt 1969, Watson & Dallwitz 1992, Nickrent 2001). They share a common growth form—obligate hemiparasitism—such that all water and minerals are obtained from their host via a specialized vascular attachment (Ehleringer & Marshall 1995, Lamont 1983b, 1985, Pate 1995). The group contains members of five families within the Santales (Kuijt 1968, 1969, Nickrent & Soltis 1995), and the aerial parasitic life-form is thought to have evolved independently four or five times (Nickrent & Franchina 1990, Nickrent et al. 1998, Nickrent 2001, Figure 1). Thus, the term mistletoe does not refer to a lineage of plants, but a functional group (like mangroves), and will be used hereafter to denote all hemiparasitic species within the Santales. Two of the constituent families—the poorly known Misodendronaceae and Eremolepidaceae—are restricted to neotropical forests, while the aerial parasitic genera within the paraphyletic Santalaceae are known from tropical forests in Latin America and Southeast Asia (Kuijt 1968, 1969, Watson & Dallwitz 1992). In contrast, the Loranthaceae and Viscaceae are well studied and distributed worldwide, comprising the majority (>98%) of mistletoe species: approximately 940 and 350 species, respectively (Watson & Dallwitz 1992, Nickrent 2001). These families are not sister taxa, and their aerial parasitic growth-form is thought to have evolved independently (Calder 1983, Kuijt 1969, Nickrent et al. 1998, Nickrent 2001, Figure 1). Based on fossils from the Cretaceous period, and the occurrence of relictual genera in Australia, New Zealand, and South America (Barlow 1983, Kuijt 1969), Loranthaceae is considered a Gondwanan lineage that subsequently dispersed to Africa, Europe, and North America (Barlow 1983, Polhill & Wiens 1998, Raven & Axelrod 1974). Conversely, Viscaceae is thought to have originated in eastern Asia, radiating through Laurasia in the early Tertiary period, secondarily dispersing to the southern continents (Barlow 1983, Raven & Axelrod 1974).

The Loranthaceae and Viscaceae are presently distributed widely throughout Europe, the Americas, Africa, Asia, and Australasia (except Tasmania), ranging from boreal climates to temperate, tropical, and arid zones, and absent only from extremely dry or cold regions (Barlow 1983, Kuijt 1969, Raven & Axelrod 1974). They are also well represented on oceanic islands, with the Azores, Madagascar, Aldabra, Comoros Islands, Mascarene Islands, Galapagos Islands, Hawaiian Islands, New Caledonia, Lord Howe Island, Norfolk Island, New Zealand, Fijian Islands, Henderson Island, Greater and Lesser Antilles, and Hispaniola all having

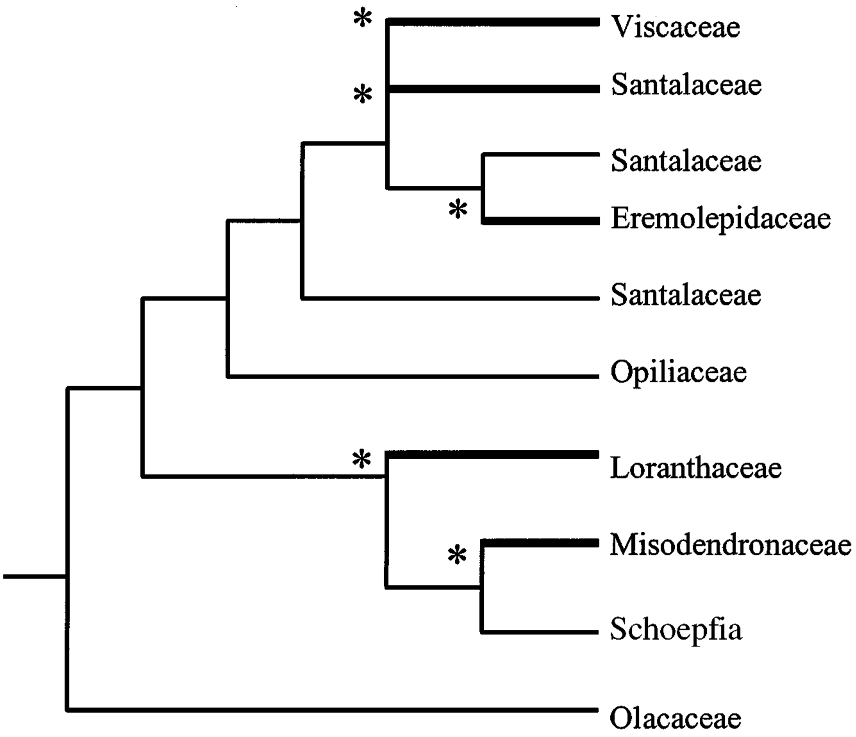

Figure 1 Consensus tree for the Santales based on data from nuclear 18S rDNA and chloroplast *rbcL* sequences (modified from Nickrent; 2001). Branches with thick lines indicate mistletoe taxa, and asterisks indicate hypothesized independent evolutionary origins of the aerial hemiparasitic habit.

representative (and principally endemic) species (Barlow 1983, Hawksworth & Wiens 1996, Kuijt 1969, Polhill & Wiens 1998). Although mistletoes are typically considered forest plants, they parasitize a wide range of hosts—coniferous trees in boreal forests (Hawksworth 1983, Hawksworth & Wiens 1996), succulent euphorbs and cacti in the deserts of Africa and Latin America (Martinez et al. 1996, Polhill & Wiens 1998), grasses and annual herbs in Australian coastal heathlands (Fineran & Hocking 1983), even orchids and ferns in Mesoamerican cloud forests (Kuijt & Mulder 1985). Most species, however, selectively parasitize trees and shrubs, and the greatest diversities of mistletoes are associated with forests and woodlands (Calder 1983, Hawksworth 1983, Kuijt 1969).

Life History and Phenology

Mistletoes are characterized by their growth habit and, excepting several root-parasitic species (Kuijt 1969, Fineran & Hocking 1983), they typically form dense clumps in the crowns of their hosts (Figures 2*a* and *c*). These clumps are generally composed of semisucculent mistletoe stems and leaves (Figures 2*a* and *b*), but for dwarf mistletoes (Viscaceae, *Arceuthobium* spp.), the resultant clump (termed a witch's broom) is actually the host tree's response to infection composed of thickened and twisted branches (Hawksworth & Wiens 1996, Schaffer et al. 1983; Figures 2*c* and *d*). Although mistletoe plants are frequently regarded as detrimental to tree health (Coleman 1949, Hawksworth 1983, Heather & Griffin 1978, Reid et al. 1994), this is not necessarily the case (Reid & Lange 1988, Reid et al. 1992, Sterba et al. 1993). Mistletoe plants have low annual survivorship (Musselman & Press 1995), with estimates of 19% and 31% for two Australian species (Reid & Lange 1988), and are considered "low-grade *K*-selected forest parasites" (Andrews & Rouse 1982). Many species are sensitive to fire (Rowe 1983, Hawksworth & Wiens 1996, Kipfmueller & Baker 1998) and frost (Hudler & French 1976, Smith & Wass 1979); these factors are cited as limiting the distribution of mistletoe in some areas (Hawksworth 1969, Hawksworth & Wiens 1996, Spooner 1983). Mistletoe seeds require high light levels for germination, establishment, and subsequent maturation (Knutson 1983, Lamont 1982, 1983a, Polhill & Wiens 1998), and they are frequently shaded out as the host canopy develops (Lamont 1982, Richards 1952). Thus, despite high rates of dispersal and successful germination, establishment is rare, and all mistletoe species studied have narrow microsite tolerances (Hawksworth & Wiens 1996, Knutson 1983, Lamont 1982, 1983a, Overton 1994, Sargent 1994, 1995, Yan & Reid 1995).

