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Comparisons of terrestrial vertebrate assemblages in temperate rainforests of North and South America

Comparaciones de ensambles de vertebrados terrestres en pluviselvas templadas de Norte y Sudamérica

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ABSTRACT

Assemblages of amphibians, reptiles, and mammals inhabiting temperate wet forests in the Pacific Northwest of North America and in southern South America were compared with respect to 1) regional species densities, 2) distributional characteristics, 3) ecological diversity, and 4) site (point) species densities. Pacific Northwest and southern temperate rainforests possess about the same numbers of amphibian species, but most in the former are salamanders while the latter has only anurans. Southern anurans tend to be more terrestrial than Pacific Northwest anurans, and more frequently have localized distributions. Pacific Northwest forests have higher numbers of reptile species overall, but fewer lizard and more snake species than southern temperate rainforests. Both regions show a decline in the importance of reptile species proceeding towards polar regions; polarward declines in numbers of amphibian species in the Pacific Northwest are largely due to the progressive loss of salamanders. Pacific Northwest forests also possess much higher total and site species densities of mammals due principally to the following groups: 1) members of the order Insectivora (shrews and moles) absent in South America, 2) higher numbers of bats, and 3) sciurids (squirrels) and arvicolids (voles) also absent in southern South America. A larger proportion of Pacific Northwest mammals are trophically insect/invertebrate consumers, and a smaller proportion are true carnivores. However, if these categories are combined, the overall proportion of broadly defined carnivores is very similar to that in southern rainforests. Proportions of herbivorous and omnivorous species are also very similar in the two regions. Both forests have at least some partially mycophagous (= fungivorous) species, and a relative scarcity of granivorous/frugivorous mammals. A smaller proportion of southern rainforest mammals are arboreal, somewhat more are fossorial, and similar proportions are terrestrial/scansorial, and aquatic. Important questions that need to be addressed include the nature of resource availability and utilization, the role of biotic interactions such as competition and predation, and the importance of coevolutionary relationships such as that suggested between mycophagous small mammals and forest tree-mycorrhizal symbionts. In addition to long-term studies, opportunities are abundant for large- and small-scale experiments despite the difficulties posed by ambient conditions.

Key words: Temperate rainforests, herpetofauna, mammals, Pacific Northwest, South America.

RESUMEN

Ensambles de anfibios, reptiles y mamíferos que habitan las pluviselvas templadas del Pacífico noroeste de Norteamérica y del sur de Sudamérica fueron comparados con respecto a: 1) densidades regionales de especies, 2) características de distribución, 3) diversidad ecológica y 4) densidad puntual (sitio-específica) de especies. Las pluviselvas templadas de Norteamérica y Sudamérica poseen similares números de especies de anfibios, pero en las primeras predominan las salamandras mientras que en las segundas hay sólo anuros. Los anuros de las pluviselvas del sur tienden a ser más terrestres que los del Pacífico noroeste y, además, presentan distribuciones más restringidas. Las pluviselvas del Pacífico noroeste tienen mayores números de especies de reptiles, pero con menos saurios y más serpientes que las del sur. Ambas regiones muestran una declinación en la cantidad de especies de reptiles hacia las latitudes polares; esta tendencia también existe en las especies de anfibios, pero en el Pacífico noroeste se debe principalmente a la desaparición de salamandras. Las pluviselvas del Pacífico noroeste también presentan mayores densidades regionales y puntuales de mamíferos, determinadas principalmente por: 1) la presencia de miembros del orden Insectivora (musarañas y topos), los que están ausentes en el sur de Sudamérica, 2) los mayores números de murciélagos, y 3) la presencia de sciúridos (ardillas) y arvicólidos (arvícolas), también ausentes en el sur de Sudamérica. Una mayor proporción de los mamíferos del Pacífico noroeste son consumidores de insectos y otros invertebrados, mientras que una menor proporción son carnívoros estrictos. Sin embargo, si ambas categorías se combinan, la proporción de carnívoros en sentido amplio es muy similar a aquélla en las pluviselvas del sur de Sudamérica. Las proporciones de mamíferos herbívoros y omnívoros son muy similares entre las dos regiones. Ambas pluviselvas tienen al menos algunas especies micófagas (o fungívoras), y una escasa representación de mamíferos granívoros o frugívoros. Una menor proporción de los mamíferos de las pluviselvas del sur son arborícolas, un poco mayor es la de fosoriales, y las proporciones de terrícolas o escansoriales y acuáticos son similares. Preguntas

que sería necesario considerar a futuro incluyen las características de la disponibilidad y consumo de recursos, el papel de interacciones bióticas, tales como competencia y depredación, y la importancia de relaciones coevolutivas, tales como aquellas sugeridas para mamíferos micófagos y micorrizas simbiontes de árboles. Además del potencial para estudios de largo alcance que presentan las pluviselvas templadas, hay abundantes oportunidades para realizar experimentos de pequeña y gran escala, a pesar de las dificultades que aportan las condiciones ambientales.

Palabras claves: Pluviselvas templadas, herpetofauna, mamíferos, Pacífico noroeste, Sudamérica.

INTRODUCTION

Temperate rainforests occur on the northern and southern continental margins of the eastern Pacific Ocean at approximately 40-50° N-S latitude. These forests are primarily included in the Pacific Northwest region of North America, and southern Chile plus the neighboring precordillera of Argentina. The climate of these regions is characterized by high precipitation as rain and/or snow (1,500-3,000 mm annually), predominantly in cooler, winter months, mild maritime conditions, and relatively dry, but not hot summers. The two temperate rainforest regions in the Western Hemisphere share a further similarity in that recent Pleistocene glaciations, orogenic uplifts of major mountain ranges, and extensive volcanism have played a major role in the development of the current topography. A fundamental difference between them is the proximity of the northern region to a large, contiguous continental land mass, whereas the southern region is in the narrowing terminus of South America. This, in addition to the historically longer isolation of South America, has had important biogeographic consequences. Although both regions presently possess temperate evergreen forests, those in northwestern North America are predominantly coniferous as opposed to predominantly broad-leaved in South America. It might be expected that regions sharing few floral and faunal elements would have few examples of convergence; such a case would be a logical consequence of the different histories of the areas and of the origins of their biotas. Conversely, we might also expect that similarities in biotas would be informative as to the extent that similar climate regimes have influenced the evolution of the biotas and ecological processes of colonization and assortative structuring of the faunal assemblages.

Herein, we compare various aspects of three classes of terrestrial vertebrates inhabiting North American and South American temperate rainforests. We consider members of the Classes Amphibia, Reptilia, and Mammalia; members of the Class Aves are analyzed separately by Jaksić & Feinsinger (1991). Our goal is to provide a broad overview of the patterns of diversity (phylogenetic and ecological), distributions, habitat useage and habit, and for the mammals, trophic specialization. From these comparisons, we make some general conclusions and suggestions for future concentration of research efforts.

METHODS

It can be operationally difficult to determine what constitutes a "temperate rainforest" at opposite ends of the Western Hemisphere. While this aspect is crucial to our comparisons, in most cases the identification of a particular set of vegetational communities as being rainforest does not influence the composition of a particular vertebrate taxon. That is, the range of faunal members is either generally much more extensive than that of the rainforest region, or is wholly enclosed within it.

This seems particularly true for the more mobile vertebrate classes such as Aves and Mammalia. In North America, we utilized the descriptions of Pacific Northwest forest prepared by Franklin (1988); from this region, we included the following types of temperate wet forests in our comparisons: 1) Douglas-fir [*Pseudotsuga menziessi* (Mirb.) Franco] - western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] forests; 2) coastal Sitka spruce [*Picea sitchensis* (Bong.) Carr.] - western hemlock forests; 3) northern Californian redwood forests [*Sequoia sempervirens* (D. Don) Endl.]; and 4) lower elevations of Pacific silver fir [*Abies amabilis* (Dougl.) Forbes] - western hemlock forests in the Cascade Mountains (up to approximately 1,000 m). While it is recognized that some forests, particularly those in the first category may not strictly be considered "rainforest", they do share basic climatological features with those in the Southern Hemisphere. We have not included mesophytic forests in the coast ranges of Canada and conterminous southwestern Alaska; available data indicates that these regions are considerably poorer in herpetofaunal and mammalian species than the Pacific Northwest (Hall 1981; Nussbaum *et al.* 1983; Cook 1984). For South America, we utilized the descriptions of Veblen *et al.* (1983) summarizing the major subdivisions of southern temperate broad-leaved forests; major categories included here were: 1) all types of forests in the Valdivian rainforest region; and 2) *Nothofagus* Blume (southern beech) dominated forest types of the north Patagonian forest region. The precise geographical limits of both these forests towards either pole does not affect the comparisons made here since few mammals, amphibians or reptiles enter the forests from only the polar ends. The approximate geographical limits of these areas analyzed are fairly similar, stretching between approximately 40-50° latitude, and usually no more than 150-200 km inland on both continents (Walter 1979; Veblen *et al.* 1983; Franklin 1988). On both continents narrow bands of similar forest may extend along the eastern flanks of cordilleran ranges, especially in southern Argentina.

