
Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities

STEPHEN C. TROMBULAK* AND CHRISTOPHER A. FRISSELL†

*Department of Biology, Middlebury College, Middlebury, VT 05753, U.S.A., email trombulak@middlebury.edu

†Flathead Lake Biological Station, University of Montana, 311 Bio Station Lane, Polson, MT 59860-9659, U.S.A.

Abstract: Roads are a widespread and increasing feature of most landscapes. We reviewed the scientific literature on the ecological effects of roads and found support for the general conclusion that they are associated with negative effects on biotic integrity in both terrestrial and aquatic ecosystems. Roads of all kinds have seven general effects: mortality from road construction, mortality from collision with vehicles, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotics, and increased use of areas by humans. Road construction kills sessile and slow-moving organisms, injures organisms adjacent to a road, and alters physical conditions beneath a road. Vehicle collisions affect the demography of many species, both vertebrates and invertebrates; mitigation measures to reduce roadkill have been only partly successful. Roads alter animal behavior by causing changes in home ranges, movement, reproductive success, escape response, and physiological state. Roads change soil density, temperature, soil water content, light levels, dust, surface waters, patterns of runoff, and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments. Roads promote the dispersal of exotic species by altering habitats, stressing native species, and providing movement corridors. Roads also promote increased hunting, fishing, passive harassment of animals, and landscape modifications. Not all species and ecosystems are equally affected by roads, but overall the presence of roads is highly correlated with changes in species composition, population sizes, and hydrologic and geomorphic processes that shape aquatic and riparian systems. More experimental research is needed to complement post-hoc correlative studies. Our review underscores the importance to conservation of avoiding construction of new roads in roadless or sparsely roaded areas and of removal or restoration of existing roads to benefit both terrestrial and aquatic biota.

Revisión de los Efectos de Carreteras en Comunidades Terrestres y Acuáticas

Resumen: Las carreteras son una característica predominante y en incremento de la mayoría de los paisajes. Revisamos la literatura científica sobre los efectos ecológicos de las carreteras y encontramos sustento para la conclusión general de que las carreteras están asociadas con efectos negativos en la integridad biótica tanto de ecosistemas terrestres como acuáticos. Las carreteras de cualquier tipo ocasionan siete efectos generales: mortalidad ocasionada por la construcción de la carretera; mortalidad debida a la colisión con vehículos; modificaciones en la conducta animal; alteración del ambiente físico; alteración del ambiente químico; dispersión de especies exóticas e incremento en el uso de áreas por humanos. La construcción de carreteras elimina a organismos sésiles y a organismos de lento movimiento, lesiona a organismos adyacentes a la carretera y altera las condiciones físicas debajo ella misma. Las colisiones con vehículos afectan la demografía de muchas especies tanto de vertebrados como invertebrados; las medidas de mitigación para reducir la pérdida de animales por colisiones con vehículos han sido exitosas solo de manera parcial. Las carreteras alteran la conducta animal al ocasionar cambios en el rango de hogar, movimientos, éxito reproductivo, respuesta de escape y estado fisiológico. Las carreteras cambian la densidad del suelo, temperatura, contenido de agua en el suelo, niveles de luz, polvo, aguas superficiales, patrones de escurrimiento y sedimentación, además de agregar metales pesados (especialmente plomo), sales, moléculas orgánicas, ozono y nutrientes a los ambientes que atraviesan. Las carreteras promueven la dispersión de especies exóticas al alterar los hábi-

Paper submitted February 8, 1999; revised manuscript accepted July 21, 1999.

tats, al estresar a las especies nativas y proveer corredores para movimiento. Las carreteras también promueven el incremento de la caza y la pesca, el hostigamiento pasivo de animales y modificaciones del paisaje. No todas las especies ni todos los ecosistemas son afectados por las carreteras de igual forma, pero en general la presencia de carreteras está altamente correlacionada con cambios en la composición de especies, los tamaños poblacionales y los procesos hidrológicos y geomorfológicos que afectan a la estructura de sistemas acuáticos y reparios. Se necesita más investigación experimental para complementar estudios correlativos post-boc. Nuestra revisión hace énfasis en que en trabajos de conservación es importante evitar la construcción de nuevas carreteras en áreas carentes de ellas o en áreas con pocas carreteras, además de remover o restaurar carreteras existentes con la finalidad de beneficiar tanto a la biota acuática como la terrestre.

Introduction

Among the most widespread forms of modification of the natural landscape during the past century has been the construction and maintenance of roads (Diamondback 1990; Bennett 1991; Noss & Cooperrider 1994). As conservation biologists seek to understand the forces that influence the viability of populations and the overall health of ecosystems, it is important that we understand the scope of the ecological effects of roads of all types, especially important as conservation biologists are asked to participate in the development and implementation of strategies to protect or restore elements of biological diversity and integrity.

Roads of all kinds affect terrestrial and aquatic ecosystems in seven general ways: (1) increased mortality from road construction, (2) increased mortality from collision with vehicles, (3) modification of animal behavior, (4) alteration of the physical environment, (5) alteration of the chemical environment, (6) spread of exotic species, and (7) increased alteration and use of habitats by humans. These general effects overlap somewhat. In some cases animals modify their behavior and avoid roads because of concentrated human activity along roads. Roads may facilitate the spread of invasive species by disrupting native communities and changing physical habitats. Roads may fragment populations through roadkill and road avoidance. Despite the difficulty of categorizing discretely the causal basis in every example, these seven categories provide a useful framework for assessing what is known and unknown about the ecological effects of roads.

Selective road removal, relocation, or remediation may provide ecological benefits in certain situations. Yet, although roads are commonly identified as important correlates or indicators of loss of ecological health (e.g., Noss & Cooperrider 1994), the specific mechanisms by which biota are affected are often complicated or uncertain. Therefore, mitigation or treatment of specific effects, whether during road design or in post-construction remediation, can be costly and fraught with uncertainty.

Mortality from Road Construction

Road construction kills any sessile or slow-moving organism in the path of the road. The extent to which road

construction contributes to direct mortality has not been estimated as has direct mortality from other forms of habitat destruction (e.g., Petranks et al. 1993). The fact that road construction kills individual organisms is obvious, however. The magnitude of such construction is not trivial; the 13,107,812 km of road lanes of all types in the conterminous United States, with an average width of 3.65 m per lane, have destroyed at least 4,784,351 ha of land and water bodies that formerly supported plants, animals, and other organisms (U.S. Department of Transportation 1996). The actual number is likely much higher because this estimate does not include shoulder pavement and land peripheral to the roadbed that is cleared during construction.

Construction may physically injure organisms adjacent to the path of construction. Roads built for extraction of white fir result in damage to trees that is visible up to 30 m from the road (Trafela 1987). Such damage contributes to a decline of up to 30% in forest productivity per rotation, due in part to a decline in growth of damaged trees. Construction also alters the physical conditions of the soil underneath and adjacent to the road. Riley (1984) showed that road construction increases soil compaction up to 200 times relative to undisturbed sites. These changes likely decrease the survival of soil biota that are not killed directly. Direct transfer of sediment and other material to streams and other water bodies at road crossings is an inevitable consequence of road construction (Richardson et al. 1975; Seyedbagheri 1996). High concentrations of suspended sediment may directly kill aquatic organisms and impair aquatic productivity (Newcombe & Jensen 1996).

Mortality from Collision with Vehicles

Mortality of animals from collision with vehicles is well documented. Many reviews of the taxonomic breadth of the victims of vehicle collision have been published (e.g., Groot Bruinderink & Hazebroek 1996). Few if any terrestrial species of animal are immune. Large mammals ranging in size from moose (*Alces alces*) to armadillos (*Dasypus novemcinctus*) are the best-documented roadkills, probably due to interest in their demography and to their size (Bellis & Graves 1971; Puglisi et al. 1974;

Reilly & Green 1974; Holroyd 1979; Wilkins & Schmidly 1980; Bashore et al. 1985; Davies et al. 1987; Bangs et al. 1989; Palomares & Delibes 1992).

Roadkill among many other species includes American Kestrels (*Falco sparverius*; Varland et al. 1993), Barn Owls (*Tyto alba*; Newton et al. 1991), Northern Saw-whet Owls and Eastern Screech Owls (*Aegolius acadicus* and *Otis asio*; Loos & Kerlinger 1993), tropical forest birds (Novelli et al. 1988), garter snakes (Dalrymple & Reichenbach 1984), granivorous birds (Dhindsa et al. 1988), American crocodile (*Crocodylus acutus*; Kushlan 1988), green iguanas (*Iguana iguana*; Rodda 1990), desert snakes (Rosen & Lowe 1994), toads (van Gelder 1973), plus a wide range of invertebrates, especially insects (H. C. Seibert & Conover 1991).

