Road Facilitation of Trematode Infections in Snails of Northern Alaska

MARK C. URBAN

Yale University, School of Forestry and Environmental Studies, Yale University, 370 Prospect Street, New Haven, CT 06511-2104, U.S.A., email mark.urban@yale.edu

Abstract: *Road disturbances can influence wildlife health by spreading disease agents and hosts or by generating environmental conditions that sustain these agent and host populations. I evaluated field patterns of trematode infections in snails inhabiting ponds at varying distances from the Dalton Highway, a wilderness road that intersects northern Alaska. I also assessed the relationships between trematode infections and snail densities and six environmental variables: calcium concentration, aquatic vegetative cover, canopy cover, temperature, pond size, and community structure. Presence of trematode infections and snail density were negatively correlated with distance from the highway. Of the pond characteristics measured, only calcium concentration and vegetation density declined with distance from road. However, neither variable was positively associated with snail density or trematode presence. One potential explanation for observed patterns is that vehicles, road maintenance, or vertebrate vectors attracted to the highway facilitate colonization of snails or trematodes. Emerging disease threats to biological diversity in northern ecosystems highlight the importance of understanding how roads affect disease transmission.*

Keywords: Alaska, Arctic ecosystems, emerging infectious disease, host–parasite interactions, pathogen pollution, pond communities, road effects

Los Caminos Facilitan las Infecciones de Trematodos en Caracoles del Norte de Alaska

Resumen: *La perturbación por caminos puede influir en la salud de la vida silvestre al propagar agentes infecciosos y huéspedes o al generar condiciones ambientales que sostienen a las poblaciones de agentes y huéspedes. Evalué los patrones de infecciones de trematodos en caracoles que habitan charcas a diferentes distancias de la Carretera Dalton, que intersecta el norte de Alaska. También evalué las relaciones entre infecciones de trematodos y las densidades de caracoles y seis variables ambientales: concentración de calcio, cobertura de vegetación acuática, cobertura del dosel, temperatura, tamaño de la charca y estructura de la comunidad. La presencia de infecciones de trematodos y la densidad de caracoles se correlacionaron negativamente con la distancia a la carretera. De las características medidas en las charcas, sólo la concentración de calcio y la densidad de la vegetación declinaron con la distancia a la carretera. Sin embargo, ninguna variable se asoció positivamente con la densidad de caracoles o con la presencia de trematodos. Una posible explicación de los patrones observados es que los vehículos, el mantenimiento de caminos o los vectores vertebrados atraídos a la carretera facilitan la colonización de caracoles o trematodos. Las amenazas de enfermedades emergentes a la diversidad biológica en ecosistemas norteños resaltan la importancia de entender el efecto de los caminos sobre la transmisión de enfermedades.*

Palabras Clave: Alaska, comunidades de charcas, ecosistemas del Ártico, efectos de caminos, enfermedad infecciosa emergente, interacciones huésped-parásito, polución por patógenos

Paper submitted July 1, 2005; revised manuscript accepted September 15, 2005.

Conservation Biology Volume 20, No. 4, 1143–1149

DOI: 10.1111/j.1523-1739.2006.00422.x

Introduction

One of the most serious consequences of anthropogenic ecosystem degradation is the emergence of novel infectious diseases. The spread of disease agents by human means, termed pathogen pollution, represents a common link between anthropogenic disturbances and disease facilitation (Daszak et al. 2000, 2001; Cunningham et al. 2003). Road construction is a global agent of anthropogenic change that frequently modifies dispersal rates among and environmental conditions within natural communities (Trombulak & Frissell 2000; Forman et al. 2003). Because road disturbances can alter ecosystems up to several kilometers away (Trombulak & Frissell 2000; Forman et al. 2003), roads affect a significant portion of the world's land surface (Forman 2000). Roads can influence disease prevalence either by facilitating movement of disease agents and hosts or by promoting environmental conditions that enhance their abundances (Patz et al. 2000; Smith 2001). For instance, mud attached to vehicles transported *Phytophthora*, a fungal pathogen, into remote stands of Port Orford Cedar (*Chamaecyparis lawsoniana* [A. Murr.]) (Jules et al. 2002) and uninfected woody plant communities in Australia (Wills 1993). Alternatively, roads can modify environments such that they provide habitat for disease agents and hosts (Patz et al. 2000; Molyneux 2003).

