Biological Conservation 142 (2009) 1628–1638

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Assessing threats to pool-breeding amphibian habitat in an urbanizing landscape

Robert F. Baldwin [a,*], Phillip G. deMaynadier [b]

[a] Department of Forestry and Natural Resources, Clemson University, 261 Lehotsky Hall, Clemson, SC 29634, United States

[b] Reptile, Amphibian, and Invertebrate Group, Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401, United States

ARTICLE INFO

Article history:
Received 3 September 2008
Received in revised form 19 February 2009
Accepted 24 February 2009
Available online 7 April 2009

Keywords:
Amphibian conservation
Threat analysis
Urbanization
Vernal pool

ABSTRACT

Geographically-based threat assessments are important for identifying natural resources at risk, yet have rarely been applied to identify habitat conservation priorities for imperiled organisms at a local scale. Pool-breeding amphibians have complex life cycles that place them at risk from habitat loss and fragmentation both in wetlands and in adjacent uplands. Because the most rapidly growing cause of habitat degradation in North America has been urbanization, a threat analysis of pool-breeding amphibian habitat should both be dynamic, i.e., sensitive to land-use change, and comprehensive, recognizing traditional protected area networks as well as less formal conservation assets (e.g., land-use regulations). To assess threats to wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) in a rapidly urbanizing, forested region of New England (USA) we examined gaps in the current protection network, as well as changing human settlement patterns. We found that greater than 50% of 542 potential breeding pools delineated using low-level infra-red aerial photography (median area 379.5 m^2) were not represented on National Wetland Inventory (U.S.FWS) maps, and thus de facto at risk. Most importantly, conservation lands and regulatory protections failed to protect 46% of potential breeding pools and 80% of adjacent non-breeding habitat. While an assessment of human settlement patterns projected that only 5% of the region contained high quality amphibian habitat under acute development pressure, nearly half of the region (44.7%) had attained a moderate threat level, highlighting the importance of conservation planning during early stages of urbanization. We conclude by illustrating the role for multiple conservation strategies when protecting functional landscapes for pool-breeding amphibians.

1. Introduction

Amphibians are threatened globally by interacting stressors, but none is so acute as physical habitat degradation and destruction (Alford and Richards, 1999; Stuart et al., 2004). Tools for identifying and prioritizing at-risk habitats in the face of expanding human activity are needed to anticipate and mitigate the effects of habitat loss on amphibians and other sensitive taxa. Most pool-breeding amphibians have complex life cycles requiring multiple habitats, including an aquatic breeding site, adjacent upland and wetland non-breeding habitat, and a permeable migration matrix to connect and buffer these elements (Semlitsch, 2002). Consequently, vernal pool amphibians are threatened in urbanizing areas by habitat loss at multiple scales: loss of small wetland breeding pools, clearing and conversion of adjacent non-breeding habitat, and loss of landscape connectivity (Gibbs, 1993, 2000; Holland et al., 1995; Semlitsch and Bodie, 1998; Dahl, 2000). Best management practices and recommendations for pool-breeding amphibian conservation have been promulgated that integrate local to landscape-scale factors (Semlitsch, 2000, 2002), however, methodologies for prioritizing their application among competing areas of the landscape are only recently being developed (Compton et al., 2007). In an era of rapid development and human competition for space (Sanderson et al., 2002a), it is increasingly necessary to prioritize and triage among potential conservation actions (Groves et al., 2002). Incorporating habitat risk assessment into the conservation planning process can allocate limited resources where conservation needs are greatest (Scott et al., 1993; Margules and Pressey, 2000; Lawler et al., 2003; Rodrigues et al., 2004).

Geographic conservation planning tools including GAP (Geographic Approach to Planning) and threat analyses are designed to help assess risk to habitat for species of potential conservation concern (Scott et al., 1993; Theobald, 2003). Traditionally, a GAP analysis compares the geographic distribution of potential habitats with the distribution of a protective network of conservation lands, and potentially less formal conservation assets (e.g., land-use regulations), in order to identify gaps in protection of priority habitats (Scott et al., 1993; Groves et al., 2000). A threat analysis moves beyond the identification of conservation gaps, to differentiating areas on the landscape where unprotected habitat is most threatened by expansion of human activities (Theobald, 2003, 2004). In a biodiversity threat analysis, habitat and protection layer information are combined with existing human population density,

* Corresponding author. Tel.: +1 864 656 4857; fax: +1 864 656 3304.
E-mail address: baldwi6@clemson.edu (R.F. Baldwin).

0006-3207/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2009.02.039

modified by projected population growth rates (Stoms, 2000; Theobald, 2003). The result is a spatially-explicit summary of where threats from anthropogenic development are most acute with respect to specific elements of biodiversity. Developed for and applied primarily at broad biogeographic scales (e.g., state-global) (Groves et al., 2002; Rodrigues et al., 2004), GAP and threat analyses have rarely been applied to inform conservation planning for individual taxa at local scales (Allen et al., 2001; Moon, 2001). To our knowledge GAP and threat analyses have yet to be applied to the problem of global amphibian declines generally, or more specifically, to the conservation of pool-breeding amphibians in rapidly developing landscapes.