This form of mortality can have substantial effects on a population's demography. Vehicle collision is the primary cause of death for moose in the Kenai National Wildlife Refuge in Alaska (Bangs et al. 1989) and for Barn Owls in the United Kingdom (Newton et al. 1991), the second highest form of mortality for Iberian lynx (*Felis pardina*) in southwestern Spain (after hunting; Ferreras et al. 1992), and the third highest form for white-tailed deer (*Odocoileus virginianus*) in New York (Sarbello & Jackson 1985) and wolves (*Canis lupus*) in Minnesota (Fuller 1989). Roadkill is a limiting factor in the recovery of the endangered American crocodile in southern Florida (Kushlan 1988) and is contributing to the endangerment of the prairie garter snake (*Thamnophis radix radix*; Dalrymple & Reichenbach 1984). Roadkill is often nonspecific with respect to age, sex, and condition of the individual animal (e.g., Bangs et al. 1989).

Amphibians may be especially vulnerable to roadkill because their life histories often involve migration between wetland and upland habitats, and individuals are inconspicuous and sometimes slow-moving. Roads can be demographic barriers that cause habitat and population fragmentation (Joly & Morand 1997). In the Netherlands, for example, roads with high traffic volume negatively affect occupancy of ponds by moor frogs (*Rana arvalis*; Vos & Chardon 1998). In Ontario, the local abundance of toads and frogs is inversely related to traffic density on adjacent roads, but the incidence of roadkill relative to abundance is higher on highly trafficked roads (Fahrig et al. 1995). Thus, even though populations in high-traffic areas have apparently already been depressed from cumulative road mortality, they continue to suffer higher proportionate rates of roadkill.

Mitigation measures have been employed in different locations with varying degrees of success (e.g., Yanes et al. 1995). For example, underpasses on Interstate 75 have been only partially successful in reducing roadkill of Florida panthers (*Felis concolor coryi*; Foster & Humphrey 1991). Despite mitigation efforts, roads are likely to be a persistent source of mortality for many species.

In general, mortality increases with traffic volume (e.g., Rosen & Lowe 1994; Fahrig et al. 1995). Some species are less likely to be killed on high-speed roads than on medium-speed roads because the former usually have vegetation cleared back further from the road's shoulder, creating less attractive habitat and greater visibility for both animals and drivers. Other species, however, are attracted to the modified habitat alongside and in the medians of high-speed roads (Cowardin et al. 1985), making them population sinks.

Modification of Animal Behavior

The presence of a road may modify an animal's behavior either positively or negatively. This can occur through five mechanisms: home range shifts, altered movement patterns, altered reproductive success, altered escape response, and altered physiological state.

Black bears (*Ursus americanus*) in North Carolina shift their home ranges away from areas with high road densities (Brody & Pelton 1989), as do grizzly bears in the Rocky Mountains (*Ursus horribilis*; McLellan & Shackleton 1988). Elk (*Cervus elaphus*) in Montana prefer spring feeding sites away from visible roads (Grover & Thompson 1986), and both elk and mule deer (*Odocoileus hemionus*) in Colorado in winter prefer areas >200 m from roads (Rost & Bailey 1979). Wolves will not establish themselves in areas with road densities greater than a region-specific critical threshold (Jensen et al. 1986; Thurber et al. 1994), probably as a result of a relationship between road density and hunting pressure. Mountain lion (*Felis concolor*) home ranges are situated in areas with lower densities of improved dirt roads and hard-surface roads (Van Dyke et al. 1986), suggesting that either mountain lions avoid these areas or road construction tends to avoid their prime habitat. Elephants (*Loxodonta africana*) in northeastern Gabon preferentially locate in forests away from both roads and villages (Barnes et al. 1991). Both Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*), on the other hand, preferentially establish home ranges in areas with greater road densities (Coleman & Fraser 1989), probably because of the increase in carrion.

Roads may also alter patterns of animal movement. Caribou (*Rangifer tarandus*) in Alaska preferentially travel along cleared winter roads that lead in the direction of their migration (Banfield 1974). Although the road may enhance caribou movement, it results in increased mortality from vehicle collisions and predation by wolves. After calving, female caribou with calves avoid roads (Klein 1991). The land snail *Arianta arbus-torum* avoids crossing roads, even those that are unpaved and as narrow as 3 m (Baur & Baur 1990), and extend their movements along road verges. Reluctance to cross roads is also seen in white-footed mice (*Peromyscus*

leucopus; Merriam et al. 1989) and many other rodent species (Oxley et al. 1974), even when the road is narrow and covered only with gravel. Cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*) avoid roads as narrow as 3 m (Swihart & Slade 1984). Black bear almost never cross interstate highways in North Carolina (Brody & Pelton 1989) but will cross roads with less traffic volume. Roads act as barriers to gene flow in the common frog (*Rana temporaria*) in Germany, leading to significant genetic differentiation among populations (Reh & Seitz 1990). Other animals that show a reluctance to cross roads include pronghorn antelope (*Antilocapra americana*; Bruns 1977) and mountain lions (Van Dyke et al. 1986).

Some animals seem unaffected by the presence of roads, at least at some spatial scales. Based on a study of 20 wolverines, Hornocker and Hash (1981) concluded that the sizes and shapes of home ranges of wolverines where they are still found in northwestern Montana are independent of the presence of highways. Similarly, the presence of highways explained none of the allelic differentiation among populations of brown hares (*Lepus europaeus*) in Austria (Hartl et al. 1989).

Roads may affect an animal's reproductive success. Productivity of Bald Eagles (*Haliaeetus leucocephalus*) in Oregon (Anthony & Isaacs 1989) and Illinois (Paruk 1987) declines with proximity to roads, and they preferentially nest away from roads. Golden Eagles (*Aquila chrysaetos*) also prefer to nest away from human disturbances, including roads (Fernandez 1993). The reduced nesting success of eagles in proximity to roads may be more a function of the presence of humans than of the road itself; nesting failure by Golden Eagles in Scotland correlates with how easy it is for people to approach but not with proximity to roads themselves (Watson and Dennis 1992). Relative to habitat availability, Sandhill Cranes (*Grus canadensis*) avoid nesting near paved and gravel public roads (Norling et al. 1992); they do not avoid private roads with low-traffic volume (Norling et al. 1992) and can habituate to roads over time (Dwyer & Tanner 1992). Mallards (*Anas platyrhynchos*) in North Dakota, on the other hand, prefer road rights-of-way for nesting (Cowardin et al. 1985), perhaps because of a lower level of predation there.

Roads can also alter escape responses. Pink-footed Geese (*Anser brachyrhynchus*) in Denmark are more easily disturbed when feeding near roads, flying away when humans approach within 500 m, a greater distance than when feeding in areas without roads (Madsen 1985). Both the Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) are more easily disturbed near roads and have disturbance distances of 480–2000 m depending on traffic volume (Van der Zande et al. 1980). Less well known is the effect of roads and vehicles on an animal's physiological state. MacArthur et al. (1979) showed that heart rate and therefore

metabolic rate and energy expenditure of female bighorn sheep (*Ovis canadensis*) increase near a road independent of any use of the road. Roads contribute to fragmentation of populations through both increased mortality and modification of behavior that makes animals less likely to cross roads. Fragmentation may be accelerated by roads when spatially critical habitat patches (e.g., "stepping stones") become unoccupied as a result of increased local mortality or reduced recolonization.

Disruption of the Physical Environment

A road transforms the physical conditions on and adjacent to it, creating edge effects with consequences that extend beyond the time of the road's construction. At least eight physical characteristics of the environment are altered by roads: soil density, temperature, soil water content, light, dust, surface-water flow, pattern of runoff, and sedimentation.

Long-term use of roads leads to soil compaction that persists even after use is discontinued. Soil density on closed forest roads continues to increase, particularly during winter months (Helvey & Kochenderfer 1990). Increased soil density can persist for decades: logging skid trails in northeastern California over 40 years old have soil that is 20% more compacted than soil in nearby areas that have not been used as trails (Vora 1988).

The reduction of water vapor transport on a road with a hard surface increases the surface temperature of a road compared to bare soil, an effect that increases with thickness of the road surface (Asaeda & Ca 1993). The heat stored on the road surface is released into the atmosphere at night, creating heat islands around roads. Animals respond to these heat islands: small birds (Whitford 1985) and snakes, for example, preferentially aggregate on or near warm roads, increasing their risk of being hit by cars and, at their northern range limits, reducing energetic demands for breeding.

During the dry season, the moisture content of soils under roads declines even if the roads are not in use (Helvey & Kochenderfer 1990), probably in response to changes in soil porosity. Roads through forests also increase the amount of light incident on the forest floor. The amount of increase depends on how much of the original canopy and lower strata remain, which depends in turn on the width of the road and roadside verge. The increase in light increases the density of species that preferentially grow where light levels are high, such as early-successional, disturbance-adapted species such as the North American orchid *Isotria medeoloides* (Mehrhoff 1989).

Road traffic mobilizes and spreads dust, which when settled on plants can block photosynthesis, respiration, and transpiration and can cause physical injuries to plants (Farmer 1993). These effects are sufficient to alter

plant community structure, especially in communities dominated by lichens and mosses (Auerbach et al. 1997). Although most sediment enters water bodies through overland flow or mass failure, dust from highly trafficked roads can serve as a source of fine sediments, nutrients, and contaminants to aquatic ecosystems (Gjessing et al. 1984).

