



Distribution of woodland amphibians along a forest fragmentation gradient

James P. Gibbs

School of Forestry and Environmental Studies, Yale University, 205 Prospect St., New Haven, CT 06511, USA; Current address: State University of New York, College of Environmental Science and Forestry, 350 Illick Hall, Syracuse, N.Y. 13210 USA; phone (315) 470-6764; e-mail jpgibbs@mailbox.syr.edu

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Abstract

Understanding how changes in land-use affect the distribution and abundance of organisms is an increasingly important question in landscape ecology. Amphibians may be especially prone to local extinction resulting from human-caused transformation and fragmentation of their habitats owing to the spatially and temporally dynamic nature of their populations. In this study, distributions of five species of woodland amphibians with differing life histories were surveyed along a 10 km, spatially continuous gradient of forest fragmentation in southern Connecticut, U.S.A. Redback salamanders (*Plethodon cinereus*) and northern spring peepers (*Pseudacris c. crucifer*) occupied available habitat along the gradient's length. Wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) were absent from portions of the gradient where forest cover was reduced to below about 30%. Red-spotted newts (*Notophthalmus v. viridescens*) did not persist below a forest cover threshold of about 50%. Correlations between species' biological traits and their fragmentation tolerance imply that low density, population variability, and high mobility coupled with restricted habitat needs predispose woodland amphibians to local extinction caused by habitat fragmentation. These patterns are in contrast to the widely held notion that populations of the best dispersers are those most tolerant of habitat fragmentation.

Introduction

How changes in land-use patterns affect the distribution and abundance of organisms is an increasingly important question in ecology (Lubchenko et al. 1991). Of particular importance is understanding the effects of human activities that fragment natural habitats and thereby alter the size, shape, and spatial arrangement of habitat types. Such properties of habitats affect extinction rates of local populations (Bolger et al. 1991, Opdam et al. 1993) and dispersal patterns (Fahrig and Merriam 1994). These processes, in turn, influence the persistence of regional metapopulations and the structure of biological communities (Andr n 1994).

Amphibian populations may be especially prone to local extinction resulting from human-caused transformation and fragmentation of their habitat owing to the

spatially and temporally dynamic nature of amphibian populations. Breeding populations of frogs and salamanders fluctuate by as much as 1–2 orders of magnitude among seasons (e.g., Pechmann et al. 1991, Blaustein et al. 1994) due to variation in factors that regulate populations of larvae, adults, or both (Wilbur 1980). Also, breeding pools used by many species of amphibians are typically ephemeral, both seasonally (Berven 1990, Gascon 1991) and over decades (Gill 1978, Zimmerman et al. 1986). Breeding sites are spatially discrete, adult fidelity to breeding sites is extremely high and interdemec migration typically is low (e.g., Gill 1978, Berven and Grudzien 1990). Thus, amphibian populations typically possess a complex population structure with semi-isolated demes that undergo frequent local extinctions, due either to demographic stochasticity (Sj gren 1991), natural

catastrophes (Gill 1978), or both (Laan and Verboom 1990). Amphibians have evolved a variety of reproductive strategies to cope with these dynamics (Wilbur 1980), but how different species respond to induced habitat subdivision is unknown.

The objective of this study was to examine how forest fragmentation might alter the local distribution patterns of woodland amphibians. To minimize the potentially confounding effects of environmental heterogeneity, studies were focused on an abrupt transitional zone in which forest cover shifted from nearly absent to nearly complete along a spatially continuous gradient (cf. Blair 1996). Distributions of five species with contrasting reproductive biologies were surveyed along the gradient to determine their thresholds of tolerance to forest fragmentation. A comparison of these species' reproductive biologies with their fragmentation tolerance was then made to identify factors that might predispose woodland amphibians to local extinction associated with land-use change.

Methods

This study was conducted in Milford and Orange, New Haven County, Connecticut, U.S.A. The predominant natural vegetative cover, oak (*Quercus* spp.) forest, showed distinct spatial trends in areal extent and degree of fragmentation along an urban-rural gradient, which extended outward from a heavily urbanized area into a rural zone. A continuous transect was established (10 km long and 2 km wide) that spanned the gradient, along which amphibian surveys were conducted (Figure 1). Trends in forest cover along the transect were quantified by measuring 1:40,000 scale, black and white aerial photographs (circa 1981) at a mapping scale of 1 hectare (source: Connecticut State Library). Information on the network of primary and secondary roads along the transect was obtained in digital form from the Connecticut Department of Environmental Protection. Forest cover and road data were entered into a geographical information system (Idrisi, Eastman 1992), which was used to estimate forest extent, a fragmentation index (Monmonier 1974), and road proximity along the gradient.

