

ROADS AND THEIR MAJOR ECOLOGICAL EFFECTS

Richard T. T. Forman and Lauren E. Alexander

Harvard University Graduate School of Design, Cambridge, Massachusetts 02138

KEY WORDS: animal movement, material flows, population effects, roadside vegetation, transportation ecology

ABSTRACT

A huge road network with vehicles ramifies across the land, representing a surprising frontier of ecology. Species-rich roadsides are conduits for few species. Roadkills are a premier mortality source, yet except for local spots, rates rarely limit population size. Road avoidance, especially due to traffic noise, has a greater ecological impact. The still-more-important barrier effect subdivides populations, with demographic and probably genetic consequences. Road networks crossing landscapes cause local hydrologic and erosion effects, whereas stream networks and distant valleys receive major peak-flow and sediment impacts. Chemical effects mainly occur near roads. Road networks interrupt horizontal ecological flows, alter landscape spatial pattern, and therefore inhibit important interior species. Thus, road density and network structure are informative landscape ecology assays. Australia has huge road-reserve networks of native vegetation, whereas the Dutch have tunnels and overpasses perforating road barriers to enhance ecological flows. Based on road-effect zones, an estimated 15–20% of the United States is ecologically impacted by roads.

INTRODUCTION

Roads appear as major conspicuous objects in aerial views and photographs, and their ecological effects spread through the landscape. Few environmental scientists, from population ecologists to stream or landscape ecologists, recognize the sleeping giant, road ecology. This major frontier and its applications to planning, conservation, management, design, and policy are great challenges for science and society.

This review often refers to The Netherlands and Australia as world leaders with different approaches in road ecology and to the United States for especially useful data. In The Netherlands, the density of main roads alone is 1.5 km/km², with traffic density of generally between 10,000 and 50,000 vehicles per commuter day (101). Australia has nearly 900,000 km of roads for 18 million people (66). In the United States, 6.2 million km of public roads are used by 200 million vehicles (85). Ten percent of the road length is in national forests, and one percent is interstate highways. The road density is 1.2 km/km², and Americans drive their cars for about 1 h/day. Road density is increasing slowly, while vehicle kilometers (miles) traveled (VMT) is growing rapidly.

The term road corridor refers to the road surface plus its maintained roadsides and any parallel vegetated strips, such as a median strip between lanes in a highway (Figure 1; see color version at end of volume). "Roadside natural strips" of mostly native vegetation receiving little maintenance and located adjacent to roadsides are common in Australia (where road corridors are called road reserves) (12, 39, 111). Road corridors cover approximately 1% of the United States, equal to the area of Austria or South Carolina (85). However, the area directly affected ecologically is much greater (42, 43).

Theory for road corridors highlights their functional roles as conduits, barriers (or filters), habitats, sources, and sinks (12, 39). Key variables affecting processes are corridor width, connectivity, and usage intensity. Network theory, in turn, focuses on connectivity, circuitry, and node functions (39, 71).

This review largely excludes road-construction-related activities, as well as affiliated road features such as rest stops, maintenance facilities, and entrance/exit areas. We also exclude the dispersed ecological effects of air pollution emissions, such as greenhouse gases, nitrogen oxides (NOX), and ozone, which are reviewed elsewhere (85, 135). Bennett's article (12) plus a series of books (1, 21, 33, 111) provide overviews of parts of road ecology.

Gaping holes in our knowledge of road ecology represent research opportunities with a short lag between theory and application. Current ecological knowledge clusters around five major topics: (a) roadsides and adjacent strips; (b) road and vehicle effects on populations; (c) water, sediment, chemicals, and streams; (d) the road network; and (e) transportation policy and planning.

Figure 1 Road corridor showing road surface, maintained open roadsides, and roadside natural strips. Strips of relatively natural vegetation are especially characteristic of road corridors (known as road reserves) in Australia. Wheatbelt of Western Australia. Photo courtesy of BMJ Hussey. See color version at end of volume.



ROADSIDE VEGETATION AND ANIMALS

Plants and Vegetation

“Roadside” or “verge” refers to the more-or-less intensively managed strip, usually dominated by herbaceous vegetation, adjacent to a road surface (Figure 1). Plants on this strip tend to grow rapidly with ample light and with moisture from road drainage. Indeed, management often includes regular mowing, which slows woody-plant invasion (1, 86). Ecological management may also maintain roadside native-plant communities in areas of intensive agriculture, reduce the invasion of exotic (non-native) species, attract or repel animals, enhance road drainage, and reduce soil erosion.

Roadsides contain few regionally rare species but have relatively high plant species richness (12, 139). Disturbance-tolerant species predominate, especially with intensive management, adjacent to highways, and exotic species typically are common (19, 121). Roadside mowing tends to both reduce plant species richness and favor exotic plants (27, 92, 107). Furthermore, cutting and removing hay twice a year may result in higher plant species richness than does mowing less frequently (29, 86). Native wildflower species are increasingly planted in dispersed locations along highways (1).

Numerous seeds are carried and deposited along roads by vehicles (70, 112). Plants may also spread along roads due to vehicle-caused air turbulence (107, 133) or favorable roadside conditions (1, 92, 107, 121, 133). For example, the short-distance spread of an exotic wetland species, purple loosestrife (*Lythrum salicaria*), along a New York highway was facilitated by roadside ditches, as well as culverts connecting opposite sides of the highway and the median strip of vegetation (133). Yet few documented cases are known of species that have successfully spread more than 1 km because of roads.

Mineral nutrient fertilization from roadside management, nearby agriculture, and atmospheric NO_x also alter roadside vegetation. In Britain, for example, vegetation was changed for 100–200 m from a highway by nitrogen from traffic exhaust (7). Nutrient enrichment from nearby agriculture enhances the growth of aggressive weeds and can be a major stress on a roadside native-plant community (19, 92). Indeed, to conserve roadside native-plant communities in Dutch farmland, fertilization and importing topsoil are ending, and in some places nutrient accumulations and weed seed banks are reduced by soil removal (86; H van Bohemen, personal communication).

Woody species are planted in some roadsides to reduce erosion, control snow accumulation, support wildlife, reduce headlight glare, or enhance aesthetics (1, 105). Planted exotic species, however, may spread into nearby natural ecosystems (3, 12). For example, in half the places where non-native woody species were planted in roadsides adjacent to woods in Massachusetts (USA), a species had spread into the woods (42).

Roadside management sometimes creates habitat diversity to maintain native ecosystems or species (1, 86, 131). Mowing different sections along a road, or parallel strips in wide roadsides, at different times or intervals may be quite effective (87). Ponds, wetlands, ditches, berms, varied roadside widths, different sun and shade combinations, different slope angles and exposures, and shrub patches rather than rows offer variety for roadside species richness.

In landscapes where almost all native vegetation has been removed for cultivation or pasture, roadside natural strips (Figure 1) are especially valuable as reservoirs of biological diversity (19, 66). Strips of native prairie along roads and railroads, plus so-called beauty strips of woodland that block views near intensive logging, may function similarly as examples. However, roadside natural strips of woody vegetation are widespread in many Australian agricultural landscapes and are present in South Africa (11, 12, 27, 39, 66, 111). Overall, these giant green networks provide impressive habitat connectivity and disperse “bits of nature” widely across a landscape. Yet they miss the greater ecological benefits typically provided by large patches of natural vegetation (39, 41).

In conclusion, roadside vegetation is rich in plant species, although apparently not an important conduit for plants. The scattered literature suggests a promising research frontier.

Animals and Movement Patterns

Mowing, burning, livestock grazing, fertilizing, and planting woody plants greatly impact native animals in roadsides. Cutting and removing roadside vegetation twice a year in The Netherlands, compared with less frequent mowing, results in more species of small mammals, reptiles, amphibians, and insects (29, 86). However, mowing once every 3–5 y rather than annually results in more bird nests. Many vertebrate species persist better with mowing after, rather than before or during, the breeding period (86, 87). The mowing regime is especially important for insects such as meadow butterflies and moths, where different species go through stages of their annual cycle at different times (83). Roadsides, especially where mowed cuttings are removed, are suitable for ~80% of the Dutch butterfly fauna (86).

Planting several native and exotic shrub species along Indiana (USA) highways resulted in higher species richness, population density, and nest density for birds, compared with nearby grassy roadsides (105). Rabbit (*Sylvilagus*) density increased slightly. However, roadkill rates did not differ next to shrubby versus grassy roadsides.

In general, road surfaces, roadsides, and adjacent areas are little used as conduits for animal movement along a road (39), although comparisons with null models are rare. For example, radiotracking studies of wildlife across the landscape detect few movements along or parallel to roads (35, 39, 93). Some exceptions are noteworthy. Foraging animals encountering a road sometimes

move short distances parallel to it (10, 106). At night, many large predator species move along roads that have little vehicular or people traffic (12, 39). Carrion feeders move along roads in search of roadkills, and vehicles sometimes transport amphibians and other animals (11, 12, 32). Small mammals have spread tens of kilometers along highway roadsides (47, 60). In addition, migrating birds might use roads as navigational cues.