Roads and bridges can alter the development of shorelines, stream channels, floodplains, and wetlands. Because of the energy associated with moving water, physical effects often propagate long distances from the site of a direct road incursion (Richardson et al. 1975). Alteration of hydrodynamics and sediment deposition can result in changes in channels or shorelines many kilometers away, both down- and up-gradient of the road crossing. The nature of such responses to channel and shoreline alteration is not always predictable; it may depend on the sequence of flood and sedimentation events after the alteration is made. Roads on floodplains can redirect water, sediment, and nutrients between streams and wetlands and their riparian ecosystems, to the detriment of water quality and ecosystem health. Roads are among the many human endeavors that impair natural habitat development and woody debris dynamics in forested floodplain rivers (Piégay & Landon 1997).

Road crossings commonly act as barriers to the movement of fishes and other aquatic animals (Furniss et al. 1991). Although many headwater populations of salmonid fishes are naturally migratory, they often persist today as fragmented headwater isolates, largely because of migration barriers created by road crossings and other human developments that fail to provide for fish passage (Kershner et al. 1997; Rieman et al. 1997). Salmonids and other riverine fishes actively move into seasonal floodplain wetlands and small valley-floor tributaries to escape the stresses of main-channel flood flows (Copp 1989), but valley-bottom roads can destroy or block access to these seasonally important habitats (Brown & Hartman 1988). Persistent barriers may encourage local selection for behaviors that do not include natural migration patterns, potentially reducing both the distribution and productivity of a population.

Roads directly change the hydrology of slopes and stream channels, resulting in alteration of surface-water habitats that are often detrimental to native biota. Roads intercept shallow groundwater flow paths, diverting the water along the roadway and routing it efficiently to surface-water systems at stream crossings (Megahan 1972; Wemple et al. 1996). This can cause or contribute to changes in the timing and routing of runoff (King & Tennyson 1984; Jones & Grant 1996; Ziemer & Lisle 1998), the effects of which may be more evident in smaller streams than in larger rivers (Jones & Grant 1996). Hydrologic effects are likely to persist for as long as the road remains a physical feature altering flow routing—often long after abandonment and revegetation of the

road surface. By altering surface or subsurface flow, roads can destroy and create wetland habitats.

Changes in the routing of shallow groundwater and surface flow may cause unusually high concentrations of runoff on hillslopes that can trigger erosion through channel downcutting, new gully or channel head initiation, or slumping and debris flows (Megahan 1972; Richardson et al. 1975; Wemple et al. 1996; Seyedbagheri 1996). Once such processes occur, they can adversely affect fishes and other biota far downstream for long periods of time (Hagans et al. 1986; Hicks et al. 1991). Roads have been responsible for the majority of hill-slope failures and gully erosion in most steep, forested landscapes subject to logging activity (Furniss et al. 1991; Hagans et al. 1986). Because most of these more catastrophic responses are triggered by the response of roads during infrequent, intense storm events, lag times of many years or decades pass before the full effects of road construction are realized.

Chronic effects also occur, however. The surfaces of unpaved roads can route fine sediments to streams, lakes, and wetlands, increasing the turbidity of the waters (Reid & Dunne 1984), reducing productivity and survival or growth of fishes (Newcombe & Jensen 1996), and otherwise impairing fishing (Buck 1956). Existing problem roads can be remediated to reduce future erosion potential (e.g., Weaver et al. 1987; Harr & Nichols 1993). The consequences of past sediment delivery are long-lasting and cumulative, however, and cannot be effectively mitigated (Hagans et al. 1986).

Alteration of the Chemical Environment

More has been written about the effects of roads on the chemical environment than on all other effects combined. Maintenance and use of roads contribute at least five different general classes of chemicals to the environment: heavy metals, salt, organic molecules, ozone, and nutrients.

A variety of heavy metals derived from gasoline additives and road deicing salts are put into the roadside environment. The most widely documented is lead, but others include aluminum, iron, cadmium, copper, manganese, titanium, nickel, zinc, and boron (Garcia-Miragaya et al. 1981; Clift et al. 1983; Gjessing et al. 1984; Oberts 1986; Araratyan & Zakharyan 1988).

Heavy metal contamination exhibits five patterns. First, the amount of contamination is related to vehicular traffic (Goldsmith et al. 1976; Dale & Freedman 1982; Leharne et al. 1992). Second, contamination of soils, plants, and animals decreases exponentially away from the road (Quarles et al. 1974; Dale & Freedman 1982). Most studies indicate that contamination declines within 20 m but that elevated levels of heavy metals often occur 200 m or more from the road. The pattern of decline is influenced

by prevailing wind patterns (Haqus & Hameed 1986). Once metals reach aquatic environments, transport rates and distances increase substantially (Gjessing et al. 1984).

Third, heavy metals can be localized in the soil, either close to the surface if downward transport has not occurred (Indu & Choudhri 1991) or deep below the surface if pollution levels in the past exceeded those in the present (Byrd et al. 1983). Transportation and localization is largely affected by the physical properties of the soil (Yassoglou et al. 1987). Metals and other persistent chemicals fixed to soils may become remobilized once they are inundated or transported to freshwater environments by wind, water, or gravity.

Fourth, heavy metals accumulate in the tissues of plants (Datta & Ghosh 1985; Beslaneev & Kuchmazokova 1991) and animals (Collins 1984; Birdsall et al. 1986; Grue et al. 1986). As with soil, contamination of plant tissue occurs up to at least 200 m from a road and is greatest for individuals along roads with high traffic volume.

Fifth, heavy metal concentrations in soil decline over time where use of leaded gasoline has been stopped and surface-water flow carries the metal ions away (Byrd et al. 1983; Tong 1990). After they leave the terrestrial environment, however, the mobilized metals may cause additional harm to aquatic biota. Also, some of the processes of metal demobilization may be reversed rapidly if environmental conditions, such as acidity of the soils, sediments, or water, change (Nelson et al. 1991).

Deicing salts, particularly NaCl but also CaCl₂, KCl, and MgCl₂, contribute ions to the soil, altering pH and the soil's chemical composition (Bogemans et al. 1989). As with lead, discontinuation of the use of deicing salts allows plants damaged by salt stress to recover (Leh 1990). The effects on aquatic biota of temporary surges of salt that often accompany runoff from roads to surface and groundwaters have received little study. Deicing salts on roadways elevate chloride and sodium concentrations in streams (Molles & Gosz 1980; Hoffman et al. 1981; Peters & Turk 1981; Mattson & Godfrey 1994) and in bogs, where road salts can alter patterns of succession in aquatic vegetation (Wilcox 1986). Accumulation of salts from chemicals used for road deicing or dust control can disrupt natural stratification patterns and thus potentially upset the ecological dynamics of meromictic lakes (Hoffman et al. 1981; Kjensmo 1997).

Organic pollutants such as dioxins and polychlorinated biphenyls are present in higher concentrations along roads (Benfenati et al. 1992). Hydrocarbons may accumulate in aquatic ecosystems near roads (Gjessing et al. 1984). In one stream along a British highway, numerous contaminants were present at elevated levels in the water column and sediments, including copper, zinc, and various hydrocarbons, but polycyclic aromatic hydrocarbons associated with stream sediments accounted for most of the observed toxicity to aquatic amphipods

(Maltby et al. 1995). Comparatively little research has focused on the questions of the fate and effects of the organic chemicals associated with roads.

Vehicles produce ozone, which increases the concentration of this harmful molecule in the air, especially in areas where vehicle exhaust accumulates (Flueckiger et al. 1984). Roads are also especially important vectors of nutrients and other materials to aquatic ecosystems, because the buffering role normally played by riparian vegetation (Correll et al. 1992) is circumvented through direct runoff of materials in water and sediment where roads abut or cross water bodies. Water moving on and alongside roadways can be charged with high levels of dissolved nitrogen in various forms, and sediment brings a phosphorus subsidy when it reaches surface waters. Road deicing salts are an additional source of phosphorus (Oberts 1986). The degree to which roads directly contribute to eutrophication problems in aquatic ecosystems has been little investigated. Because roads deliver nutrients that originate in the contributing slope area, the nutrient burden is probably largely controlled by surrounding vegetation and land use. An increased density of road crossings of water bodies can be expected to increase delivery of nutrients.

The alteration of the chemical environment by roads results in a number of consequences for living organisms. First, in the terrestrial environment the chemical composition of some woody plants changes in response to pollution. These changes include increased concentrations of chemicals produced by plants, such as terpenoids, which help them resist the toxic effects of pollution (Akimov et al. 1989) and salts (Bogemans et al. 1989), and decreased production of other chemicals, such as soluble protein and chlorophyll *a*, which are necessary for plant function (Banerjee et al. 1983).

Second, organisms may be killed or otherwise displaced as a result of chemical exposure. Virtually all measures of soil biotic diversity and function decline in contaminated soil, including abundance, number of species, species composition, index of species diversity, index of equability, and bulk soil respiration (Muskett & Jones 1981; Guntner & Wilke 1983; Krzysztofak 1991).