Road building is one of many disturbances associated with conversion of wilderness to human land use (Hope et al. 2003). Often these correlated disturbances impede one's ability to discern among potential explanations of disease emergence (Schauber et al. 2005; Skelly et al. 2006). The Dalton Highway in northern Alaska (Fig. 1) has few outlying roads, bisects a vast wilderness area, and is of recent origin (1974) and thus provides a good opportunity to study road effects on disease in a relatively undisturbed system. Road construction in northern Alaska has generated particular concern because Arctic and sub-Arctic biota are thought to be exceptionally sensitive to disturbance (Truett & Johnson 2000; Kutz et al. 2004). I addressed the effects of roads on disease emergence and on the ecosystem surrounding the Dalton Highway. I evaluated relationships between digenetic trematode infections in freshwater snail populations and the distance of these populations from the Dalton Highway.

Digenetic trematodes are multihost parasites that generally infect aquatic snails during their intermediate life stages and vertebrates during adult stages. Digenetic trematodes comprise a widespread agent of wildlife and human disease that has been linked to environmental degradation (Patz et al. 2000; Johnson & Chase 2004). Trematode infections can impact host population dynamics (Jokela et al. 2005), cause amphibian deformities (Johnson et al. 2002), modify aquatic communities (Mouritsen & Poulin 2005; Thompson et al. 2005), impair human health (Patz et al. 2000), and threaten endangered species (Mitchell et al. 2000; Prenter et al. 2004). In general, the prevalence of trematode infections increases with snail density (Patz et al. 2000; Smith 2001).

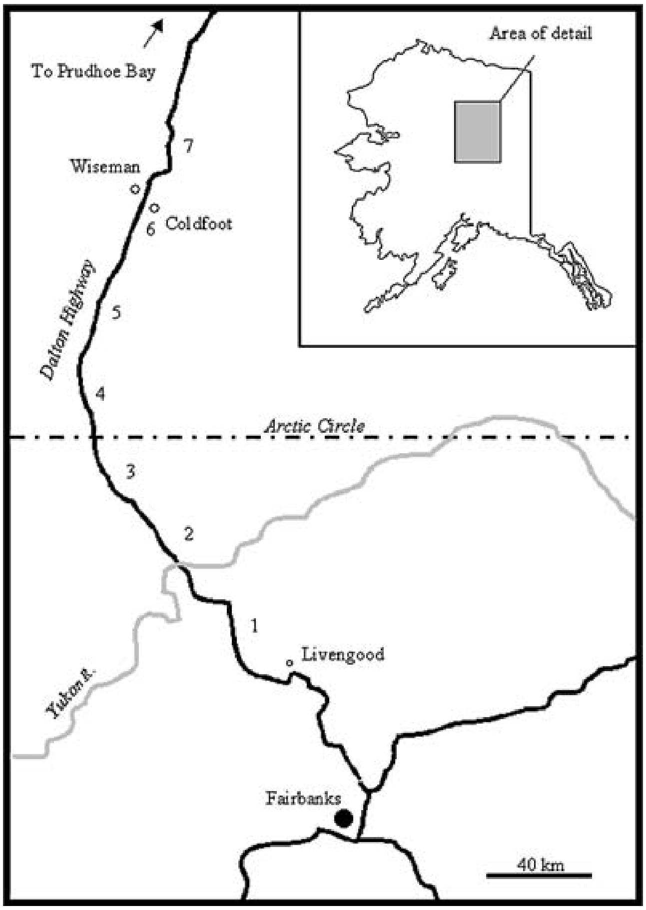

Figure 1. The Dalton Highway and locations of study transects in northern Alaska (U.S.A.).