Intensive surveys of all forested habitats occurring along the transect were made for five species of amphibians (three salamanders and two frogs). The species chosen were forest-dwellers whose presence or absence could be determined readily during field surveys. Moreover, these species exhibited widely di-

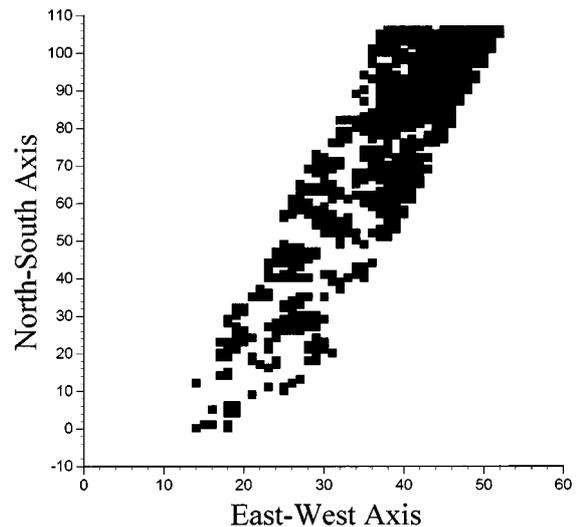


Figure 1. Trends in forest cover along a continuous transect (10 km long by 2 km wide) that spanned an urban-rural forest fragmentation gradient along which amphibian surveys were conducted in Milford and Orange, Connecticut, U.S.A., 1992–1994. Map is in units of 100 m.

vergent reproductive biologies (Table 1). The species were: the redback salamander (*Plethodon cinereus*), red-spotted newt (*Notophthalmus v. viridescens*), spotted salamander (*Ambystoma maculatum*), northern spring peeper (*Pseudacris c. crucifer*), and wood frog (*Rana sylvatica*). Ostensibly suitable breeding habitat was available throughout the gradient for all species. Specifically, temporary pools for wood frogs, spring peepers, and spotted salamanders and semi-permanent ponds for red-spotted newts and spring peepers occurred within 1 km of all forested blocks. Mature, close-canopied forest with an intact litter layer suitable for redback salamanders also occurred throughout the gradient.

Redback salamanders and red-spotted newts were surveyed by visiting each forest patch along the gradient during daylight hours between 1 May and 15 June, 1992–1994, and turning over cover objects (logs, rocks, and refuse) to find dormant individuals. Surveys were standardized by conducting searches for up to 2.5 hours per forest patch or until all moveable cover objects had been overturned and replaced. Because most occupied sites were so classified within 10 minutes of the survey's start for red-backed salamanders, and 30 minutes for newts, most unoccupied determinations made after 2.5 hours of searching were likely correct. All forested lands and adjacent meadows along the gradient were visited during April-May of either 1992

Table 1. General comparison of life-history characteristics of the five woodland amphibian species surveyed along a forest fragmentation gradient in southern Connecticut, 1992–1994¹.

Characteristic	Red-spotted Newt	Redback salamander	Spotted salamander	Spring peeper	Wood frog
Relative density	Low	High	Low	Intermediate	Low
Dispersal tendency	High	Low	Intermediate	Intermediate	Intermediate
Life-cycle	Bi-phasic	Uni-phasic	Bi-phasic	Bi-phasic	Bi-phasic
Adult habitat	Forest	Forest	Forest	Mixed	Forest

¹Based on Gill (1978), Healy (1978), Jaeger (1980), Wyman (1988), Berven (1990), Berven and Grudzien (1991), Conant and Collins (1991).

or 1993 to complete a census of potential breeding pools for wood frogs and spotted salamanders. A survey of the pools thus identified was conducted in April, 1994, immediately after wood frogs and spotted salamanders had bred in the area, during which the number of egg masses in each pool was counted. Presence of egg masses was assumed to be a valid indicator of presence of adult populations in adjacent upland habitats. Spring peepers were surveyed by visiting all pools and ponds along the gradient for at least 10 minutes on 3–5 separate occasions between dusk and 2200 h during April–May, 1994, and listening for calling males. The metric used for describing the incidence of amphibians along the gradient was the proportion of forested habitat along each segment of the gradient that supported populations of each species.