Third, the growth (Petersen et al. 1982) and overall physical health (Flueckiger et al. 1984; Moritz & Breitenstein 1985) of many plants is depressed, even to the point of death (Fleck et al. 1988). The sensitivity of plants to pollutants may change during development; for example, seedlings are more sensitive to salt than are adults (Liem et al. 1984), which influences juvenile recruitment. Pollutants may affect plant health by damaging fine roots, mycorrhizae (Majdi & Persson 1989), and leaves (Simini & Leone 1986) and by changing salt concentrations in plant tissues (Northover 1987). Secondary effects on plant health include decreased resistance to pathogens (Northover 1987), causing further declines. In aquatic environments, plant (and animal) assemblages

may change due to direct and indirect responses to nutrient increases and due to growth suppression or mortality caused by other chemicals introduced by roads.

Fourth, plants (Graham & Kalman 1974; Nasralla & Ali 1985; Dickinson et al. 1987; Guttormsen 1993) and animals (Robel et al. 1981; Collins 1984; Harrison & Dyer 1984; Krzysztofiak 1991; Marino et al. 1992), including those cultivated or raised for agriculture, may accumulate toxins at levels that pose health hazards, including those for humans that consume exposed organisms (Jarosz 1994).

Fifth, increased concentrations near roadsides of some pollutants, particularly salt, attract large mammals, putting them more at risk of being killed by vehicles (Fraser & Thomas 1982). Spills of edible products from trucks and trains also attract wildlife to roadsides. Finally, evolutionary processes may be affected through altered selection pressures that result in local differentiation of populations of both plants (Kiang 1982) and animals (Minoranskii & Kuzina 1984).

Spread of Exotic Species

Roads provide dispersal of exotic species via three mechanisms: providing habitat by altering conditions, making invasion more likely by stressing or removing native species, and allowing easier movement by wild or human vectors. It is often difficult to distinguish among these factors. Soils modified during road construction can facilitate the spread of exotic plants along roadsides (Greenberg et al. 1997). Some exotic plants establish themselves preferentially along roadsides and in other disturbed habitats (Wester & Juvik 1983; Henderson & Wells 1986; Tyser & Worley 1992; Wein et al. 1992). The spread of exotic diseases (Dawson & Weste 1985; Gad et al. 1986) and insects (Pantaleoni 1989; Schedl 1991) is facilitated by increased density of roads and traffic volume. Road construction that alters the canopy structure of forests promotes invasion by exotic understory plants, which affects animal communities (Gaddy & Kohlsaat 1987). Some roadside verges have been invaded by maritime plants because of their ability to tolerate saline soil (Scott & Davison 1982). Feral fruit trees are found preferentially along roadsides, and some populations are maintained solely by seeds in fruit waste thrown from vehicles (Smith 1986).

Exotic species are sometimes introduced along roadsides for the purpose of erosion control (Niordson 1989). Native species are now more widely preferred for this purpose, but Dunlap (1987) argues that in some cases the need for rapid establishment of plant cover requires the use of exotic species.

In another form of deliberate introduction, roads provide easy access to streams and lakes for fishery manag-

ers to stock nonnative hatchery fish (Lee et al. 1997), which adversely affect native biota and disrupt aquatic ecosystems in many ways (Allan & Flecker 1993). Unsanctioned, illegal, and unintentional introductions of fishes, mollusks, plants, and other aquatic organisms also occur frequently (Allan & Flecker 1993), and they are facilitated by public road access to water bodies.

The dispersal of a biological agent such as a pathogen along a roadway can affect both terrestrial and aquatic ecosystems far from the road. In northern California and southwest Oregon, for example, vehicle traffic and roadway drainage along logging and mining roads during the wet season disperse spores of an exotic root disease (*Phytophthora lateralis*) that infects the endemic Port Orford cedar (*Chamaecyparis lawsoniana*; Zobel et al. 1985). Transfer of the water-borne spores from forest roads into headwater stream crossings can result in the infection and nearly complete mortality of Port Orford cedars along a much larger network of downstream channel margins and floodplains, even deep inside otherwise roadless areas. The progressive loss of this important conifer species from riparian ecosystems may engender substantial long-term consequences for the integrity of stream biota, including endangered salmon species, for which the Port Orford cedar provides shade, large and long-lasting coarse woody debris, and stabilization of channels and floodplains.

Changes in Human Use of Land and Water

Roads facilitate increased use of an area by humans, who themselves often cause diverse and persistent ecological effects. New roads increase ease of access by humans into formerly remote areas. Perhaps more important, roads often increase the efficiency with which natural resources can be exported. At least three different kinds of human use of the landscape, made increasingly possible by roads, can have major ecological effects: hunting and fishing, recreation, and changes in use of land and water.

Roads open up areas to increased poaching and legal hunting. Hunting reduces population sizes of many game species, including brown bear (*Ursus arctos*; Camarra & Parde 1990), Iberian lynx (Ferreras et al. 1992), wolves (Fuller 1989), black bear (Manville 1983), and Egyptian mongooses (*Herpestes ichneumon*; Palomares & Delibes 1992). Roads also increase both legal and illegal fishing in streams and lakes. Native fish populations in previously inaccessible areas are often vulnerable to even small increases in fishing effort. Increased fishing then often gives rise to public demand for fish stocking as an attempt to artificially compensate for the effects of unsustainable harvest, at the further expense of native fishes and other species (e.g., Gresswell & Varley 1988).

Visitors increase when roads make areas more accessible, leading to increased passive harassment of animals—such as elk on Mount St. Helens in Washington State (Czech 1991) and the Oregon Coast Range (Witmer & DeCalesta 1985), brown bear in Europe (Del Campo et al. 1990), and mountain goats (*Oreamnos americanus*) in Montana (Pedevillano & Wright 1987)—and damage to plant communities (Matlack 1993).

Roads are often built into areas to promote logging, agriculture, mining, and development of homes or industrial or commercial projects. Such changes in land cover and land and water use result in major and persistent adverse effects on the native flora and fauna of terrestrial (Van Dyke et al. 1986; Karnefelt & Mattsson 1989; P. Seibert 1993) and freshwater ecosystems (Schlosser 1991; Allan & Flecker 1993; Roth et al. 1996).

Numerous studies have demonstrated declines in stream health associated with roads. Because the nature and extent of land use within a region tend to be highly correlated with road networks, however, it is often difficult or impossible to separate the direct ecological effects of roads from those of the accompanying land-use activities. For example, Eaglin and Hubert (1993) reported that trout biomass and streambed habitat quality in Wyoming streams declined in relation to the number of road crossings and to the proportion of area logged in the contributing catchment. Findlay and Houlihan (1997) found that herpetile species diversity in wetlands declined in relation to the density of roads within 2 km of the perimeter. Among streams in the Pacific Northwest, the status or abundance of bull trout populations has been inversely correlated to road density (Rieman et al. 1997; Baxter et al. 1999); these studies used roads as the best available general proxy of cumulative effects associated with land use and human access. On the other hand, some studies (e.g., Roth et al. 1996) have demonstrated correlations of stream biotic integrity with land-use pat-

terns across large catchments but did not investigate the specific roles that roads might play in mediating the causes and effects.

It appears that roads can serve as useful indicators of the magnitude of land-use changes, but it remains unclear to what degree the associated ecological responses result directly from roads themselves. If roads are largely responsible, effects could be ameliorated through altered road design, placement, remediation, or road removal. Strong interactions between roads and land use are likely, however. Forest roads in Idaho, for example, are less prone to erosion when the surrounding landscape remains in natural forest cover (Seyedbagheri 1996).

Discussion and Conclusions

Roads have diverse and systemic effects on many aspects of terrestrial and aquatic ecosystems. The ecological effects of roads can resonate substantial distances from the road in terrestrial ecosystems, creating habitat fragmentation and facilitating ensuing fragmentation through support of human exploitative activities (Fig. 1a). Habitat deterioration is not widely appreciated as an aspect of ecological fragmentation in aquatic ecosystems. At the scale of an extensive landscape or stream network, however, roads produce a pattern of aquatic habitat loss that differs from the terrestrial pattern yet nevertheless results in the ecological fragmentation of aquatic ecosystems (Fig. 1b). We coin the term *hyperfragmentation* to describe the multidimensional view of ecological fragmentation and habitat loss that emerges when the consequences of roads or any habitat alteration for terrestrial and aquatic ecosystems are considered simultaneously (Fig. 1c). Hyperfragmentation is the result of a spatial footprint of ecological effect that propagates across the landscape differently in freshwater and