We first inventoried each region to prepare species lists of amphibians, reptiles, and mammals. Valuable references providing information on the distributions and ecology of South American amphibians and reptiles include Cei (1962, 1979), Donoso-Barros (1966), and Formas (1979). Counterpart publications for the Pacific Northwest include Stebbins (1966), Nussbaum *et al.* (1983), and Brown (1985). For South American mammals, we utilized Osgood (1943), Miller & Rottmann (1978), Meserve *et al.* (1982, 1991, in press), Campos (1985), Pearson & Pearson (1982), Pearson (1983, 1984), and Patterson *et al.* (1989). For the Pacific Northwest mammals, we consulted Ingles (1965), Larrison (1976), and Brown (1985). Information on mammalian habits and diets was found in the previously mentioned sources, and Meserve *et al.* (1988). For amphibians, nomenclature follows Frost (1985) with revisions indicated by J.R. Formas (pers. comm.); for mammals, nomenclature follows Honacki *et al.* (1982). Since no synopsis currently exists for reptiles, nomenclature for South America follows Donoso-Barros (1966), Field Museum of Natural History catalogue, Chicago, Illinois, with revisions indicated by J.C. Ortiz (pers. comm.); that for North America follows Nussbaum *et al.* (1983).

Vertebrates were tabulated as being present if they spent al least a major part of their life cycle in temperate rainforests. They were characterized as being "Widespread" in distribution if they: 1) occurred in a major portion of the rainforest area; and/or 2) had much wider distributions elsewhere. Vertebrates were characterized as "Local" in distribution if they had very isolated/endemic ranges wholly within the rainforest; we omitted introduced species in comparisons of these distributions. Habit characterization was based on where the major portion of the life cycle was spent, and (for mammals) the way in which the habitat was used including vertical dimensions. Trophic specializations were based on relatively standard categories in the literature.

Initially, we attempted to quantitatively compare results on vertebrate density, biomass, and diversity at specific sites in North American and South American rainforests. However, since studies differ widely in methodologies and intensity of sampling, we were limited in our ability to make direct comparisons of biomass and densities. Therefore, we have focused on numbers of species recorded at each site without attempting to be overly quantitative in site comparisons. The objective here was to emphasize salient features of terrestrial vertebrate structure in representative localities within the biomes.

RESULTS

Total species density

Tables 1 and 2 list the reptiles and amphibians known from temperate rainforests in North America and South America. It is immediately apparent that numbers of amphibians are similar between the two regions while numbers of reptiles are higher in North America. Significantly, a major proportion of the amphibian diversity in Pacific Northwest forests is made up of salamanders (18 species, or 69.2% of the 26 species), while all amphibians in southern forests are anurans. Members of the family Leptodactylidae alone account for 82.1% of southern temperate amphibians; for South America as a whole, 37.5% are in this family (Duellman 1979a). Although there are somewhat fewer species of reptiles in southern rainforests, more noteworthy is the paucity of snakes, and the presence of all but one of the lizard species in one genus, *Liolaemus.* Interestingly, there are more species of lizards overall in southern temperate rainforests. Turtles are entirely absent in southern temperate forests, and only two reptile families represented (as opposed to five in the Pacific Northwest). South America as a whole has a smaller proportion of reptiles of the world total than it does of either birds or amphibians (Duellman 1979a).

Tables 3 and 4 present tabulations for mammal species known from temperate rainforest regions of North America and South America. The total number of potential species in South American forests is much smaller than that for North American ones (37 versus 73 species). Most of this difference in species richness is due to: 1) the lack of members of the order Insectivora (shrews and moles) in southern temperate rainforests; 2) a less diverse Chiropteran (bat) fauna (5 vs. 13 species); and 3) fewer rodent species in South America, largely due to the absence of members of the family Sciuridae (squirrels) and Arvicolidae (voles). These differences account for a total of 35 species in the greater number found in Pacific Northwest forests. Other noteable differences include the predominance of members of the family Cricetidae (= Sigmodontinae) among south temperate Rodentia (eight out of 11 native species) as opposed to only four species in the Pacific Northwest. This group is particularly diverse in South America; approximately half of the > 400 known species are present here (Hershkovitz 1972). Other orders are somewhat smaller in South America (Carnivora), or about the same size (Lagomorpha, Artiodactyla, Marsupialia).

Distributional characteristics

Using the arbitrary characterizations of distribution described earlier, 14/28 (50.0%) species of amphibians and 1/10 (10.0%) species of reptiles may be considered to have highly localized or isolated distributions in southern temperate rainforests. In contrast, 9/26 (34.6%) amphibian species and no reptile species have highly localized distributions in the Pacific Northwest. Thus, the southern temperate rainforest herpetofauna appears to include a greater proportion of species with geographically restricted ranges. Similarly, mammals show a greater proportion of localized distributions in South America. Ignoring introduced species, 7/29 species (24.1%) may be considered to have highly localized distributions in southern temperate rainforests. The comparable figure for Pacific Northwest mammals is 10/69 species (14.5%). It should be noted however that given the uncertain distributional status of many vertebrates in southern South America, these comparisons may be rendered less meaningful with further work.

Ecological diversity

In comparing habit or habitat useage by amphibians, it must be remembered that a specific taxon may be constrained in patterns of breeding and feeding habitat use. For example, the North American ranid frogs are highly aquatic in virtually all habitats and make up a large proportion of the aquatic species in Pacific Northwest forests (five of nine species; Table 1). On the other hand, the leptodactylids are an

TABLE 1

Species list of amphibians and reptiles, general distribution, and habit/habitat characteristics for Pacific Northwest temperate forests, USA. See end of table for codes

Lista de anfibios y reptiles, su distribución general, y características de su hábito/hábitat en bosques templados del Noroeste Pacífico, EE.UU. Véase el pie de la tabla para los códigos.

Taxa		Distribution	Habit/ Habitat
Class Amphibia			
Order Urodela			
Family Ambystomatidae			
Ambystoma gracile	Northwestern Salamander	W	T
Ambystoma macrodactylum	Long-toed Salamander	W	T
Dicamptodon copei	Cope's Salamander	L	A
Dicamptodon ensatus	Pacific Giant Salamander	W	T
Rhyacotriton olympicus	Olympic Salamander	W	A
Batrachoseps attenatus	California Slender Salamander	W	T
Batrachoseps wrighti	Oregon Slender Salamander	L	T
Family Salamandridae			
Taricha granulosa	Rough-skinned Newt	W	T
Family Plethodontidae			
Plethodon dunni	Dunn's Salamander	L	A
Plethodon vehiculum	Western Red-backed Salamander	W	T
Plethodon elongatus	Del Norte Salamander	L	T
Plethodon larselli	Larch Mountain Salamander	L	T
Plethodon stormi	Siskiyou Mountains Salamander	L	T
Plethodon vandykei	Van Dyke's Salamander	L	T
Ensatina eschscholtzi	Ensatina	W	T
Aneides ferreus	Clouded Salamander	W	T
Aneides flavipunctatus	Black Salamander	L	T
Aneides lugubris	Arboreal Salamander	W	T
Order Anura			
Family Ascaphidae			
Ascaphus truei	Tailed Frog	W	A
Family Bufonidae			
Bufo boreas	Western Toad	W	T
Family Hylidae			
Hyla regilla	Pacific Treefrog	W	T
Family Ranidae			
Rana aurora	Red-legged Frog	W	A
Rana pretiosa	Spotted Frog	W	A
Rana boylei	Foothill Yellow-legged Frog	W	A
Rana cascadae	Cascades Frog	L	A
Rana catesbeiana	Bullfrog	W	A
Class Reptilia			
Order Testudinata			
Family Emydidae			
Chrysemys picta	Painted Turtle	W	A
Clemmys marmorata	Western Pond Turtle	W	A
Order Squamata			
Family Iguanidae			
Sceloporus occidentalis	Western Fence Lizard	W	T
Sceloporus graciosus	Sagebrush Lizard	W	T
Eumeces skiltonianus	Western Skink	W	T
Gerrhonotus multicarinatus	Southern Alligator Lizard	W	T
Gerrhonatus coeruleus	Northern Alligator Lizard	W	F
Family Boidae			
Charina bottae	Rubber Boa	W	F
Family Colubridae			
Diadophis punctatus	Ringneck Snake	W	F
Coluber constrictor	Racer	W	T
Contia tenuis	Sharptail Snake	W	F
Pituophis melanoleucus	Gopher Snake	W	T
Thamnophis sirtalis	Common Garter Snake	W	T-A
Thamnophis couchi	Western Aquatic Garter Snake	W	A
Thamnophis elegans	Western Terrestrial Garter Snake	W	T
Thamnophis ordinoides	Northwestern Garter Snake	W	T
Lampropeltis getulus	Common Kingsnake	W	T
Lampropeltis zonata	California Mountain Kingsnake	W	T
Family Viperidae			
Crotalus viridis	Western Rattlesnake	W	T

N = 26 species of amphibians + 19 species of reptiles.