Experimental, observational, and modeling approaches have been used to study beetle movement along roadsides in The Netherlands (125–127). On wide roadsides, fewer animals disappeared into adjacent habitats. Also, a dense grass strip by the road surface minimized beetle susceptibility to roadkill mortality (126, 127). Long dispersals of beetles were more frequent in wide (15–25 m) than in narrow (<12 m) roadsides. Nodes of open vegetation increased, and narrow bottlenecks decreased, the probability of long dispersals. The results suggest that with 20–30-m-wide roadsides containing a central suitable habitat, beetle species with poor dispersal ability and a good reproductive rate may move 1–2 km along roadsides in a decade (127).

Adjacent ecosystems also exert significant influences on animals in corridors (39). For example, roadside beetle diversity was higher near a similar patch of sandy habitat, and roadsides next to forest had the greatest number of forest beetle species (127). In an intensive-agriculture landscape (Iowa, USA), bird-nest predation in roadsides was highest opposite woods and lowest opposite pastures (K Freemark, unpublished data). Finally, some roadside animals also invade nearby natural vegetation (37, 47, 54, 60, 63, 127).

The median strip between lanes of a highway is little studied. A North Carolina (USA) study found no difference in small-mammal density between roadsides on the median and on the outer side of the highway (2). This result was the same whether comparing mowed roadside areas or unmowed roadside areas. Also, roadkill rates may be affected by the pattern of wooded and grassy areas along median strips (10).

In conclusion, some species move significant distances along roadsides and have major local impacts. Nevertheless, road corridors appear to be relatively unimportant as conduits for species movement, although movement rates should be better compared with those at a distance and in natural-vegetation corridors.

ROAD AND VEHICLE EFFECTS ON POPULATIONS

Roadkilled Animals

Sometime during the last three decades, roads with vehicles probably overtook hunting as the leading direct human cause of vertebrate mortality on land. In addition to the large numbers of vertebrates killed, insects are roadkilled in prodigious numbers, as windshield counts will attest.

Estimates of roadkills (faunal casualties) based on measurements in short sections of roads tell the annual story (12, 39, 123): 159,000 mammals and 653,000 birds in The Netherlands; seven million birds in Bulgaria; five million frogs and reptiles in Australia. An estimated one million vertebrates per day are killed on roads in the United States.

Long-term studies of roadkills near wetlands illustrate two important patterns. One study recorded >625 snakes and another >1700 frogs annually roadkilled per kilometer (8, 54). A growing literature suggests that roads by wetlands and ponds commonly have the highest roadkill rates, and that, even though amphibians may tend to avoid roads (34), the greatest transportation impact on amphibians is probably roadkills (8, 28, 34, 128).

Road width and vehicle traffic levels and speeds affect roadkill rates. Amphibians and reptiles tend to be particularly susceptible on two-lane roads with low to moderate traffic (28, 34, 57, 67). Large and mid-sized mammals are especially susceptible on two-lane, high-speed roads, and birds and small mammals on wider, high-speed highways (33, 90, 106).

Do roadkills significantly impact populations? Measurements of bird and mammal roadkills in England illustrate the main pattern (56, 57). The house sparrow (*Passer domesticus*) had by far the highest roadkill rate. Yet this species has a huge population, reproduces much faster than the roadkill rate, and can rapidly recolonize locations where a local population drops. The study concluded, based on the limited data sets available, that none of the >100 bird and mammal species recorded had a roadkill rate sufficient to affect population size at the national level.

Despite this overall pattern, roadkill rates are apparently significant for a few species listed as nationally endangered or threatened in various nations (~9–12 cases) (9, 39, 43; C Vos, personal communication). Two examples from southern Florida (USA) are illustrative. The Florida panther (*Felis concolor coryi*) had an annual roadkill mortality of approximately 10% of its population before 1991 (33, 54). Mitigation efforts reduced roadkill loss to 2%. The key deer (*Odocoileus virginianus clavium*) has an annual roadkill mortality of ~16% of its population. Local populations, of course, may suffer declines where the roadkill rate exceeds the rates of reproduction and immigration. At least a dozen local-population examples are known for vertebrates whose total populations are not endangered (33, 39, 43).

Vehicles often hit vertebrates attracted to spilled grain, roadside plants, insects, basking animals, small mammals, road salt, or dead animals (12, 32, 56, 87). Roadkills may be frequent where traffic lanes are separated by impermeable barriers or are between higher roadside banks (10, 106).

Landscape spatial patterns also help determine roadkill locations and rates. Animals linked to specific adjacent land uses include amphibians roadkilled

near wetlands and turtles near open-water areas (8). Foraging deer are often roadkilled between fields in forested landscapes, between wooded areas in open landscapes, or by conservation areas in suburbs (10, 42, 106). The vicinity of a large natural-vegetation patch and the area between two such patches are likely roadkill locations for foraging or dispersing animals. Even more likely locations are where major wildlife-movement routes are interrupted, such as roads crossing drainage valleys in open landscapes or crossing railway routes in suburbs (42, 106).

In short, road vehicles are prolific killers of terrestrial vertebrates. Nevertheless, except for a small number of rare species, roadkills have minimal effect on population size.

Vehicle Disturbance and Road Avoidance

The ecological effect of road avoidance caused by traffic disturbance is probably much greater than that of roadkills seen splattered along the road. Traffic noise seems most important, although visual disturbance, pollutants, and predators moving along a road are alternative hypotheses as the cause of avoidance.

Studies of the ecological effects of highways on avian communities in The Netherlands point to an important pattern. In both woodlands and grasslands adjacent to roads, 60% of the bird species present had a lower density near a highway (102, 103). In the affected zone, the total bird density was approximately one third lower, and species richness was reduced as species progressively disappeared with proximity to the road. Effect-distances (the distance from a road at which a population density decrease was detected) were greatest for birds in grasslands, intermediate for birds in deciduous woods, and least for birds in coniferous woods.

Effect-distances were also sensitive to traffic density. Thus, with an average traffic speed of 120 km/h, the effect-distances for the most sensitive species (rather than for all species combined) were 305 m in woodland by roads with a traffic density of 10,000 vehicles per day (veh/day) and 810 m in woodland by 50,000 veh/day; 365 m in grassland by 10,000 veh/day and 930 m in grassland by 50,000 veh/day (101–103). Most grassland species showed population decreases by roads with 5000 veh/day or less (102). The effect-distances for both woodland and grassland birds increased steadily with average vehicle speed up to 120 km/h and also with traffic density from 3000 to 140,000 veh/day (100, 102, 103). These road effects were more severe in years when overall bird population sizes were low (101).

Songbirds appear to be sensitive to remarkably low noise levels, similar to those in a library reading room (100, 102, 103). The noise level at which population densities of all woodland birds began to decline averaged 42 decibels (dB), compared with an average of 48 dB for grassland species. The most sensitive

woodland species (cuckoo) showed a decline in density at 35 dB, and the most sensitive grassland bird (black-tailed godwit, *Limosa limosa*) responded at 43 dB. Field studies and experiments will help clarify the significance of these important results for traffic noise and birds.

Many possible reasons exist for the effects of traffic noise. Likely hypotheses include hearing loss, increase in stress hormones, altered behaviors, interference with communication during breeding activities, differential sensitivity to different frequencies, and deleterious effects on food supply or other habitat attributes (6, 101, 103, 130). Indeed, vibrations associated with traffic may affect the emergence of earthworms from soil and the abundance of crows (*Corvus*) feeding on them (120). A different stress, roadside lighting, altered nocturnal frog behavior (18). Responses to roads with little traffic may resemble behavioral responses to acute disturbances (individual vehicles periodically passing), rather than the effects of chronic disturbance along busy roads.

Response to traffic noise is part of a broader pattern of road avoidance by animals. In the Dutch studies, visual disturbance and pollutants extended outward only a short distance compared with traffic noise (100, 103). However, visual disturbance and predators moving along roads may be more significant by low-traffic roads.

Various large mammals tend to have lower population densities within 100–200 m of roads (72, 93, 108). Other animals that seem to avoid roads include arthropods, small mammals, forest birds, and grassland birds (37, 47, 73, 123). Such road-effect zones, extending outward tens or hundreds of meters from a road, generally exhibit lower breeding densities and reduced species richness compared with control sites (32, 101). Considering the density of roads plus the total area of avoidance zones, the ecological impact of road avoidance must well exceed the impact of either roadkills or habitat loss in road corridors.

Barrier Effects and Habitat Fragmentation

All roads serve as barriers or filters to some animal movement. Experiments show that carabid beetles and wolf spiders (*Lycosa*) are blocked by roads as narrow as 2.5 m wide (73), and wider roads are significant barriers to crossing for many mammals (11, 54, 90, 113). The probability of small mammals crossing lightly traveled roads 6–15 m wide may be <10% of that for movements within adjacent habitats (78, 119). Similarly, wetland species, including amphibians and turtles, commonly show a reduced tendency to cross roads (34, 67).