Mistletoes obtain all of their water and minerals from the host through a vascular connection termed a haustorium (Calder 1983, Press & Graves 1995; Figure 2*b*). This swollen holdfast serves both to attach the mistletoe plant to the host and to divert water and minerals to the parasite. The term hemiparasitic is used because most mistletoes photosynthesize, although they may obtain up to 60% of their carbohydrates from the host (Hull & Leonard 1964, Lamont 1983b). The consequence of this growth-form is that mistletoes are less affected by the edaphic, hydrological, and nutritional factors that limit the distribution, growth, and phenology of most plants; the host plant buffers the parasite against large-scale fluctuations in resource availability (Ehleringer & Marshall 1995).

Restrepo's (1987) research in Colombian cloud forests revealed that five mistletoe species had continuous fruiting seasons with a generalized peak during the wet season. Flowering seasons were similarly continuous, with nectar and fruit resources available year-round. Data from elsewhere in the Neotropics fit the same pattern, flowering and fruiting seasons ranging from 10 to 12 months (Feinsinger 1978, Leck 1972, Sargent 1994, Skutch 1980, Stiles 1985) with a pronounced wet-season peak. Mistletoes in southern Africa also have prolonged fruiting seasons, ranging from three months to year-round (Godschalk 1983a, Polhill & Wiens 1998), while those in Burkhina Faso exhibit staggered fruiting patterns throughout the year (Boussim 1991). Dwarf mistletoes in the Palearctic have more limited flowering and fruiting seasons, lasting from 4 to 6 months; flowering typically peaks in early to mid autumn, with peak fruiting in late autumn to early winter (Hawksworth & Wiens 1996). Davidar (1983) recorded phenologies for six mistletoe species in southern India, with flowering ranging from 3 to 9 months and fruiting seasons of from 4 to 7 months. These species displayed complementary peaks in fruit and nectar availability such that nectar and fruit were available from at least two species at any time. Reid (1986) summarized phenologies of 13 Australian loranthaceous species and demonstrated that the flowering season for several species extended throughout the year, with different patterns associated with regional climates. A pronounced summer peak in wetter areas graded into a winter peak in drier areas, corresponding to seasons when little nectar is available from other sources. Fruiting was similarly widespread throughout the year, and Reid (1986) noted that there was always nectar and fruit available from at least one mistletoe species within a region.

Fruit Dispersal and Pollination

Although several lineages of mistletoe (notably within the Viscaceae) use hydrostatic explosion to disperse seeds, birds play a subsequent role in long-distance dispersal (Hawksworth & Geils 1996) and mistletoes generally are regarded as bird-dispersed (Calder 1983, Hawksworth 1983, Kuijt 1969, Reid 1986). A recent evaluation of New World mistletoes (Restrepo et al, in press) suggests that vertebrate dispersers may have played a key role in the diversification of mistletoes—those lineages dispersed by vertebrates having higher diversities. Most studies of mistletoe dispersal have focused on a small number of highly specialized birds (Reid 1989, 1990, Sargent 1994, Snow & Snow 1984, Walsberg 1977). This research has involved documenting the pattern (Godschalk 1983, Liddy 1983, Snow & Snow 1988), assessing the physiological, anatomical, and behavioral traits associated with obligate frugivory (Reid 1989, Richardson & Wooller 1988, Snow & Snow 1984, Walsberg 1975), and evaluating the coevolutionary potential of such interactions (Reid 1987, 1991, Restrepo et al, in press; Snow 1971).

The fruits of many mistletoe species show a range of attributes consistent with ornithochory: large, sweet, conspicuous in color when ripe, with small peduncles or borne directly on the branch. Fruit pulp compositions vary, but most have high fractions of soluble carbohydrates, typically from 40% to 60% dry weight (Godschalk 1983b, Lamont 1983b, Restrepo 1987) but as high as 74% (Snow & Snow 1988). Fruits of some loranthaceous species are high in lipids (up to 35% dry mass; Godschalk 1983b, Restrepo 1987), with fruits of *Loranthus europaeus* containing droplets of pure fat (Chiarlo & Cajelli 1965). Fruits of viscaceous species tend to have much higher fractions of protein than other fruits (Wheelright et al. 1984)—an average of 22% in three species of *Phoradendron* (Restrepo 1987)—comprising up to 18 free amino acids (Chiarlo & Cajelli 1965, Godschalk 1983b). Indeed, detailed biochemical analyses of mistletoe fruits have identified all 10 essential amino acids as originally defined by Rose and coworkers (Rose et al. 1948, Womack & Rose 1947), especially arginine, lysine, and phenylalanine (Bushueva et al. 1990, Chiarlo & Cajelli 1965, Godshalk 1983b). As with other mistletoe tissues, fruits also contain high concentrations of minerals (notably P and K) and micronutrients (e.g., Mn and Fe) (Lamont 1983b, Pate 1995). Despite the poisonous reputation of mistletoe, toxins have been isolated from only a small number of species within the Viscaceae, and toxicity is rare within mistletoes generally (Barlow & Wiens 1977, Bushueva et al. 1990). Many mistletoe species display discontinuous ripening such that individual plants have ripe fruits available throughout the fruiting season, with the timing of peak-fruiting varying between individual plants and separate populations (Reid 1986, Restrepo 1987). Combining this within-species variation with the between-species complementarity noted earlier, fruit (and floral) resources are often available year-round within a given region (Boussim 1991, Davidar 1983, Polhill & Wiens 1998, Reid 1986)

Whereas most species of mistletoe are pollinated by birds, members of the Viscaceae are pollinated primarily by wind and insects (Hawksworth & Wiens 1996, Kuijt 1969, Polhill & Wiens 1998, Whittaker 1984). Whether anemophily or entomophily is the prime means of pollen transfer remains controversial, with many species displaying a mosaic of features that variously favors the two agents, and most species-specific studies have implicated both (Hawksworth & Wiens 1996, Penfield et al. 1976). The more speciose Loranthaceae are pollinated primarily by birds (Calder 1983, Davidar 1985, Kuijt 1969, Ladley et al. 1997, Reid 1986, Robertson et al. 1999) and display the typical suite of characteristics associated with ornithophilous pollination—large odorless flowers that are typically brightly colored (yellow, orange, red) with robust corollas, short pedicels, and often in massed inflorescences (Reid 1986, Watson & Dallwitz 1992; see Figure 2*b*). Nectar secretions are typically abundant and rich in sugars—glucose, sucrose, and especially fructose (up to 60% total sugar content; Baker et al. 1998, Reid 1986, Stiles & Freeman 1993). Unlike fruit dispersers, no species (of bird, insect, or other group) is known to be wholly dependent on mistletoe nectar as a primary food source (Davidar 1983, 1985, Reid 1986). Rather, a wide range of species pollinates mistletoes, some of which may depend on the nectar during particular seasons (Davidar 1985, Feinsinger 1978, Ford et al. 1979, Ladley et al. 1997, Stiles 1985, Robertson et al. 1999, Watson 1997).