Codes: Distribution: W = Widespread; L = Highly localized or regional
Habitat + Habit: A = Aquatic; T = Terrestrial; C = Climbing;
F = Forest-dwelling; S = Shrub-dwelling.

TABLE 2

Species list of amphibians and reptiles, general distribution, and habit/habitat characteristics for temperate rainforests of southern South America. See end of table for codes

Lista de especies de anfibios y reptiles, su distribución general y características de su hábito/hábitat en bosques templados lluviosos del sur de Sudamérica. Véase el pie de la tabla para los códigos

Taxa	Distribution	Habit/ Habitat
Class Amphibia		
Order Anura		
Family Leptodactylidae		
Alsodes monticola	W	T-F
Alsodes barrioi	L	T-F
Alsodes gargola	L	A
Alsodes vanzolinii	L	T-F
Atelognathus grandisonae	L	A?
Atelognathus nitoi	L	A
Batrachyla antartandica	L	T-F
Batrachyla leptopus	W	C-F
Batrachyla taeniata	W	T-F
Hylorina sylvatica	W	C-F
Caudiverbera caudiverbera	W	A
Eupsophus roseus	W	T-F
Eupsophus emiliopugini	W	T-F
Eupsophus calcaratus	W	T-F
Eupsophus vertebralis	W	T-F
Eupsophus migueli	L	T-F
Eupsophus contulmoensis	L	T-F
Insuetophrynus acarpicus	L	A
Pleurodema bufonina	W	T-F
Pleurodema thaul	W	T-F
Telmatobufo australis	L	T-F-A
Telmatobufo venustus	L	A-F
Telmatobufo bullocki	L	A-F
Family Rhinodermatidae		
Rhinoderma darwini	W	T-F
Rhinoderma rufum	L	T-F
Family Bufonidae		
Bufo chilensis	W	T-F
Bufo rubropunctatus	L	T-F
Bufo variegatus	W	T-F
Class Reptilia		
Order Squamata		
Family Tropiduridae		
Liolaemus chiliensis	W	C-S
Liolaemus cyanogaster	W	C-S
Liolaemus lemniscatus	W	T
Liolaemus monticola villaricensis	W	T
Liolaemus nitidus	W	T
Liolaemus pictus	W	C-S-F
Liolaemus tenuis	W	C-S
Pristidactylus torquatus	L	C-F
Family Colubridae		
Philodryas chamissonis	W	F-S
Tachymenis chilensis	W	F

N = 28 species of amphibians (all anurans) + 10 species of reptiles.

Codes: Distribution: W = Widespread; L = Highly localized or regional
Habitat + Habit: A = Aquatic; T = Terrestrial; C = Climbing;
F = Forest-dwelling; S = Shrub-dwelling.

TABLE 3

Species list of mammals, general distribution, habit/habitat characteristics, and their trophic characteristics in Pacific Northwest temperate forests, USA. See end of table for codes

Lista de especies de mamíferos, su distribución general, características de sus hábitos/hábitat, y sus características tróficas en bosques templados del Noroeste Pacífico, EE.UU. Véase el pie de la tabla para los códigos

Taxa		Distribution	Habit	Trophic
Order Marsupialia				
Family Didelphidae				
Didelphis virginiana	Virginia Opossum	W	C-T	O
Order Insectivora				
Family Talpidae				
Neurotrichus gibbsi	Shrew Mole	W	F	I
Scapanus orarius	Coast Mole	W	F	I
Scapanus townsendii	Townsend's Mole	W	F	I
Scapanus latimanus	Broad-footed Mole	W	F	I
Family Soricidae				
Sorex bendirii	Pacific Water Shrew	W	T	I
Sorex cinereus	Masked Shrew	W	T	I
Sorex monticolus	Dusky Shrew	W	T	I
Sorex pacificus	Pacific Shrew	L	T	I
Sorex palustris	Water Shrew	L	A	I
Sorex trowbridgii	Trowbridge's Shrew	W	T	I
Sorex vagrans	Wandering Shrew	W	T	I
Order Chiroptera				
Family Vespertilionidae				
Antrozous pallidus	Pallid Bat	W	AR	I
Myotis californicus	California Myotis	W	AR	I
Myotis evotis	Long-eared Myotis	W	AR	I
Myotis lucifugus	Little Brown Bat	W	AR	I
Myotis keenii	Keen's Myotis	W	AR	I
Myotis volans	Long-legged Bat	W	AR	I
Myotis thysanodes	Fringed Myotis	W	AR	I
Myotis subulatus	Small-footed Myotis	W	AR	I
Myotis yumanensis	Yuma Myotis	W	AR	I
Eptesicus fuscus	Big Brown Bat	W	AR	I
Lasionycteris noctivagans	Silver-haired Bat	W	AR	I
Lasiurus cinereus	Hoary Bat	W	AR	I
Plecotus townsendii	Townsend's Big-eared Bat	W	AR	I
Order Lagomorpha				
Family Leporidae				
Lepus americanus	Snowshoe Hare	W	T	H
Order Rodentia				
Family Aplodontidae				
Aplodontia rufa	Mountain Beaver	L	T	H
Family Sciuridae				
Eutamias townsendii	Townsend's Chipmunk	W	C	O-M
Eutamias amoenus	Yellow Pine Chipmunk	W	C	O-M
Glaucomys sabrinus	Northern Flying Squirrel	W	C	M-L
Tamiasciurus douglasi	Chickaree/Douglas Squirrel	W	C	M-O
Sciurus griseus	Western Gray Squirrel	W	C	G-M
Spermophilus lateralis	Golden-mantled Ground Squirrel	W	T	G
Spermophilus saturatus	Cascade Golden-mantled Ground Squirrel	L	T	M
Family Castoridae				
Castor canadensis	Beaver	W	A	H
Family Cricetidae				
Neotoma fuscipes	Dusky-footed Woodrat	W	T	H
Neotoma cinerea	Bushy-tailed Woodrat	W	T	H-M
Peromyscus maniculatus	Deer Mouse	W	T	O
Peromyscus oreas	Forest Deer Mouse	L	T	O
Family Arvicolidae				
Arborimus albipes	White-footed Vole	L	C	H
Arborimus longicaudus	Red Tree Vole	L	C	H
Clethrionomys californicus	Western Red-backed Vole	W	T	M
Clethrionomys gapperi	Red-backed Vole	W	T	H-M

Taxa		Distribution	Habit	Trophic
Microtus longicaudus	Long-tailed Vole	W	T	H-M
Microtus oregoni	Oregon Vole	W	T	H-M
Microtus townsendii	Townsend's Vole	W	T	H
Phenacomys intermedius	Heather Vole	L	T	H-M
Ondatra zibethica	Muskrat	W	A	H-I
Family Muridae				
Mus musculus	House Mouse	W (I)	T	O
Rattus rattus	Black Rat	W (I)	T	O
Rattus norvegicus	Norway Rat	W (I)	T	O
Family Zapodidae				
Zapus trinotatus	Pacific Jumping Mouse	W	T	G
Family Erethizontidae				
Erethizon dorsatum	Porcupine	W	T	H
Order Carnivora				
Family Canidae				
Canis latrans	Coyote	W	T	C
Vulpes fulva	Red Fox	W (I)	T	C
Urocyon cinereoargenteus	Gray Fox	W	T	C
Family Procyonidae				
Procyon lotor	Raccoon	W	T	O
Bassariscus astutus	Ringtail	L	T	O
Family Ursidae				
Ursus americanus	Black Bear	W	T	O
Ursus arctos	Grizzly Bear	L	T	O
Family Mustelidae				
Lutra canadensis	River Otter	W	A	C
Martes americanus	Marten	W	T	C
Martes pennanti	Fisher	W	T	C
Mephitis mephitis	Striped Skunk	W	T	O
Spilogale putorius	Spotted Skunk	W	T	O
Mustela erminea	Ermine	W	T	C
Mustela frenata	Long-tailed Weasel	W	T	C
Mustela vison	Mink	W	A	C
Family Felidae				
Felis concolor	Puma	W	T	C
Lynx rufus	Bobcat	W	T	C
Lynx canadensis	Canadian Lynx	W	T	C
Order Artiodactyla				
Family Cervidae				
Cervus canadensis	Canadian Elk	W	T	H
Odocoileus hemionus	Black-tailed Deer	W	T	H
N = 73 species				