Disturbance associated with Dalton Highway has the potential to elicit conditions associated with elevated snail densities, such as increased calcium concentration, aquatic vegetative cover, temperature, and pond size (Alexander & Miller 1977; Auerbach et al. 1997; Dillon 2000; Skelly et al. 2006). However little is known about the species composition and distribution of digenetic trematodes or their snail hosts in northern Alaska except that moose (*Alces alces*), caribou (*Rangifer tarandus*), and wolves (*Canis lupis*) have been identified as final hosts for a limited number of species (Barrett & Dau 1981). This study provides initial baseline data on snail–trematode associations in northern Alaska.

I considered four competing hypotheses about snail infection by digenetic trematodes along the Dalton Highway: (1) the null hypothesis, no relationship exists between population distance from road and trematode infection; (2) roads facilitate trematode dispersal alone, thereby generating a negative correlation between snail infections and distance from road; (3) roads promote snail dispersal, which leads to higher snail densities that also support trematode populations (Patz et al. 2000; Smith 2001); and (4) road disturbances modify nearby pond conditions to favor higher snail density which, in turn, increases trematode infections. These hypotheses were evaluated with field correlations. Although correlative results cannot reveal causal mechanisms, observational studies of this kind are important because they inform the development of appropriate hypotheses for future experimentation.

Methods

Study Area and Sampling

Prior to sampling, I identified areas in which to place seven transects at 40-km intervals from the beginning of the Dalton Highway just north of Fairbanks, Alaska (Fig. 1, 65.5°N, 148.8°W), to the foothills of the Brooks Range (67.5°N, 150.1°W). If a proposed transect site did not include both a roadside pond and three ponds total, I relocated the transect as close as possible to the original point so that these criteria were met. I surveyed an area bounded by the road and 0.1 km north and south of a 2-km transect (east from roadbed) for ponds with maximum depth > 0.1 m. In two cases, ponds west of the highway were sampled. I surveyed 30 ponds located 0–2.24 km from the road (median = 0.65 km). I also sampled four urban ponds in Fairbanks (2000 population density = 366 people/km^2) so I could compare Dalton Highway effects with the amalgamated effects of urbanization (Skelly et al. 2006).

The location, shortest distance to highway, and elevation of each pond were recorded with a global positioning unit. I also estimated maximum depth, temperature (10 cm below surface at maximum depth), pond area, percent emergent vegetation, and percent canopy cover. Wind can transport calcium dust from road gravel and road salts 300 m away from the road (Alexander & Miller 1977; Auerbach et al. 1997). Therefore, I measured calcium concentration from a 100-mL water sample I collected 10 cm below the surface in each pond's center. Water samples were digested with 1.0% nitric acid at 120.0° C (Clesceri et al. 1998) and then analyzed in an Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES) (Perkin Elmer Optima 3000, Boston) with standard methods (Varma 1991). Calcium concentrations were corrected using the mean of two deionized water blanks treated in the same manner as environmental samples.

Community Structure and Infection

I surveyed pond communities with 17 × 25 cm dipnet sweeps (1.4-mm mesh) stratified across pond microhabitats with standardized effort (15 minutes). All ponds were sampled within 9 days. Organisms were preserved in 70% EtOH for later identification (Clarke 1981; Merritt & Cummins 1996). A maximum of 20 snails per species were dissected after being selected randomly from sections of a numbered grid across which the total sample had been homogenized. Snails were removed from shells and systematically fragmented with a dissecting needle. I then spread the fragmented tissue across a petri dish, and extracted and counted trematodes under a 10.5–50× stereoscope. An infection was registered for a population whenever a trematode was identified with a 70–350× compound microscope. I categorized cercariae by morphotype (Schell 1970). Because most samples contained trematode sporocysts and rediae that cannot be identified to lower taxonomic levels (Table 1), I estimated infection risk as the pooled presence and prevalence (percent infected snails per pond) of trematode infections in the numerically dominant snail species (*Stagnicola elodes*) and all snail species.