MISTLETOE-VERTEBRATE INTERACTIONS

Mistletoe as a Food Source

The importance of mistletoe as a food source was assessed for all birds and mammals, with information on other groups included incidentally. I systematically surveyed dietary information in handbooks, species accounts, and autecological studies for records of species consuming mistletoe nectar, flowers, fruit, seeds, or foliage. I restricted this review to the family level, indicating the recorded frequency of mistletoe consumption within the family and providing a species exemplar (Table 1). Whereas few families are likely to have been neglected, this summary is

TABLE 1 List of families recorded feeding on mistletoe

Family	Feeding	Frequency	Species exemplar	Citation
Characinidae	F	R	*Triportheus angulatus*	Goulding 1980
Casuariidae	F	R	*Casuarius casuarius*	Bentrupperbaumer 1997
Dromaiidae	F	—	*Dromaius novaehollandiae*	Berney 1907
Tinamidae	L	R	*Eudromia elegans*	Bohl 1970
Columbidae	F	S	*Columba flavirostris*	Skutch 1983
Cacatuidae	F	S	*Callocephalon fimbriatum*	Coleman 1949
Psittacidae	F, Fl	S	*Pionopsitta haematotis*	Eitnier et al. 1994
Loriidae	N	S	*Glosopsitta porphyrocephala*	Paton & Ford 1977
Musophagidae	F	V	*Tauraco corythaix*	Godschalk 1986
Cuculidae	F	S	*Scythrops novaehollandiae*	Lord 1956
Cracidae	F	R	*Ortalis vetula*	Lopez de Buen & Ornelas 1999
Tetraonidae	F, L	S	*Bonasa umbellus*	Skinner 1928
Odontophoridae	F	S	*Callipepla gambelii*	Rosenberg et al. 1991
Phasianidae	F, L	S	*Lophura leucomelana*	Ali & Ripley 1978
Trochilidae	N	C	*Heliodaxa jacula*	Stiles 1985
Coliidae	F	V	*Colius indicus*	Godschalk 1986
Trogonidae	F	R	*Trogon violaceus*	Dickey & van Rossem 1978
Bucerotidae	F	R	*Anthracoceros malayanus*	McConkey 1999
Ramphastidae	F	S	*Semnornis frantzii*	Sargent 1994
Lybiidae	F	C	*Pogoniulus bilineatus*	Van Someren 1956
Indicatoridae	F, I	S	*Prodotiscus zambesiae*	Fry et al. 1988
Picidae	F	C	*Colaptes auratus*	Rosenberg et al. 1991
Eurylaimidae	F, N	R	*Philepitta castanea*	Prum & Razafindratsita 1997
Tyrannidae	F, I	C	*Tyranniscus vilissimus*	Leck 1972
Cotingidae	F	C	*Phibalura flavirostris*	Snow 1982
Oxyruncidae	F	—	*Oxyruncus cristatus*	Nadkarni & Matelson 1989
Pipridae	F	S	*Manacus vitellinus*	Leck 1972
Pardalotidae	N, I	S	*Acanthiza uropygialis*	Reid 1986
Meliphagidae	F, N, I	C	*Grantiella picta*	Reid 1986
Pachycephalidae	F, N, I	S	*Mohoua ochrocephala*	O’Donnell & Dilks 1989
Vireonidae	F	S	*Vireo olivaceus*	Leck 1972
Oriolidae	F	R	*Oriolus sagittatus*	Liddy 1982
Artamidae	N	S	*Artamus superciliosus*	Barker & Vestjens 1990
Cracticidae	F	S	*Strepera graculina*	Reid 1986
Ptilonorhynchidae	F	C	*Chlamydera nuchalis*	Barker & Vestjens 1990
Corvidae	F	S	*Perisoreus canadensis*	Punter & Gilbert 1989
Paridae	F, S, I	C	*Parus caeruleus*	Heine de Balsac & Mayaud 1930
Remizidae	F	R	*Auriparus flaviceps*	Restrepo et al., unpublished data
Aegithalidae	F	R	*Psaltriparus minimus*	Sutton 1951
Sittidae	F	R	*Sitta canadensis*	Punter & Gilbert 1989
Certhiidae	F	R	*Certhia americana*	Punter & Gilbert 1989

TABLE 1 (*Continued*)

Family	Feeding	Frequency	Species exemplar	Citation
Troglodytidae	F	R	*Campylorhynchus brunneicapillus*	Austin 1970
Campephagidae	F	R	*Lalage leucomela*	Crome 1978
Pycnonotidae	F	S	*Pycnonotus capensis*	Godschalk 1986
Chloropseidae	N	S	*Chloropsis aurifrons*	Ali & Ripley 1996
Sylviidae	F, I	R	*Sylvia atricapilla*	Hein de Balsac 1930
Turdidae	F	C	*Sialia mexicanus*	Rosenberg et al. 1991
Timaliidae	N, F	S	*Turdoides squamiceps*	Cramp & Perrins 1993
Dicaeidae	F, N, I	V	*Dicaeum cruentatum*	Ali & Ripley 1999
Melanocharitidae	N	S	*Toxorhamphus poliopterus*	Mack & Wright 1996
Nectariniidae	N, I	C	*Nectarinia lotenia*	Ali & Ripley 1999
Zosteropidae	F	S	*Zosterops lateralis*	Barker & Vestjens 1990
Mimidae	F	C	*Mimus polyglottos*	Rosenberg et al. 1991
Sturnidae	F	S	*Cinnyricinclus leucogaster*	Godschalk 1986
Prunellidae	F	R	*Prunella collaris*	Cramp 1988
Bombycillidae	F	C	*Bombycilla cedrorum*	Rosenberg et al. 1991
Ptilogonatidae	F, N	V	*Ptilogonys cinereus*	Sutton 1951
Parulidae	F, I	S	*Dendroica petechia*	Ostry & Nichols 1979
Thraupidae	F, N	V	*Euphonia lauta*	Sutton 1951
Coerebidae	F, N	—	*Coereba flaveola*	Snow & Snow 1971
Emberizidae	F	S	*Junco hymenalis*	Punter & Gilbert 1989
Cardinalidae	F	S	*Pheucticus melanocephalus*	Marshall 1957
Icteridae	N	S	*Icterus bullockii*	Howell 1972
Fringillidae	F	S	*Carpodacus mexicanus*	Weathers 1983
Passeridae	F	R	*Passer montanus*	Cramp & Perrins 1994
Ploceidae	F	R	*Malimbus rubriceps*	Godschalk 1986
Estreldidae	F	R	*Lonchura punctulata*	Alam & Rahman 1988
Microbiotheriidae	F	—	*Dromiciops australis*	Amico & Aizen 2000
Phascolarctidae	L	—	*Phascolarctos cinereus*	H.E. Young, unpublished data
Phalangeridae	L, Fl	S	*Ailurops ursinus*	Dwiyarheni et al. 1999
Pseudocheiridae	L, Fl	S	*Pseudocheirus peregrinus*	Choate et al. 1987
Petauridae	Fl	S	*Petaurus australis*	Reid 1986
Pteropodidae	F	S	*Rousettus aegyptiacus*	Herzig-Streschil & Robinson 1978
Lemuridae	F, Fl, N	C	*Eulemur fulvus*	Overdorff 1993
Indriidae	L, F	C	*Propithecus diadema*	Hemmingway 1998
Cebidae	L, F	S	*Alouatta palliata*	Stoner 1996
Callitrichidae	F	C	*Saguinus fuscicollis*	Soini 1987
Cercopithecidae	L, Fl	C	*Cercopithecus aethiops*	Kavanagh 1978
Hylobatidae	L, Fl	R	*Hylobates mulleri* x *agilis*	McConkey 1999
Pongidae	L	C	*Gorilla gorilla*	Goodall 1977

(*Continued*)

TABLE 1 (*Continued*)

Family	Feeding	Frequency	Species exemplar	Citation
Hominidae	F, L	—	*Homo sapiens*	Morgan 1981
Procyonidae	F	S	*Bassariscus astutus*	Taylor 1954
Mustelidae	F	S	*Martes americana*	Nichols et al. 1984
Elephantidae	W	R	*Loxodonta africana*	Bax 1963
Equidae	L	S	*Equus asinus*	Fowler de Neira & Johnson 1985
Rhinocerotidae	W	R	*Diceros bicornis*	Goddard 1968
Suidae	L	R	*Sus scrofa*	Knott 1908
Camellidae	L	R	*Camellus camellus*	Morgan 1981
Giraffidae	L	R	*Giraffa camelopardalis*	Wiens 1978
Cervidae	W	C	*Oedocoileus hemionus*	Riney 1951
Antilocapridae	L	—	*Antilocapra americana*	Russel 1964
Bovidae	L	S	*Ovis canadensis*	Halloran & Crandell 1953
Sciuridae	F, S	S	*Tamiasciurus hudsonicus*	Nichols et al. 1984
Heteromyidae	F, S	S	*Perognathus parvus*	Burt 1934
Muridae	F, S, L	S	*Neotoma stephensi*	Vaughan 1982
Anomaluridae	F	R	*Anomalurus derbianus*	Kingdon 1974
Erethizontidae	W	R	*Erethizon epixanthum*	Taylor 1935