Results

Forest cover increased linearly over the 10 km gradient from about 5% at the urban terminus to 95% at the rural terminus (Figure 2a). Degree of fragmentation remained uniformly high while forest cover increased to a threshold of about 60%, whereupon fragmentation dropped sharply (Figure 2b). Mean proximity of upland habitats to paved roads, a measure of the density of dispersal barriers to amphibians, was high over much of the gradient, except at the rural terminus (Figure 2c).

Field surveys revealed that the redback salamander and spring peeper were the species most resistant to habitat fragmentation (Figure 3). Available forested habitat was largely occupied along the gradient's length, although habitat saturation along the urban segment of the gradient was uneven. Wood frogs and spotted salamanders displayed an intermediate sensitivity to forest fragmentation (Figure 3),

and were absent from portions of the gradient where forest cover was reduced to below about 30% (Figure 2a). Red-spotted newts were least resistant to forest fragmentation. Populations did not persist (Figure 3) below a forest cover threshold of about 50% (Figure 2a).

Discussion

This study was strictly correlational in nature and therefore mechanisms that might have produced the distributional patterns observed can only be speculated upon. Nonetheless, woodland amphibians responded to forest fragmentation in ways perhaps not obvious from an inspection of their reproductive biologies. Specifically, a comparison of the reproductive biologies of the species surveyed (Table 1) with their incidence along the fragmentation gradient (Figure 2) suggests, somewhat non-intuitively, that dispersal ability was inversely related to fragmentation resistance. The most sedentary species, the redback salamander, was among the two species most resistant to fragmentation of its habitat, whereas the most dispersive species, the red-spotted newt, was least resistant. These patterns are in contrast to the widely held notion that populations of the best dispersers are those most resistant to habitat fragmentation (Kareiva and Wennergren 1995, McCarthy et al. 1997).

The high fragmentation sensitivity of the red-spotted newt is particularly intriguing, given that this species has a life stage dedicated to dispersal, that is, the 'eft' stage, which lasts about four years and comprises the bulk, numerically speaking, of a newt population at any given time (Gill 1978). In heavily forested regions, having a large proportion of the population dedicated to dispersal likely facilitates recolonization of newly created or newly vacant sites. In