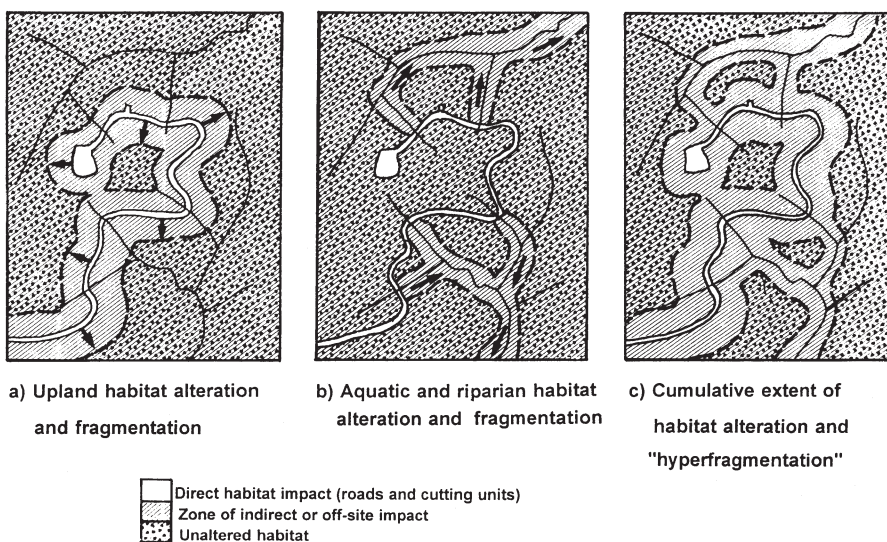


Figure 1. Spatial pattern of direct and indirect habitat alteration caused by human disturbance in a forested watershed: (a) classical forest edge effects contributing to terrestrial habitat fragmentation, (b) downstream-propagating hydrologic and biotic effects leading to large-scale fragmentation of freshwater habitats and populations, (c) combined terrestrial-aquatic view of landscape alteration that we term hyperfragmentation because it considers multiple ecosystem dimensions on the same landscape. Arrows indicate pre-dominant spatial vector of effects.

aquatic ecosystems than in terrestrial systems. Even where only a small percentage of the land's surface is directly occupied by roads, few corners of the landscape remain untouched by their off-site ecological effects. The breadth of these effects cannot be appreciated unless one takes a broadly transdisciplinary view of ecosystems and biological communities.

Road design, management, and restoration need to be more carefully tailored to address the full range of ecological processes and terrestrial and aquatic species that may be affected. Deliberate monitoring is necessary to ensure that projects have robust ecological benefits and minimal adverse effects and that they are cost-efficient relative to their actual benefits (e.g., Weaver et al. 1987). Of course, such assessments require time and money that are usually unavailable. Most funds used to remediate problem roads are earmarked for actual field operations and are not available to support such assessment and monitoring. Few of the experts building roads or "restoring" them are trained to recognize and address the full spectrum of ecological issues that we have identified. Moreover, by their nature roads have systemic ecological effects that, even if recognized, cannot be overcome.

If a broad view of the ecological effects of roads reveals a multiplicity of effects, it also suggests that it is unlikely that the consequences of roads will ever be completely mitigated or remediated. Thus, it is critical to retain remaining roadless or near-roadless portions of the landscape in their natural state. Because of the increasing rarity of roadless areas, especially roadless watersheds, conservation efforts cannot rely entirely on protection of existing natural areas. But neither can conservation efforts depend entirely on tenuous and unexamined assumptions about the capability of site- and species-specific mitigation and remediation measures to reduce the ecological consequences of existing and proposed roads.

Acknowledgments

We thank M. Hourdequin for organizing the symposium at the 1997 annual meeting of the Society for Conservation Biology at which we originally presented much of this material and for her patience during the preparation of this manuscript. We also thank R. Noss and an anonymous reviewer for improvement of the paper. The second author's contribution to this paper and his participation in the symposium were supported by The Pacific Rivers Council.

Literature Cited

- Akimov Y. A., V. V. Pushkar, and S. I. Kuznetsov. 1989. The content and composition of volatile terpenoids in woody plants under conditions of air pollution. *Sbornik Nauchnykh Trudov* 109:70-79.
- Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. *BioScience* 43:32-43.
- Anthony, R. G., and F. B. Isaacs. 1989. Characteristics of bald eagle nest sites in Oregon. *Journal of Wildlife Management* 53:148-159.
- Aratyan, L. A., and S. A. Zakharyan. 1988. On the contamination of snow along main highways. *Biologicheskii Zhurnal Armenii* 41:514-519.
- Asaeda, T., and V. A. Ca. 1993. The subsurface transport of heat and moisture and its effect on the environment: a numerical model. *Boundary Layer Meteorology* 65:159-179.
- Auerbach, N. A., M. D. Walker, and D. A. Walker. 1997. Effects of road-side disturbance on substrate and vegetation properties in arctic tundra. *Ecological Applications* 7:218-235.
- Banerjee, A., R. K. Sarkar, and S. Mukherji. 1983. Reduction in soluble protein and chlorophyll contents in a few plants as indicators of automobile exhaust pollution. *International Journal of Environmental Studies* 20:239-243.
- Banfield, A. W. F. 1974. The relationship of caribou migration behavior to pipeline construction. Pages 797-804 in V. Geist and F. Walther, editors. *The behavior of ungulates and its relation to management*. International Union for the Conservation of Nature Press, Morges, Switzerland.
- Bangs, E. E., T. N. Bailey, and M. F. Portner. 1989. Survival rates of adult female moose on the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 53:557-563.
- Barnes, R. F. W., K. L. Barnes, M. P. T. Alers, and A. Blom. 1991. Man determines the distribution of elephants in the rain forests of north-eastern Gabon. *African Journal of Ecology* 29:54-63.
- Bashore, T. L., W. M. Tzilkowski, and E. D. Bellis. 1985. Analysis of deer-vehicle collision sites in Pennsylvania. *Journal of Wildlife Management* 49:769-774.
- Baur, A., and B. Baur. 1990. Are roads barriers to dispersal in the land snail *Arianta arbustorum*? *Canadian Journal of Zoology* 68:613-617.
- Baxter, C. V., C. A. Frissell, and F. R. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout (*Salvelinus confluentus*) spawning in a forested river basin: implications for management and conservation. *Transactions of the American Fisheries Society* 128:854-867.
- Bellis, E. D., and H. B. Graves. 1971. Deer mortality on a Pennsylvania interstate highway. *Journal of Wildlife Management* 35:232-237.
- Benfenati, E., S. Valzacchi, G. Maniani, L. Airolidi, and R. Farnelli. 1992. PCDD, PCDF, PCB, PAH, cadmium and lead in roadside soil: relationship between road distance and concentration. *Chemosphere* 24:1077-1083.
- Bennett, A. F. 1991. Roads, roadsides, and wildlife conservation: a review. Pages 99-118 in D. A. Saunders and R. J. Hobbes, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Beslaneev, V. D., and F. A. Kuchmazokova. 1991. The effect of motorways on the accumulation of toxic substances in walnuts. *Sadovodstvo i Vinogradarstvo* 5:38.
- Birdsall, C. W., C. E. Grue, and A. Anderson. 1986. Lead concentrations in bullfrog *Rana catesbeiana* and green frog *Rana clamitans* tadpoles inhabiting highway drainages. *Environmental Pollution Series A Ecological and Biological* 40:233-248.
- Bogemans, J., L. Nierinck, and J. M. Stassart. 1989. Effect of deicing chloride salts on ion accumulation in spruce (*Picea abies* (L.) sp.). *Plant and Soil* 113:3-11.
- Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* 17:5-10.
- Brown, T. G., and G. F. Hartman. 1988. Contribution of seasonally flooded lands and minor tributaries to coho (*Oncorhynchus kisutch*) salmon smolt production in Carnation Creek, a small coastal stream in British Columbia. *Transactions of the American Fisheries Society* 117:546-551.
- Bruns, E. H. 1977. Winter behavior of pronghorns in relation to habitat. *Journal of Wildlife Management* 41:560-571.
- Buck, D. H. 1956. Effects of turbidity on fish and fishing. *Transactions of the North American Wildlife Conference* 21:249-261.