Road width and traffic density are major determinants of the barrier effect, whereas road surface (asphalt or concrete versus gravel or soil) is generally a minor factor (34, 39, 73, 90). Road salt appears to be a significant deterrent to amphibian crossing (28, 42). Also, lobes and coves in convoluted outer-roadside boundaries probably affect crossing locations and rates (39).

The barrier effect tends to create metapopulations, e.g. where roads divide a large continuous population into smaller, partially isolated local populations (subpopulations) (6, 54, 128). Small populations fluctuate more widely over time and have a higher probability of extinction than do large populations (1, 88, 115, 122, 123). Furthermore, the recolonization process is also blocked by road barriers, often accentuated by road widening or increases in traffic. This well-known demographic threat must affect numerous species near an extensive road network, yet is little studied relative to roads (6, 73, 98).

The genetics of a population is also altered by a barrier that persists over many generations (73, 115). For instance, road barriers altered the genetic structure of small local populations of the common frog (*Rana temporaria*) in Germany by lowering genetic heterozygosity and polymorphism (97, 98). Other than the barrier effect on this amphibian and roadkill effects on two southern Florida mammals (20, 54), little is known of the genetic effects of roads.

Making roads more permeable reduces the demographic threat but at the cost of more roadkills. In contrast, increasing the barrier effect of roads reduces roadkills but accentuates the problems of small populations. What is the solution to this quandary (122, 128)? The barrier effect on populations probably affects more species, and extends over a wider land area, than the effects of either roadkills or road avoidance. This barrier effect may emerge as the greatest ecological impact of roads with vehicles. Therefore, perforating roads to diminish barriers makes good ecological sense.

WATER, SEDIMENT, CHEMICALS, STREAMS, AND ROADS

Water Runoff

Altering flows can have major physical or chemical effects on aquatic ecosystems. The external forces of gravity and resistance cause streams to carve channels, transport materials and chemicals, and change the landscape (68). Thus, water runoff and sediment yield are the key physical processes whereby roads have an impact on streams and other aquatic systems, and the resulting effect-distances vary widely (Figure 2).

Roads on upper hillslopes concentrate water flows, which in turn form channels higher on slopes than in the absence of roads (80). This process leads to smaller, more elongated first-order drainage basins and a longer total length of the channel network. The effects of stream network length on erosion and sedimentation vary with both scale and drainage basin area (80).

Water rapidly runs off relatively impervious road surfaces, especially in storm and snowmelt events. However, in moist, hilly, and mountainous terrain, such

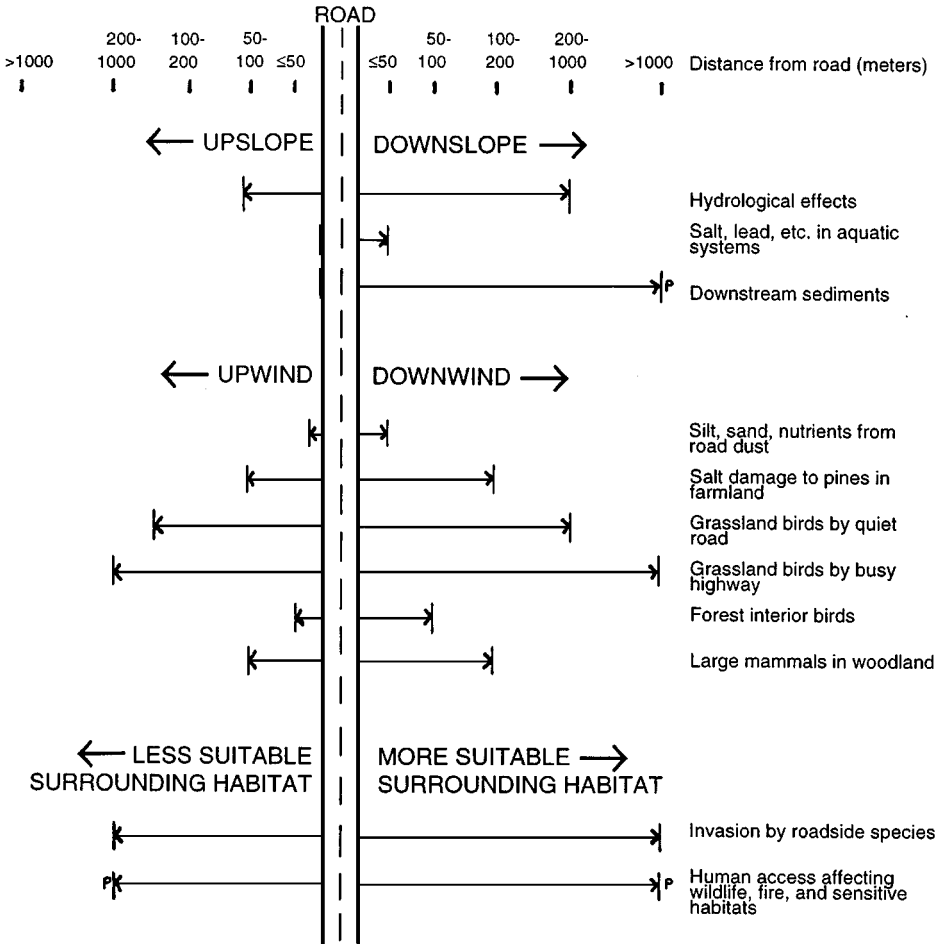


Figure 2 Road-effect zone defined by ecological effects extending different distances from a road. Most distances are based on specific illustrative studies (39); distance to left is arbitrarily half of that to right. (P) indicates an effect primarily at specific points. From Forman et al (43).

runoff is often insignificant compared with the conversion of slow-moving groundwater to fast-moving surface water at cutbanks by roads (52, 62, 132). Surface water is then carried by roadside ditches, some of which connect directly to streams while others drain to culverts with gullies incised below their outlets (132). Increased runoff associated with roads may increase the rates and extent of erosion, reduce percolation and aquifer recharge rates, alter channel morphology, and increase stream discharge rates (13, 14). Peak discharges or

floods then restructure riparian areas by rearranging channels, logs, branches, boulders, fine-sediment deposits, and pools.

In forests, the combination of logging and roads increases peak discharges and downstream flooding (62, 132). Forest removal results in lower evapotranspiration and water-storage capabilities, but roads alone may increase peak discharge rates (62). Also, flood frequency apparently correlates with the percentage of road cover in a basin (52, 62, 110).

Roads may alter the subsurface flow as well as the surface flow on wetland soils (116). Compacted saturated or nearly saturated soils have limited permeability and low drainage capacity. Wetland road crossings often block drainage passages and groundwater flows, effectively raising the upslope water table and killing vegetation by root inundation, while lowering the downslope water table with accompanying damage to vegetation (116, 118).

Streams may be altered for considerable distances both upstream and downstream of bridges. Upstream, levees or channelization tend to result in reduced flooding of the riparian zone, grade degradation, hydraulic structural problems, and more channelization (17). Downstream, the grade change at a bridge results in local scouring that alters sedimentation and deposition processes (17, 49). Sediment and chemicals enter streams where a road crosses, and mathematical models predict sediment loading in and out of reaches affected by stream crossings (5). The fixed stream (or river) location at a bridge or culvert reduces both the amount and variability of stream migration across a floodplain. Therefore, stream ecosystems have altered flow rates, pool-riffle sequences, and scour, which typically reduce habitat-forming debris and aquatic organisms.

Sediment

The volume of sediment yield from a road depends on sediment supply and transport capacity (5). Sediment yield is determined by road geometry, slope, length, width, surface, and maintenance (5, 51), in addition to soil properties and vegetation cover (59). Road surfaces, cutbanks, fillslopes, bridge/culvert sites, and ditches are all sources of sediment associated with roads. The exposed soil surfaces, as well as the greater sediment-transport capacity of increased hydrologic flows, result in higher erosion rates and sediment yields (99).

Road dust as a little-studied sediment transfer may directly damage vegetation, provide nutrients for plant growth, or change the pH and vegetation (109). Effect-distances are usually <10–20 m but may extend to 200 m downwind (Figure 2). In arid land, soil erosion and drainage are common road problems (61).

Arctic roads also are often sources of dust. Other ecological issues include change in albedo, flooding, erosion and thermokarst, weed migration, waterfowl and shorebird habitat, and altered movement of large mammals (129).

Landsliding or mass wasting associated with roads may be a major sediment source (13, 117). Some of this sediment accumulates on lower slopes and is subject to subsequent erosion. The rest reaches floodplains or streams, where it alters riparian ecosystems, channel morphology, or aquatic habitat. Although gradual sediment transport and episodic landslides are natural processes affecting streams, elevated levels caused by roads tend to disrupt aquatic ecosystems. Indeed, logging roads commonly produce more erosion and sediment yield, particularly by mass wasting, than do the areas logged (45, 51, 104, 117).