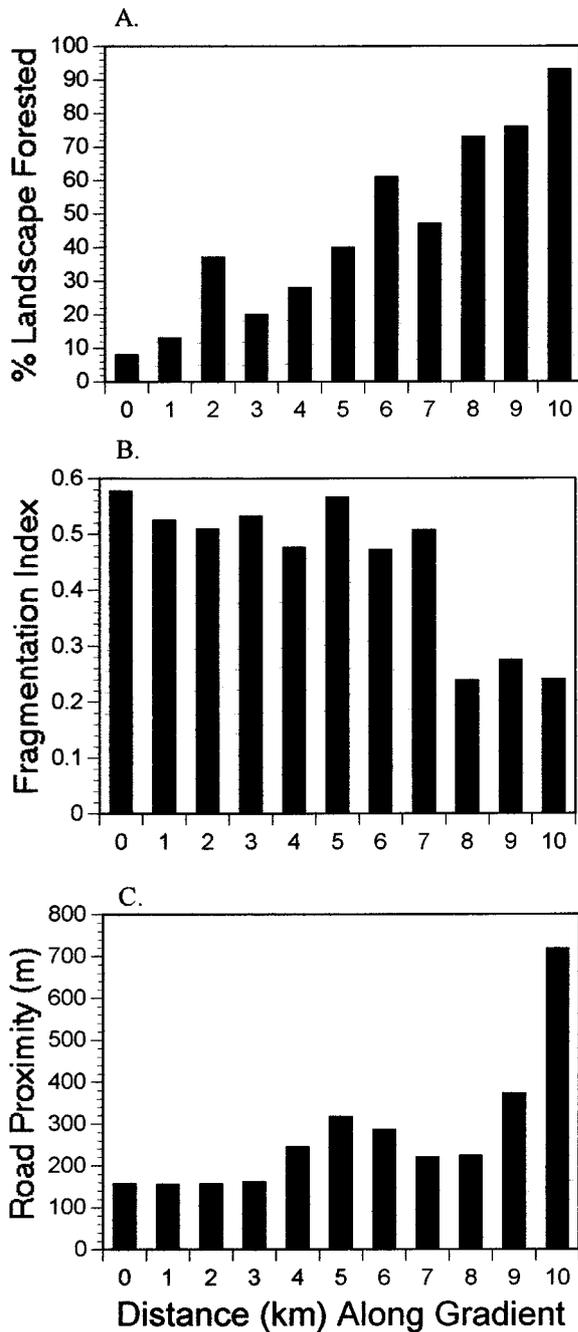


Figure 2. Trends in the forest mosaic along the fragmentation gradient studied in Milford and Orange, Connecticut, U.S.A. Trends are depicted in (a) forest cover, (b) forest fragmentation using Monmonier's index (Monmonier 1974), and (c) road proximity.

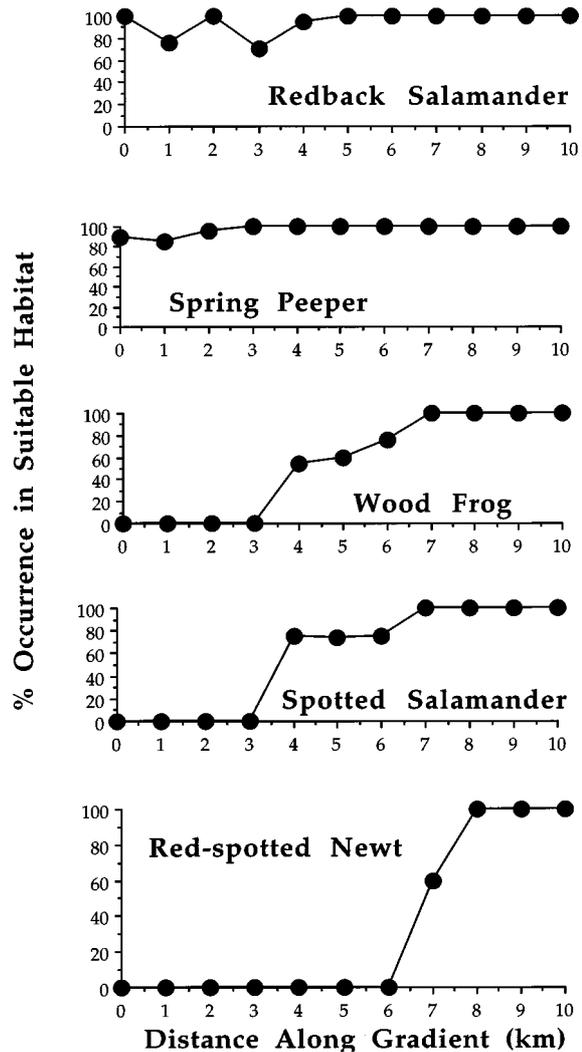


Figure 3. Patterns of incidence of five woodland amphibians along a forest fragmentation gradient in Milford and Orange, Connecticut, U.S.A., 1992–1994.

fragmented habitats, however, most dispersers likely end their migration forays in unsuitable habitats or become stranded in open habitats between forested areas, and subsequently fail to recruit into breeding populations. Thus, a high dispersal tendency that may represent a valuable trait in red-spotted newts for exploiting ephemeral breeding areas in continuous habitats (Gill 1978) may become a liability in fragmented environments. Landscape connectivity may be particularly important to sustaining newt populations, which perhaps is indicated by the close correspondence between the fragmentation threshold tolerated by red-spotted newts and the threshold in forest cover

at which the fragmentation index increased sharply (Figures 1c and 2).

The open land between habitat fragments may serve as a demographic 'drain' for many species of woodland amphibians, such as wood frogs, spotted salamanders, and red-spotted newts, whose life cycles include an annual exodus from natal areas of migrants that lack the ability to sample and select among potential dispersal destinations. For spring peepers, however, which occur most abundantly in woodland areas but also use a variety of open lands as recent metamorphs and adults (DeGraaf and Rudis 1990, Klemens 1993), the open areas adjacent to forest fragments occur may not be as inhospitable and hence not serve to deplete populations. Redback salamanders do not undergo pronounced annual migrations and therefore populations would not be expected to be depleted by unsuitable habitats adjacent to forest fragments.