In the feeding mode column, F = fruit, Fl = flower, N = nectar, S = seed, W = whole plant, and I = insects on mistletoe. In terms of frequency, R denotes rare within the family, S denotes several records, C denotes common in family, V is very common and — is for monotypic families.

only as complete as the available dietary information. Such data are patchy, with the diets of species from some areas (e.g., Australia, North America, Europe) very well described compared with other regions (notably southeast Asia, Africa, and Latin America). In addition to regional variation, there is a taxonomic bias, with the diets of some groups (e.g., primates, galliformes) well studied compared with others. Thus, rather than considering this summary an exhaustive list, it is more appropriately viewed as an indication of the breadth of taxa that include mistletoe in their diets.

Species from 66 families of birds and 30 families of mammals have been recorded consuming mistletoe, spanning 12 and 10 orders, respectively. I also encountered a record of the Amazonian characinoid fish *Triportheus angulatus* feeding on mistletoe fruits during high seasonal floods (Goulding 1980). Frugivory and nectarivory were the most common modes of consumption among birds, whereas folivory and frugivory accounted for most of the mammalian records. Although it is generally accepted that all mistletoe-fruit specialists are birds, recently published information (Amico & Aizen 2000) suggests that the monito del monte *Dromiciops australis*—sole living member of the ancient marsupial order Microbiotheria—acts as exclusive disperser of mistletoe fruits in southern Andean cloud forests. Amico & Aizen (2000) speculated that this interaction may be indicative of an early association between mistletoes and marsupials, with both taxa originating in Gondwanaland. Although many reptiles are frugivorous or folivorous (Rand 1978), dietary composition data are incomplete for most species, and I did not find reliable records of mistletoe in the diet of any wild reptilian.

Given the year-round availability of mistletoe fruits in many regions, there is a diverse range of species that depend on mistletoe when little else is available. Many of these consumers may act as occasional dispersers, but most are more appropriately viewed as fruit predators. The diversity of these opportunistic frugivores was unexpected, given the prevailing view that mistletoes have highly specific dispersal systems, refined over evolutionary time to deter generalist frugivores (Herrera 1985a, McKey 1975, Reid 1991, Wheelwright 1988, but see Moermond & Denslow 1985). Reid (1991) noted that fruits of many mistletoe species are large, sticky, and relatively cryptic—attributes that would exclude most potential dispersers in favor of a small group of specialists (McKey 1975, Wheelwright 1988). Data summarized here suggest that many organisms regularly consume mistletoe fruit, indicating that it may not be as difficult to locate and process as previously considered. These two ideas are not mutually incompatible, the widespread consumption of mistletoe fruit is independent of the reciprocal specificity between mistletoes and dispersers as long as these coevolved specialists remain the primary dispersers. Available data suggest this is the case, with mistletoe plants in many regions reliant on a small number of specialized frugivorous birds for successful dispersal (Davidar 1987, Godschalk 1983a, 1986, Heine de Blasac & Mayaud 1930, Liddy 1983, Reid 1986, 1989, 1990, Restrepo 1987, Sargent 1994, Snow & Snow 1984, 1988, Walsberg 1975; but see Punter & Gilbert 1989).

Mistletoes also provide abundant nectar, and in addition to many nectarivorous species (Davidar 1983, Ladley et al. 1997, Reid 1986, Snow & Snow 1971, Stiles 1985), a broad range of insectivorous and generalist species have been recorded feeding from mistletoe flowers (Barker & Vestjens 1989, 1990, Crome 1978, O'Donnell & Dilks 1989, Reid 1986, Rosenberg et al. 1991). Several mammals are also known to feed on mistletoe nectar (more commonly consuming the entire flower; Dwiyarheni et al. 1999, Hemmingway 1998, Kavanagh 1978, McConkey 1999, Overdorff 1993). There are no confirmed records of mammals functioning as pollinators.

The leaves of mistletoe plants are considered highly favored browse in dietary studies of many folivorous mammals ranging from deer and rhinoceroses to gorillas and possums (Table 1). Brushtail possums, *Trichosaurus vulpeca*, introduced from Australia are thought to have decimated populations of endemic mistletoe in New Zealand (Norton 1991, Ogle & Wilson 1985), although declines in pollinating bird species may also be involved (Robertson et al. 1999). Indeed, mammalian folivory has been proposed as the primary selective force driving host-mimicry patterns displayed by many mistletoes (Barlow & Wiens 1977, Choate et al. 1987, Kavanagh & Lambert 1990, Pasteur 1982, Wiens 1978), but there are several other competing hypotheses (Atsatt 1977, 1983, Canyon & Hill 1997). No mammal is known to specialize on mistletoe foliage, but several species appear to be seasonally dependent on it (Quinton & Horejsi 1977, Riney 1951). There are several records of birds feeding on mistletoe leaves (Ali & Ripley 1978, Bohl 1970, Skinner 1928, Takatsukasa 1967), but folivory generally is rare in the group (Morton 1978).

Mistletoe clumps are often used as a foraging substrate by insectivorous species. As indicated earlier, a diverse range of insects is associated with mistletoes as both pollinators and herbivores, and mistletoe clumps often have abundant insect assemblages (Bennetts 1991, de Baar 1985, Mushtaque & Baloch 1979, Whittaker 1984). Insectivorous birds including several highly specialized species (e.g., *Prodotiscus regulus*, *Arachnothera longirostris*) (Ali & Ripley 1999, Fry et al. 1988) use mistletoe clumps for foraging activities (Bennetts 1991, Heine de Balsac & Mayaud 1930, O'Donnell & Dilks 1989, Turner 1991). Foraging substrate is rarely recorded in dietary studies of insectivores, however, and the extent of this foraging mode is presumably much greater than the 10 recorded families. There is also a record of a predatory lizard, *Varanus albigularis*, using mistletoe clumps as sites for hunting birds (Rose 1962). Probably a rare instance, this further highlights the importance and complexity of the habitat provided by mistletoes.

Mistletoes as Nest Sites

Mistletoes are used extensively as sites for nesting and roosting, and whereas many researchers have reported this for individual species (Bull et al. 1989, Farentinos 1972, Ralph 1975, Reynolds et al. 1982, Skutch 1969, Thompson & Owen 1964, Weathers 1983) or regions (Fry et al. 1988, Mamone 1996, North 1906, Parks et al. 1999, van Someren 1956), use of mistletoe for nest sites has never been assessed generally. I reviewed the literature on life histories of birds and mammals, collating records of species recorded using mistletoe as nesting/roosting sites. Again, I restricted this review to the family-level, with representative species listed in Table 2. Nesting records in witches' brooms as well as regular mistletoe clumps

TABLE 2 Families recorded nesting and roosting in mistletoe clumps

Family	Nesting frequency	Species exemplar	Citation
Ardeidae	R	*Egretta novaehollandiae*	Marchant & Higgins 1990
Threskiornithidae	R	*Threskiornis molucca*	Marchant & Higgins 1990
Accipitridae	C	*Accipiter cooperi*	Reynolds et al. 1982
Tetraonidae	S*	*Dendrapagus obscurus*	Pekins et al. 1991
Phasianidae	S*	*Syrmaticus soemmerringi*	Takatsukasa 1967
Alcidae	R	*Brachyramphus marmoratus*	Nelson 1997
Columbidae	S	*Zenaida macroura*	Bennetts & Hawksworth 1992
Musophagidae	V	*Corythaeola cristata*	Fry et al. 1988
Cuculidae	S	*Coccyzus pumilus*	Ralph 1975
Neomorphidae	S	*Geococcyx californianus*	Weathers 1983
Strigidae	C	*Asio otus*	Bull et al. 1989
Trochilidae	R	*Stellula calliope*	Bent 1940