Statistical Analyses

Linear regressions were used to assess relationships between infection prevalence and snail diversity, density, and distance from the road. I used logistic regression to evaluate trematode infections in the subset of ponds inhabited by snails. The distance over which road disturbances influenced infection was measured as the inflection point for the estimated logistic curve. I used redundancy analysis (RDA) to evaluate multivariate relationships between environmental variables and distance from road (5000 permutations). I calculated Fisher's alpha to measure pond community diversity. Relationships among community trophic traits (shredder, collector, grazer, predator [Merritt & Cummins 1996]), distance

Table 1. Number of individuals of each snail species collected along the Dalton Highway, Alaska, that were infected by trematode sporocysts, rediae, or cercarial morphotypes.*

Intermediate host species	*Sporocysts or rediae (%)*	*Cercarial morphotype*			
		Armatae	*Amphistome*	*Monostome*	*Strigeidae*
S. elodes	21 (18.4)	5 (4.3)	3 (2.6)	2 (1.7)	2 (1.7)
G. parvus	3 (15.8)	—	2 (10.5)	1 (5.3)	—
V. sincera	2 (20)	—	2 (20)	—	—

**All snails infected by cercariae also contained sporocysts or rediae. Two* S. elodes *individuals had multiple infections (Armatae and Amphistome).*

from road, and community composition were evaluated with fourth corner statistics (Legendre & Legendre 1998). One pond was removed from the calcium dataset following outlier detection (Cook's distance, Neter et al. 1996). This point corresponded to a pond 1.42 km from the Dalton Highway located on a secondary gravel road. Proportions were arc-sine transformed and pond area and snail density were ln transformed to address detected nonnormality. Neither latitude nor its interaction with distance from road explained significant variation in environmental variables, pond communities, snail densities, or infection characteristics. Thus, I report only results for distance from road.

Results

Environmental and Community Variation

Ponds varied in area (range: 12–4000 m^2), surface temperature (8.5–22.0° C), percent emergent vegetation, canopy cover (0–100%), and calcium concentration (0–68 mg/L). Among the 76 macroinvertebrate taxa identified, the most abundant orders were Diptera (33%), Odonata (20%), Ephemeroptera (11%), and Gastropoda (10%). In this last group, I identified 6 snail species: *Stagnicola elodes* (65%), *Aplexa elongata* (12%), *Gyraulus parvus* (11%), *Valvata sincera* (10%), *Lymnaea stagnalis* (2%), and *Physa gyrina* (1%).

Overall, 16% of all snails and 50% of snail populations collected along the Dalton Highway were infected by trematodes (Table 1). Within populations, trematode infection prevalence ranged from 0 to 83%. Armatae, Amphistome, Monosotome, and Strigeid cercarial morphotypes were identified in *S. elodes*, *G. parvus*, and *V. sincera* from the Dalton Highway (Table 1). A similar community composition, excluding Strigeid cercarial morphotypes, characterized Fairbanks collections.

Distance from Road and Infection

The presence of trematode infections in ponds with potential snail hosts was negatively correlated with distance from road (Fig. 2; logistic regression: slope = −5.88, $F_{1,10} = 7.5; p = 0.021$). This result remained significant when restricted to the most common snail species (*S. elodes*; slope = −35.5, $F_{1,5} = 4.7; p < 0.001$). The distance at which roads influenced disease occurrence was estimated to be 310 m based on the inflection point (infection probability = 50%) from logistic regression (Fig. 2). Distance from the road was not associated with infection prevalence ($F_{1,10} = 2.2; p = 0.17$).