- Byrd, D. S., J. T. Gilmore, and R. H. Lea. 1983. Effect of decreased use of lead in gasoline on the soil of a highway. *Environmental Science and Technology* 17:121-123.
- Camarra, J. J., and J. M. Parde. 1990. The brown bear in France—status and management in 1985. *Aquilo, Serie Zoologica* 27:93-96.
- Clift, D., I. E. Dickson, T. Roos, P. Collins, M. Jolly, and A. Klindworth. 1983. Accumulation of lead beside the Mulgrave Freeway, Victoria. *Search* 14:155-157.
- Coleman, J. S., and J. D. Fraser. 1989. Habitat use and home ranges of Black and Turkey Vultures. *Journal of Wildlife Management* 53:782-792.
- Collins, J. A. 1984. Roadside lead in New Zealand and its significance for human and animal health. *New Zealand Journal of Science* 27:93-98.
- Copp, G. H. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes* 26:1-27.
- Correll, D. L., T. E. Jordan, and D. E. Weller. 1992. Cross media inputs to eastern US watersheds and their significance to estuarine water quality. *Water Science and Technology* 26:2675-2683.
- Cowardin, L. M., D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs* 92:1-37.
- Czech, B. 1991. Elk behavior in response to human disturbance at Mount St. Helens National Volcanic Monument. *Applied Animal Behavior Science* 29:269-277.
- Dale, J. M., and B. Freedman. 1982. Lead and zinc contamination of roadside soil and vegetation in Halifax, Nova Scotia. *Proceedings of the Nova Scotian Institute of Science* 32:327-336.
- Dalrymple G. H., and N. G. Reichenbach. 1984. Management of an endangered species of snake in Ohio, USA. *Biological Conservation* 30:195-200.
- Datta, S. C., and J. J. Ghosh. 1985. A study of the distribution pattern of lead in the leaves of banyan trees (*Ficus benghalensis*) from different traffic density regions of Calcutta. *Ecotoxicology and Environmental Safety* 9:101-106.
- Davies, J. M., T. J. Roper, and D. J. Shepherdson. 1987. Seasonal distribution of road kills in the European badger (*Meles meles*). *Journal of Zoology (London)* 211:525-530.
- Dawson, P., and G. Weste. 1985. Changes in the distribution of *Phytolophora cinnamomi* in the Brisbane Ranges National Park between 1970 and 1980-81. *Australian Journal of Botany* 33:309-315.
- Del Campo, J. C., J. L. Marquez, J. Naves, and G. Palomero. 1990. The brown bear in the Cantabrian Mountains. *Aquilo, Serie Zoologica* 27:97-101.
- Dhindsa, M. S., J. S. Sandhu, P. S. Sandhu, and H. S. Toor. 1988. Roadside birds in Punjab (India): relation to mortality from vehicles. *Environmental Conservation* 15:303-310.
- Diamondback. 1990. Ecological effects of roads (or, the road to destruction). Pages 1-5 in J. Davis, editor. *Killing roads: a citizen's primer on the effects and removal of roads*. Biodiversity special publication. Earth First!, Tucson, Arizona.
- Dickinson, N. M., N. W. Lepp, and G. T. K. Surtan. 1987. Lead and potential health risks from subsistence food crops in urban Kenya. *Environmental Geochemistry and Health* 9:37-42.
- Dunlap, D. W. 1987. Development of grass-seeding specifications for use on Texas highway rights-of-way: erosion control—you're gambling without it. *International Erosion Control Association* 18:161-172.
- Dwyer, N., and G. W. Tanner. 1992. Nesting success in Florida Sandhill Cranes. *Wilson Bulletin* 104:22-31.
- Eaglin, G. S., and W. A. Hubert. 1993. Effects of logging roads on substrate and trout in streams of the Medicine Bow National Forest, Wyoming. *North American Journal of Fisheries Management* 13:844-846.
- Fahrig, L., J. H. Pedlar, S. E. Pope, P. D. Taylor, and J. F. Wenger. 1995. Effect of road traffic on amphibian density. *Biological Conservation* 73:177-182.
- Farmer, A. M. 1993. The effects of dust on vegetation—a review. *Environmental Pollution* 79:63-75.
- Fernandez, C. 1993. The choice of nesting cliffs by golden eagles *Aquila chrysaetos*: the influence of accessibility and disturbance by humans. *Alauda* 61:105-110.
- Ferreras, P., J. J. Aldama, J. F. Beltran, and M. Delibes. 1992. Rates and causes of mortality in a fragmented population of Iberian lynx *Felis pardina* Temminck, 1824. *Biological Conservation* 61:197-202.
- Findlay, C. S., and J. Houlihan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology* 11:1000-1009.
- Fleck, A. M., M. J. Lacki, and J. Sutherland. 1988. Response of white birch (*Betula papyrifera*) to road salt applications at Cascade Lakes, New York. *Journal of Environmental Management* 27:369-377.
- Flueckiger, W., H. Fluckiger Keller, and S. Braun. 1984. Untersuchungen ueber waldschaeden in der Nordwestschweiz. *Schweizerische Zeitschrift fuer Forstwesen* 135:389-444.
- Foster, M. L., and S. R. Humphrey. 1991. Effectiveness of wildlife crossing structures on Alligator Alley (I-75) for reducing animal/auto collisions. Report. Florida Game and Fresh Water Fish Commission and Florida Department of Transportation, Tallahassee.
- Fraser, D., and E. R. Thomas. 1982. Moose-vehicle accidents in Ontario: relation to highway salt. *Wildlife Society Bulletin* 10:261-265.
- Fuller, T. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105:1-41.
- Furniss, M. J., T. D. Roeloffs, and C. S. Yee. 1991. Road construction and maintenance. Pages 297-323 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. Special publication 19. American Fisheries Society, Bethesda, Maryland.
- Gad, A. M., F. M. Feinsod, I. H. Allam, M. Eisa, A. N. Hassan, B. A. Soliman, S. El Said, A. J. Saah, S. El Said, R. F. Sellers, and H. Hoogstraal. 1986. A possible route for the introduction of Rift Valley fever virus into Egypt during 1977. *Journal of Tropical Medicine and Hygiene* 89:233-236.
- Gaddy, L. L., and T. L. Kohlsaat. 1987. Recreational impact on the natural vegetation, avifauna, and herpetofauna of four South Carolina barrier islands (USA). *Natural Areas Journal* 7:55-64.
- Garcia-Miragaya, J., S. Castro, and J. Paolini. 1981. Lead and zinc levels and chemical fractionation in road-side soils of Caracas, Venezuela. *Water, Air and Soil Pollution* 15:285-297.
- Gjessing, E., E. Lygren, L. Berglund, T. Gulbrandsen, and R. Skanne. 1984. Effect of highway runoff on lake water quality. *Science of the Total Environment* 33:247-257.
- Goldsmith, C. D., P. F. Scanlon, and W. R. Pirie. 1976. Lead concentrations in soil and vegetation associated with highways of different traffic densities. *Bulletin of Environmental Contamination and Toxicology* 16:66-70.
- Graham, D. L., and S. M. Kalman. 1974. Lead in forage grass from a suburban area in northern California. *Environmental Pollution* 7:209-215.
- Greenberg, C. H., S. H. Crownover, and D. R. Gordon. 1997. Roadside soil: a corridor for invasion of xeric scrub by nonindigenous plants. *Natural Areas Journal* 17:99-109.
- Gresswell, R. E., and J. D. Varley. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. Pages 45-52 in Symposium 4. American Fisheries Society, Bethesda, Maryland.
- Groot Bruinderink, G. W. T. A., and E. Hazebroek. 1996. Ungulate traffic collisions in Europe. *Conservation Biology* 10:1059-1067.
- Grover, K. E., and M. J. Thompson. 1986. Factors influencing spring feeding site selection by elk in the Elkhorn Mountains, Montana. *Journal of Wildlife Management* 50:466-470.
- Grue, C. E., D. J. Hoffman, W. N. Beyer, and L. P. Franson. 1986. Lead concentrations and reproductive success in European starlings, *Sturnus vulgaris*, nesting within highway roadside verges. *Environmental Pollution Series A Ecological and Biological* 42:157-182.
- Guntner, M., and B. M. Wilke. 1983. Effects of de-icing salt on soil enzyme activity. *Water, Air and Soil Pollution* 20:211-220.
- Guttormsen, G. 1993. The content of lead, cadmium and PAH in vegetables and strawberries alongside the E18 motorway. *Norsk Landbruksforskning* 7:175-189.