Buffer strips between roads and streams tend to reduce sediments reaching aquatic ecosystems (77, 91). Buffers may be less effective for landslides than for arresting water and sediment from culverts and roadside ditches. Good road location (including avoiding streambanks and narrow floodplains for many ecological reasons), plus good ecological design of roadsides relative to slope, soil, and hydrology, may be a better strategy than depending on wide buffers to absorb sediment.

Water from road ditches tends to deposit finer sediment in streams, whereas landslides generally provide coarser material. Fine sediment increases turbidity (51), which disrupts stream ecosystems in part by inhibiting aquatic plants, macro-invertebrates, and fish (14, 16, 31, 99). Coarse deposits such as logs and boulders help create deep pools and habitat heterogeneity in streams. During low-flow periods, fine-sediment deposits tend to fill pools and smooth gravel beds, hence degrading habitats and spawning sites for key fish (13, 14, 31). During high-discharge events, accumulated sediment tends to be flushed out and redeposited in larger water bodies.

In short, roads accelerate water flows and sediment transport, which raise flood levels and degrade aquatic ecosystems. Thus, local hydrologic and erosion effects along roads are dispersed across the land, whereas major impacts are concentrated in the stream network and distant valleys.

Chemical Transport

Most chemical transport from roads occurs in stormwater runoff through or over soil. Runoff pollutants alter soil chemistry, may be absorbed by plants, and affect stream ecosystems, where they are dispersed and diluted over considerable distances (16, 50, 66, 137, 138). Deicing salt and heavy metals are the two main categories of pollutants studied in road runoff.

The primary deicing agent, NaCl, corrodes vehicles and bridges, contaminates drinking water supplies, and is toxic to many species of plants, fish, and other aquatic organisms (4, 16, 84). Calcium magnesium acetate (CMA) is a more effective deicer, less corrosive, less mobile in soil, biodegradable, and less toxic to aquatic organisms (4, 84, 89). Also, CaCl used to decrease dust may inhibit amphibian movement (28).

Airborne NaCl from road snowplowing may cause leaf injury to trees (e.g. *Pinus strobus*) up to 120 m from a road, especially downwind and downslope (58, 84). Trees seem to be more sensitive to chloride damage than are common roadside shrubs and grasses. Sodium accumulation in soils, mainly within 5 m of a road, alters soil structure, which affects plant growth (84). Road salt has facilitated the spread of three coastal exotic plants as much as 150 km in The Netherlands (1).

Deicing agents tend to increase the mobility of chemical elements in soil, such as heavy metals (by NaCl) and Na, Cl, Ca, and Mg (by CMA) (4). This process facilitates contamination of groundwater, aquifers, and streams. Because of dilution, the chemical effects of road runoff on surface water ecosystems may be primarily confined to small streams, particularly where they run adjacent to roads (36, 84).

Heavy metals are relatively immobile and heterogeneously distributed in roadsides, especially due to drainage ditch flows (15, 55, 80). Soils adjacent to the road surface typically contain the greatest mass (136). Elevated concentrations in grass tissue may occur within 5–8 m of a road, although high lead levels have been found in soil out to 25 m (30, 65, 82). Elevated lead concentrations were found in tissue of several small-mammal species in a narrow zone by roads, with higher lead levels by busy roads (48).

Highway roadsides of 5–15-m width next to traffic densities of 11,000–124,000 veh/day in The Netherlands had somewhat higher heavy-metal accumulations on the downwind side, but no correlation with traffic density was found (30). All average levels of Pb, Cd, Zn, Cr, Ni, and As in cut grass (hay) from these roadsides were below the Dutch maximum-acceptable-levels for livestock fodder and “clean compost.” Only Zn in some roadsides studied exceeded the maximum for “very clean compost.”

Many other chemicals enter roadsides. Herbicides often kill non-target plants, particularly from blanket applications in drifting air. For polycyclic aromatic hydrocarbons from petroleum (136), the preliminary conclusion for the Dutch highways was that levels in roadside hay “do not seem to give cause for alarm” (30). Fertilizer nutrients affect roadside vegetation (19, 86, 92), and nitrogen from vehicular NOX emission altered vegetation up to 100–200 m from a highway in Britain (7). Acidic road runoff may have impacts on stream ecosystems (36, 81). Of the hazardous materials transported on roads, e.g. >500,000 shipments moved each day in the United States, a small fraction is spilled, although occasional large spills cause severe local effects (85).

Typical water-quality responses to road runoff include altered levels of heavy metal, salinity, turbidity, and dissolved oxygen (16, 23, 81). However, these water-quality changes, even in a wetland, tend to be temporary and localized due to fluctuations in water quantity (23). Road runoff is a major source of heavy

metals to stream systems, especially Pb, Zn, Cu, Cr, and Cd (16, 50, 64, 137). Fish mortality in streams has been related to high concentrations of Al, Mn, Cu, Fe, or Zn, with effects on populations reorded as far as 8 km downstream (81). Both high traffic volume and high metal concentration in runoff have correlated with mortality of fish and other aquatic organisms (59). Floodplain soil near bridges may have high heavy-metal concentrations (138). Although highway runoff generally has little adverse effect on vegetation or plant productivity, it may change the species composition of floodplain plant communities, favoring common species (138).

Overall, terrestrial vegetation seems to be more resistant than aquatic organisms to road impacts (59, 138). Drainage of road runoff through grassy channels greatly reduces toxic solid- and heavy-metal concentrations (59). Furthermore, dense vegetation increases soil infiltration and storage. Therefore, instead of expensive detention ponds and drainage structures to reduce runoff impacts, creative grassland designs by roads, perhaps with shrubs, may provide both sponge and biodiversity benefits. The wide range of studies cited above lead to the conclusion that chemical impacts tend to be localized near roads.

THE ROAD NETWORK

New Roads and Changing Landscape Pattern

Do roads lead to development, or does development lead to roads? This timeless debate in the transportation community has greater ramifications as environmental quality becomes more important in the transportation–land-use interaction (114). For example, new roads into forested landscapes often lead to economic development as well as deforestation and habitat fragmentation (22).

At the landscape scale, the major ecological impacts of a road network are the disruption of landscape processes and loss of biodiversity. Interrupting horizontal natural processes, such as groundwater flow, streamflow, fire spread, foraging, and dispersal, fundamentally alters the way the landscape works (40, 53). It truncates flows and movements, and reduces the critical variability in natural processes and disturbances. Biodiversity erodes as the road network impacts interior species, species with large home ranges, stream and wetland species, rare native species, and species dependent on disturbance and horizontal flows.

A new road system in the Rondonia rainforest of Brazil illustrates such effects. By 1984, road construction and asphalt paving had stimulated a major influx of people and forest clearing (25). A regular pattern of primary roads plus parallel secondary roads 4 km apart was imposed on the land. Commonly, small forest plots of ~5 ha were gradually converted to grass and joined with neighboring plots to form large pastures (26). Simulation models of this typical scenario were compared with models of a worst-case scenario and an “innovative

farming” scenario with perennial crops and essentially no fire or cattle (25, 26). Species requiring a large area and having poor “gap-crossability” disappeared in all model scenarios after road construction. Species with moderate requirements for area and gap-crossability persisted only in the innovative farming scenario. Reestablishing the connectivity of nature with a network of wildlife corridors was proposed as a solution to maintain the first group of species, which are of conservation importance.

The closure and removal of some roads in the grid is an alternative ecological approach. Natural landscape processes and biodiversity are both inhibited by a rigid road grid. Closing and eliminating some linkages would permit the reestablishment of a few large patches of natural rainforest (39, 41, 43). Such a solution helps create a road network with a high variance in mesh size. Large natural-vegetation patches in areas remote from both roads and people are apparently required to sustain important species such as wolf, bear, and probably jaguar (*Canis lupus*, *Ursus*, *Felis onca*) (39, 76). Temporary road closures could, for example, enhance amphibian migration during the breeding phase (67). In contrast, road closure and removal could eliminate motorized vehicle use, thus reducing numerous disturbance effects on natural populations and ecosystems.

A general spatial-process model emphasizes that roads have the greatest ecological impact early in the process of land transformation (39, 41). They dissect the land, leading to habitat fragmentation, shrinkage, and attrition. Forest road networks may also create distinctive spatial patterns, such as converting convoluted to rectilinear shapes, decreasing core forest area, and creating more total edge habitat by roads than by logged areas (79, 96).

Forest roads as a subset of roads in general are characterized as being narrow, not covered with asphalt, lightly traveled, and remote (98). Among the wide range of ecological effects of roads (39, 95), forest roads have a distinctive set of major ecological effects: (a) habitat loss by road construction, (b) altered water routing and downstream peak flows, (c) soil erosion and sedimentation impacts on streams, (d) altered species patterns, and (e) human access and disturbance in remote areas (43, 45, 62, 132). Thus, an evaluation of logging regimes includes the ecological effects of both the road network and forest spatial patterns (45, 69). In conclusion, a road network disrupts horizontal natural processes, and by altering both landscape spatial pattern and the processes, it reduces biodiversity.