Codes: Distribution: W = Widespread; L = Highly localized or regional distribution;
Habit: F = Fossorial; SF = Semifossorial; A = Aquatic; C = Climbing/Arboreal;
T = Terrestrial/Scansorial; AR = Flying
Trophic: F = Frugivore; H = Herbivore/Folivore; G = Granivore;
I = Insectivore/Invertebrate; M = Mycophagous; O = Omnivore;
C = Carnivore
(I) = Introduced

extremely diversified group that utilize both aquatic and terrestrial habitats; most southern temperate rainforest species tend to be primarily terrestrial. Combined with the bufonids and rhinodermatids, a minimum of 20 of the 28 southern amphibians are terrestrial (Table 2). In Pacific Northwest forests, these anuran groups are largely replaced by salamanders; of the 18 species, 15 species are primarily terrestrial. Combined with the bufonid and hylid frogs, these constitute 17 terrestrial species out of a total of 26 (Table 1). Most. of these species are forest dwellers and have therefore not been further subdivided. Terrestrial habitat subdivisions are somewhat more difficult to assess among reptiles, but southern temperate rainforests unlike those in the Pacific Northwest appear to lack deep forest-dwelling

TABLE 4

Species list of mammals, general distribution, habit/habitat characteristics, and their trophic characteristics in temperate rainforests of southern South America. See end of table for codes

Lista de especies de mamíferos, su distribución general, características de sus hábitos/hábitat, y sus características tróficas en bosques templados lluviosos del sur de Sudamérica. Véase el pie de la tabla para los códigos

Taxa		Distribution	Habit	Trophic
Order Marsupialia				
Family Microbiotheriidae				
Dromiciops australis	Colocolo Opossum	W	C	I
Family Caenolestidae				
Rhyncholestes raphanurus	Long-Snout Rat-opossum	W	T	I
Order Chiroptera				
Family Vesptertilionidae				
Myotis chiloensis	Chiloé Bat	W	AR	I
Histiotus montanus	Big-eared Bat	W	AR	I
Lasiurus borealis	Red Bat	W	AR	I
Lasiurus cinereus	Hoary Bat	W	AR	I
Family Molossidae				
Tadarida brasiliensis	Free-tailed Bat	W	AR	I
Order Lagomorpha				
Family Leporidae				
Lepus europaeus	European Hare	W (I)	T	H
Oryctolagus cuniculus	European Rabbit	W (I)	T	H
Order Rodentia				
Family Cricetidae				
Oryzomys longicaudatus	Long-tailed Mouse	W	T	G
Akodon longipilis	Long-haired Mouse	W	T	O-M
Akodon sanborni	Sanborn's Mouse	L	T	O-M
Akodon olivaceus	Olivaceous Field Mouse	W	T	O-M
Geoxus valdivianus	Mole Mouse Valdivian	W	SF	I
Chelemys macronyx	Mole Mouse Mountain	L	SF	F-O
Irenomys tarsalis	Arboreal Mouse	W	C	F-G
Auliscomys micropus	Austral Greater Mouse	L	T	F-G
Family Muridae				
Mus musculus	House Mouse	W (I)	T	O
Rattus rattus	Black Rat	W (I)	T	O
Rattus norvegicus	Norway Rat	W (I)	T	O
Family Myocastoridae				
Myocastor coypus	Nutria (Coypu)	W	A	H
Family Octodontidae				
Aconaemys fuscus	Great Rock-rat	L	SF	H
Aconaemys sagei	Sage's Rock-rat	L	SF	H
Octodon bridgesi + *Octodon* sp. (Argentina)	Bridges' degu + Degu sp. Argentina)	L	T	H
Order Carnivora				
Family Canidae				
Pseudalopex (=Dusicyon) culpaeus	Colpeo Fox	W	T	C
Pseudalopex (=Dusicyon) griseus	Gray Fox	W	T	C
Pseudalopex (=Dusicyon) fulvipes	Chiloé Fox	L	T	C
Family Mustelidae				
Galictis cuja	Lesser Grison	W	T	C
Conepatus chinga	Hog-nosed Skunk	W	T	C
Lutra provocax	River Otter Southern	W	A	C
Mustela frenata	Long-tailed Weasel	L (I)	T	C
Mustela vison	Mink	W (I)	T	C
Family Felidae				
Felis concolor	Puma	W	T	C
Felis guigna	Austral Spotted Cat	W	T	C
Order Artiodactyla				
Family Cervidae				
Pudu pudu	Sourthern Pudu	W	T	H
Hippocamelus bisculus	Southern guemal	W	T	H
Cervus elaphus	Red Deer	W (I)	T	H

N = 37 species.

Codes:
- Distribution: W = Widespread; L = Highly localized or regional distribution;
- Habit: F = Fossorial; SF = Semifossorial; A = Aquatic; C = Climbing/Arboreal; T = Terrestrial/Scansorial; AR = Flyin
- Trophic: F = Frugivore; H = Herbivore/Folivore; G = Granivore; I = Insectivore/Invertebrate; M = Mycophagous; O = Omnivore; C = Carnivore
- (I) = Introduced

lizards; both areas have at least two forest-dwelling snakes (Tables 1 and 2).

Patterns of functional habit are a bit more complex among mammals. Excluding volant mammals (bats), a somewhat lower proportion of species are fossorial or semi-fossorial in Pacific Northwest forests (4/60 species or 6.7%; Table 3) vs. southern temperate rainforests (4/32 species, 12.5%; Table 4). This is counterbalanced by a higher proportion of climbing or arboreal species in Pacific Northwest forests, most of them sciurids (8/60 species or 13.3%; Table 4). In contrast, only two species in South America are at least partially arboreal (*Dromiciops australis* and *Irenomys tarsalis*; 2/32 species or 6.3%; Table 4). Virtually all remaining mammal species in both forests are terrestrial/scansorial with the exception of two to five aquatic species in each. Volant mammals make up a larger proportion of species in Pacific Northwest forests (13/73 or 17.8%, versus 5/37 or 13.5% in southern temperate forests; Tables 3 and 4).

Trophically, 32.9% of Pacific Northwest forest mammals are primarily insect/invertebrate consumers (n = 24; Table 3); without bats, the proportion is still high (18.3%, n = 11). This is largely due to the importance of members of the order Insectivora which are always insect/invertebrate consumers. In southern temperate forests, eight mammal species (21.6%) are insect/invertebrate consumers; this figure drops to three species (9.4%) if bats are excluded (Table 4). While the proportion of true carnivore species (i.e., flesh eaters) is lower in North America vs. South America (12/73 species or 16.4% versus 10/37 species or 27.0%, respectively), if we include insect/invertebrate eating species (following Harris 1984), the number and proportion of broadly defined carnivore species is virtually identical in Pacific Northwest and southern temperate rainforests (36/73, and 18/37 or 49.3%, and 48.7%, respectively). The proportion of herbivorous species is also very similar in each region (16/73, and 9/37 or 21.9%, and 24.3%, respectively). However, mammal species classified as herbivores here are usually not occupants of deep forest but rather of forest edges, clearings, meadows, and running water adjacent to forests. Finally, the proportions of omnivorous species are similar in each region (14/73 or 19.2%, and 7/37 or 16.2% for Pacific Northwest, and southern temperate forests, respectively; Tables 3 and 4). Frugivory and granivory are generally rare among small mammals of both forest regions –4.1% to 10.8%. Although only four species (5.5%) in the Pacific Northwest are primarily mycophagous, a total of 12 species (16.4%) are at least partially mycophagous; for southern temperate forests, three species (8.1%) are partially mycophagous. Calvo *et al.* (1989) reported the fungi in stomachs of three additional rainforest rodents in Argentina (*Chelemys, Auliscomys,* and *Oryzomys*; Table 4), but it is unclear if this constitutes a significant proportion of the diet. Here we have considered mycophagy a feeding specialization separate from frugivory unlike Pearson (1983).

Site species density

Because of differences in methodology, it is difficult to make direct comparisons of site diversities, biomass, and densities of vertebrate taxa between temperate rainforests of different continents. For reptiles and amphibians on southern forests, we used the list of Cei (1962), Meserve (pers. observ.), local authorities (amphibians: Dr. J. Ramón Formas, Universidad Austral de Chile, Valdivia; reptiles: Dr. Juan Carlos Ortiz, Universidad de Concepción), and records from the Field Museum of Natural History, Chicago, Illinois to obtain inventories for six areas. In Pacific Northwest forests, we used the results of intensive surveys of amphibians and reptiles of Welsh & Lind (1988), Bury & Corn (1988), Bury *et al.* (1991a, 1991b) in northwestern California, the Washington and Oregon Cascades, the Oregon Coast Range, and Cascade aquatic communities, respectively. The sequence of results of these surveys is presented in Tables 5 and 6 in approximately latitudinal order from more equatorial sites to more polar ones. Generally, sites in both regions have about 8-14

TABLE 5

Summary of amphibian and reptile inventories in four Pacific Northwest temperate forests in northwestern California (NW Cal.), Oregon Cascades (OR Cas.), Oregon Coastal Range (OR Ct. Rg.), the southern Washington Cascades (WA Cas.), and aquatic areas in both Oregon and Washington (Aquat.), USA. Data from Welsh & Lind (1988), Bury & Corn (1988) and Bury *et al.* (1991a) [next three localities], and Bury *et al.* (1991b), respectively. Dashes indicate that inventories of a particular taxon (i.e., reptiles) were not available