Density would appear to be another important correlate of fragmentation sensitivity in the woodland amphibians studied. The most fragmentation-resistant species, redback salamanders and spring peepers, generally occur at higher densities than those species observed to be more sensitive to fragmentation (wood frogs, spotted salamanders, and red-spotted newts) (Heatwole 1962, Wyman and Hawksley-Lescault 1987, Burton and Likens 1975, Klemens 1993). Higher average densities would translate into larger effective population sizes in habitat fragments, which may buffer fragmented populations from local extinctions caused by environmental variation and demographic stochasticity (Burgman et al. 1993).

Whereas interactions between habitat fragmentation and demographic processes may underlie much of the variation in sensitivity to habitat fragmentation observed, other factors may also be involved, such as differential vulnerability to predation by birds and mammals and sensitivity to edge effects such as forest drying (Yahner 1988). Many ground-dwelling, omnivorous predators that are known to depress reproduction in ground-nesting birds nesting near forest edges (Yahner 1988), also eat amphibians (Klemens 1993). These predators, including opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) thrive in fragmented forests. Changes in these predator communities along the fragmentation gradient, however, may be discounted as a factor influencing distributional patterns for all species except the wood frog. Redback salamanders and spotted salamanders are largely fossorial, and spring peepers are highly cryptic and largely arboreal. Red-spotted newts

are mostly surface-active and vulnerable to ground-based predators but are distasteful to most avian and mammalian predators (Brodie 1968). Thus, wood frogs are likely the only species surveyed that might be sensitive to changes in these predator communities along the fragmentation gradient. Changes in other predator communities, however, such as those of shrews and snakes, also might exert an influence on amphibian distributions along fragmentation gradients.

Road proximity and water quality may further influence amphibian distributions along the gradient studied (Fahrig et al. 1995). Road proximity may best reflect trends in landscape dissection (Forman and Godron 1986) to dispersing amphibians because roads often are physical barriers to dispersal by woodland amphibians and also agents of mortality (e.g., van Gelder 1973, Cooke 1988). Landscape permeability would be particularly important for sustaining populations of those species observed to be most sensitive habitat fragmentation, that is, wood frogs, spotted salamanders, and red-spotted newts, which are more migratory than redback salamanders. Whereas spring peepers also possess a bi-phasic life cycle that includes annual migrations that could be impeded by roads, spring peepers are adept at climbing and likely can better cope with barrier effects of roads than the other, seasonally migratory species examined. Declines in water quality in breeding pools, particularly at the urban end of the fragmentation gradient, were not considered in this study but might also influence distributions of the pool-breeding species along the gradient.

This study of a limited number of species indicates that two, quite contrasting life cycles may confer resistance to habitat fragmentation upon woodland amphibians: restricted dispersal ability and restricted habitat use (e.g., redback salamanders), or extensive dispersal ability in conjunction with habitat flexibility (e.g., spring peepers). Furthermore, low population density apparently predisposes populations to fragmentation sensitivity (e.g., wood frog, spotted salamander, and red-spotted newt), particularly when coupled with habitat specificity and high dispersal tendency (e.g., red-spotted newt). Further research involving surveys in areas with more species-rich communities along similar disturbance gradients would be revealing, particularly if done in conjunction with analyses that quantify natural history traits (local survival, fecundity, and dispersal rates) and correlate them with inflection points for species' incidences

along those gradients (cf. Whitcomb et al. 1981). Measures of fitness (e.g., survival rates, length-mass ratios, and egg hatching success) along the gradient might also better elucidate the mechanisms by which landscape fragmentation influences amphibian distributions. Nevertheless, despite the explanatory limitations imposed by the correlative nature of this study, these empirical data (Figure 3) on fragmentation tolerances characteristic of various amphibian species represent information useful for conservation planning (Wyman 1990, Blair 1996).