Road Density

Road density, e.g. measured as km/km², has been proposed as a useful, broad index of several ecological effects of roads in a landscape (39, 43, 44, 95). Effects are evident for faunal movement, population fragmentation, human access, hydrology, aquatic ecosystems, and fire patterns.

A road density of approx. 0.6 km/km^2 (1.0 mi/mi^2) appears to be the maximum for a naturally functioning landscape containing sustained populations of large predators, such as wolves and mountain lions (*Felis concolor*) (43, 76, 124). Moose (*Alces*), bear (*Ursus*) (brown, black, and grizzly), and certain other populations also decrease with increasing road density (11, 43, 72). These species are differentially sensitive to the roadkill, road-avoidance, and human-access dimensions of road density. Species that move along, rather than across, roads presumably are benefitted by higher road density (12, 39).

Human access and disturbance effects on remote areas tend to increase with higher road density (39, 72, 76). Similarly, human-caused fire ignitions and suppressions may increase, and average fire sizes decrease (111).

Aquatic ecosystems are also affected by road density. Hydrologic effects, such as altered groundwater conditions and impeded drainage upslope, are sensitive to road density (116, 118). Increased peak flows in streams may be evident at road densities of $2\text{--}3 \text{ km/km}^2$ (62). Detrimental effects on aquatic ecosystems, based on macro-invertebrate diversity, were evident where roads covered 5% or more of a watershed in California (75). In southeastern Ontario, the species richness of wetland plants, amphibians/reptiles, and birds each correlated negatively with road density within 1–2 km of a wetland (38).

Road density is an overall index that averages patterns over an area. Its effects probably are sensitive to road width or type, traffic density, network connectivity, and the frequency of spur roads into remote areas. Thus network structure, or an index of variance in mesh size, is also important in understanding the effect of road density (39, 76, 79, 96). Indeed, although road density is a useful overall index, the presence of a few large areas of low road density may be the best indicator of suitable habitat for large vertebrates and other major ecological values.

TRANSPORTATION POLICY AND PLANNING

Environmental Policy Dimensions

Ecological principles are increasingly important in environmental transportation policy, and Australia, The Netherlands, and the United States highlight contrasting approaches. Australian policy has focused on biodiversity, including wildflower protection. An enormous network of road reserves with natural-vegetation strips 10–200 m wide (Figure 1) stands out in many agricultural landscapes (66, 92, 111). Public pressure helped create this system, which “helps to prevent soil erosion” and “where wildflowers can grow and flourish in perpetuity” (111). Diverse experimental management approaches involve burning, weed control, planting native species, and nature restoration. Ecological

scientists commonly work side by side with civil engineers in transportation departments at all levels of government.

In contrast, Dutch policy has focused on the open roadside vegetation, road-kills, animal movement patterns, and nature restoration (1, 21, 29, 86). This approach reflects the stated national objectives of (a) recreating “nature, including natural processes and biodiversity; and (b) enhancing the national ecological network,” mainly composed of large natural-vegetation patches and major wildlife and water corridors (1, 46). An impressive series of mitigation overpasses, tunnels, and culverts provide for animal and water movement where interrupted by road barriers (24, 43, 44, 86). Environmental activities in transportation revolve around a group of environmental scientists in the national Ministry of Transport who work closely with engineers and policy-makers at both local and national levels.

In the United States, environmental transportation policy focuses on vehicular pollutants, as well as engineering solutions for soil erosion and sedimentation (85). A few states have built wildlife underpasses and overpasses to address local roadkill or wildlife movement concerns. A 1991 federal law—the Intermodal Surface Transportation Efficiency Act (ISTEA)—establishes policy for a transportation system that is “economically efficient and environmentally sound,” considers the “external benefits of reduced air pollution, reduced traffic congestion and other aspects of the quality of life,” considers transportation in a region-wide metropolitan area, and links ecological attributes with the aesthetics of a landscape (43). Thus, US transportation policy largely ignores biodiversity loss, habitat fragmentation, disruption of horizontal natural processes, natural stream and wetland hydrology, streamwater chemistry, and reduction of fish populations, a range of ecological issues highlighted in the transportation community in 1997 (85).

Of course, many nations use ecological principles in designing transportation systems (21, 33, 63, 95, 134), and environmental scientists, engineers, and policy-makers in Europe have united to “conserve biodiversity and reduce . . . fauna casualties” at the international level (21; H van Bohemen, personal communication). The successful removal of lead from petroleum led to less lead in roadside ecosystems worldwide. Nevertheless, the huge Australian road-reserve system and the Dutch mitigation system for animal and water flows are especially ambitious and pioneering.

Spatial Planning and Mitigation

Most existing roads were built before the explosion in ecological knowledge, and many are poorly located ecologically (43). Yet the Dutch have developed a promising transportation planning process for the movement of both people and natural processes across the land (40, 44, 86). In essence, the ecological network, consisting of large natural-vegetation patches plus major corridors for

water and wildlife movement, is mapped. The road network is then superimposed on the ecological network to identify bottlenecks. Finally, mitigation or compensation techniques are applied to eliminate designated percentages of bottlenecks in a time sequence. The earlier such spatial planning begins, the greater its effect (41).

Compensation is proposed where bottlenecks apparently cannot be overcome by mitigation. The principle of no-net-loss has been used internationally for wetlands with varying success (46, 94), whereas no-net-loss of natural processes and biodiversity by roads is a concept only beginning to be applied (1, 24, 46, 86). The loss, e.g. of biodiversity or groundwater flow, is compensated by increasing an equivalent ecological value nearby. Options include protection of an equivalent amount of high-quality habitat, reestablishment of another wildlife corridor, or creation of new habitat. Mitigation, on the other hand, attempts to minimize detrimental ecological impacts and is illustrated by the varied wildlife passages (tunnels, pipes, underpasses, overpasses) operating for animal movement (21, 86).

Diverse tunnel designs focus on small and mid-sized animals. Amphibian tunnels, generally 30–100 cm wide and located where roads block movement to breeding ponds or wetlands, are widespread in Europe and rare in the United States (33, 43, 67). “Ecopipes,” or badger tunnels, are pipes ~40 cm in diameter mainly designed for movement of mid-sized mammals across Dutch roads, and located where water can rarely flow through (9, 44, 46, 86). In contrast, Dutch wildlife culverts are ~120 cm wide, with a central channel for water flow between two raised 40-cm-wide paths for animal movement. “Talus tunnels” are designed for a mid-sized mammal that lives and moves in rock talus slopes in Australia (74).

Wildlife underpasses, generally 8–30 m wide and at least 2.5 m high, have been built for large mammals in southern Florida and scattered locations elsewhere in the United States, Canada, and France (33, 43, 54, 63, 93, 113). Wildlife overpasses, also designed for large mammals, range in width up to 200 m and are scarce: approximately 6 in North America (New Jersey, Utah, Alberta, British Columbia) (33, 43; BF Leeson, personal communication) and 17 in Europe (Germany, France, The Netherlands, Switzerland) (44, 46, 63, 86, 134). The minimum widths for effectiveness may be 30–50 m in the center and 50–80 m on the ends (33, 46, 86). The two Swiss overpasses of 140-m and 200-m width remind us that ultimately the goal should be “landscape connectors” that permit all horizontal natural processes to cross roads (43, 44).

These mitigation structures are normally combined with fencing and vegetation to enhance animal crossing (86). Almost all such passages are successful in that the target species crosses at least occasionally, and most are used by many other species. Florida underpasses are used by the Florida panther (*Felis concolor coryi*), nearly the whole local terrestrial fauna, and groundwater as

well (33, 54). Underpasses and overpasses are used by almost all large mammal species of a region. Yet, little information exists on crossing rates relative to population sizes, movement rates away from roads, predation rates, home range locations, and so forth. Nevertheless, mitigation passages are effective in perforating road barriers to maintain horizontal natural processes across the land.

The Road-Effect Zone

Roads and roadsides cover 0.9% of Britain and 1.0% of the United States, while road reserves (Figure 1) cover 2.5% of the State of Victoria, Australia (12, 85, 131). Yet how much of the land is ecologically impacted by roads with vehicles?

The road-effect zone is the area over which significant ecological effects extend outward from a road and typically is many times wider than the road surface plus roadsides (Figure 2) (39, 95, 101, 134). The zone is asymmetric with convoluted boundaries, reflecting the sequence of ecological variables, plus unequal effect-distances due to slope, wind, and habitat suitability on opposite sides of a road (40, 43). Knowing the average width of the road-effect zone permits us to estimate the proportion of the land ecologically affected by roads (43). For example, based on the traffic noise effect-distances of sensitive bird species described above, road-effect zones cover ~10–20% of The Netherlands (101).

Finally, a preliminary calculation for the United States was made based on nine water and species variables in Massachusetts (USA), plus evidence from the Dutch studies (42). An estimated 15–20% of the US land area is directly affected ecologically by roads. These estimates reemphasize the immensity and pervasiveness of ecological road impacts. Moreover, they challenge science and society to embark on a journey of discovery and solution.