Resumen de inventarios de anfibios y reptiles en cuatro bosques templados del Noroeste Pacífico, en el noroeste de California (NW Cal.), las Oregon Cascades (OR Cas.), la Sierra Costera de Oregon (OR Ct. Rg.), las Washington Cascades del Sur (WA Cas.), y áreas acuáticas de Oregon y Washington (Aquat.), EE.UU. Datos de Welsh & Lind (1988), Bury & Corn (1988) y Bury *et al.* (1991a) [próximas tres localidades], y Bury *et al.* (1991), respectivamente. Las líneas cortadas indican que no había datos disponibles para el taxon (i.e., reptiles)

Taxa	NW Cal.	OR Cas.	OR Ct.Rg.	WA Cas.	Aquat.
Class Amphibia					
Order Urodela					
Family Ambystomatidae					
Ambystoma gracile	X	X	X	X	
Dicamptodon copei					X
Dicamptodon ensatus	X	X	X	X	X
Rhyacotriton olympicus	X		X	X	X
Batrachoseps attenatus	X				
Batrachoseps wrighti		X			
Family Salamandridae					
Taricha granulosa	X	X	X	X	
Family Plethodontidae					
Plethodon dunni		X			X
Plethodon vehiculum		X	X	X	
Plethodon elongatus	X				
Plethodon larselli				X	
Ensatina eschscholtzi	X	X	X	X	
Aneides ferreus	X	X	X		
Aneides flavipunctatus	X				
Aneides lugubris	X				
Order Anura					
Family Ascaphidae					
Ascaphus truei	X	X	X	X	X
Family Bufonidae					
Bufo boreas	X				
Family Hylidae					
Hyla regilla	X	X	X	X	
Family Ranidae					
Rana aurora		X	X	X	
Rana boyley	X				
Class Reptilia					
Order Squamata					
Family Iguanidae					
Sceloporus occidentalis	X	X	–		–
Eumeces skiltonianus	X	X	–		–
Gerrhonotus multicarinatus	X		–		–
Gerrhonotus coeruleus	X	X	–	X	–
Family Boidae					
Charina bottae	X	X	–	X	–
Family Colubridae					
Diadophis punctatus	X		–		–
Contia tenuis	X		–		–
Thamnophis sirtalis	X	X	–	X	–
Thamnophis couchi	X		–		–
Thamnophis elegans	X		–		–
Thamnophis ordinoides	X	X	–	X	–
Number of Amphibian Species	14	11	10	10	5*
Number of Reptile Species	11	6	–	4	–
Total Number of Species	25	17	–	14	–

* Incomplete tabulation of species present.

TABLE 6

Summary of amphibian and reptilian inventories in six temperate rainforests of southern South America. Localities are in northern Valdivian forest (Malleco and Concepción Provinces, Chile: Angol), in central Valdivian forests (Valdivia, Osorno, Llanquihue, and Chiloé: Vald., LaPic, Llan. and Chiloé), and in northern Patagonian forest (Aysén Province: Aysén). Data from Cei (1962), Meserve (pers. observ.), Drs. J. Ramón Formas and Juan Carlos Ortiz (pers. comm.), and Field Museum of Natural History records, Chicago, Illinois (USA)

Resumen de inventarios de anfibios y reptiles en seis bosques templados lluviosos del sur de Sudamérica. Las localidades están en el bosque valdiviano del norte (Provincias de Malleco y Concepción, Chile: Angol), en el bosque valdiviano central (Provincias de Valdivia, Osorno, Llanquihue y Chiloé: Vald., LaPic, Llan. y Chiloé), y en el bosque patagónico del norte (Provincia de Aysén: Aysén). Datos de Cei (1962), Meserve (observ. pers.), Drs. J. Ramón Formas y Juan Carlos Ortiz (com. pers.) y de los archivos del Field Museum of Natural History, Chicago, Illinois (EE.UU.)

Taxa	Angol	Vald.	LaPic	Llan.	Chiloé	Aysén
Class Amphibia						
Order Anura						
Family Leptodactylidae						
Alsodes monticola			X			
Alsodes barrioi	X					
Batrachyla antartandica			X	X	X	
Batrachyla leptopus		X	X	X	X	
Batrachyla taeniata	X	X	X	X	X	
Hylorina sylvatica		X	X	X	X	X
Caudiverbera caudiverbera	X	X		X		
Eupsophus roseus	X	X				
Eupsophus emiliopugini			X	X	X	
Eupsophus calcaratus			X	X	X	
Eupsophus vertebralis		X				
Eupsophus migueli		X				
Insuetophrynus acarpicus		X				
Pleurodema bufonina						X
Pleurodema thaul	X	X	X	X	X	X
Telmatobufo bullocki	X					
Family Rhinodermatidae						
Rhinoderma darwini	X	X	X	X	X	X
Family Bufonidae						
Bufo chilensis	X					
Bufo rubropunctatus		X				
Bufo variegatus			X	X		X
Class Reptilia						
Order Squamata						
Family Tropiduridae						
Liolaemus chiliensis	X	X				
Liolaemus cyanogaster	X	X			X	
Liolaemus lemniscatus	X					
Liolaemus monticola villaricensis			X			
Liolaemus nitidus	X					
Liolaemus pictus	X	X	X	X	X	
Liolaemus tenuis	X	X	X			
Liolaemus sp.	X	X	X	X	X	X
Pristidactylus torquatus	X	X			X	
Family Colubridae						
Philodryas chamissonis	X					
Tachymenis chilensis	X	X	X	X	X	
Number of Amphibian Species	8	11	10	10	8	5
Number of Reptile Species	10	7	5	3	5	1
Total Number of Species	18	18	15	13	13	6

species of amphibians; in Pacific Northwest forests, these are dominated by salamanders, while all amphibians in southern temperate rainforests are anurans. As noted previously, the southern temperate rainforest region in general lacks many aquatic species such as the ranids, and this contributes some of the difference in total species numbers between the two regions. In terrestrial situations, Aubrey & Hall (1989), and Gilbert & Allwine (1989) noted strong correlations between amphibian species number and moisture (positive), and elevation (negative). A similar situation was reported by Formas (1979) for southern forest amphibians. Amphibian assemblages in precordilleran forests on the eastern side of the Argentine Andes are extremely similar in composition and richness (R.D. Sage, pers. comm.). Interestingly, both Pacific Northwest and southern temperate forests show little change in amphibian species numbers except at the most polar sites. That observed in the Pacific Northwest is primarily due to the loss of salamanders (Table 6). Numbers of reptiles decline substantially in more polar forests on both continents; therefore, this group seems particularly sensitive to changes related to latitude in temperate rainforests. It should be noted that on both continents, reptiles are rare faunal members of deep forest; for example, their abundances in northwestern California where species density is highest (Table 5) average only 1-2% of amphibian densities (Welsh & Lind 1988), and apparently decline with stand age (Raphael 1988). A similar pattern is present in southern temperate rainforests, and reptiles seem to be only secondary components of the forest herpetofauna preferring rather, rocky areas, open, shrubby clearings, and regions above timberline (Formas 1979).

The situation with respect to the availability of point (= site) estimates for mammals is somewhat better. Meserve *et al.* (1982, 1991, in press), Pearson & Pearson (1982), Pearson (1983), Murúa & González (1985, 1986), Murúa *et al.* (1986, 1987), and Patterson *et al.* (1989) have provided descriptions and species lists for three Valdivian rainforests in Chile and Argentina. In North America, Raphael (1988), Gilbert (1989), Corn & Corn (1989) and Corn & Bury (1991), Gashwiler (1959, 1970) and Tevis (1956), and West (1991) have reported on results of intensive surveys in northwestern California, the Oregon Cascades, the Oregon Coast Range, Washington and Oregon Douglas-fir forests, and the southern Washington Cascades, respectively. Surprisingly, there still remains no quantitative inventory of specific sites in Olympic rainforests, and Pearson (1983) utilized the data of Svihla & Svihla (1933); Johnson & Johnson (1952) is an additional reference. For larger mammals, only data from northwestern California, and the Washington Cascades are presented from Raphael (1984, 1988), and Dr. Steven D. West (pers. comm.), respectively, in Table 7.

In general, small mammal assemblages are very similar between forests within a continent with respect to number of species; interestingly, whereas Pacific Northwest forests tend to have a higher species richness, there are many species not shared between specific sites. In contrast, southern temperate rainforests tend to have lower species richness, and virtually all the same species (i.e., they have lower beta or between habitat diversity) as compared to Pacific Northwest forests. This finding is similar to that reported by Cody *et al.* (1977) for mediterranean scrub communities in Chile and California. In comparisons of point diversity between the three southern temperate forests given in Table 8, Meserve *et al.* (in press) noted that although total species richness was about the same, primary growth forests (La Picada in Chile, and Puerto Blest + Río Castaño Overo in Argentina) have much higher species diversity (H') due primarily to differences in evenness (J'). Secondary growth forests such as those in San Martín, Chile tend to be numerically dominated by only two or three small mammal species.