- Hagans, D. K., W. E. Weaver, and M. A. Madej. 1986. Long-term on-site and off-site effects of logging and erosion in the Redwood Creek Basin, northern California. Pages 38–65 in Papers presented at the American Geophysical Union meeting on cumulative effects. Technical bulletin 490. National Council for Air and Stream Improvement, New York.
- Haqus, M. D., and H. A. Hameed. 1986. Lead content of green forage growing adjacent to expressways and roads connecting Erbil City (Northern Iraq). *Journal of Biological Science Research* **17**:151–164.
- Harr, R. D., and R. A. Nichols. 1993. Stabilizing forest roads to help restore fish habitat: a northwest Washington example. *Fisheries* **18**:18–22.
- Harrison, P. D., and M. I. Dyer. 1984. Lead in mule deer forage in Rocky Mountain National Park, Colorado. *Journal of Wildlife Management* **48**:510–517.
- Hartl, G. B., F. Suchentrunk, R. Willing, and M. Grillitsch. 1989. Biochemical-genetic variability and differentiation in the brown hare (*Lepus europaeus*) of lower Austria. *Wiener Tierärztliche Monatsschrift* **76**:279–284.
- Helvey, J. D., and J. N. Kochenderfer. 1990. Soil density and moisture content on two unused forest roads during first 30 months after construction. Research paper NE-629. U.S. Forest Service, Northeast Forest Experiment Station, Broomhall, Pennsylvania.
- Henderson, L., and M. J. Wells. 1986. Alien plant invasions in the grassland and savanna biomes. Pages 109–117 in I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. *The ecology and management of biological invasions in southern Africa*. Oxford University Press, Capetown.
- Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Response of salmonids to habitat change. Pages 483–518 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. Special publication 19. American Fisheries Society, Bethesda, Maryland.
- Hoffman, R. W., C. R. Goldman, S. Paulson, and G. R. Winters. 1981. Aquatic impacts of deicing salts in the central Sierra Nevada Mountains, California. *Water Resources Bulletin* **17**:280–285.
- Holroyd, G. L. 1979. The impact of highway and railroad mortality on the ungulate populations in the Bow Valley, Banff National Park. Environment Canada, Canadian Wildlife Service, Edmonton, Alberta.
- Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology* **59**:1286–1301.
- Indu, B., and G. N. Choudhri. 1991. Impact of automobile effusion on plant and soil. *International Journal of Ecology and Environmental Sciences* **17**:121–127.
- Jarosz, W. 1994. Heavy metals contamination of grass growing at the road edges. *Medycyna Weterynaryjna* **50**:23–26.
- Jensen, W. F., T. K. Fuller, and W. L. Robinson. 1986. Wolf, *Canis lupus*, distribution on the Ontario-Michigan border near Sault Ste. Marie. *Canadian Field Naturalist* **100**:363–366.
- Joly, P., and A. Morand. 1997. Amphibian diversity and land-water ecotones. Pages 161–182 in J.-P. Bravard and R. Juge, editors. *Biodiversity in land-water ecotones. Man and biosphere series*. Volume 18. United Nations Educational, Scientific and Cultural Organization, Paris.
- Jones, J. A., and G. E. Grant. 1996. Cumulative effects of forest harvest on peak streamflow in the western Cascades of Oregon. *Water Resources Research* **32**:959–974.
- Karnefelt, I., and J. E. Mattsson. 1989. *Cetraria cucullata* and *Cetraria nivalis*, two vanishing lichens from southernmost Sweden. *International Journal of Mycology and Lichenology* **4**:299–306.
- Kershner, J. L., C. M. Bischoff, and D. L. Horan. 1997. Population, habitat, and genetic characteristics of Colorado River cutthroat trout in wilderness and nonwilderness stream sections in the Uinta Mountains of Utah and Wyoming. *North American Journal of Fisheries Management* **17**:1134–1143.
- Kiang, Y. T. 1982. Local differentiation of *Antboxanthum odoratum* L. populations on roadsides. *American Midland Naturalist* **107**:340–350.
- King, J. G., and L. C. Tennyson. 1984. Alteration of streamflow characteristics following road construction in north central Idaho. *Water Resources Research* **20**:1159–1163.
- Kjensmo, J. 1997. The influence of road salts on the salinity and the meromictic stability of Lake Svinsjøen, Norway. *Oecologia* **347**:151–158.
- Klein, D. R. 1991. Caribou in the changing North. *Applied Animal Behavior Science* **29**:279–291.
- Krzysztofak, L. 1991. The effect of habitat pollution with heavy metals on ant populations and ant-hill soil. *Ekologia Polska* **39**:181–202.
- Kushlan, J. A. 1988. Conservation and management of the American crocodile. *Environmental Management* **12**:777–790.
- Lee, D. C., et al. 1997. Broad-scale assessment of aquatic species and habitats. Pages 1057–1496 in T. M. Quigley and S. J. Arbelbide, editors. *An assessment of ecosystem components in the interior Columbia River Basin and portions of the Klamath and Great Basins*. Volume 3. General technical report PNW-GTR-405. U.S. Forest Service, Portland, Oregon.
- Leh, H. O. 1990. Investigations on health conditions of street trees after discontinued use of de-icing salts on streets in Berlin. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* **42**:134–142.
- Leharne, S., D. Charlesworth, and B. Chowdhry. 1992. A survey of metal levels in street dusts in an inner London neighbourhood. *Environment International* **18**:263–270.
- Liem, A. S. N., A. Hendriks, H. Kraal, and M. Loenen. 1984. Effects of de-icing salt on roadside grasses and herbs. *Plant and Soil* **84**:299–310.
- Loos, G., and P. Kerlinger. 1993. Road mortality of saw-whet and Screech Owls on the Cape May peninsula. *Journal of Raptor Research* **27**:210–213.
- MacArthur, R. A., R. H. Johnston, and V. Geist. 1979. Factors influencing heart rate in free ranging bighorn sheep: a physiological approach to the study of wildlife harassment. *Canadian Journal of Zoology* **57**:2010–2021.
- Madsen, J. 1985. Impact of disturbance on field utilization of pink-footed geese in West Jutland, Denmark. *Biological Conservation* **33**:53–64.
- Majdi, H., and H. Persson. 1989. Effects of road-traffic pollutants (lead and cadmium) on tree fine-roots along a motor road. *Plant and Soil* **119**:1–5.
- Maltby, L., A. B. A. Boxall, D. M. Farrow, P. Calow, and C. I. Betton. 1995. The effects of motorway runoff on freshwater ecosystems. 2. Identifying major toxicants. *Environmental Toxicology and Chemistry* **14**:1093–1101.
- Manville, A. M. 1983. Human impact on the black bear in Michigan's lower peninsula. *International Conference on Bear Research and Management* **5**:20–33.
- Marino, F., A. Ligerio, and D. J. Diaz Cosin. 1992. Heavy metals and earthworms on the border of a road next to Santiago (Galicia, Northwest of Spain): initial results. *Soil Biology and Biochemistry* **24**:1705–1709.
- Matlack, G. R. 1993. Sociological edge effects: spatial distribution of human impact in suburban forest fragments. *Environmental Management* **17**:829–835.
- Mattson, M. D., and P. J. Godfrey. 1994. Identification of road salt contamination using multiple regression and GIS. *Environmental Management* **18**:767–773.
- McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries: effects of roads on behavior, habitat use and demography. *Journal of Applied Ecology* **25**:451–460.
- Megahan, W. F. 1972. Subsurface flow interception by a logging road in mountains of central Idaho. Pages 350–356 in *Proceedings of a national symposium on watersheds in transition*. American Water Resources Association, Bethesda, Maryland.
- Mehrhoff, L. A. 1989. Reproductive vigor and environmental factors in populations of an endangered North American orchid, *Isotria medeoloides* (Pursh) Rafinesque. *Biological Conservation* **47**:281–296.