ACKNOWLEDGMENTS

Virginia H Dale, Robert D Deblinger, Malcolm L Hunter, Jr, and Julia A Jones provided terrific reviews, which we deeply appreciate.

Visit the *Annual Reviews* home page at
<http://www.AnnualReviews.org>

Literature Cited

1. Aanen P, Alberts W, Bekker GJ, van Bohemen HD, Melman PJM, et al. 1991. *Nature Engineering and Civil Engineering Works*. Wageningen, Netherlands: PU-DOC
2. Adams LW. 1984. Small mammal use of an interstate highway median strip. *J. Appl. Ecol.* 21:175–78
3. Amor RL, Stevens PL. 1976. Spread of weeds from a roadside into sclerophyll forests at Dartmouth, Australia. *Weed Res.* 16:111–18

4. Amrhein C, Strong JE, Mosher PA. 1992. Effect of deicing salts on metal and organic matter mobilization in roadside soils. *Environ. Sci. Technol.* 26:703–9
5. Anderson B, Simons DB. 1983. Soil erosion study of exposed highway construction slopes and roadways. *Transp. Res. Rec.* 948:40–47
6. Andrews A. 1990. Fragmentation of habitat by roads and utility corridors: a review. *Aust. J. Zool.* 26:130–41
7. Angnold PG. 1997. The impact of road upon adjacent heathland vegetation: effects on plant species composition. *J. Appl. Ecol.* 34:409–17
8. Ashley EP, Robinson JT. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point causeway, Lake Erie, Ontario. *Can. Field Nat.* 110:403–12
9. Bekker H, Canters KJ. 1997. The continuing story of badgers and their tunnels. See Ref. 21, pp. 344–53
10. Bellis ED, Graves HB. 1971. Deer mortality on a Pennsylvania interstate highway. *J. Wildl. Manage.* 35:232–37
11. Bennett AF. 1988. Roadside vegetation: a habitat for mammals at Naringal, southwestern Victoria. *Victorian Natur.* 105: 106–13
12. Bennett AF. 1991. Roads, roadsides and wildlife conservation: a review. See Ref. 111, pp. 99–117
13. Beschta R. 1978. Long-term patterns of sediment production following road construction and logging in the Oregon Coast Range. *Water Resour. Res.* 14:1011–16
14. Bilby RE, Sullivan K, Duncan SH. 1989. The generation and fate of road-surface sediment in forested watersheds in southwestern Washington. *For. Sci.* 35:453–68
15. Black FM, Braddock JN, Bradow R, Ingalls M. 1985. Highway motor vehicles as sources of atmospheric particles: projected trends 1977–2000. *Environ. Int.* 11:205–33
16. Brown KJ. 1994. River-bed sedimentation caused by off-road vehicles at river fords in the Victorian Highlands, Australia. *Water Resour. Bull.* 30:239–50
17. Brown SA. 1982. Prediction of channel bed grade changes at highway stream crossings. *Transp. Res. Rec.* 896:1–11
18. Buchanan BW. 1993. Effects of enhanced lighting on the behaviour of nocturnal frogs. *Anim. Behav.* 43:893–99
19. Cale P, Hobbs RJ. 1991. Condition of roadside vegetation in relation to nutrient status. See Ref. 111, pp. 353–62
20. Calvo RN, Silvy NJ. 1996. Key deer mortality, U.S. 1 in the Florida Keys. See Ref. 33, pp. 337–48
21. Canters K, ed. 1997. *Habitat Fragmentation & Infrastructure*. Minist. Transp., Public Works & Water Manage., Delft, Netherlands. 474 pp.
22. Chomitz KM, Gray DA. 1996. Roads, land use, and deforestation: a spatial model applied to Belize. *World Bank Econ. Rev.* 10:487–512
23. Cramer GH, Hopkins WC. 1982. Effects of a dredged highway construction on water quality in a Louisiana wetland. *Transp. Res. Rec.* 896:47–51
24. Cuperus R, Piepers AAG, Canters KJ. 1997. Elaboration of the compensation principle in the Netherlands: outlines of the draft manual *Ecological Compensation in Road Projects*. See Ref. 21, pp. 308–15
25. Dale VH, O'Neill RV, Southworth F, Pedlowski M. 1994. Modeling effects of land management in the Brazilian Amazonian settlement of Rondonia. *Conserv. Biol.* 8:196–206
26. Dale VH, Pearson SM, Offerman HL, O'Neill RV. 1994. Relating patterns of land-use change to faunal biodiversity in the Central Amazon. *Conserv. Biol.* 8:1027–36
27. Dawson BL. 1991. South Africa road reserves: valuable conservation reserves? See Ref. 111, pp. 119–30
28. deMaynadier PG, Hunter ML Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environ. Rev.* 3:230–61
29. Dienst Weg- en Waterbouwkunde. 1994. *Managing Roadside Flora in The Netherlands*. DWW Wijzer 60. Delft, Netherlands. 4 pp.
30. Dienst Weg- en Waterbouwkunde. 1994. *The Chemical Quality of Verge Grass in The Netherlands*. DWW Wijzer 62. Delft, Netherlands. 4 pp.
31. Eaglin GS, Hubert WA. 1993. Effects of logging and roads on substrate and trout in streams of the Medicine Bow National Forest, Wyoming. *North Am. J. Fish. Manage.* 13:844–46
32. Ellenberg H, Muller K, Stottele T. 1991. Strassen-Ökologie. In *Ökologie und Strasse*, pp.19–115. Broschurenreihe de Deutschen Strassenliga, Bonn, Ger.
33. Evink GL, Garret P, Zeigler D, Berry J, eds. 1996. *Trends in Addressing Transportation Related Wildlife Mortality*. No. FL-ER-58-96. Florida Dep. Transp. Tallahassee, FL. 395 pp.

34. Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF. 1995. Effect of road traffic on amphibian density. *Biol. Conserv.* 73:177–82
35. Feldhamer GA, Gates JE, Harman DM, Loranger AJ, Dixon KR. 1986. Effects of interstate highway fencing on white-tailed deer activity. *J. Wildl. Manage.* 50:497–503
36. Fennessey TW. 1989. Guidelines for handling acid-producing materials on low-volume roads. *Transp. Res. Rec.* 1291:186–89
37. Ferris CR. 1979. Effects of Interstate 95 on breeding birds in northern Maine. *J. Wildl. Manage.* 43:421–27
38. Findlay CS, Houlahan J. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conserv. Biol.* 11:1000–9
39. Forman RTT. 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge, UK: Cambridge Univ. Press
40. Forman RTT. 1998. Horizontal processes, roads, suburbs, societal objectives, and landscape ecology. In *Landscape Ecological Analysis: Issues and Applications*, ed. JM Klopatek, RH Gardner. New York: Springer-Verlag. In press
41. Forman RTT, Collinge SK. 1997. Nature conserved in changing landscapes with and without spatial planning. *Landscape Urban Plan.* 37:129–35
42. Forman RTT, Deblinger RD. 1998. The ecological road-effect zone for transportation planning, and a Massachusetts highway example. In *Proc. Int. Conf. Wildlife and Transportation, Rep. FL-ER-69-98*, ed. GL Evink, P Garrett, D Zeigler, J Berry. Florida Dep. Transp. Tallahassee, FL. In press
43. Forman RTT, Friedman DS, Fitzhenry D, Martin JD, Chen AS, Alexander LE. 1997. Ecological effects of roads: toward three summary indices and an overview for North America. See Ref. 21, pp. 40–54
44. Forman RTT, Hersperger AM. 1996. Road ecology and road density in different landscapes, with international planning and mitigation solutions. See Ref. 33, pp. 1–22
45. Forman RTT, Mellinger AD. 1998. Road networks and forest spatial patterns in ecological models of diverse logging regimes. In *Nature Conservation in Production Environments: Managing the Matrix*, ed. DA Saunders, J Craig, N Mitchell. Chipping Norton, Australia: Surrey Beatty. In press
46. Friedman DS. 1997. *Nature as Infrastructure: The National Ecological Network and Wildlife-crossing Structures in The Netherlands*. Rep. 138, DLO Winand Staring Centre. Wageningen, Netherlands. 49 pp.
47. Getz LL, Cole FR, Gates DL. 1978. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *J. Mammal.* 59:208–12
48. Getz LL, Verner L, Prather M. 1977. Lead concentrations in small mammals living near highways. *Environ. Pollut.* 13:151–57
49. Gilje SA. 1982. Stream channel grade changes and their effects on highway crossings. *Transp. Res. Rec.* 895:7–15
50. Gilson MP, Malivia JF, Chareneau RJ. 1994. Highway runoff studied. *Water Environ. Technol.* 6:37–38
51. Grayson RB, Haydon SR, Jayasuriya MDA, Enlayson BC. 1993. Water quality in mountain ash forests—separating the impacts of roads from those of logging operations. *J. Hydrol.* 150:459–80
52. Harr RD, Harper WC, Krygier JT, Hsieh FS. 1975. Changes in storm hydrographs after road building and clear-cutting in the Oregon Coast Range. *Water Resour. Res.* 11:436–44
53. Harris LD, Hctor TS, Gergel SE. 1996. Landscape processes and their significance to biodiversity conservation. In *Population Dynamics in Ecological Space and Time*, ed. O Rhodes Jr, R Chesser, M Smith, pp. 319–47. Chicago: Univ. Chicago Press
54. Harris LD, Scheck J. 1991. From implications to applications: the dispersal corridor principle applied to the conservation of biological diversity. See Ref. 111, pp. 189–220
55. Hewitt CN, Rashed MB. 1991. The deposition of selected pollutants adjacent to a major rural highway. *Atmos. Environ.* 35A(5–6):979–83
56. Hodson NL. 1962. Some notes on the causes of bird road casualties. *Bird Study* 9:168–73
57. Hodson NL. 1966. A survey of road mortality in mammals (and including data for the grass snake and common frog). *J. Zool., Lond.* 148:576–79
58. Hofstra G, Hall R. 1971. Injury on roadside trees: leaf injury on pine and white cedar in relation to foliar levels of sodium chloride. *Can. J. Bot.* 49:613–22
59. Horner RR, Mar BW. 1983. Guide for assessing water quality impacts of highway operations and maintenance. *Transp. Res. Rec.* 948:31–39
60. Huey LM. 1941. Mammalian invasion via