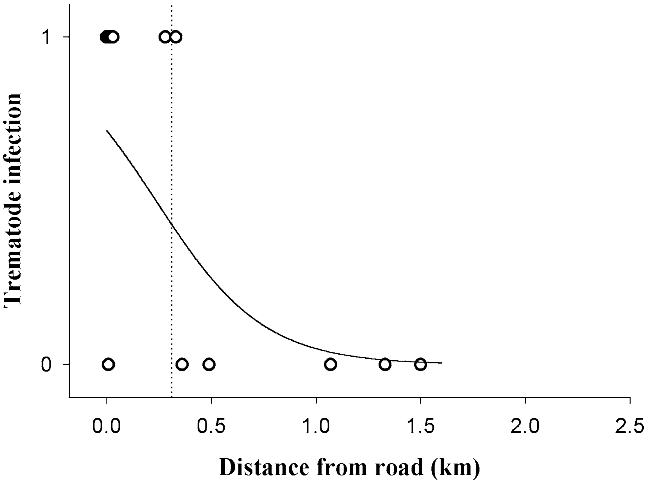

Figure 2. Presence (1) or absence (0) of snail trematode infections in pond snails plotted by distance from the Dalton Highway. Solid line indicates the probability of an event occurring based on the fit obtained by logistic regression. Dotted line provides a reference to the point (0.31 km) at which the probability of infection equals 0.5. Random deviations were added to data at 0 km to facilitate interpretation. Ponds without snails were excluded from this analysis.

Distance from Road, Snail Density, and Infection

Snail density significantly decreased with distance from the Dalton Highway (Fig. 3; slope = −0.93; $F_{1,28} = 5.9; p = 0.022$). This also was true for the dominant snail species (*S. elodes*; slope = −0.77; $F_{1,28} = 4.8; p = 0.037$). Densities of both pooled snail species and *S. elodes* alone were positively associated with trematode infection (logistic regressions: slope = +3.25, $F_{1,10} = 6.1$, $p = 0.033$; slope: +211.0; $F_{1,5} = 4.7; p < 0.001$). The interaction between snail density and distance from road did not explain presence of infections ($F_{1,8} = 0.0; p = 1.00$). The

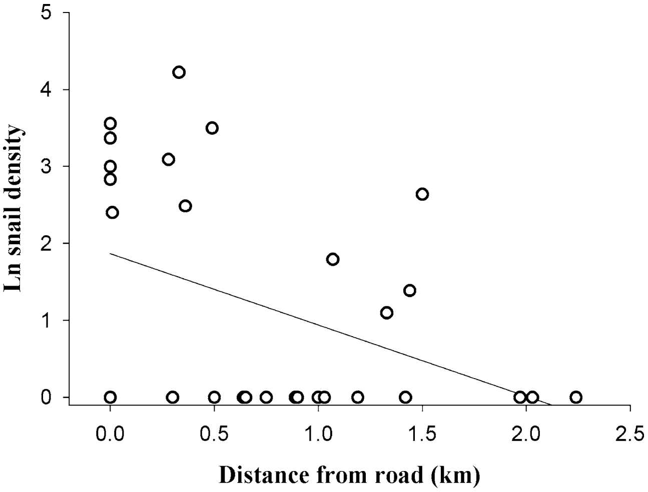

Figure 3. Snail density (ln transformed) in sampled ponds by distance from the Dalton Highway. Line indicates the estimated linear relationship between snail density and distance from road.

best model based on Akaike information criteria included both distance from road and snail density but not their interaction. Distance from road and snail density together explained 99% of the variation in infection occurrence based on McFadden's ρ^2, an analog of R^2 for logistic regression (model chi-square $p < 0.001$). Snail density and its interaction with distance from road did not predict infection prevalence (linear regression: $F_{1,10} = 3.3,1.2$; $p > 0.10$). Snail taxa richness marginally decreased with distance from road ($F_{1,28} = 3.5$; $p = 0.07$).

Compared with Fairbanks, ponds along the Dalton Highway had significantly lower snail density and diversity (analysis of variance: $F_{1,32} = 9.1, p = 0.005$; $F_{1,32} = 10.6, p = 0.003$, respectively) but were similar in infection prevalence ($F_{1,14} = 0$; $p = 0.85$). Seventy-five percent of sampled snail populations from Fairbanks were infected with trematodes. Fifty percent of snail populations along the Dalton Highway were infected with trematodes. However, no Dalton Highway populations located more than 330 m from the highway were infected (Fig. 2).