Thomas (1988) and Thomas & West (1989) report some of the first quantitative species lists of chiropterans in

TABLE 7

Summary of mammal inventories in five Pacific Northwest temperate forests in northwestern California (NW Cal.), the Oregon Cascades (OR Cas.), Oregon and California Douglas-fir forests (Doug-fir), Oregon Coast Range (OR Ct. Rg.), and the southern Washington Cascades (WA Cas,). Data from Raphael (1988), Gilbert (1989), Tevis (1956) and Gashwiler (1970), Corn & Corn (1989) and Corn & Bury (1991), and West (1991), respectively. Additional data on larger mammals from Raphael (1984, 1988), and West (pers. comm.) for northwestern California, and Washington Cascades, respectively. Dashes indicate data was not available for larger mammals

Resumen de inventarios de mamíferos en cinco bosques templados del Noroeste Pacífico, EE.UU., en el noroeste de California (NW Cal.), las Oregon Cascades (OR Cas.), bosques de Douglas-fir en Oregon y California (Doug-fir), la Sierra Costera de Oregon (OR Ct. Rg.), y las Washington Cascades del sur (WA Cas.). Datos de Raphael (1988), Gilbert (1989), Tevis (1956) y Gashwiler (1970), Corn & Corn (1989) y Corn & Bury (1991), y West (1991), respectivamente. Datos adicionales para grandes mamíferos de Raphael (1984, 1988), y West (pers. comm.) para el noroeste de California, y las Washington Cascades, respectivamente. Las líneas cortadas indican que no existen datos para grandes mamíferos

Taxa	NW Cal.	OR Cas.	Doug-Fir	OR Ct. Rg.	WA Cas.
Order Insectivora					
Family Talpidae					
Neurotrichus gibbsi	X	X	X		X
Scapanus orarius	X	X			X
Scapanus townsendii					X
Scapanus latimanus			X		
Family Soricidae					
Sorex bendirii					X
Sorex cinereus					X
Sorex monticolus		X			X
Sorex pacificus	X			X	
Sorex palustris					X
Sorex trowbridgii	X	X	X	X	X
Sorex vagrans			X		X
Order Lagomorpha					
Family Leporidae					
Lepus americanus			X		X
Order Rodentia					
Family Aplodontidae					
Aplodontia rufa					X
Family Sciuridae					
Eutamias townsendii	X		X		
Eutamias amoenus					X
Glaucomys sabrinus	X	X	X		X
Tamiasciurus douglasi	X	X	X		X
Sciurus griseus		X			X
Spermophilus saturatus					X
Family Cricetidae					
Neotoma cinerea	X		X		X
Neotoma fuscipes			X		
Peromyscus maniculatus	X	X	X	X	X
Peromyscus boylei	X				
Peromyscus truei	X				
Peromyscus oreas					X
Family Arvicolidae					
Arborimus longicaudus	X	X	X	X	
Clethrionomys californicus	X	X	X		
Clethrionomys gapperi	X			X	X
Microtus longicaudus					X
Microtus oregoni	X		X	X	X
Microtus richarsonii					X
Phenacomys intermedius					X
Family Zapodidae					
Zapus trinotatus	X		X		X
Family Erethizontidae					
Erethizon dorsatum	X	–	–	–	X
Order Carnivora					
Family Canidae					
Canis latrans	X	–	–	–	X

Taxa	NW Cal.	OR Cas.	Doug-Fir	OR Ct. Rg.	WA Cas.
Vulpes vulpes		–	–	–	X
Urocyon cinereoargenteus	X	–	–	–	
Family Procyonidae					
Procyon lotor	X	–	–	–	X
Bassariscus astutus	X	–	–	–	
Family Ursidae					
Ursus americanus	X	–	–	–	X
Ursus arctos		–	–	–	X
Family Mustelidae					
Lutra canadensis		–	–	–	X
Martes pennanti	X	–	–	–	X
Mephitis mephitis	X	–	–	–	X
Spilogale putorius	X	–	–	–	X
Mustela erminea	X	–	–	–	X
Mustela frenata	X	–	–	–	X
Mustela vison	X	–	–	–	X
Family Felidae					
Felis concolor		–	–	–	X
Lynx rufus	X	–	–	–	X
Order Artiodactyla					
Family Cervidae					
Cervus elaphus		–	–	–	X
Odocoileus hemionus	X	–	–	–	X
Number of Small Mammal Species	16	17*	15	6**	25
Total Number of Mammal Species	30	–	–	–	42

* Not all species identified in tabulations; total species number given.
** Total species number was not reported.

TABLE 8

Summary of small mammal inventories in three temperate rainforests in Chile and Argentina. Forests are: coastal secondary growth forest, San Martín, Chile (SanMt); precordilleran primary forest, La Picada, Chile (LaPic); montane primary growth forests, Puerto Blest, and Río Castaño Overo, Argentina (Argt.). Data are from Murúa & González (1985, 1986), Murúa *et al.* (1986, 1987), and Meserve (pers. observ.) for San Martín; Meserve *et al.* (1982, 1991) and Patterson *et al.* (1989) for La Picada; and Pearson & Pearson (1982) and Pearson (1983) for Argentina

Resumen de inventarios de mamíferos en tres bosques templados lluviosos del sur de Sudamérica. Los bosques son: bosque secundario de la costa, San Martín, Chile (SanMt); bosque primario de la precordillera, La Picada, Chile (LaPic); y bosques primarios montañosos, Puerto Blest y Río Castaño Overo, Argentina (Argt.). Datos de Murúa & González (1985, 1986), Murúa *et al.* (1986, 1987) y Meserve (observ. pers.) para San Martín; Meserve *et al.* (1982, 1991, en prensa) y Patterson *et al.* (1989) para La Picada; y Pearson & Pearson (1982) y Pearson (1983) para Argentina

Taxa	SanMt	LaPic	Argt.
Order Marsupialia			
Family Microbiotheriidae			
Dromiciops australis	X	X	X
Family Caenolestidae			
Rhyncholestes raphanurus		X	
Order Rodentia			
Family Cricetidae			
Oryzomys longicaudatus	X	X	X
Akodon longipilis	X	X	X
Akodon sanborni	X	X	
Akodon olivaceus	X	X	X
Geoxus valdivianus	X	X	X
Chelemys macronyx	X		X
Irenomys tarsalis	X	X	X
Auliscomys micropus	X	X	X
Family Muridae			
Rattus sp.	X		X
Number of Small Mammal Species	10	9	9

Pacific Northwest forests. These are summarized in Table 9; between eight and 11 species of bats may be present in Pacific Northwest forests although usually at low densities, indicating that they utilize this habitat primarily for roosting sites (Thomas 1988). Virtually nothing is known of bat species numbers in southern temperate rainforests, but with a maximum of only five species present in the entire region (Table 4), potential species richness at specific sites is at least considerably lower.

Total mammal species number at specific sites in Pacific Northwest forests is probably around 40-45 (Tables 7 and 9). Pearson (1983), using Svihla & Svihla (1933), concluded that there were about 32 species in Olympic forests excluding bats. Table 7 provides an estimate of 30 non-volant mammals from northwestern California, and 42 species in the Washington Cascades; if bats were added (Table 9), the total number would probably be about to 40-50 species for each area, respectively. The estimate of 57 species given by Harris (1984) for Oregon forests seems high probably due to use of cumulative records from many sites. The comparable number of mammals for specific sites in southern temperate forests is probably about 25 (Tables 4 and 8); the figure of 31 species for temperate rainforests in Malleco given by Lacher & Mares (1986) from the list of Greer (1965) may also be an overestimate due to the inclusion of non-forest species. Excluding bats, Pearson (1983) reported that only 16 mammal species were present in southern Argentina. He also noted that very small bodied mammals (< 25 g) and larger bodied ones (> 100 g) were poorly represented there, as compared to Olympic forests; the fauna of the latter area also has a more uniform distribution of body sizes among resident mammals (Pearson 1983).