TABLE 2 (*Continued*)

Family	Nesting frequency	Species exemplar	Citation
Coliidae	C	*Colius striatus*	Van Someren 1956
Tyrannidae	S	*Camptostoma imberbe*	Bleitz 1955
Cotingidae	R	*Pachyramphus polychopterus*	Skutch 1969
Maluridae	R	*Malurus lamberti*	McDonald 1973
Acanthizidae	R	*Acanthiza chrysorrhoa*	Beruldson 1980
Eupetidae	V	*Psophodes cristatus*	McDonald 1973
Meliphagidae	C	*Prosthemadera novaeseelandiae*	Soper 1976
Pachycephalidae	S	*Pachycephala rufiventris*	McDonald 1973
Laniidae	R	*Lanius ludovicianus*	Weathers 1983
Malaconotide	S	*Chlorophoneus sulfureopectus*	Harris & Franklin 2000
Vireonidae	R	*Vireo huttoni*	Davis 1995
Artamidae	S	*Artamus tenebrosus*	North 1906
Cracticidae	S	*Cracticus torquatus*	North 1906
Ptilonorhynchidae	C	*Ptilonorhynchus violaceus*	McDonald 1973
Corvidae	S	*Cyanocitta stelleri*	Brandt 1951
Remizidae	R	*Auriparus flaviceps*	Jaeger 1947
Aegithalidae	R	*Psaltriparus minimus*	Bendire 1887
Troglodytidae	S	*Campylorhynchus brunneicapillus*	Anderson & Anderson 1973
Campephagidae	R	*Lalage sueurii*	Beruldson 1980
Sylviidae	R	*Polioptila melanura*	Rosenberg et al. 1991
Muscicapidae	R	*Muscicapa adusta*	Van Someren 1956
Turdidae	S	*Catharus guttatus*	Bennetts et al. 1992
Mimidae	S	*Mimus polyglottos*	Sutton 1967
Ptilogonatidae	C	*Phainopepla nitens*	Rea 1983
Parulidae	R	*Dendroica nigrescens*	Guzy & Lowther 1997
Thraupidae	S	*Piranga rubra*	Brandt 1951
Emberizidae	S	*Pipilo aberti*	Finch 1985
Cardinalidae	S	*Cardinalis sinuatus*	Bleitz 1955
Icteridae	R	*Icterus bullockii*	Rosenberg et al. 1991
Fringillidae	S	*Carpodacus cassinii*	Bennetts et al. 1992
Estreldidae	S	*Emblema guttata*	North 1906
Erethizodontida	R*	*Erethizon epixanthum*	Smith 1982
Pseudocheiridae	R	*Pseudocheirus peregrinus*	Thompson & Owen 1964
Sigmodontidae	S	*Neotoma floridanum*	Mamone 1996
Arvicolidae	S	*Arborimus longicaudus*	Mamone 1996
Mustelidae	R*	*Martes americana*	Parks & Bull 1997
Phascolarctidae	—*	*Phascolarctos cinereus*	S.J. Cox, unpublished observation
Sciuridae	C	*Sciurus aberti*	Farentinos 1972

In the nesting frequency column, R denotes rare within the family, S denotes several records, C denotes common in family, V is very common with the family and — is for monotypic families.

*Denotes record is only of roosting—all other records pertain to nesting (rearing young in a nest).

are included. Information on nesting is highly variable across regions. Thus, although there have been several separate treatments of the nests and eggs of Australian birds (e.g., Beruldson 1980, Campbell 1900, North 1906), there is not a single such publication for Asia, Africa, or Latin America. As more research is conducted in these regions, species from many other families will probably be added and the list provided here is clearly provisional.

Species from 43 families of birds and 7 families of mammals have been recorded using mistletoe as a nesting or roosting site (Table 2). No groups are obligate mistletoe nesters, but species from several avian lineages (notably Coccyzinae, Musophagidae, Striginae, Accipitrinae, Ptilogonatidae, and Ptilonorhynchidae) favor nesting in mistletoe (Beruldson 1980, Fry et al. 1988, North 1906, Parks et al. 1999). It is unclear which attributes of mistletoe clumps are most important in nest-site selection, but many authors comment on their dense, evergreen habit and the enlarged host branches associated with the haustorium (Bleitz 1955, Jaeger 1947, McDonald 1973, Rosenberg et al. 1991, Sutton 1967, van Someren 1956). For example, long-eared owls (*Asio otus*) use witches' brooms as the primary structural support for their stick nests, with one study finding 19 of 20 nests associated with mistletoe (Bull et al. 1989). Alternatively, smaller nests can be concealed within foliose mistletoe clumps, a strategy used by many passerines (Anderson & Anderson 1973, Bennetts et al. 1996, Bleitz 1955, Brandt 1961, McDonald 1973, North 1906). In addition to such structural factors, microclimate may also be involved. Porcupines (*Erethizon epixanthum*), pine martens (*Martes americana*), and several species of squirrel have been recorded using witches' brooms as hibernaculae (Mamone 1996, Parks et al. 1999, Parks & Bull 1997, Smith 1982, Taylor 1935), and several species of birds and mammals shelter in mistletoe clumps during extremely hot weather (Brandt 1951, Jaeger 1947, Stoner 1932, SJ Cox, unpublished observations). Other than this anecdotal information, there has been only one study on the nesting of organisms in mistletoe clumps (Parks et al. 1999), so the relative importance of structure and microclimate cannot be assessed.

In addition to using mistletoe as a nest site, there are records from Africa and North America of birds using fresh mistletoe sprigs as nest lining. Whereas the behavior of using green foliage as a nest lining is widespread in birds, at least seven species of raptor have been recorded selecting viscaceous mistletoe as nest lining, often replacing it daily (Brandt 1951, Fry et al. 1988, van Someren 1956). There is evidence that extracts of *Viscum* spp. have antibacterial activity (Grainge & Ahmed 1988), and clinical trials have found some of these chemicals to act as immunostimulants (Fischer et al. 1997, Rentea et al. 1981, Stoffel et al. 1997, Wagner & Proksch 1985). Experimental studies with common starlings (*Sturnus vulgaris*) indicate that fledglings have higher immune function in the presence of various aromatic herbs in the nest; Gwinner et al. (2000) speculated that mistletoe foliage may have a similar effect. Other than isolated records in species accounts, this intriguing behavior has been completely overlooked and merits greater attention. The fact that it has been recorded solely from raptors and scavengers further suggests that viscaceous mistletoe may have a key role in nest hygiene, and that the popularity of mistletoe as a nest site may have a biochemical component in addition to structure and microclimate.

Mistletoe infection has been associated with the formation of hollows and snags (Bennetts 1991, Bennetts et al. 1996, Hawksworth & Wiens 1996), which are limiting resources in many forests (Raphael & White 1984). Mistletoes are considered critical in creating hollows used by a broad range of species for nesting and roosting (Bennetts et al. 1996, Hawksworth & Geils 1996, Mamone 1996, Parks et al. 1996), and influencing larger-scale distributions (Bennetts 1991, Bennetts et al. 1996). A close correlation was found between intensity of mistletoe infection and diversity and abundance of cavity-nesting birds (Bennetts 1991, Bennetts & Hawksworth 1992, Bennetts et al. 1996), suggesting that mistletoe may be important both directly and indirectly in providing nesting and roosting locations for vertebrates.