Distance from Road and Environmental Modification

Multivariate RDA indicated that distance from road was marginally related to pond temperature, size, percent emergent vegetation, percent canopy cover, calcium concentration, and community diversity ($p = 0.08$). Negative univariate relationships characterized distance from road, calcium concentration, and aquatic vegetation. The significant relationship (slope = +0.03, $F_{1,28} = 16.4$; $p < 0.001$) between calcium concentration and percent emergent vegetation may indicate calcium subsidization of aquatic emergent vegetation or associated nutrient inputs. Univariate relationships between pond temperature, area, canopy cover, and community diversity and distance from road were not statistically significant (all $p > 0.15$). Community trophic structure also did not vary with distance from road (fourth corner statistic: $p = 0.85$). Only pond area was significantly associated with snail density (slope = +0.62, $F_{1,28} = 31.5$; $p < 0.0001$). Pond characteristics were not significantly associated with presence of trematode infection (logistic regressions: all $p > 0.09$).

Discussion

Wildlife disease often has been attributed to anthropogenic alteration of host and agent ecologies (Daszak et al. 2000, 2001). Roads can modify dispersal rates among and environmental conditions within roadside communities (Forman et al. 2003). In my study, trematode infections in snails occurred only in ponds located within 330 m of the highway. A statistical model that included distance from road and snail density explained 99% of variation in infection occurrence. Although some environmental variables were significantly correlated with distance from road (calcium, vegetation) and snail density (area), none were correlated with both variables. Hence, evidence did not strongly support the hypothesis that roads modify six important environmental variables that, in turn, support higher snail host and disease abundances. Instead, evidence was consistent with the facilitation of snail and trematode colonization by road disturbances. However, these conclusions are based on field observations. Due to the correlative nature of field observations, results cannot be used to infer direct causation without support from results of manipulative experiments.

The absence of trematodes in ponds far from the highway could indicate the influence of one or more mechanisms: (1) an initial wave of infection that has yet to spread laterally from the road; (2) increased rates of snail host and trematode colonization in ponds near the highway relative to background extinction rates; or (3) decreased extinction rates in roadside ponds due to environmental modification. The first hypothesis suggests that patterns of the spread of infection coincide with an invasion of snail or trematode species. All the snail species I collected were native. For trematodes, I cannot draw any conclusions about potential invasions because little is known about the composition of trematode communities in northern Alaska before the highway was built. However, the diversity of cercarial morphotypes, which contributed to infection patterns (Table 1), suggests a generalized correlation between road distance and trematode occurrences, rather than specific invasion of a single trematode species. Future data collection will offer important insights about subsequent spatiotemporal dynamics of these infection patterns.

My results support increased colonization rates in roadside ponds as an explanation for infection patterns. Along the Dalton Highway, mud attached to vehicles (e.g., Wills 1993; Jules et al. 2002) and water collected from wild sources and sprayed as dust palliative (personal observation) could facilitate dispersal of microscopic life stages into roadside ponds. However, these dispersal mechanisms do not explain long-distance trematode dispersal beyond the reach of road spray. Movement of vertebrate definitive hosts along road corridors offers an additional hypothesis for longer distance dispersal that operates alone or in conjunction with road travel and maintenance. Roads may attract definitive hosts by providing travel corridors (e.g., wolves [*Canis lupis*], Forman et al. 2003), navigational cues (e.g., migrating birds, Forman & Alexander 1998), and anthropogenic food sources (e.g., foxes [*Aloplex lagopus*], Truett & Johnson 2000).

None of the pond characteristics significantly associated with pond distance also predicted snail density or trematode infection. However, unmeasured environmental conditions may have contributed to observed patterns. The similarity between the distances over which road dust settled and infections occurred (~300 m) indicates the potential for environmental influences of roads on snail and trematode distributions (Auerbach et al. 1997). Future research should evaluate temporal variation in dust inputs and additional environmental factors such as phosphorus concentrations (Johnson & Chase 2004).