Related to the above, the Douglas-fir forests as a whole have 22 native mammal species exceeding 1 kg; of these, 16 are Carnivora, and at least 12 may be considered true carnivores (Harris 1984). Added to the Insectivora plus reptiles and amphibians which may be considered broadly "carnivorous", 65% of the terrestrial vertebrates in the western Cascade forests may be considered carnivorous (Harris 1984). A similar calculation for southern temperate rainforests for broadly carnivorous mammals plus reptiles and amphi-

TABLE 9

Summary of bats netted and detected with ultrasonic detectors in the Pacific Northwest temperate forests, USA, in the western Cascades (West. Cas.), and Coast Range of Washington and Oregon (Cst. Rg.). Data from Thomas (1988) and Thomas & West (1989)

Resumen de murciélagos atrapados en redes y descubiertos con detectores ultrasónicos en los bosques templados del Noroeste Pacífico, EE.UU. en los Cascades del Oeste (West. Cas.), y la Sierra Costera de Washington y Oregón (Cst. Rg.). Datos de Thomas (1988), y Thomas & West (1989)

Taxa		West. Cas.	Cst. Rg.
Order Chiroptera			
Family Vespertilionidae			
Myotis californicus	California Myotis	X	X
Myotis evotis	Long-eared Myotis	X	X
Myotis lucifugus	Little Brown Bat	X	
Myotis volans	Long-legged Bat	X	X
Myotis thysanodes	Fringed Myotis	X	X
Myotis subulatus	Western Small-footed Myotis	X	X
Myotis yumanensis	Yuma Myotis	X	X
Eptesicus fuscus	Big Brown Bat	X	X
Lasionycteris noctivagans	Silver-haired Bat	X	X
Lasiurus cinereus	Hoary Bat	X	
Plecotus townsendii	Townsend's Big-eared Bat	X	
Total Number of Bat Species		11	8

bians yields a figure of 69.5% indicating that the same pattern prevails. With respect to habit, Pearson (1983) commented on the low number of arboreal forms in southern temperate rainforests; a similar observation was made by Glanz (1982), and is generally confirmed here.

DISCUSSION

A number of potentially significant patterns emerges from this consideration of terrestrial vertebrate assemblages in northern and southern temperate rainforests. Regional species richness of amphibians is similar, but a majority of species in Pacific Northwest forests are salamanders while all those in southern temperate forests are anurans. Although anurans are usually considered more dependent on water for at least a portion of their life cycle, a lower proportion of the southern temperate amphibian fauna is aquatic. Species richness in specific forests is somewhat higher in the Pacific Northwest, but the proportion of localized distributions among native amphibians is lower. Although reptile species richness is higher in Pacific Northwest forests, this class contributes little to total herpetofaunal diversity within forested areas on both continents. Snakes are more important in Pacific Northwest forests, and lizards more so in southern temperate ones; however, the latter group does not occupy dense forest habitats of South America.

Among mammals, regional and point (site) species richness is much higher in Pacific Northwest forests; this is primarily due to the contributions of members of the Insectivora (shrews and moles), Sciuridae (squirrels), Arvicolidae (voles), and Chiroptera (bats). Members of the first three taxa are entirely absent in southern temperate rainforests. The lack of sciurids in southern South America contributes particularly to the noteable absence of arboreal mammals in southern temperate forests. Using Harris's (1984) categorization of broadly carnivorous mammals as including insectivorous groups, trophically there is a large proportion of carnivorous forms and a relatively low proportion of frugivorous-granivorous mammals in both regions. Mycophagous habits are also important in mammals inhabitating forests of both regions although apparently more so in the Pacific Northwest.

In attempting to explain these differences, it is useful to examine the influence of three potential factors: geological history, geographic isolation, and resource availability.

It has already been noted that the Pacific Northwest and southern South American temperate forests share similar geological histories and climates; to the extent that such factors may have influenced the development of their respective faunas, we might have expected the similarities documented to exist. As a reference point, it is useful to note comparisons that have been made with faunas of other Western Hemispheric forest regions. Fleming (1973) compared trends in mammal species numbers in seven forests ranging from northern boreal to tropical forests in North and Central America. He noted an increase in species number from 16 in Alaska to 31-35 in mid-latitudinal temperate deciduous forests; Barbour (1951) reported a similar number of mammal species (31) in a Kentucky deciduous forest. As noted before, specific sites in Pacific Northwest forests appear to support a somewhat higher number (40-50) of species. Tropical forests in Panama, Brazil, and Peru clearly have more mammal species than either group of temperate forests (Fleming 1973; Glanz 1982; Lacher & Mares 1986) —up to 70 or more species. The fact that Pacific Northwest forests are noteably richer in mammal species number than either temperate deciduous forests elsewhere in North America or southern temperate rainforests suggests that historical patterns of evolution and diversification may be important. Simpson (1964), and Hagmeier & Stults (1964) called attention to the increase in species density and percentage of endemic mammal species in the Pacific Northwest, and the western forest province generally relative to the rest of North America. The dissimilarity between mammal species numbers in temperate rainforests in North and South America might argue against a major role for similar recent geological events in affecting diversity in both regions. On the other hand, Kiester (1971) noted a decrease in amphibian and reptile species density proceeding towards the Pacific Northwest. Given the similarity of amphibian species numbers between temperate rainforests in North and South America, it might be tempting to attribute this to convergent geological histories; since amphibians are a much older group, relatively recent geological events may have had less impact on them in contrast to more ancient continental drift events. Again, similar to mammals, tropical areas have much higher total numbers of amphibian species –between 126 and 225 species in three South American forests (Lynch 1979).

Geographic isolation could partially account for the differences in species numbers between forests. The southern temperate rainforest is much more isolated due to a gap of at least 1,000 km from all other South American forests. Duellman (1979b) has noted the effectiveness of high altitude passes in reducing herpetofaunal dispersal between opposite sides of the Andes; however, passes are low enough in the southern temperate rainforest district to allow interchange and a high degree of similarity between assemblages on opposite sides. Regionally, the southern temperate rainforest herpetofauna shows the least faunal similarity to other South American assemblages indicating that isolation could indeed have influenced its composition; yet at least for amphibians, total species richness is not discernibly poorer than that of Pacific Northwest forests. Salamanders are replaced by anuran frogs, most in the family Leptodactylidae, which are considered to be an ancient Gondwanaland element (Cracraft 1974). Within the southern temperate rainforests, the effects of isolation may also be reflected in relatively localized distributions among many anuran species and genera. The herpetofauna of Pacific Northwest forests shows a pronounced decrease in species number proceeding northward which is due primarily to the loss of reptile and urodele components (Table 5). In the southern temperate forests, there is a similar loss of reptile species to the south, but little change in amphibian (anuran) species numbers until the extreme southern end (Table 6) even though most are terrestrial (Table 2). It may be significant that there appears to be relatively little change in mean annual temperature within lower elevational southern temperate rainforests even as far south as Puerto Aysén due to proximity to the sea and moderating effects of high rainfall (Miller 1976; Prohaska 1976; Meserve *et al.* 1991; these conditions may ameliorate normal latitudinal effects on amphibian diversity.

For mammals, the role of isolation has been more dramatic. Modern mammal groups entered South America relatively recently, and a number of originally Laurasian groups are still poorly represented (or entirely absent) on the continent as a whole (e.g., Insectivora, Sciuridae, Arvicolidae, Heteromyidae). The absence of the first three groups accounts for much of the difference in species richness between Pacific Northwest and southern temperate forests. The family Cricetidae entered South America in the early to mid-Pliocene, but underwent spectacular radiation such that half of the known New World species are now found there (Hershkovitz 1972). This group accounts for most of the rodent genera in southern temperate forests; in Pacific Northwest forests, they make up a small proportion of the Rodentia. Interestingly though, relatively few southern temperate forest mammals have highly localized distributions; in fact many have extremely wide distributions frequently extending into northern semiarid desert, high Andean puna, and southern Patagonia.

The fact that small mammal species numbers decline from south to north in the northern Chilean semiarid region (Meserve & Glanz 1978) have led some to conclude that this is a historical consequence of relatively long-term elevational barriers to trans-Andean dispersal (i.e., Caviedes & Iriarte 1989). Yet, the same process occurs from north to south in the transition between southern Valdivian and northern

Patagonian rainforests for small mammals (Meserve *et al.* 1991) where the Andes become progressively lower. Additionally, near the southern end of this region, mammal species richness rises sharply as Patagonian steppe species become influential (Kelt 1989). Thus, at the southern end of the temperate rainforest in South America, isolation could be important; additionally, Patagonian steppe species show virtually no penetration into temperate rainforest regions (Pearson & Pearson 1982, Pearson 1987, Kelt 1989).

Related to the foregoing, information on ecological specializations of terrestrial vertebrates is intriguing. In particular, Harris (1984) has called attention to the high proportion of carnivorous (including insectivorous) species in Pacific Northwest forests. Including insectivorous and carnivorous birds, 65% of the vertebrates are carnivorous (Harris 1984), but this observation is apparently not unique to Pacific Northwest forests. Jaksić & Feinsinger (1991) reported an even higher figure for insectivorous birds alone (74-89%) in southern temperate rainforests, and this combined with the figure of 69.5% broadly carnivorous terrestrial vertebrates would suggest that the overall figure is somewhat higher on southern forests. In turn, Harris (1984) noted a very small proportion of herbivorous species (28% among terrestrial vertebrates; 24% among all Oregon vertebrates including birds). Our results here confirm the general scarcity of herbivorous species in temperate forests of both regions, but this need not be viewed as necessarily suprising. It should be recognized that the many insectivorous and omnivorous species present are also a potential prey base in addition to insects themselves. Further, alternative foraging groups such as detritivores may be more important in such communities (Harris 1984).