HYPOTHESIS

Having summarized the life-history of mistletoes and documented the breadth of interactions between mistletoe and vertebrates throughout the world, I propose the following general hypothesis:

Mistletoes function as keystone resources in many forests and woodlands worldwide.

This hypothesis will be evaluated with existing data (both qualitative and quantitative) to allow the first explicit assessment of the importance of mistletoe in forests and woodlands worldwide. Although several researchers have noted the importance of mistletoe in particular regions (Anderson et al. 1978, Bennetts 1991, Reid 1986, Snow & Snow 1988, Turner 1991), the generality of this phenomenon has apparently never been proposed nor evaluated.

This hypothesis builds on work by Terborgh (1986), in which he documented the importance of figs, palm nuts, and nectar to a wide range of vertebrates in neotropical forests. His paper expanded on earlier research by Leighton & Leighton (1983), who proposed that “the reproductive biology of figs makes them uniquely suited to play roles as keystone mutualists for many vertebrates”—one of the earliest examples of applying the “keystone species” concept to a suite of resources. Terborgh (1986) estimated that this resource-base, despite accounting for less than 1% of local plant diversity, supported the majority of frugivorous vertebrates during seasonal periods of scarcity in two neotropical forests. He concluded that figs and other fruit resources were of critical importance to most frugivores, and that fruits function as keystone resources in tropical forests generally.

MISTLETOE AS A KEYSTONE RESOURCE

Since its introduction by Paine (1969), the concept of an ecological keystone has been applied to a wide variety of groups spanning predators, prey, parasitoids, modifiers, links, and resources. Some authors (e.g., Mills et al. 1993) have suggested that the term has become so widely used that it has become too generic and unwieldy. Provided explicit criteria are used to define them, keystones remain useful heuristics both in comparing the structure and function of communities and in identifying priority groups for directed management. Power and associates (1996, p. 609) defined a keystone as a group "whose impact on its community or ecosystem is large and disproportionately large relative to its abundance." Mills and coauthors (1993) stated that an important component of defining keystones was interaction strength, measured by quantifying the community-wide effect of keystone removal that "would likely precipitate loss of obligate and possibly opportunistic users" (p. 220, after Redford 1984).

There have been several small-scale removal experiments to assess the effect of mistletoe infection on various host parameters, but the level of treatment was the tree (Reid et al. 1992, 1994, Shea 1964, Sterba et al. 1993). These data cannot be used to quantify the strength of interactions at the community level, nor address the hypothesis of mistletoe as a keystone resource in forested habitats. This lack of explicit data notwithstanding, the keystone hypothesis can still be assessed. It was primarily on the basis of observational and qualitative data that Terborgh (1986) proposed that figs be considered a keystone resource in tropical forests, with subsequent studies and reviews lending support (Antsett et al. 1997, Nason et al. 1998, but see Gautier-Hion & Michaloud 1989). I examine two well-studied habitats as case studies, summarize relevant data on the role of mistletoes in both systems, and evaluate the validity of the keystone hypothesis.

Case Study 1: Mesquite Woodland of the Southwestern USA

This semiarid habitat is dominated by shrubs and small trees, principally mesquite (*Prosopis* spp.), acacia (*Acacia* spp.), and creosote bush (*Larrea tridentata*), intergrading with different associations in riparian zones and upland areas (Anderson et al. 1979, Blake 1984, Jaeger 1947, Rosenberg et al. 1991, Stamp 1978). Of the two viscaceous genera in the region—*Arceuthobium* and *Phoradendron*—the former is restricted to conifers and is rare to absent in mesquite woodlands. *Phoradendron* species parasitize a broad range of host trees, with *P. californicum* and *P. tomentosum* most common on mesquite trees. Insects (chiefly Diptera and Hymenoptera) are the main pollen vectors (Whittaker 1984), with birds acting as principal fruit dispersers (Rea 1983, Rosenberg et al. 1991, Spooner 1983). The phainopepla (*Phainopepla nitens*) relies on *Phoradendron* berries as its main food source (Walsberg 1975), and several other species (western bluebird *Sialia mexicanus*, cedar waxwing *Bombycilla cedrorum*, northern mockingbird *Mimus polyglottos*, and several species of woodpecker) are partially dependent on the fruits (Rea 1983, Rosenberg et al. 1991, Sutton 1967). Although these species act as primary dispersal agents, many other insectivorous and generalist bird species have been recorded consuming the fruits. Few other fruit resources are available during the winter (Anderson et al. 1979, Austin 1970, Rice et al. 1981), so some birds actively defend mistletoe clumps (Walsberg 1977). During summer, mistletoe fruits are also widely consumed as a source of water (Jaeger 1947, Walsberg 1975). The fruits and leaves are consumed by several mammals (e.g., pronghorn antelope *Antilocapra americana*—Russell 1964; mule deer *Oedocoileus hemionus*—Riney 1951; Great Basin pocket mouse *Perognathus parvus*—Burt 1934), and also feature in the diets of indigenous people as both food and medicine (Curtin 1949, Timbrook 1990). Some mammals appear to be seasonally dependent on mistletoe: *Phoradendron* seeds dominate scats of cacomistles (*Bassariscus astutus*) during peak fruiting (Taylor 1954) and according to Quinton & Horejsi (1977), *P. tomentosum* foliage comprizes up to 65% of the winter diet of white-tailed deer (*Oedocoileus virginianus*). *Phoradendron* clumps are used by many species for nesting (Bleitz 1955, Brandt 1951, Rea 1983, Weathers 1983) and are regarded as preferred nesting sites for several species. A study of phainopeplas in Arizona found 80% of nests in mesquites, of which 80% were in or under mistletoe clumps (Rea 1983); 18% of cactus wren (*Campylorhynchus brunneicappilus*) roosting nests were located in *P. californicum* clumps (Anderson & Anderson 1973). In a study of Abert's towhee (*Pipilo aberti*), 50% of nests were within *P. californicum* clumps, their evergreen habit allowing breeding to commence earlier; the author considered them the most desirable nest site (Finch 1985). Moreover, several birds of prey commonly nest in mistletoe clumps, with other species recorded using fresh sprigs of *Phoradendron* as nest lining (Brandt 1951, Stoner 1932).

Many authors have commented on the interactions between vertebrates and *Phoradendron* in mesquite woodlands, with several spatial and temporal associations between mistletoe and species distributions noted. Austin (1970) reported an increase in abundance of several avian species in response to a major fruiting event of *P. californicum*, and Anderson & Ohmart (1978) and Rice et al. (1981) found *P. californicum* to be a critical habitat component for 15 of 20 species. They noted that *P. californicum* berries constituted the only reliable source of fruit in the area, and thus they determined the distribution of frugivores in mesquite woodlands. This finding was confirmed by Rosenberg et al. (1991), who found the berries to dominate the diets of 11 species and to be of particular importance during winter. Density of *Phoradendron* plants in this habitat varies, with reported values ranging from 1 to 17 plants per hectare in one study (Blake 1984), with another reporting from 0.5% to 8.7% of trees contained mistletoe plants (Stamp 1978).