Vernal pool ecosystems of northeastern North America provide breeding habitat for a wide diversity of amphibian species (~27 spp.; Colburn, 2004; Semlitsch and Skelly, 2008) and are under threat from expanding exurban development (Homan et al., 2004; Skidds et al., 2007). We assess risk to breeding and non-breeding habitat of two of the region's most ubiquitous and better studied pool-breeding species, wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*). The life history and habitat associations of these species are representative of many other vernal pool amphibians, in that breeding occurs primarily in seasonal, isolated wetlands followed by extensive use of neighboring post-breeding forested habitat (Petranka, 1998; Hunter et al., 1999). Breeding and post-breeding habitat are connected by overland migrations often over 100 m (Semlitsch and Bodie, 2003), with juvenile dispersal from natal pools likely exceeding 1000 m (Gordon, 1968; Berven and Grudzien, 1990; Gamble et al., 2007). Movements at these scales make pool-breeding amphibians especially vulnerable to potential landscape barriers such as roads (Fahrig et al., 1995; Clevenger et al., 2001), which in turn affect dispersal success and genetic linkages at the population level (Reh and Seitz, 1990; Hitchings and Beebee, 1998; Gibbs and Reed, 2008). Heavily fragmented landscapes have reduced populations of pool-breeding amphibians (Kolozsvary and Swihart, 1999; Lehtinen et al., 1999; Marsh and Trenham, 2001; Porej et al., 2004), intensifying the need to understand how land-use change will influence the quality and distribution of vernal pool habitat in the future.

By developing these two geographically-based conservation planning tools, GAP and threat analyses, for two vernal pool focal species, we seek to advance amphibian conservation planning so that it includes an explicit assessment of habitat risk. We use fine-scale spatial data available from regional conservation groups, and in so doing, meet a secondary goal of providing a repeatable model of scientific collaboration in which locally-generated land protection data are incorporated into regional conservation planning efforts (Theobald et al., 2000; Farnsworth, 2004). Finally, we propose a conservation triage (Hobbs and Kristjanson, 2003) for pool-breeding amphibians, in which information about current habitat protection levels and future risk is used to recommend specific conservation actions.

2. Methods

2.1. Study area

As is the case for much of eastern North America, southern Maine is undergoing rapid urbanization, resulting in significant threats to wildlife (Krohn and Hepinstall, 2000). Some coastal Maine towns experienced growth rates in excess of 30% over the past decade (Plantinga et al., 1999). Floristically, the region is more similar to central than to northern New England, with repeated fire and land clearing in recent centuries influencing species composition (Foster, 1992; Copenheaver et al., 2000). The coastal portions of the region are dominated by red oak (*Quercus rubra*) – pine (*Pinus* spp.) forests, with inland regions dominated by eastern hemlock (*Tsuga canadensis*) – beech (*Fagus grandifolia*) associations. For this study, four southern Maine towns (North Berwick, Kennebunkport, Biddeford and Falmouth) were selected non-randomly to represent a gradient of development present in the region (Fig. 1). The current land-use pattern is characterized by single-family developments and small subdivisions accessed by secondary rural roads on the margins of mostly large forest blocks of an average size of 289 ha (range: 13–742 ha).

2.2. Data layers

The following five data layers were assembled as a basis for conducting fine-scale GAP and threat analyses for pool-breeding amphibian habitat in southern Maine: (1) development pressure, (2) potential habitat value, (3) land-use intensity, (4) actual habitat value, and (5) land protection level.

2.2.1. Development pressure (DP)

Development pressure is an estimate of potential land-use change based on current population density and growth trends (Theobald, 2003). In Maine, the State Planning Office used US Census data to project growth trends for the period 2000–2015 as percentage increases in population (MESPO, 2003). We multiplied these growth trends by human population density from 2000 US Census Blocks to produce a generalized Development Pressure map (using 100 m grids). This index represents areas from which new residential development is likely to radiate, because it incorporates both an area's current land-use and its likelihood for future growth. Thus, an area with dense population but a low rate of development will be less likely to present new threats in the future than an area with low or moderate population and high growth rates. Original development pressure values for the four study towns (range: 0–13,133) were placed in five classes (0–4) to approximate the scale of other components (see below) used in the model depicting threats to pool-breeding amphibian habitat (Fig. 1).

2.2.2. Potential habitat value (PHV)

The basis of the potential habitat layer were vernal pools delineated from low-level (1:12,000) color infra-red (CIR) air photos, commissioned for the four study towns. These photos were taken under leaf off and high-water conditions in the early spring of 2001, and then delineated for potential vernal pools by a professional consulting firm (http://www.woodlotalt.com/). The vernal pool density of the four towns (1.77/km^2) is comparable to those summarized for other New England municipalities (1.47/km^2), and median pool size (379.5 m^2) was in the range of that reported elsewhere in the region (town median range: 294.5–392.2 m^2) (Calhoun et al., 2003).

Species-specific migration and dispersal distances were used to approximate non-breeding habitat surrounding delineated potential breeding pools (Semlitsch and Bodie, 2003). For our purposes, migration was defined as the annual adult movements between breeding pools and adjacent non-breeding habitat, and dispersal as the unidirectional movements of juveniles away from natal breeding pools (Hunter, 1997). For wood frogs, we used a conservative genetic neighborhood estimate of 1126 m (Berven and Grudzien, 1990) to represent dispersal, and the longest telemetry-documented, straight-line migration movement in our study area of 340 m to represent migration (Baldwin et al., 2006), a distance similar to that published for wood frogs elsewhere (Rittenhouse and Semlitsch, 2007a) and for many other anurans (Semlitsch and Bodie, 2003). For spotted salamanders, there are no published genetic neighborhoods, nor did we study their migra-