- the highway. *J. Mammal.* 22:383–85
61. Iverson RM, Hinckley BS, Webb RM. 1981. Physical effects of vehicular disturbances on arid landscapes. *Science* 212:915–17
 62. Jones JA, Grant GE. 1996. Peak flow responses to clearcutting and roads in small and large basins, Western Cascades, Oregon. *Water Resour. Res.* 32:959–74
 63. Keller V, Pfister HP. 1997. Wildlife passages as a means of mitigating effects of habitat fragmentation by roads and railway lines. See Ref. 21, pp. 70–80
 64. Kerri KD, Racine JA, Howell RB. 1985. Forecasting pollutant loads from highway run off. *Transp. Res. Rec.* 1017:39–46
 65. Lagerwerff JV, Specht AN. 1970. Contamination of roadside soil and vegetation with cadmium, nickel, lead, and zinc. *Environ. Sci. Technol.* 4:583–86
 66. Lamont DA, Blyth JD. 1995. Roadside corridors and community networks. In *Nature Conservation 4: The Role of Networks*, ed. DA Saunders, JL Craig, EM Mattiske, pp. 425–35. Chipping Norton, Australia: Surrey Beatty
 67. Langton TES, ed. 1989. *Amphibians and Roads*. ACO Polymer Products, Shefford, Bedfordshire, UK. 202 pp.
 68. Leopold LB, Wolman MG, Miller JP. 1964. *Fluvial Processes in Geomorphology*. San Francisco: Freeman
 69. Li H, Franklin JF, Swanson FJ, Spies TA. 1993. Developing alternative forest cutting patterns: a simulation approach. *Landsc. Ecol.* 8:63–75
 70. Lonsdale WM, Lane AM. 1994. Tourist vehicles as vectors of weed seeds in Kakadu National Park, northern Australia. *Biol. Conserv.* 69:277–83
 71. Lowe JC, Moryadas S. 1975. *The Geography of Movement*. Boston: Houghton Mifflin
 72. Lyon LJ. 1983. Road density models describing habitat effectiveness for elk. *J. For.* 81:592–95
 73. Mader HJ. 1984. Animal habitat isolation by roads and agricultural fields. *Biol. Conserv.* 29:81–96
 74. Mansergh IM, Scotts DJ. 1989. Habitat-continuity and social organization of the mountain pygmy-possum restored by tunnel. *J. Wildl. Manage.* 53:701–7
 75. McGurk B, Fong DR. 1995. Equivalent roaded area as a measure of cumulative effect of logging. *Environ. Manage.* 19:609–21
 76. Mech LD. 1989. Wolf population survival in an area of high road density. *Am. Midl. Nat.* 121:387–89
 77. Megahan WF, Ketcheson GL. 1996. Predicting downslope travel of granitic sediments from forest roads in Idaho. *Water Resour. Bull.* 32:371–82
 78. Merriam G, Kozakiewicz M, Tsuchiya E, Hawley K. 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Landsc. Ecol.* 2:227–35
 79. Miller JR, Joyce LA, Knight RL, King RM. 1996. Forest roads and landscape structure in the southern Rocky Mountains. *Landsc. Ecol.* 11:115–27
 80. Montgomery D. 1994. Road surface drainage, channel initiation, and slope instability. *Water Resour. Res.* 30:192–93
 81. Morgan E, Porak W, Arway J. 1983. Controlling acidic-toxic metal leachates from southern Appalachian construction slopes: mitigating stream damage. *Transp. Res. Rec.* 948:10–16
 82. Motto HL, Daines RL, Chilko DM, Motto CK. 1970. Lead in soils and plants: its relationship to traffic volume and proximity to highways. *Environ. Sci. Technol.* 4:231–37
 83. Munguira ML, Thomas JA. 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. *J. Appl. Ecol.* 29:316–29
 84. National Research Council. 1991. *Highway Deicing: Comparing Salt and Calcium Magnesium Acetate*. Spec. Rep. 235, Transp. Res. Board, Washington, DC. 170 pp.
 85. National Research Council. 1997. *Toward a Sustainable Future: Addressing the Long-term Effects of Motor Vehicle Transportation on Climate and Ecology*. Washington, DC: Natl. Acad. Press
 86. *Natuur Over Wegen (Nature Across Motorways)*. 1995. Dienst Weg- en Waterbouwkunde, Delft, Netherlands. 103 pp.
 87. Oetting RB, Cassel JF. 1971. Waterfowl nesting on interstate highway right-of-way in North Dakota. *J. Wildl. Manage.* 35:774–81
 88. Opdam P, van Apeldoorn R, Schotman A, Kalkhoven J. 1993. Population responses to landscape fragmentation. In *Landscape Ecology of a Stressed Environment*, ed. CC Vos, P Opdam, pp. 147–71. London: Chapman & Hall
 89. Ostendorf DW, Pollack SJ, DeCheke ME. 1993. Aerobic degradation of CMA in roadside soils: field simulations from soil microcosms. *J. Environ. Qual.* 22:299–304
 90. Oxley DJ, Fenton MB, Carmody GR. 1974. The effects of roads on populations

- of small mammals. *J. Appl. Ecol.* 11:51–59
91. Packer PE. 1967. Criteria for designing and locating logging roads to control sediment. *For. Sci.* 13:1–18
 92. Panetta FD, Hopkins AJM. 1991. Weeds in corridors: invasion and management. See Ref. 111, pp. 341–51
 93. Paquet PC, Callaghan C. 1996. Effects of linear developments on winter movements of gray wolves in the Bow River Valley of Banff National Park, Alberta. See Ref. 33, pp. 51–73
 94. Race MS, Fonseca MS. 1995. Fixing compensatory mitigation: What will it take? *Ecol. Appl.* 6:94–101
 95. Reck H, Kaule G. 1993. Strassen und Lebensraume: Ermittlung und Beurteilung strassenbedingter Auswirkungen auf Pflanzen, Tiere und ihre Lebensraume. *Forschung Strassenbau und Strassenverkehrstechnik*, Heft 654. Herausgegeben vom Bundesminister für Verkehr, Bonn-Bad Godesberg, Ger. 230 pp.
 96. Reed RA, Johnson-Barnard J, Baker WL. 1996. Contribution of roads to forest fragmentation in the Rocky Mountains. *Conserv. Biol.* 10:1098–106
 97. Reh W. 1989. Investigations into the influences of roads on the genetic structure of populations of the common frog *Rana temporaria*. See Ref. 67, pp. 101–13
 98. Reh W, Seitz A. 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biol. Conserv.* 54:239–49
 99. Reid LM, Dunne T. 1984. Sediment production from forest road surfaces. *Water Resour. Res.* 20:1753–61
 100. Reijnen MJSM, Veenbaas G, Foppen RPB. 1995. *Predicting the Effects of Motorway Traffic on Breeding Bird Populations*. DLO Inst. For. Nat. Res., Ministry Transp. Public Works, Delft, The Netherlands. 92 pp.
 101. Reijnen R. 1995. *Disturbance by car traffic as a threat to breeding birds in The Netherlands*. PhD thesis, DLO Inst. For. Nat. Res., Wageningen, Netherlands. 140 pp.
 102. Reijnen R, Foppen R, Meeuwssen H. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biol. Conserv.* 75:255–60
 103. Reijnen R, Foppen R, ter Braak C, Thissen J. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *J. Appl. Ecol.* 32:187–202
 104. Rice RM, Lewis J. 1991. Estimating erosion risks associated with logging and forest roads in northwestern California. *Water Resour. Bull.* 27:809–18
 105. Roach GL, Kirkpatrick RD. 1985. Wildlife use of roadside woody plantings in Indiana. *Transp. Res. Rec.* 1016:11–15
 106. Romin LA, Bissonette JA. 1996. Temporal and spatial distribution of highway mortality of mule deer on newly constructed roads at Jordanelle Reservoir, Utah. *Gt. Basin Nat.* 56:1–11
 107. Ross SM. 1986. Vegetation change on highway verges in south-east Scotland. *J. Biogeogr.* 13:109–13
 108. Rost GR, Bailey JA. 1979. Distribution of mule deer and elk in relation to roads. *J. Wildl. Manage.* 43:634–41
 109. Santelman MV, Gorham EV. 1988. The influence of airborne road dust on the chemistry of *Sphagnum* mosses. *J. Ecol.* 76:1219–31
 110. Sauer VB, Thomas EO Jr, Stricker VA, Wilson KV. 1982. Magnitude and frequency of urban floods in the United States. *Transp. Res. Rec.* 896:30–33
 111. Saunders DA, Hobbs RJ, eds. 1991. *Nature Conservation 2: The Role of Corridors*. Chipping Norton, Australia: Surrey Beatty
 112. Schmidt W. 1989. Plant dispersal by motor cars. *Vegetatio* 80:147–52
 113. Singer FJ, Langlitz WL, Samuelson EC. 1985. Design and construction of highway underpasses used by mountain goats. *Transp. Res. Rec.* 1016:6–10
 114. Skinner RE Jr, Moore T, Cervero R, Landis J, Giuliano G, Leinberger CB, Epstein LR. 1996. The transportation–land use interaction. *TR News (Washington)* 187:6–17
 115. Soule ME, ed. 1987. *Viable Populations for Conservation*. Cambridge, UK: Cambridge Univ. Press
 116. Stoeckeler JH. 1965. Drainage along swamp forest roads: lessons from Northern Europe. *J. For.* 63:771–76
 117. Swanson FJ, Dyrness CT. 1975. Impact of clear-cutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. *Geology* 3:393–96
 118. Swanson GA, Winter TC, Adomaitis VA, LaBaugh JW. 1988. *Technical characteristics of prairie lakes in south-central North Dakota—their potential for influencing use by fish and wildlife*. Tech. Rep. 18, US Fish Wildl. Serv., Washington, DC
 119. Swihart RK, Slade NA. 1984. Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. *J. Mammal.* 65:357–60