Recent reports of disease outbreaks in northern wildlife populations, including in salmon (Kocan et al. 2004), herring (Marty et al. 2003), and muskoxen (Kutz et al. 2004) indicate the possible emergence of multiple wildlife diseases in Arctic and near-Arctic regions. Disease emergence could be fueled by rapid warming associated with climate change or anthropogenic disturbances associated with resource extraction (Kutz et al. 2004). My results indicated that parasite infections in northern snail populations were negatively correlated with distance from roads. Although correlative, the patterns I found suggest a link between roads and trematode infections not directly explained by environmental modification. My results and results from other studies (Wills 1993; Jules et al. 2002; Forman et al. 2003) suggest that roads may facilitate wildlife disease by enhancing movement of disease agents and hosts. Roads often constitute one of the earliest and most common forms of anthropogenic disturbances in wilderness areas (Forman & Alexander 1998). In the United States, 600,000 km of roads intersect national forests (Forman et al. 2003) and 954 km of roads support oil exploration and extraction on Alaska's North Slope (NRC 2003). Pathogen pollution associated with roads can impair local wildlife populations and cause species extinctions (Cleaveland et al. 2002). By spreading disease into undisturbed regions, wilderness roads may threaten biological diversity even within protective reserves. Therefore, designating roadless wilderness areas may constitute an effective means of biological conservation.

Acknowledgments

Research support was provided by Carpenter-Sperry-Mellon and Jubitz Family Foundation grants. M.C.U. was supported by a National Science Foundation graduate fellowship and a Centers for Disease Control training fellowship in vector-borne disease. L. Middle identified ponds in Fairbanks. H. Hu, J. Karosas, and R. Schiff assisted with chemical analyses. S. Bolden, P. Daszak, K. Freidenburg, M. Holland, E. Lee, J. MacLellan, D. Skelly, and two anonymous reviewers greatly improved the manuscript.

Literature Cited

Alexander, V., and M. C. Miller. 1977. Effects of the pipeline haul road on nearby ponds and lakes across Alaska's north slope. Report RLO-2220-T9-2. U.S. Energy Research and Development Administration, Washington, D.C.

Auerbach, N. A., M. D. Walker, and D. A. Walker. 1997. Effects of roadside disturbance on substrate and vegetation properties in Arctic tundra. Ecological Applications **7:**218–235.

Barrett, R., and J. Dau. 1981. Parasitic diseases. Pages 79–186 in R. A. Dieterich, editor. Alaskan wildlife diseases. University of Alaska, Fairbanks.

Clarke, A. H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, Ottawa, Canada.

Cleaveland, S., G. R. Hess, A. P. Dobson, M. K. Laurenson, H. I. McCallum, M. G. Roberts, and R. Woodroffe. 2002. The role of pathogens in biological conservation. Pages 139–150 in P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek, and A. P. Dobson, editors. The ecology of wildlife disease. Oxford University Press, New York.

Clesceri, L. S., A. E. Greenberg, and A. H. Eaton. 1998. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, D.C.

Cunningham, A. A., P. Daszak, and J. P. Rodriguez. 2003. Pathogen pollution: defining a parasitological threat to biodiversity conservation. Journal of Parasitology **89:**S78–S83.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife-threats to biodiversity and human health. Science **287:**443–449.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2001. Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta Tropica **78:**103–116.

Dillon, J., R. T. 2000. The ecology of freshwater molluscs. Cambridge University Press, New York.

Forman, R. T. T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology **14:**31–35.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29:**207–231.

Forman, R. T. T., et al. 2003. Road ecology: science and solutions. Island Press, Washington, D.C.

Hope, D., C. Gries, W. Zhu, W. F. Fagan, C. L. Redman, N. B. Grimm, A. L. Nelson, C. Martin, and A. Kinzig. 2003. Socioeconomics drive urban plant diversity. Proceedings of the National Academy of Science **100:**8788–8792.

Johnson, P. T. J., and J. M. Chase. 2004. Parasites in the food web: linking amphibian malformations and aquatic eutrophication. Ecology Letters **7:**521–526.