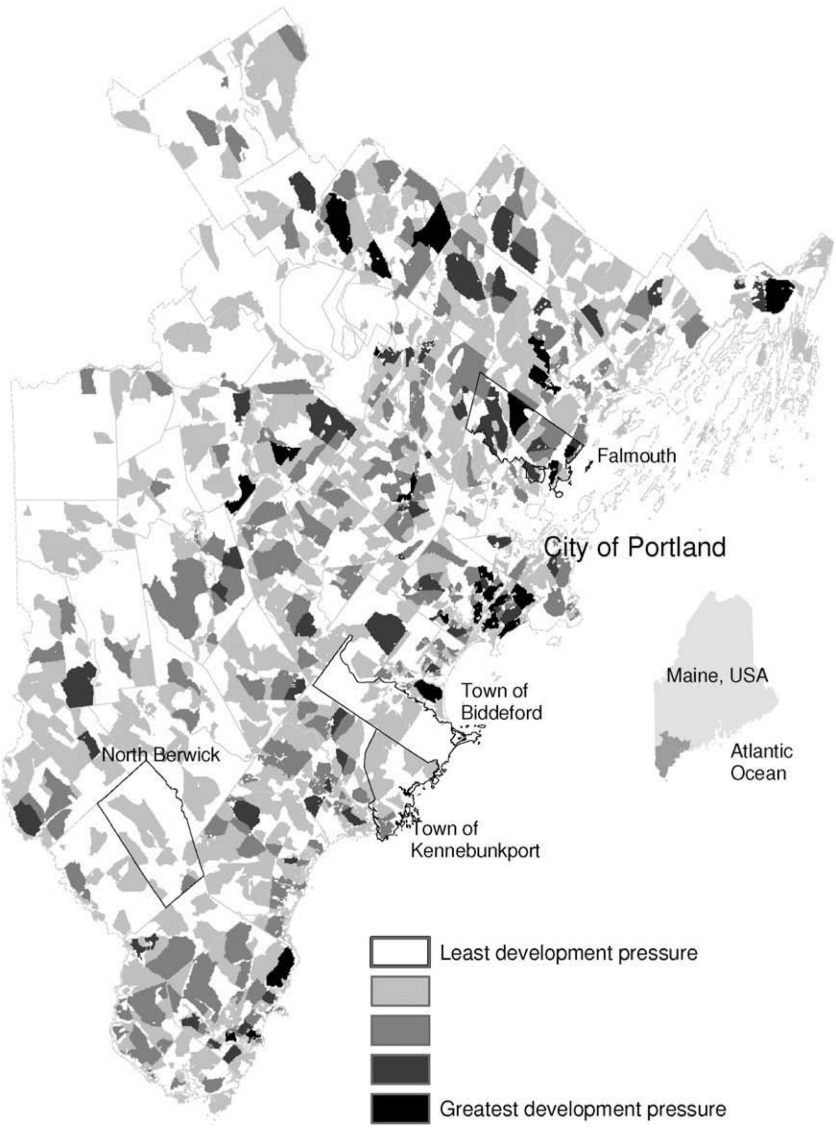

Fig. 1. Four study towns shown in the context of regional development pressure (see Methods). The largest regional metropolitan center (city of Portland) has a population of 230,000. The inset shows the US State of Maine, with southern study area.

tion or dispersal in the study area. Instead, we used the farthest documented upland occurrence of a spotted salamander from a breeding pool, ~800 m (Gordon, 1968), as a proxy for dispersal potential, and estimated migration at 250 m based on recent findings that core terrestrial habitat zones commonly used for salamanders (164–218 m: Semlitsch and Bodie, 1998; Semlitsch and Bodie, 2003) are inadequate (Gamble et al., 2006; McDonough and Paton, 2007). By selecting movement estimates for our analysis in no way do we imply that they should be the exact distances used for all modeling or management applications. Amphibian movement data is rapidly accumulating through recent field telemetry and mark-recapture studies (reviewed by Semlitsch and Bodie, 2003; Semlitsch and Skelly, 2008) and models incorporating movement data should be subject to revision as field data emerge. Likewise, distribution of amphibians around breeding habitats is not uniform and management approaches should be based on as spatially explicit an approach as allowable given available data (Baldwin et al., 2006; Compton et al., 2007; Rittenhouse and Semlitsch, 2007b).

As a consequence of (a) the high density of vernal pools in our study area, (b) the relatively long-ranging frog and salamander movement estimates described above, and (c) the decision to apply a uniform radial movement approach often promulgated in the literature (but see Compton et al., 2007), a large portion of our study area was mapped as potential dispersal habitat: 89.5% for wood frogs and 75.1% for spotted salamanders. By contrast the more restricted seasonal migration distances used to define non-breeding "life zone" or "critical terrestrial habitat" (Semlitsch and Bodie, 2003) encompassed 32.3% and 21.3% of the study area for wood frogs and spotted salamanders, respectively.

For the purposes of building the habitat threat model described below, potential breeding pools were buffered by both the species-specific migration and dispersal distances and each buffer assigned a habitat value of "1". A habitat value of 0 was the minimal value, assigned to areas where no pools or buffers are present. If potential breeding or non-breeding habitat of a single focal species were present, 1 was the minimal value, while values of 6 occurred when the maximum of 6 buffers overlapped. Pool buffer polygons were converted to 100 m grids and these layers were then added when overlapping to produce a density surface of cumulative potential habitat value (the "PHV" component of the threat model, ranging from 0 to 6), incorporating potential breeding and non-breeding habitat for both wood frogs and spotted salamanders.