- Merriam, G., M. Kozakiewicz, E. Tsuchiya, and K. Hawley. 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Landscape Ecology* 2:227-236.
- Minoranskii, V. A., and Z. R. Kuzina. 1984. Effect of environmental pollution by motor transport on the reproduction and development of *Opatrum sabulosum*. *Biologicheskii Nauki (Moscow)* 11:43-47.
- Molles, M. C., Jr., and J. R. Gosz. 1980. Effects of a ski area on the water quality and invertebrates of a mountain stream. *Water, Air, and Soil Pollution* 14:187-205.
- Moritz, K., and J. Breitenstein. 1985. Damage by spreading salt on West German federal trunk roads and possibilities of avoiding it. *Allgemeine Forstzeitschrift* 44:1192-1193.
- Muskett, C. J., and M. P. Jones. 1981. Soil respiratory activity in relation to motor vehicle pollution. *Water, Air and Soil Pollution* 23:231-242.
- Nasralla, M. M., and E. A. Ali. 1985. Lead accumulation in edible portions of crops grown near Egyptian traffic roads. *Agriculture Ecosystems and Environment* 13:73-82.
- Nelson, R. L., M. L. McHenry, and W. S. Platts. 1991. Mining. Pages 425-457 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. Special publication 19. American Fisheries Society, Bethesda, Maryland.
- Newcombe, C. P., and J. O. T. Jensen. 1996. Channel suspended sediment and fisheries: a synthesis for quantitative assessment of risk. *North American Journal of Fisheries Management* 16:693-727.
- Newton, I., I. Wyllie, and A. Asher. 1991. Mortality causes in British barn owls *Tyto alba*, with a discussion of aldrin-dieldrin poisoning. *Ibis* 133:162-169.
- Niordson, N. 1989. *Glyceria grandis* found in south Sweden. *Svensk Botanisk Tidskrift* 83:357-360.
- Norling, B. S., S. H. Anderson, and W. A. Hubert. 1992. Roost sites used by Sandhill Crane staging along the Platte River, Nebraska. *Great Basin Naturalist* 52:253-261.
- Northover, J. 1987. NaCl injury to dormant roadside peach trees and its effect on the incidence of infections by *Leucostoma* spp. *Phytopathology* 77:835-840.
- Noss, R. F., and A. Y. Cooperrider. 1994. *Saving nature's legacy*. Island Press, Washington, D.C.
- Novelli, R., E. Takase, and V. Castro. 1988. Study of birds killed by collision with vehicles in a stretch of Highway BR-471, between Quinta and Taim, Rio Grande do Sul, Brazil. *Revista Brasileira De Zoologia* 5:441-454.
- Oberts, G. L. 1986. Pollutants associated with sand and silt applied to roads in Minnesota. *Water Resources Bulletin* 22:479-483.
- Oxley, D. J., M. B. Fenton, and G. R. Carmody. 1974. The effects of roads on population of small mammals. *Journal of Applied Ecology* 11:51-59.
- Palomares, F., and M. Delibes. 1992. Some physical and population characteristics of Egyptian mongooses (*Herpestes ichneumon* L., 1758) in southwestern Spain. *Zeitschrift fuer Säugetierkunde* 57:94-99.
- Pantaleoni, R. A. 1989. Ways of invasion of a new area by *Metacalfa pruinosa* (Say, 1830) (Auchenorrhyncha, Flatidae). *Bollettino Dell'istituto Di Entomologia Della Università Degli Studi Di Bologna* 43:1-8.
- Paruk, J. D. 1987. Habitat utilization by Bald Eagles wintering along the Mississippi River (USA). *Transactions of the Illinois State Academy of Science* 80:333-342.
- Pedevillano, C., and R. G. Wright. 1987. The influence of visitors on mountain goat activities in Glacier National Park, Montana. *Biological Conservation* 39:1-11.
- Peters, N. E., and J. T. Turk. 1981. Increases in sodium and chloride in the Mohawk River, New York, from the 1950s to the 1970s attributed to road salt. *Water Resources Bulletin* 17:586-598.
- Petersen, A., D. Eckstein, and W. Liese. 1982. Holzbiologische Untersuchungen ueber den Einfluss von Auftausalz auf Hamburger Strassenbaeume. *Forstwissenschaftliches Centralblatt* 101:353-364.
- Petranks, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on Southern Appalachian salamanders. *Conservation Biology* 7:363-370.
- Piégay, H., and N. Landon. 1997. Promoting ecological management of riparian forests on the Drôme River, France. *Aquatic Conservation: Marine and Freshwater Ecosystems* 7:287-304.
- Puglisi, M. J., J. S. Lindzey, and E. D. Bellis. 1974. Factors associated with highway mortality of white-tailed deer. *Journal of Wildlife Management* 38:799-807.
- Quarles, H. D., R. B. Hanawalt, and W. E. Odum. 1974. Lead in small mammals, plants and soil at varying distances from a highway. *Journal of Applied Ecology* 11:937-949.
- Reh, W., and A. Seitz. 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* 54:239-249.
- Reid, L. M., and T. Dunne. 1984. Sediment production from forest road surfaces. *Water Resources Research* 20:1753-1761.
- Reilly, R. E., and H. E. Green. 1974. Deer mortality on a Michigan interstate highway. *Journal of Wildlife Management* 38:16-19.
- Richardson, E. V., B. Simons, S. Karaki, M. Mahmood, and M. A. Stevens. 1975. *Highways in the river environment: hydraulic and environmental design considerations training and design manual*. U.S. Department of Transportation, Federal Highway Administration, Washington, D.C.
- Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River Basins. *North American Journal of Fisheries Management* 17:1111-1125.
- Riley, S. J. 1984. Effect of clearing and roading operations on the permeability of forest soils, Karuah catchment, New South Wales, Australia. *Forest Ecology and Management* 9:283-293.
- Robel, R. J., C. A. Howard, M. S. Udevitz, and B. Cumutte, Jr. 1981. Lead contamination in vegetation, cattle dung, and dung beetles near an interstate highway, Kansas. *Environmental Entomology* 10:262-263.
- Rodda, G. H. 1990. Highway madness revisited: roadkilled *Iguana iguana* in the llanos of Venezuela. *Journal of Herpetology* 24:209-211.
- Rosen, P. C., and C. H. Lowe. 1994. Highway mortality of snakes in the Sonoran desert of southern Arizona. *Biological Conservation* 68:143-148.
- Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* 43:634-641.
- Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* 11:141-156.
- Sarbello, W., and L. W. Jackson. 1985. Deer mortality in the town of Malone, N. Y. *Fish and Game Journal* 32:141-157.
- Schedl, W. 1991. Invasion of the American buffalo treehopper (*Stictoccephala bisonia* Kopp and Yonke, 1977) into Austria (Homoptera, Auchenorrhyncha, Membracidae). *Anzeiger fuer Schaedlingkunde, Pflanzenschutz, Umweltschutz* 64:9-13.
- Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704-712.
- Scott, N. E., and A. W. Davison. 1982. De-icing salt and the invasion of road verges by maritime plants. *Watsonia* 14:41-52.
- Seibert, H. C., and J. H. Conover. 1991. Mortality of vertebrates and invertebrates on an Athens County, Ohio, highway. *Ohio Journal of Science* 91:163-166.
- Seibert, P. 1993. Vegetation and man in South America from a historical perspective. *Phytocoenologia* 23:457-493.
- Seyedbagheri, K. A. 1996. Idaho forestry best management practices: compilation of research on their effectiveness. General technical report INT-GTR-339. U.S. Forest Service, Intermountain Research Station, Ogden, Utah.
- Simini, M., and I. A. Leone. 1986. Studies on the effects of de-icing salts on roadside trees. *Arboricultural Journal* 10:221-231.
- Smith, J. M. B. 1986. Feral fruit trees on New England roadsides. Page 158 in R. H. Groves and J. J. Burdon, editors. *Ecology of biological invasions*. Cambridge University Press, New York.
- Swihart, R. K., and N. A. Slade. 1984. Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. *Journal of Mammalogy* 65:357-360.
- Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22:61-68.

- Tong, S. T. Y. 1990. Roadside dusts and soils contamination in Cincinnati, Ohio, USA. *Environmental Management* **14**:107-114.
- Trafela, E. 1987. The influence of the construction of forest roads on forest production. *Zbornik Gozdarstva Lesarstva* **29**:85-140.
- Tyser, R. W., and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). *Conservation Biology* **6**:253-262.
- U.S. Department of Transportation. 1996. Highway statistics 1996. FHWA-PL-98-003. U.S. Department of Transportation, Office of Highway Information Management, Washington, D.C.
- Van der Zande, A. N., W. J. ter Keurs, and W. J. Van der Weijden. 1980. The impact of road on the densities of four bird species in an open field habitat—evidence of a long-distance effect. *Biological Conservation* **18**:299-321.
- Van Dyke, F. G., R. H. Brocke, and H. G. Shaw. 1986. Use of road track counts as indices of mountain lion presence. *Journal of Wildlife Management* **50**:102-109.
- van Gelder, J. J. 1973. A quantitative approach to the mortality resulting from traffic in a population of (*Bufo bufo*) L. *Oecologia* **13**:93-95.
- Varland, D. E., E. E. Klaas, and T. M. Loughin. 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledgling American Kestrels. *Journal of Field Ornithology* **64**:169-178.
- Vora, R. S. 1988. Potential soil compaction forty years after logging in northeastern California. *Great Basin Naturalist* **48**:117-120.
- Vos, C. C., and J. P. Chardon. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog, *Rana arvalis*. *Journal of Applied Ecology* **35**:44-56.
- Watson, J., and R. H. Dennis. 1992. Nest-site selection by Golden Eagles in Scotland. *British Birds* **85**:469-481.
- Weaver, W. E., M. M. Hektner, D. K. Hagans, L. J. Reed, R. A. Sonnevile, and G. J. Bundros. 1987. An evaluation of experimental rehabilitation work, Redwood National Park. Technical report 19. Redwood National Park, Arcata, California.
- Wein, R. W., G. Wein, S. Bahret, and W. J. Cody. 1992. Northward invading non-native vascular plant species in and adjacent to Wood Buffalo National Park, Canada. *Canadian Field Naturalist* **106**:216-224.
- Wemple, B. C., J. A. Jones, and G. E. Grant. 1996. Channel network extension by logging roads in two basins, western Cascades, Oregon. *Water Resources Bulletin* **32**:1195-1207.
- Wester, L., and J. O. Juvik. 1983. Roadside plant communities on Mauna Loa, Hawaii. *Journal of Biogeography* **10**:307-316.
- Whitford, P. C. 1985. Bird behavior in response to the warmth of blacktop roads. *Transactions of the Wisconsin Academy of Sciences Arts and Letters* **73**:135-143.
- Wilcox, D. A. 1986. The effects of deicing salts on vegetation in Pinhook Bog, Indiana. *Canadian Journal of Botany* **64**:865-874.
- Wilkins, K. T., and D. J. Schmidly. 1980. Highway mortality of vertebrates in southeastern Texas. *Texas Journal of Science* **4**:343-350.
- Witmer, G. W., and D. S. DeCalesta. 1985. Effect of forest roads on habitat use by Roosevelt elk. *Northwest Science* **59**:122-125.
- Yanes, M., J. M. Velasco, and F. Suárez. 1995. Permeability of roads and railways to vertebrates: the importance of culverts. *Biological Conservation* **71**:217-222.
- Yassoglou, N., C. Kosmas, J. Asimakopoulou, and C. Kallianou. 1987. Heavy metal contamination of roadside soils in the Greater Athens (Greece) area. *Environmental Pollution* **47**:293-304.
- Ziemer, R. R., and T. E. Lisle. 1998. Hydrology. Pages 43-68 in R. J. Naiman and R. E. Bilby, editors. *River ecology and management: lessons from the Pacific coastal ecosystem*. Springer-Verlag, New York.
- Zobel, D. B., L. F. Roth, and G. M. Hawk. 1985. Ecology, pathology, and management of Port Orford cedar (*Chamaecyparis lawsoniana*). General Technical report PNW-184. U.S. Forest Service, Portland, Oregon.