Johnson, P. T. J., et al. 2002. Parasite (*Ribeiroia ondatrae*) infection linked to amphibian malformations in the western United States. Ecological Monographs **72:**151–168.

Jokela, J., J. Taskinen, P. Mutikainen, and K. Kopp. 2005. Virulence of parasites in hosts under environmental stress: experiments with anoxia and starvation. Oikos **108:**156–164.

Jules, E. S., M. J. Kauffman, W. D. Ritts, and A. L. Carroll. 2002. Spread of an invasive pathogen over a variable landscape: a nonnative root rot on Port Orford Cedar. Ecology **83:**3167–3181.

Kocan, R., P. Hershberger, and J. Winton. 2004. Ichthyophoniasis: an emerging disease of Chinook salmon in the Yukon River. Journal of Aquatic Animal Health **16:**58–72.

Kutz, S. J., E. P. Hoberg, J. Nagy, L. Polley, and B. Elkin. 2004. "Emerging" parasitic infections in Arctic ungulates. Integrative and Comparative Biology **44:**109–118.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier, New York.

Marty, G. D., T. J. Quinn, G. Carpenter, T. R. Meyers, and N. H. Willits. 2003. Roles of disease in abundance of a Pacific herring (*Clupea pallasi*) population. Canadian Journal of Fisheries and Aquatic Science **60:**1258–1265.

Merritt, R. W., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing, Dubuque, Iowa.

Mitchell, A. J., M. J. Salmon, D. G. Huffman, A. E. Goodwin, and T. M. Brandt. 2000. Prevalence and pathogenicity of a heterophyid trematode infecting the gills of an endangered fish, the fountain darter, in two central Texas spring-fed rivers. Journal of Aquatic Animal Health **12:**283–289.

Molyneux, D. H. 2003. Common themes in changing vector-borne disease scenarios. Transactions of the Royal Society of Tropical Medicine and Hygiene **97:**129–132.

Mouritsen, K. N., and R. Poulin. 2005. Parasite boosts biodiversity and changes animal community structure by trait-mediated indirect effects. Oikos **108:**344–350.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. McGraw-Hill, Boston.

NRC (National Resource Council). 2003. Cumulative environmental effects of oil and gas activities on Alaska's north slope. The National Academies Press, Washington, D.C.

Patz, J. A., T. K. Graczyk, N. Geller, and A. Y. Vittor. 2000. Effects of environmental change on emerging parasitic diseases. International Journal for Parasitology **30:**1395–1405.

Prenter, J., C. MacNeil, J. T. A. Dick, and A. M. Dunn. 2004. Roles of parasites in animal invasions. Trends in Ecology & Evolution **19:**385–390.

Schauber, E. M., R. S. Ostfeld, and A. S. Evans. 2005. What is the best predictor of annual Lyme disease incidence: weather, mice, or acorns? Ecological Applications **15:**575–586.

Schell, S. C. 1970. The trematodes. William C. Brown, Dubuque, Iowa.

Skelly, D. K., S. R. Bolden, M. P. Holland, L. K. Freidenburg, N. A. Freidenfelds, and T. R. Malcolm. 2006. Urbanization and disease in amphibians. Pages 153–167 in S. K. Collinge and C. Ray, editors. Community ecology of disease. Oxford University Press, New York.

Smith, N. F. 2001. Spatial heterogeneity in recruitment of larval trematodes to snail intermediate hosts. Oecologia **127:**115–122.

Thompson, R. M., K. N. Mouritsen, and R. Poulin. 2005. Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. Journal of Animal Ecology **74:**77–85.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14:**18–30.

Truett, J. C., and S. R. Johnson. 2000. The natural history of an Arctic oil field: development and biota. Academic Press, New York.

Varma, A. 1991. Handbook of inductively coupled plasma atomic emission spectroscopy. CRC Press, Boca Raton, Florida.

Wills, R. T. 1993. The ecological impact of *Phytophthora-Cinnamomi* in the Stirling Range National Park, Western-Australia. Australian Journal of Ecology **18:**145–159.