Case Study 2: Eucalypt Forests of Southeastern Australia

These sclerophyllous forests are found throughout eastern Australia, grading into woodlands and savannas inland. The canopies are dominated by *Eucalyptus* spp., with smaller trees and shrubs (e.g., *Acacia* spp., *Leptospermum* spp., *Casuarina* spp.) often forming a subcanopy, and different associations in gulleys and drier slopes (Smith 1984, Thompson & Owen 1964, Turner 1991). More than 20 loranthaceous species of mistletoe are known from this region, of which seven widespread species commonly parasitize eucalypts [*Amyema bifurcatum*, *A. miquelii*, *A. pendulum*, *Dendrophthoe glabrescens*, *D. vitellina*, *Diplatia grandibractea*, and *Muellerina eucalyptoides*; Downey (1998)]. All species are bird-pollinated (Ford et al. 1979, Reid 1986), with insects also playing a role for some species. In addition to nectarivores (primarily in the Meliphagidae, Paton & Ford 1977, Reid 1986), a broad range of birds has been recorded feeding opportunistically on mistletoe flowers (Barker & Vestjens 1989, 1990, Ford et al. 1979, Reid 1986, Turner 1991), especially during summer when nectar availability in these forests is lowest (Paton & Ford 1977). Birds also act as sole fruit dispersers, with two mistletoe-dependent specialists (mistletoebird *Dicaeum hirundaceum* and painted honeyeater *Grantiella picta*) inhabiting these forests. Many other species have been recorded feeding on the fruits (Barker & Vestjens 1989, 1990, Reid 1986) and mistletoe is one of the few reliable fruit sources in this region (Reid 1986). Several mammals regularly consume mistletoe foliage and flowers (Canyon & Hill 1997, Choate et al. 1987, Kavanagh & Lambert 1990, Reid 1986), and may reduce the abundance of mistletoe in some areas. Mistletoes are also used as a foraging substrate by many insectivorous species, and probably represent a concentration of insects (Turner 1991). Mistletoe clumps are noticeably denser than eucalypt foliage (see Figure 2*a*) and are frequently used as nest sites by a broad range of species (Beruldson 1980, Campbell 1900, North 1906, Thompson & Owen 1964). While mostly opportunistic, some species appear to prefer nesting in mistletoe clumps—Ford (1999) reported 28% of noisy friarbird and 29% of red wattlebird nests in northern New South Wales were inside mistletoe clumps.

Numerous qualitative datasets have been collected demonstrating a close temporal and spatial relationship between faunal distributions and mistletoe in eucalypt forests, for both particular species (Thompson & Owen 1964, Watson 1997) and entire assemblages (Liddy 1983, Smith 1984, Turner 1991). Thompson & Owen (1964) found ringtail possums (*Pseudocheirus peregrinus*) nested almost exclusively within mistletoe clumps and reported a close correlation in the spatial distribution of the two. Turner (1991) described the importance of mistletoe as a food resource for birds, accounting for the majority of foraging records in terms of both individuals and species. There was a significant relationship between density of mistletoe plants and number of species observed foraging in foliage ($N = 18$, $R = 0.564$, $P \simeq 0.007$ (one-tailed), recalculated from Turner 1991), with almost four times more records in mistletoe than in eucalypts. This involved nectarivores, frugivores, and insectivores, and Turner (1991) proposed that mistletoe be regarded as a critical resource for birds in eucalypt forests. Mistletoe density in eucalypt forests ranges from fewer than three to more than one hundred plants per hectare. These high values are from degraded or highly perturbed habitat (Heather & Griffin 1978, Norton & Stafford Smith 1999); values from intact forest are typically fewer than 10 plants per hectare (Turner 1991).

Inference—Mistletoe as a Keystone Resource

In terms of the qualitative criterion of Power et al. (1996), there is unambiguous support for treating mistletoe as a keystone resource in both habitats. Mistletoe is uncommon in both systems and can be considered a minor to extremely minor vegetational component in terms of abundance, species richness, and biomass. The plants provide a broad range of high-quality nutritional resources that support several obligate and many partially dependent species, especially during periods of seasonal scarcity. They also create habitat used by many species for nesting and roosting. As such, mistletoe is considered a keystone resource in both habitats, having a large and disproportionate impact on both.

The similar role mistletoes play in these two habitats is striking, given the broad differences between the habitats. One is a semiarid, shrub-dominated habitat in which the viscaceous mistletoes are mostly insect-pollinated. The other is temperate mesic forest, with loranthaceous mistletoes pollinated primarily by birds. Ongoing research in the coniferous forests of the Rocky Mountains has also focused on the role of mistletoe (Bennetts 1991, Bennetts & Hawksworth 1992, Bennetts et al. 1996, Hawksworth & Geils 1996) and comprises the most detailed research on the effects of mistletoe density on vertebrate diversity. Bennetts and associates (1996) reported dwarf mistletoe density to be a highly significant predictor of avian richness, positively affecting the abundance of 24 of 28 bird species. Mistletoe density was also correlated with number of snags, cavity nests, and total number of nests and was identified as the single most important variable affecting avian diversity in these boreal forests.

Further case studies supporting the keystone resource hypothesis could have been drawn from studies of mistletoe-vertebrate interactions in savannas of southern Africa (Dean et al. 1994, Fry et al. 1988, Godschalk 1983a,b, 1986, van Someren 1956), acacia shrublands in central Australia (Barker & Vestjens 1989, 1990, Beruldson 1980, North 1906, Reid 1989, 1990), tropical forests in India (Ali & Ripley 1996, 1999, Davidar 1978, 1983, 1985, Mushtaque & Baloch 1979), cactus-dominated deserts in Chile (Martinez del Rio et al. 1995, 1996), or subtropical cloud-forests in Costa Rica (Feinsinger 1978, Sargent 1994, 1995, Skutch 1969, 1980, 1983, Stiles 1985). Thus, given the widespread qualitative and quantitative support, the conclusion that mistletoes function as keystone resources can be provisionally accepted and adopted as a working hypothesis to guide further research.

Beyond Evaluation—Mechanisms and Causation

Although several studies have found greater vertebrate richnesses associated with higher mistletoe densities, few have examined the mechanistic basis of the pattern. In a study of woodland remnants in southern Australia (Watson 1994, Watson et al. 2000), mistletoe density contributed to a vegetation classification that explained the distribution of 12 of 29 common woodland bird species. Avian richnesses increased with mistletoe density until a threshold of approximately 20 plants per ha was reached. Patches with higher densities (up to 93 plants per ha) were characteristically heavily grazed and contained depauperate avian assemblages (Watson 1994, Watson et al. 2000). This pattern has been noted by researchers in other areas (Heather & Griffin 1978, Norton et al. 1995, Norton & Reid 1997, Norton & Stafford Smith 1999), indicating that the mistletoe-diversity association is not a simple linear relationship. In addition to measuring mistletoe density, Watson

(1994) also quantified mistletoe richness and presented the only dataset permitting analysis of the effect of mistletoe richness on vertebrate diversity. The 27 woodland remnants contained between 0 and 4 species of mistletoe, with an associated increase in avian richness (ANOVA, df $= 26; 4$, F $= 3.875$, P $\simeq 0.012$, recalculated from Watson 1994). Mean richness of birds in patches with four species of mistletoe was 63% greater than in patches with a single species, suggesting that mistletoe richness may contribute to the mistletoe-diversity patterns noted earlier. As well as increasing net availability of resources, an increase in mistletoe richness may expand the temporal extent of resource availability, given interspecies variation in phenology described earlier.

Although more mistletoes may entail more resources that can potentially support greater richnesses, this assumes no interaction between the consumers. Several researchers have noted birds actively defending fruiting mistletoe plants (Snow & Snow 1984, Walsberg 1977), driving alpha diversities down in the immediate area. Moreover, in many ecosystems the patterns of causal interdependence are unclear. Are areas with more mistletoe more attractive to vertebrates and hence more diverse, or is mistletoe secondarily introduced into diverse areas by seed-dispersing species? For example, data from southern Africa indicate a close relationship between mistletoe distribution and soil type (Dean et al. 1994), revealing mistletoes are more common on more fertile soils. Research in Australia and New Zealand has demonstrated the complex interaction of factors that influence mistletoe distribution, mediated both by environmental factors and interactions with hosts, pollinators, and fruit dispersers (Norton et al. 1995, Norton & Reid 1997). With changes related to European settlement, mistletoe has become more common in eastern Australia (Heather & Griffin 1978, Reid et al. 1994), less common in New Zealand (Ogle & Wilson 1985, Norton 1991), and either absent or superabundant in forest fragments in western Australia (Norton et al. 1995). Associated with these ecosystem-scale changes in vegetation cover have been concomitant changes in the distribution and abundance of animals (Norton & Reid 1997) that may or may not be related to mistletoe distribution.