2.2.3. Land-use intensity index (LUI)

Most satellite imagery is inadequate for representing land-use and habitat availability at a scale that is meaningful for pool-breeding amphibians. Therefore, land-use polygons were manually classified from the same 1:12,000-scale CIR photos used for delineating potential breeding pools. To recognize the added importance of roads as potential fragmenting elements for amphibians, road classifications were also used. By adapting the continuum approach to assessing human influence in which an ordinal scale is used to indicate relative strength of influences (Sanderson et al., 2002a; Woolmer et al., 2008), an index of land-use intensity was applied to each of eight classified land uses and six road classes. We created the index using literature on amphibian landscape permeability (e.g., Gibbs, 1998; Rothermel and Semlitsch, 2002), amphibian–habitat relationships (e.g., Faccio, 2003; Regosin et al., 2003), and personal observations obtained during field research on these species (Table 1). We recognize that the understanding of amphibian-landscape permeability relationships is only now developing, particularly in relation to cumulative effects (Forman et al., 2003); nonetheless we felt our additive index captured the trends emerging from the literature. Implicit in our approach is the assumption that land-use intensity reaches an asymptote at the maximum value of 16, where urban areas are combined with interstate highways; a landscape we assume is completely inhospitable for pool-breeding amphibians. Land-use intensity and road coverages were converted to 100 m-scale grids and the indexed grids were added together to produce a final 1–16 Land-Use Intensity Index (LUI).

2.2.4. Actual habitat value (AHV)

Instead of using the idealized potential habitat values (described previously) in our analysis, we derived a more realistic habitat value that we refer to as actual habitat value (AHV), informed by local land-use intensity, analogous to but computationally simpler than the "resistant-kernel" approach used by Compton et al. (2007). Actual habitat value was specifically derived by dividing potential habitat value by land-use intensity (PHV/LUI; range 0–6), with the assumption that increasing land-use intensity degrades the current value of pool-breeding amphibian habitat.

2.2.5. Land protection level (PL)

Existing land protection levels were assessed based on fee and easement status of conservation lands and presence of regulated wetland, shoreland, and wildlife habitats. Fine scale (tax-parcel) data indicating the conservation status of individual landholdings – e.g., conservation easement, National Wildlife Refuge, or tree farm – were obtained from local organizations, specifically the Wells National Estuarine Research Reserve (S. Smith, WNERR) and The Nature Conservancy (D. Coker, Maine TNC). Regulated wetlands, shoreland zones, and endangered species habitats were obtained from state agencies (Departments of Environmental Protection, and Inland Fisheries and Wildlife).

A range of protection levels was assigned on an ordinal scale, from none (1) to high (4), to all lands in the study area based on expert opinion of the data compilers. Protection level 2 is low and includes managed lands with conservation restrictions (i.e., tree farms and open space easements) that allow periodic tree harvesting, cultivation and limited development. Protection level 2 also includes wetlands above a critical regulatory size threshold (400 m^2; 0.1 acre) whereby state wetland policy can require environmental review and permitting for proposed impacts. By contrast, wetlands < 400 m^2 are generally not subject to either notification or review in Maine and many other states and thus are considered largely unprotected by existing regulations (DEP, 2002).

Protection level 3 is moderate and includes land owned by towns that is not in conservation easement but is generally managed as municipal open space. The risk of habitat conversion for these lands is less immediate but still real as municipalities occasionally convert portions of this land base to public works and recreation, e.g., school grounds and ball fields. Also in protection level 3 are state regulated shoreland zones (22.9 m for perennial streams, 76.2 m for coastal wetlands, and freshwater wetlands and great ponds over 4.05 ha) (DEP, 2003), within which development is restricted but permissible on a limited basis.

Protection level 4 offers a high level of protection and includes those lands explicitly managed for biodiversity and conservation purposes. Specifically, protection level 4 covers both fee and easement conservation lands managed by land trusts, state or federal governments. Also receiving protection level 4 are mapped wetlands that occur within state-mandated shoreland zones (but not the zones themselves, which are intermediate; see above). Wetlands occurring within shoreland zones receive extra regulatory protection during permitting reviews. In practice, this law and many others related to land-use are not always applied as intended. We chose to follow intent rather than practice as is generally the case when using GIS databases including protection levels (e.g., IUCN status). Also receiving the highest protection level were

Table 1
A land-use intensity index for pool-breeding amphibians applied to fine-scale polygons and used to quantify actual habitat values (AHV) surrounding potential breeding pools. The ordinal index is specific for wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*), derived from published literature (as listed) and field observations in the study area.

Land-use	Road class	Land-use intensity index	Permeability and Habitat Studies
Lightly managed forest	_	1	deMaynadier and Hunter (1998, 1999); Gibbs (1998); Patrick et al. (2006); reviewed by deMaynadier and Houlahan (2008)
Intensively managed forest (heavy partial and clearcut harvesting)	_	2	Means et al. (1996); deMaynadier and Hunter (1998, 1999); Gibbs (1998); Morris and Maret (2007); Patrick et al. (2006); reviewed by deMaynadier and Houlahan (2008)
Old fields, scrub-shrub areas	Discontinued	3	Gibbs (1998); deMaynadier and Hunter (1999); Rothermel and Semlitsch (2002); Marsh et al. (2004)
Low density residential in forest matrix	Gravel	4	Gibbs (1998); deMaynadier and Hunter (2000); Marsh et al. (2005); reviewed by Windmiller and Calhoun (2008)
Hayfields and Pasture	Forested secondary and paved	5	Shoop (1965); Gibbs (1998); deMaynadier and Hunter (2000); Rothermel and Semlitsch (2002); Marsh et al. (2004, 2005)
Lawns, golf course	Open secondary and paved	6	Gibbs (1998); Rothermel and Semlitsch (2002); Marsh et al. (2005); Montieth and Paton (2006)
Dense residential (suburban)	Interstate with no median	7	Reh and Seitz (1990); Hitchings and Beebee (1998); Carr and Fahrig (2001); reviewed by Windmiller and Calhoun (2008) and Gibbs and Reed (2008)
Urban/industrial (primarily impervious)	Large interstate with median	8	Reh and Seitz (1990); Hitchings and Beebee (1998); Carr and Fahrig (2001); reviewed by Windmiller and Calhoun (2008) and Gibbs and Reed (2008)

mapped endangered wildlife habitats. In our study area, the latter consisted entirely of wetlands hosting state-endangered Blanding's turtles (*Emydoidea blandingii*) surrounded by a 76.2 m buffer within which little or no development activity is permitted under jurisdiction of the state Endangered Species Act.