Perhaps more interestingly, whereas the proportion of insectivorous birds is similar between Pacific Northwest and southern temperate rainforests (71-84%; Harris 1984; Jaksić & Feinsinger 1991), the proportion of insectivorous small mammals is discernibly lower in southern forests. While much of this can be attributed to the lack of members of the order Insectivora, it is also perhaps significant that sigmodontine rodent species that are strongly insectivorous elsewhere in Chile (i.e., *Akodon olivaceus* and *A. longipilis*; Meserve 1981a; Glanz 1984) along with related species (*A. sanborni*) are much more omnivorous in southern forests (Meserve *et al.* 1988). Thus, lack of mammalian insectivory may indicate a relative scarcity of this resource in southern temperate forests; significantly perhaps, the consumption of insects and other invertebrates among southern rainforest small mammals increases in warmer summer months (Meserve *et al.* 1988). On the other hand, these forests have a wholly endemic family of ground-feeding insectivorous birds, the Rhinocryptidae, which have no equivalents in Pacific Northwest forests, and which may form an important group of competitors for insectivorous mammals (Jaksić & Feinsinger 1991). Unfortunately, there is virtually no quantitative information on insect availability in temperate rainforests in general, and therefore, conclusions about the relative importance or abundance of insects must be necessarily speculative.

Fogel & Trappe (1978), Maser *et al.* (1978a, 1978b) and Maser & Maser (1987) have strongly emphasized the importance of mycophagy among Pacific Northwest small mammals including squirrels and mice, and possible coevolutionary relationships between consumers and myocorrhizal fungi and ultimately, host trees. A number of southern rainforest small mammals are also mycophagous especially in cooler winter months (Meserve *et al.* 1988, Calvo *et al.* 1989), but it is difficult to determine if a potential coevolutionary relationship exists there as well. Jaksić & Fesinger (1991) noted the absence of mycophagous birds in both regions, but this trophic habit is rare among birds generally. Cork & Kenagy (1989) found that hypogeous fungi are not a high quality dietary item for mycophagous Cascade golden-mantled ground squirrels (*Spermophilus saturatus*) in Washington Douglas-fir forests; therefore, their dietary value is derived from high availability and relatively low energetic cost of consumption. A similar situation probably exists in southern temperate rainforests for small mammal consumers especially in wetter winter months when insect/invertebrate abundance appears to be lower. Finally, the conspicuous absence of granivorous/frugivorous forms in temperate forests of both regions is noteworthy. Although non-volant mammals in the Pacific Northwest show a larger proportion of arboreal species chiefly composed of sciurids, this is not balanced by any noteable increase in granivory/frugivory due to greater utilization of nuts or seeds of coniferous tree species. In southern temperate rainforests, only one of the four granivorous/frugivorous small mammals is arboreal (i.e., *Irenomys tarsalis*); although *Dromiciops australis* is predominantly arboreal/scansorial, and captive animals readily consume fruits and seed (Kelt & Martínez, 1989), summer diets were strongly insectivorous (Meserve *et al.* 1988). Mares & Rosenzweig (1978), and Brown & Ojeda (1987) have noted the conspicuous lack of mammalian granivores in southern temperate regions generally. This occurs despite the fact that seed availability appears to be at least comparable in semiarid areas (Mares & Rosenzweig 1978; Meserve 1981b). Armesto *et al.* (1987) commented on the wide availability of fruits in southern temperate rainforests; they suggest that in addition to birds, small mammal consumers could be important. However, this is not confirmed in dietary analyses (Meserve *et al.* 1988); only *Oryzomys longicaudatus*, and the relatively uncommon *I. tarsalis* and *Auliscomys micropus* are significant consumers of seeds and fruits; the granivore status of the first species has been confirmed elsewhere in secondary growth rainforests (Murúa & González 1981), and northern semiarid communities (Meserve 1981a).

GENERAL QUESTIONS

This treatment of patterns of species richness, distributions, and ecological attributes of the terrestrial vertebrates in northern and southern temperate rainforests has suggested several questions that are of considerable interest for future research. Unfortunately, questions dealing with the role of evolutionary and assortive processes ("ghosts of competition/predation past") in the development of current faunal assemblages in both regions are difficult to test. While we recognize the importance of such processes, we focus on questions relating to the current structure of these asemblages, their dynamics, and possible explanations for major ecological differences.

1) Are there different levels of specific resources available to consumers in each forest region? What is the availability of insects, seeds, and fruits in each area, and their patterns of temporal and spatial variability throughout the year?

2) What is the proportion of those resources identified in 1) that are actually consumed by vertebrates? Are there periods of the year when the availability of specific types of resources are potentially limited for major consumer groups?

3) To what extent have different evolutionary histories, biogeographical processes, and ecological interactions influenced the direction of assortive processes in structuring vertebrate assemblages? Is there a greater importance of competition, predation or other biotic interactions in different forests? If so, what are the possible explanations for this? Have there been any consequences for the structure and composition of vertebrate assemblages in each?

4) Related to 3), have "tighter" coevolutionary relationships developed in some forests or groups of organisms than others (e.g., small mammal mycophagy and mycorrhizal-host tree relationships)? Are possible differences in such hypothesized relationships related to the relative length of time that the involved organisms have been associated?

In order to begin addressing particularly questions 1) and 2), we need better quantitative estimates of resource availability and utilization by consumers. While some initial efforts have been reported in northern coniferous forests (Wiens & Nussbaum 1975; Long 1982) and in southern temperate rainforests (Armesto *et al.* 1987; Jaksić & Feinsinger 1991), we still lack precise estimates of seed, fruit, and insect availability collected concurrently with consumer group abundance and utilization. Estimates of consumption could be derived from differences between seed and fruit collections in open, unscreened collection devices versus those in netted or otherwise selectively screened collections designed to exclude specific consumer groups. For largely terrestrial consumers, insect and invertebrate availability (and utilization) could be assessed from traps placed in screened and unscreened cages placed around areas of soil and litter on the forest floor. Similarly, soil samples could be used to yield estimates of invertebrate abundance and consumption. Given the high precipitation and rates of decomposition experienced in such forests, collections and small scale experiments such as these must be maintained religiously and collections conducted frequently on a year-round basis.

We also need imaginative applications of large scale experimental techniques in these forests. Field experiments are difficult but not impossible to conduct here (e.g., Murúa *et al.* 1987) It is surprising that despite the recent resurgence of interest in Pacific Northwest forests and their indigenous faunas, there have been very few experimental studies conducted in field situations. This would seem to be necessary in order to begin to assess the importance of biotic interactions such as competition and predation. Experimental manipulations involving exclusions or introductions of indigenous species into specific areas may be the only way to operationally test hypotheses of interspecific competition or the impact of predators on prey populations.

Related to the above, hypotheses of coevolution between, for example, small mammal consumers, mycorrhizal fungi, and their host trees require careful studies of proposed relationships. Again, small scale but carefully replicated experiments involving the exclusion of suggested crucial components of the hypothesized interactions such as small mammals would be highly informative as to the nature of such associations. It may be that the relatively recent arrival of mycophagous sigmodontine rodents and their highly flexible dietary habits in southern temperate rainforests may have led to a less "tight" coevolutionary relationship with fungi and host plants than that suggested by Maser *et al.* (1978a, 1978b) for Pacific Northwest forests. Experiments in both regions would be highly informative here.

There is a certain urgency in this work both in Pacific Northwest and southern temperate rainforests. It was estimated recently that only 7-8% of old growth Douglas-fir forests were left uncut in the Pacific Northwest. Brun (1975; cited in Veblen & Ashton 1978) provided the long outdated estimate of 16% of primary growth temperate rainforests left uncut in southern Chile as of 1952; that figure is certainly much less today (Veblen *et al.* 1983). Pacific Northwest forests have been demonstrated to have significant compositional changes in faunas with logging; a similar process has probably already occurred in logged-over areas in southern temperate regions (Meserve *et al.* 1991). D.A. Kelt (pers. comm.) inventoried a number of forest "islands" in the southern central valley of Chile, and found that they contained an impoverished subset of typical rainforest small mammals. The failure of older (> 80 years) secondary growth forests such as San Martin to reach small mammal diversity levels comparable to those in primary growth forests suggests that such effects may be long-term, and potentially irreversible. The fact that the Chilean government has made colonization of previously undisturbed southern rainforests in the continental "Chile Chico" region part of national policy while at the same time these forests have been shown to possess a reduced herpetofauna and mammalian fauna (Formas 1979; Meserve *et al.* 1991; this paper) indicates the alarm with which we must view the future status of these forests and their biotas. While much attention has rightfully been focused on tropical rainforests, temperate rainforests in much of the world may be in far greater danger of disappearing due to their more restricted distribution and lack of appreciation for their unique indigenous biotas.

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