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References

- Andr n, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.
- Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71: 1599–1608.
- Berven, K.A. and Grudzien, T.A. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44: 2047–2056.
- Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. *Ecol. Appl.* 6: 506–519.
- Blaustein, A.R., D.B. Wake and W.P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Cons. Biol.* 8: 60–71.
- Bolger, D.T., A.C. Alberts and M.E. Soul . 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. *Am. Nat.* 137: 155–156.
- Brodie, E.D. 1968. Investigations on the skin toxin of the red-spotted newt, *Notophthalmus viridescens viridescens*. *Am. Midl. Nat.* 80: 276–280.
- Burgman, M.A., Ferson, S. and Ak akaya, H.R. 1993. Risk assessment in conservation biology. Chapman Hall, London.
- Burton, T.M. and G.E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. *Copeia* 1975: 541–546.
- Cooke, A.S. 1988. Mortality of toads (*Bufo bufo*) on roads near a Cambridgeshire breeding site. *Brit. Herpetol. Soc.* 26: 29–30.
- DeGraaf, R.M. and D.D. Rudis. 1990. Herpetofaunal species composition and relative abundance among three New England forest types. *For. Ecol. Manage.* 32: 155–165.
- Eastman, J.R. 1992. IDRISI. Clark University, Graduate School of Geography, Worcester, Massachusetts.
- Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. *Cons. Biol.* 8: 50–59.
- Fahrig, L., J.H. Pedlar, S.E. Pope, P.D. Taylor and J.F. Wegner. 1995. Effect of road traffic on amphibian density. *Biological Conservation* 73: 177–182.
- Forman, R.T.T. and M. Godron. 1986. *Landscape Ecology*. John Wiley and Sons, New York.
- Gascon, C. 1991. Population- and community-level analysis of species occurrences of central Amazonian rainforest tadpoles. *Ecology* 72: 1731–1746.
- Gill, D.E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecol. Mono.* 48: 145–166.
- Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. *Ecology* 43: 460–472.
- Kareiva, P. and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373: 299–302.
- Klemens, M.W. 1993. Amphibians and reptiles of Connecticut and adjacent regions. State Geological and Natural History Survey of Connecticut Bulletin 112.
- Laan, R. and B. Verboom. 1990. Effects of pool size and isolation on amphibian communities. *Biol. Conserv.* 54: 251–262.
- Lubchenko, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J. and Risser, P.G. 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* 72: 371–412.
- McCarthy, M.A., D.B. Lindenmayer and M. Drechsler. 1997. Extinction debts and risks faced by abundant species. *Conservation Biology* 11: 221–226.
- Monmonier, M.S. 1974. Measures of pattern complexity for chloropleth maps. *The American Cartographer* 2: 159–169.
- Opdam, P., Van Apeldoorn, R., Schotman, A. and Kalkhoven, J. 1993. Population responses to landscape fragmentation. pp. 147–171. *In* Landscape Ecology of a Stressed Environment. Edited by C.C. Vos and P. Opdam. Chapman Hall, London.
- Pechmann, J.H.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt and J.W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253: 892–894.
- Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biol. J. Linnean Soc.* 42: 135–147.
- van Gelder, J.J. 1973. A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo* L. *Oecologia* 13: 93–95.
- Whitcomb, R.F., Robbins, C.F., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. and Bystrak, D. 1981. Effects of forest fragmentation on the avifauna of eastern deciduous forest. pp. 125–205. *In* Forest Island Dynamics in Man-Dominated Landscapes. Edited by R.L. Burgess and D. Sharpe. Springer-Verlag, New York.
- Wilbur, H.M. 1980. Complex life cycles. *Ann. Rev. Ecol. Syst.* 11: 67–93.
- Wyman, R.L. 1990. Multiple threats to wildlife: climate change, acid precipitation and habitat fragmentation. pp. 134–155. *In* Global Climate Change and Life on Earth. Edited by R.L. Wyman. Routledge, Chapman and Hall, New York.
- Wyman, R.L. and Hawksley-Lescault, D. 1987. Soil acidity affects distributions, behavior, and physiology of the salamander *Plethodon cinereus*. *Ecology* 68: 1819–1827.
- Yahner, R.H. 1988. Changes in wildlife communities near edges. *Cons. Biol.* 2: 333–339.
- Zimmerman, B.L. and Bierregaard, R.O. 1986. Relevance of the equilibrium theory of island biogeography with an example from Amazonia. *J. Biogeography* 13: 133–143.