2.2.6. Mapping validation

The mapping project was carried out concurrently with a field study in the same area (Baldwin et al., 2006) and followed a validation of the remote vernal pool detection methods (Calhoun et al., 2003). There were few errors of commission (what was identified as a potential breeding wetland usually was), but omissions of vernal pools were moderately common – estimated by Calhoun et al. (2003) at 25%. Development pressure maps correspond well with what we observed in the field and learned through discussions with landowners and local officials. Protected lands data were mapped at the tax parcel level by a regional land trust, and captured eight times more area than did the public source (i.e., U.S.G.S. GAP).

2.3. GAP analysis

The first step of our GAP analysis was to assess omissions in detection of potential breeding pools by conventional map data. We did this under the assumption that, if the resource could not be detected using publicly available data (U.S.F.W.S National Wetland Inventory maps or NWI's), it represented a de facto gap in protection as NWI maps are widely used by consultants, planners, and regulatory officials as the starting point, and often the ending point, for identifying project area wetlands. To this end, we compared the aerial photo-delineated pool layer (1:12,000 CIR spring leaf off aerial photography) with the coarser scale NWI maps (1:58,000 CIR spring leaf off aerial photography).

The next step was to assess gaps in existing protections for pool-breeding amphibian habitat using traditional GAP methods of layering resource and protection data (Scott et al., 1993). Specifically, data layers for state-mandated shoreland zones, tax-parcel-level conservation lands and endangered species habitat were layered with breeding and non-breeding habitat zones (prior to inclusion in the PHV) for vernal pool amphibians thereby summarizing potential gaps in the existing protection network.

2.4. Threat analysis

The premise of our threat model is that development pressure serves to compromise existing habitat values that lie outside of existing protection layers and results in the greatest threat values when both development pressure and adjusted habitat values are estimated to be high, and existing protection low, as follows:

$$\textbf{Threat value} = (\textbf{D}\text{evelopment }\textbf{P}\text{ressure}) * (\textbf{A}\text{ctual }\textbf{H}\text{abitat }\textbf{V}\text{alue})/\textbf{P}\text{rotection }\textbf{L}\text{evel}$$

The model produces as output a map where the confluence of development pressure and high-value, unprotected habitat have the greatest output "threat" value, at a resolution of 10,000 m^2 (1 ha). To reduce the output to a scale of threat similar to our scale of protection, the raw threat quotients 0–20 were rescaled to just 5 levels, 0 (lowest) to 4 (highest threat). We felt that simplifying the output in this manner would facilitate application of the model to real world planning. Zero (no threat) values were produced in two ways: (1) when there were no actual habitat values present (e.g., no breeding pools present, or complete coverage by urban/industrial land-use), or (2) when there was no predicted development pressure, which only occurs when human population in a census block is zero as each town has a projected growth rate > 0.

2.5. Economic characteristics of towns

In order to better understand the underlying socioeconomic causes for patterns of threat, we investigated the economic characteristics of towns using data from the 2000 US Census (MESPO, 2001). Tax valuation/housing unit were taken as an indicator of property value, and average per capita income were compared to town-level habitat threat levels in combination with the components of development pressure (town-level growth rate and US census block population density). Sensitivity of the threat model to two primary variables was assessed by increasing and decreasing values for development pressure and protection level by 25%.

2.6. Conservation triage

To demonstrate one approach to applying threat assessment results to conservation strategies for pool-breeding amphibians, we undertook a conservation triage (Hobbs and Kristjanson, 2003). Conservation triage applies medical disaster terminology to allocating resources for conservation action based on urgency. It differs from prioritization in that it attempts to assign "treatments" to varying landscape "conditions". In our triage high-threat, high-value landscapes are considered in need of more urgent care, while other landscapes are not considered for immediate treatment either because they have high ecological value but face little current threat, or are considered beyond ecological recovery (e.g., urban and/or industrial locales).

3. Results

3.1. Gaps in detection

The U.S.F.W.S National Wetland Inventory maps (1:58,000) did not include over half (55.3%) of the pools that were delineated for the study area using a finer scale of aerial photography (1:12,000). Predictably, those pools not captured by the NWI but detected by lower-level flights were significantly smaller ($\bar{x} = 442.92$ m^2, SD = 597.50) than those included ($\bar{x} = 963.08$ m^2, SD = 1151.78; $t = -6.774$, $df = 540$, $p < 0.001$). Furthermore, we found no vernal pool-type wetlands indicated by the NWI that were not identified by our own finer scale, remote delineation layer.

3.2. Gaps in protection

Of the 542 potential breeding pools delineated for the study area, 249 or approximately half (46%) received no formal protection from any mechanism (Fig. 2). Of the 293 pools that received some form of protection (54% of total), more than a third (106 pools; 19.6% of total) were captured by the regulatory review afforded by their size alone (>400 m^2). Conservation lands of all protection levels captured 21% of all 542 pools. Most of this protection was provided by multiple use land; less than 2% of all pools were captured by conservation land managed primarily for biodiversity (highest protection level of 4; Fig. 2). In total, only 15.2% of all pools were captured by the three sources for highest levels of protection (level 4): (1) lands specifically managed for biodiversity conservation (1.8% of total; 3.4% of those protected), (2) regulated endangered species habitat (2% of total; 3.8% of those protected), and (3) pools located inside regulated shoreland zones (11.4% of total; 21.1% of those protected).