Although identifying the causal influence of mistletoe on diversity remains elusive, it is clear that mistletoe does have an important role in many habitats throughout the world. As a direct source of nutritional resources, as a provider of nesting and roosting microhabitats, and as an indirect modifier of habitat structure, mistletoes have a pervasive effect in many forests and woodlands. Having identified mistletoes as keystone resources, the next step is to explore the underlying mechanisms and further our understanding of their role in forested ecosystems worldwide.

PRIORITIES FOR FUTURE RESEARCH

Whereas the vast majority of studies that have included mistletoe have found it important in the structure and function of forest and woodland communities, exceptions may emerge as more research is conducted. Tropical regions, in particular, are underrepresented in the mistletoe literature, and it is unclear if mistletoe is as important in structuring these highly diverse ecosystems as in less diverse temperate areas. Despite the occurrence of mistletoe on many oceanic islands, the role of mistletoes in these simpler communities is not known. Multitaxon studies are rare, and it is unknown how mistletoe affects diversity patterns of different groups within the same habitat. Many of these gaps can be addressed by modifying ongoing studies. Of the many studies examining diversity patterns of selected faunal groups in forests and woodlands throughout the world, almost all collect a range of habitat metrics, but mistletoe is rarely included. Given the breadth of interactions with pollinators, dispersers, and herbivores, mistletoe density depends on an array of factors and represents a sensitive and accurate assay of many community-level effects (Anderson et al. 1979, Norton et al. 1995, Norton & Reid 1997, Robertson et al. 1999). By incorporating measurements or estimates of mistletoe density into inventory-based field studies, the representation of habitats and faunal groups will be expanded greatly, yielding a broader understanding of mistletoes as keystone resources.

To complement correlational data collected by descriptive studies, manipulative experiments are essential to measure the direct effects of mistletoe on diversity and ecosystem function. Although transplanting is not possible and inoculation difficult, mistletoe plants are relatively easy to remove allowing “replicated” patches of forest to be manipulated and subsequently monitored. As Bennetts et al. (1996) discussed, this is not practical for some habitats where mistletoe infection and resultant habitat change may take centuries. There are other habitats (including the two used here as case studies) in which manipulative experiments would be tractable, with several studies at the individual-tree scale demonstrating the potential feasibility of such an approach (Reid et al. 1992, 1994, Sterba et al. 1993).

To guide future experimental studies, a series of explicit predictions can be made regarding the long-term consequences of removing mistletoes from forested habitats. Compared with control plots (with the usual density and diversity of mistletoe plants), test plots (in which all mistletoe plants have been removed) would be expected to have:

1. lower abundances of mistletoe-obligate frugivores and folivores, with local populations declining toward local extinction;
2. lower abundances of regular mistletoe foragers (folivores, frugivores, and nectarivores);
3. fewer fallen branches, hollows, and snags over the long term;
4. lower abundances of birds and mammals that nest in mistletoe clumps and hollows;
5. lower richness of vertebrates generally; and
6. communities with increased sensitivity to drought and other rare events.

In addition to these research questions, a range of management-oriented applications remain unexplored. Mistletoe density in fragmented habitats is often unusually high or low, revealing the disturbed nature of these landscapes (Heather & Griffin 1978, Norton & Reid 1997, Norton et al. 1995). Could this imbalance be corrected by removing excess plants, or selectively inoculating trees in areas where mistletoe has been extirpated? Some researchers have advocated mistletoe as an integral part of revegetation programs (Anderson et al. 1979). Similar approaches could be extended to commercial plantations, introducing mistletoe to enhance their value for native fauna. Although this may not be applicable to many systems, data from a commercial forest in eastern Australia demonstrate that mistletoe and forestry can coexist (Turner 1991), and the topic merits further exploration.

Finally, the widespread perception of mistletoes as destructive weeds needs to be challenged. Many landholders, managers, and even biologists regard mistletoes as invasive pests, damaging to individual trees and detrimental to forest health. Rather than being viewed as the cause of disturbance or disease, mistletoes need to be promoted as an indicator of habitat health, or in superabundance as a signal of landscape perturbation (Norton & Reid 1997). As demonstrated in this review, mistletoes have a substantial positive role in many forests and woodlands, and should be given appropriate recognition. Effecting such attitudinal changes will take considerable effort, but recognizing mistletoes as a keystone resource is an important first step.

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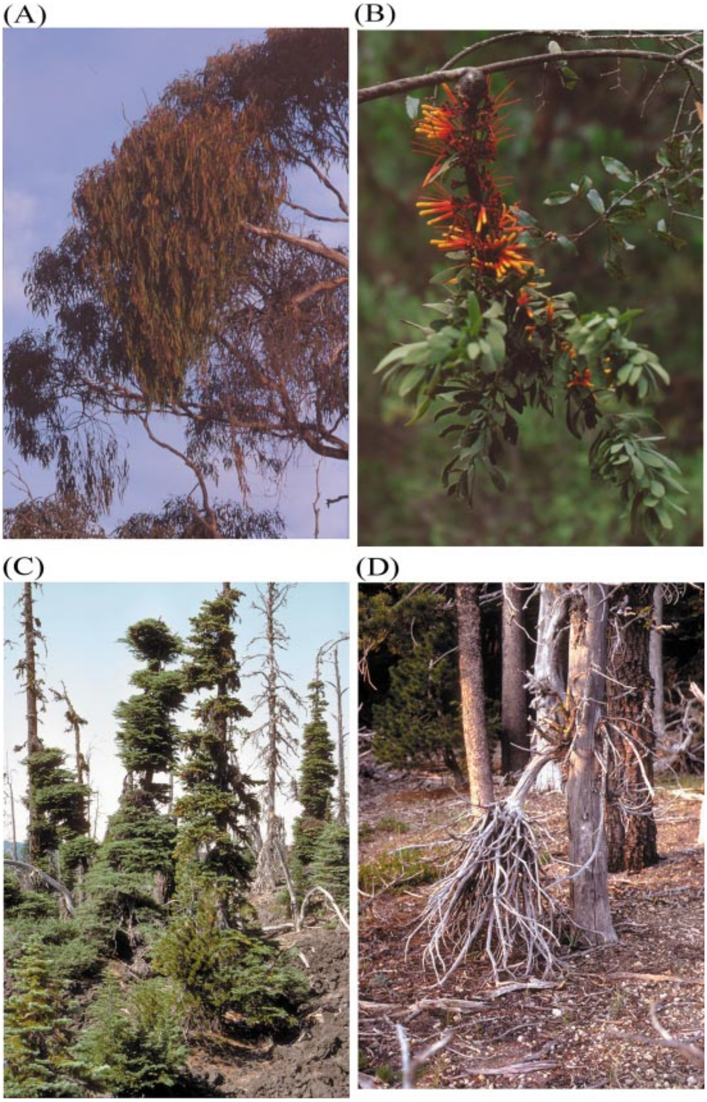

Figure 2 (*A*) Large *Amyema pendulum* parasitizing eucalyptus tree, New South Wales, Australia. Photograph by author. (*B*) *Psittacanthus* spp. parasitising an oak tree in Oaxaca, Mexico. Note the abundant colorful flowers with short pedicels typical of Loranthaceae, and haustorium at junction with host. Photograph by author. (*C*) Coniferous trees displaying the characteristic dense clumps associated with dwarf mistletoe infection known as witches' brooms. Oregon, USA, photograph by D.L. Nickrent. (*D*) Detail of a dead witch's broom on a pine tree, caused by *Arceuthobium tsugense*. Note the thickened, dense branches associated with the infection, used as a nesting/roosting site by a variety of animals in this habitat. Oregon, USA, photograph by D.L. Nickrent.