120. Tabor R. 1974. Earthworms, crows, vibrations and motorways. *New Sci.* 62: 482–83
121. Tyser RW, Worley CA. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). *Conserv. Biol.* 6:253–62
122. van Apeldoorn RC. 1997. Fragmented mammals: What does that mean? See Ref. 21, pp. 121–26
123. van der Zande AN, ter Keurs J, van der Weijden WJ. 1980. The impact of roads on the densities of four bird species in an open field habitat—evidence of a long distance effect. *Biol. Conserv.* 18:299–321
124. van Dyke FB, Brocke RH, Shaw HG, Ackerman BB, Hemker TP, Lindzey FG. 1986. Reactions of mountain lions to logging and human activity. *J. Wildl. Manage.* 50:95–102
125. Vermeulen HJW. 1993. The composition of the carabid fauna on poor sandy road-side-verges in relation to comparable open areas. *Biodiv. Conserv.* 2:331–50
126. Vermeulen HJW. 1994. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (*Carabidae*). *Biol. Conserv.* 69:339–49
127. Vermeulen HJW, Opdam PFM. 1995. Effectiveness of roadside verges as dispersal corridors for small ground-dwelling animals: a simulation study. *Landscape Urban Plan.* 31:233–48
128. Vos CC. 1997. Effects of road density: a case study of the moor frog. See Ref. 21, pp. 93–97
129. Walker DA, Walker MD. 1991. History and pattern of disturbance in Alaskan arctic terrestrial ecosystems: a hierarchical approach to analysing landscape change. *J. Appl. Ecol.* 28:244–76
130. Wasser S, Bevis K, King G, Hanson E. 1997. Noninvasive physiological measures of disturbance in the northern spotted owl. *Conserv. Biol.* 11:1019–22
131. Way JM. 1977. Roadside verges and conservation in Britain: a review. *Biol. Conserv.* 12:65–74
132. Wemple BC, Jones JA, Grant GE. 1996. Channel network extension by logging roads in two basins, Western Cascades, Oregon. *Water Resour. Bull.* 32:1195–207
133. Wilcox DA. 1989. Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. *Environ. Manage.* 13:365–70
134. *Wildtiere, Strassenbau und Verkehr*. 1995. Schweiz. Ges. Wildtierbiol., Zurich. 53 pp.
135. Winner WE. 1994. Mechanistic analysis of plant responses to air pollution. *Ecol. Appl.* 4:651–61
136. Wust W, Kern U, Hermann R. 1994. Street wash-off behavior of heavy metals, polyaromatic hydrocarbons and nitrophenols. *Sci. Total Environ.* 147:457–63
137. Yousef YA, Wanielista MP, Harper HH. 1985. Removal of highway contaminants by roadside swales. *Transp. Res. Rec.* 1017:62–68
138. Yousef YA, Wanielista MP, Harper HH, Skene ET. 1983. Impact of bridging on floodplains. *Transp. Res. Rec.* 948:26–30
139. Zwaenepoel A. 1997. Floristic impoverishment by changing unimproved roads into metalled roads. See Ref. 21, pp. 127–37



CONTENTS

MOLECULAR TRANS-SPECIES POLYMORPHISM, <i>Jan Klein, Akie Sato, Sandra Nagl, Colm O'hUigín</i>	1
PRINCIPLES OF PHYLOGEOGRAPHY AS ILLUSTRATED BY FRESHWATER AND TERRESTRIAL TURTLES IN THE SOUTHEASTERN UNITED STATES, <i>DeEtte Walker, John C. Avise</i>	23
THE FUNCTIONAL SIGNIFICANCE OF THE HYPORHEIC ZONE IN STREAMS AND RIVERS, <i>Andrew J. Boulton, Stuart Findlay, Pierre Marmonier, Emily H. Stanley, H. Maurice Valett</i>	59
ENDANGERED MUTUALISMS: The Conservation of Plant-Pollinator Interactions, <i>Carol A. Kearns, David W. Inouye, Nickolas M. Waser</i>	83
THE ROLE OF INTRODUCED SPECIES IN THE DEGRADATION OF ISLAND ECOSYSTEMS: A Case History of Guam, <i>Thomas H. Fritts, Gordon H. Rodda</i>	113
EVOLUTION OF HELPING BEHAVIOR IN COOPERATIVELY BREEDING BIRDS, <i>Andrew Cockburn</i>	141
THE ECOLOGICAL EVOLUTION OF REEFS, <i>Rachel Wood</i>	179
ROADS AND THEIR MAJOR ECOLOGICAL EFFECTS, <i>Richard T. T. Forman, Lauren E. Alexander</i>	207
SEX DETERMINATION, SEX RATIOS, AND GENETIC CONFLICT, <i>John H. Werren, Leo W. Beukeboom</i>	233
EARLY EVOLUTION OF LAND PLANTS: Phylogeny, Physiology, and Ecology of the Primary Terrestrial Radiation, <i>Richard M. Bateman, Peter R. Crane, William A. DiMichele, Paul R. Kenrick, Nick P. Rowe, Thomas Speck, William E. Stein</i>	263
POSSIBLE LARGEST-SCALE TRENDS IN ORGANISMAL EVOLUTION: Eight "Live Hypotheses", <i>Daniel W. McShea</i>	293
FUNGAL ENDOPHYTES: A Continuum of Interactions with Host Plants, <i>K. Saikkonen, S. H. Faeth, M. Helander, T. J. Sullivan</i>	319
FLORAL SYMMETRY AND ITS ROLE IN PLANT-POLLINATOR SYSTEMS: Terminology, Distribution, and Hypotheses, <i>Paul R. Neal, Amots Dafni, Martin Giurfa</i>	345
VERTEBRATE HERBIVORES IN MARINE AND TERRESTRIAL ENVIRONMENTS: A Nutritional Ecology Perspective, <i>J. H. Choat, K. D. Clements</i>	375
CARBON AND CARBONATE METABOLISM IN COASTAL AQUATIC ECOSYSTEMS, <i>J.-P. Gattuso, M. Frankignoulle, R. Wollast</i>	405
THE SCIENTIFIC BASIS OF FORESTRY, <i>David A. Perry</i>	435

PATHWAYS, MECHANISMS, AND RATES OF POLYPLOID FORMATION IN FLOWERING PLANTS, <i>Justin Ramsey, Douglas W. Schemske</i>	467
BACTERIAL GROWTH EFFICIENCY IN NATURAL AQUATIC SYSTEMS, <i>Paul A. del Giorgio, Jonathan J. Cole</i>	503
THE CHEMICAL CYCLE AND BIOACCUMULATION OF MERCURY, <i>François M. M. Morel, Anne M. L. Kraepiel, Marc Amyot</i>	543
PHYLOGENY OF VASCULAR PLANTS, <i>James A. Doyle</i>	567