As expected, gaps in existing protection for terrestrial non-breeding habitat were more extensive than for the breeding pools themselves (Fig. 3). In contrast to the nearly half of all potential breeding pools that received at least partial protection, only 20% of all delineated non-breeding habitat received some level of pro-

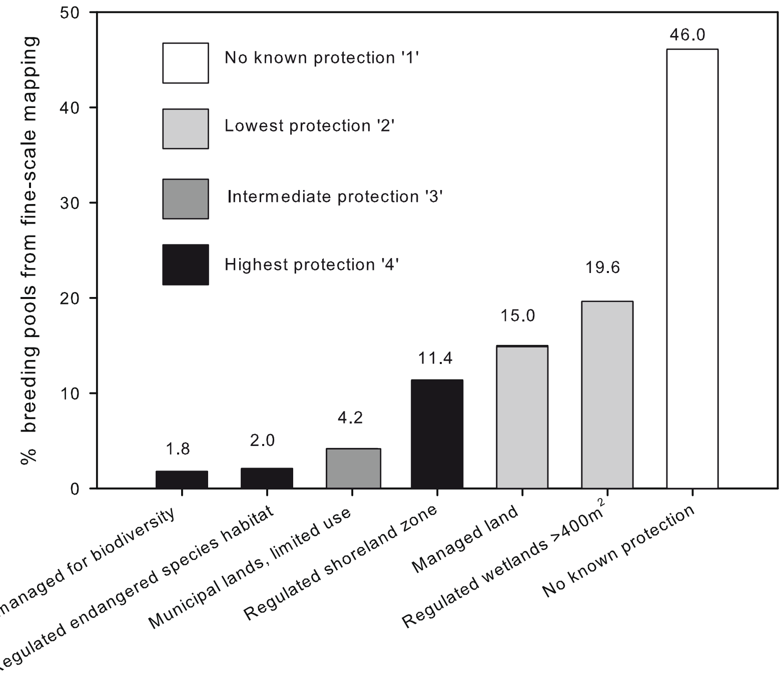

Fig. 2. The existing protection network of conservation and regulated lands for mapped amphibian breeding pools in an urbanizing, forested region of New England (USA). Pools were delineated from fine-scale, color infra-red, high-water aerial photography. Protection level categories range from 1 (no known) to 4 (highest; managed for biodiversity). Mapped lands include Regulated Endangered Species Habitat (occupied wetlands and adjacent habitat zone of 76.2 m), fee and easement conservation lands (varied levels of protection including Lands Managed for Biodiversity, Municipal Lands, and Managed Land), Regulated Shoreland Zones (riparian lands subject to regulatory review and limited development), Regulated Wetlands (wetlands > 400 m^2 subject to increased regulatory scrutiny) and No Known Protection.

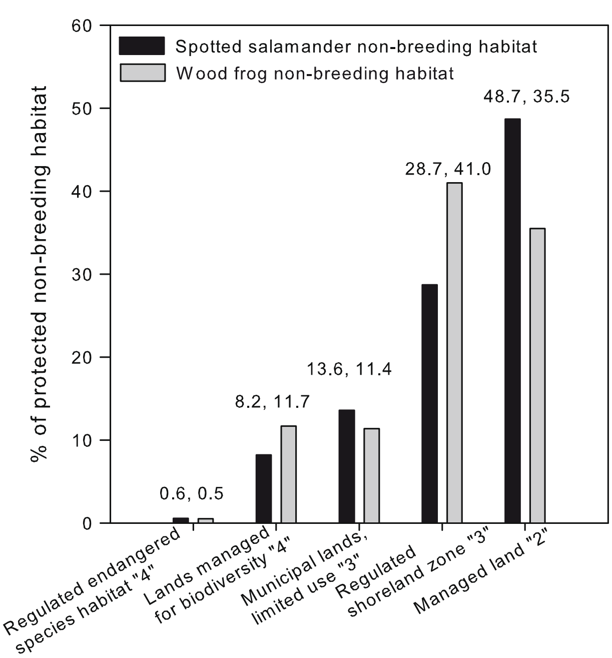

Fig. 3. The existing protection network of conservation and regulated lands influencing non-breeding habitat for pool-breeding amphibians in an urbanizing, forested region of New England (USA). Non-breeding habitat is delineated as species-specific radial maximum migration zones, i.e., 340 m for wood frogs (*Rana sylvatica*) and 250 m for spotted salamanders (*Ambystoma maculatum*).

tection. Because non-breeding habitat is extensive spatially, it was captured roughly in proportion to the amount of landscape covered by managed and regulated lands (20%). Depending on species, between 20.2% (wood frog), and 22.8% (spotted salamander) of non-breeding habitat received some level of protection. Of this, most was protected by managed forest and agricultural lands, and lands subject to regulated development. For example, 91% of the protected spotted salamander, and 87.9% of the protected wood frog non-breeding habitat was protected by tree farms, tax credit farmlands, municipal (no easement) lands, and regulated shoreland zones, while only 8.8% (spotted salamander) to 12.2% (wood frog) was protected at the highest level (Fig. 3).

3.3. Threat analysis

The results of the threat assessment point to two tiers of landscape threat for pool-breeding amphibians: (1) a relatively small percentage (5.1%; 1547 ha) of the four study towns acutely threatened (level 3 and 4 threat), and (2) a relatively large land area (44.4%; 13,419 ha) at low to moderate threat levels (level 1 and 2 threat). The remainder (50.3%) of the land area was not threatened (level 0 threat), due to (a) naturally low habitat potential combined with low development pressure, (b) lands already protected at the highest level (4), or (c) very high current land-use intensity combined with low habitat value (e.g., an urban center). Within each of the four study towns, areas most threatened were generally characterized by landscapes where individual houses and smaller subdivisions bordered otherwise unfragmented forest matrix blocks of 1–5 km^2 (the darkest blocks in Fig. 4).

Our sensitivity analysis suggests that development pressure is more influential than land protection level in determining overall landscape threat levels for pool-breeding amphibians. For example, to achieve a decrease in threat level of 50%, either a 50% decrease in development pressure, or 80% increase in protection level, are needed.

When evaluating sociodemographic characteristics of our study towns, the greatest threat values appeared to result from a combination of intermediate population density and high growth rates. For example, the town of Falmouth (population density 13.5 people/km^2 and growth rate 23.5%) had the greatest threat levels

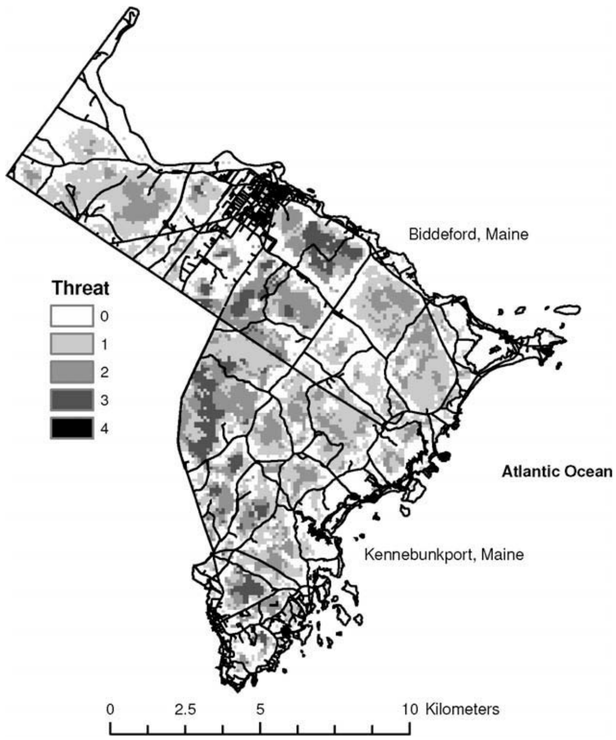

Fig. 4. Threats to pool-breeding amphibian habitat in adjacent southern Maine (USA) towns. Darker areas represent identified 1–5 km^2 blocks of relatively unfragmented pool-breeding amphibian habitat that are more threatened by growth rates on their margins. The major road network is shown to emphasize the importance of roadless areas for amphibian conservation in urbanizing landscapes.

(Fig. 5). By contrast, Biddeford had a higher population density (26.8 people/km^2), but a lower growth rate (5.9%), resulting in much lower levels of threat. Rural towns such as North Berwick, with a high growth rate (23%) but low population density (4.4 people/km^2), may be most dynamic in terms of development potential, but present relatively little overall threat to vernal pool amphibian habitat in the near future (Fig. 5). By contrast, towns with intermediate levels of settlement (those with some quality habitat remaining) combined with high growth rates (e.g., Falmouth) may be the kinds of places most urgently in need of conservation action, today.

4. Discussion

Our GAP and Threat assessments suggest that the current framework of conservation lands and regulations provides only limited protections for pool-breeding amphibian habitat in rapidly urbanizing landscapes. Nearly half of the 542 delineated potential breeding pools and 80% of delineated non-breeding habitat assessed in southern Maine (USA) currently receive no known form of protection. Further, many breeding pools and associated habitats are de facto unprotected because they are undetectable by conventional mapping products (e.g., National Wetlands Inventory; NWI) and when planning for the conservation of wetlands, remote detection and mapping using these products are generally the first steps in the delineation process (Tiner, 1999). We note a two-fold improvement in vernal pool detection using 1:12,000 aerial photography over the NWI's 1:58,000 scale, while Calhoun et al. (2003) found that an even finer scale of aerial photography (1:4800) detected nearly four times as many pools. The first step in conservation planning is being able to identify habitats and many low-cost alternatives to custom aerial CIR photography exist (Burne and Lathrop, 2008). For pool-breeding amphibians, simple wetland detectability may be a major hurdle to overcome considering that even when detected, nearly half may remain unprotected.

While it is generally recognized that state and federal wetland regulations need to be strengthened to protect small, isolated wetlands (Gibbs, 1993; Semlitsch and Bodie, 1998; Zedler, 2003), our results provide a measure of just how significant an impact stronger regulations could have. Of the protected pools in southern Maine, we found that greater than a third (36.2%) receive protection only because of minimal regulatory oversight based on size (>400 m^2), which still allows for potential impact during the state's permitting process. Similarly, pools eligible for protection under state-mandated shoreland zoning do not uniformly receive it, as rigor of local enforcement varies widely. Thus, our estimates of protection levels for pools are probably high. Regulations designed to specifically protect the unique values associated with smaller isolated wetlands would improve protection for these, and the remaining 2/3 of the vernal pools in our study area. Following enactment of new regulations in 2007 for high-value vernal pools that qualify as Significant Wildlife Habitat (http://www.maine.gov/dep/blwq/docstand/nrpa/vernalpools/index.htm), including an

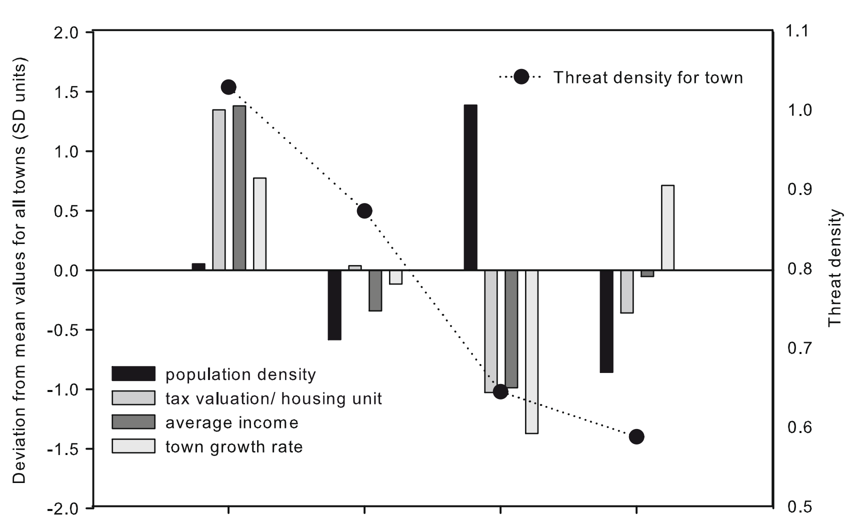

Fig. 5. Relationship among socioeconomic conditions and degree of threat to pool-breeding amphibian habitat in southern Maine (USA). Bars show extent to which towns deviate positively or negatively from the mean socioeconomic values across four municipalities (horizontal solid line). Filled circles show mean density of threat for each town (∑threat index for all 1 ha cells in town/town area).

adjacent terrestrial habitat zone of 76 m, the US State of Maine arguably now hosts one of the strongest regulatory safety nets for vernal pools in North America.

Conservation of pool-breeding amphibians must take into account that many species make far-ranging movements, requiring relatively intact forest landscapes enveloping their breeding wetlands (Semlitsch and Bodie, 1998; Semlitsch, 2000; Gamble et al., 2007). In contrast to the protection coverage we assessed for breeding pools themselves (nearly 50%), only 20% of non-breeding habitat for pool-breeding amphibians received some protection. This was not "hard" protection, but primarily resulted from shoreland zoning regulations and lower-level conservation lands where management for biodiversity is secondary to other objectives (e.g., silviculture). Tree farms and shoreland zones allow several land-use activities detrimental to pool-breeding amphibians including partial canopy clearing, road building, and limited residential development. The detrimental effects of roads and development have been increasingly documented for pool-breeding amphibians (reviewed by Semlitsch, 2000; Windmiller and Calhoun, 2008). While forest management is among the more compatible consumptive land-use activities for conserving amphibian habitat, it can have negative impacts if not practiced in an ecological manner (reviewed by deMaynadier and Hunter, 1995; deMaynadier and Houlahan, 2008). Nonetheless, tree farms, shoreland zones and other low to moderate-level conservation lands not traditionally quantified in large-scale GAP analyses, clearly play an immediate role in the protective network that currently exists for pool-breeding amphibians; one that could be enhanced over time through additional purchase of development rights by federal, state, or local conservation interests.

The most rapid land-use conversion typically occurs in the rural-urban (exurban) fringe where current human population densities may be moderate but growth rates are rapid due to a combination of land value and availability (Bell and Irwin, 2002; Hansen et al., 2005). We observed the greatest threats to pool-breeding amphibians where these same exurban zones overlapped portions of the landscape supporting high habitat values for amphibians. Specifically, threat was greatest where intermediate human densities (~10–30 people/km^2) were combined with high projected growth rates (>20%) and high density of breeding and non-breeding habitat in remaining forest blocks sized 1–5 km^2. In the American West, exurban development has been rapidly overtaking sensitive habitat at coarse (e.g., county) scales (e.g., riparian areas on the outskirts of sprawling cities; Theobald, 2003). Our results from the densely settled Northeast suggest the same processes underway at much finer scales (i.e., amphibian habitat within New England towns). In the long-settled Northeast (European settlement since the 1600's), there is an abundant supply of forested land from reverted farmlands (Foster, 1992) that can serve as "habitat" for both subdivisions and, where moderately sized patches > 1 km^2 remain, pool-breeding amphibians. Given our results, it appears that a promising strategy for conserving pool-breeding amphibian habitat in developing landscapes is to strengthen protections for remaining intact forest matrix blocks hosting wetland complexes in areas where human population densities remain low to intermediate but projected growth rates are high – thus preventing large portions of the landscape from slipping into the highest risk status for imminent development (Fig. 4).

While our analysis may seem parochial (e.g., integrating local conservation lands data and state-level regulations), assessing risk is scale-dependent. For small, terrestrial vertebrates such as pool-breeding amphibians, fine-scale habitat and protective network data are required. These are often only available through partnerships with local environmental groups and agencies that collect and maintain valuable, fine-scale geographic data (Allen et al., 2001). We were able to use data at a much finer scale than the 30-m resolution Landsat-TM and conservation lands data that are typically employed for coarser scale analyses (Woolmer et al., 2008). For pool-breeding amphibians and other localized habitat specialists, a comprehensive assessment of the protection network requires fine-scale data on wetlands and their regulations as well as conservation lands under ownerships not typically tracked (e.g., local land trusts and town governments). Such fine-scale

Table 2
A conservation triage for pool-breeding amphibian habitat in a rapidly urbanizing region (southern Maine, USA), based on results of a threat analysis. Conservation actions are ordered vertically with increasing levels of urgency, and horizontally using a medical metaphor from "preventative" (i.e., longer term actions designed to reduce threats over broad geographic areas) to "emergency" (i.e., local and urgent actions to address acute levels of threat).

			Preventative			Emergency	
			Conservation strategy				
Level of urgency	**Land area (ha)**	**Percent of study area**	**Outreach**	**State and federal wetland regulation**	**Local conservation**	**Private land incentives**	**Fee and easement purchase**
Higher threat = combination of greater habitat value and development pressure			• Education	• Improved regulation for small, isolated wetlands	• Improved ordinances and code enforcement	• Managed land tax credits (e.g., open space, tree farm, farmland)	• Federal, state, and private conservation groups
			• Promulgation of Best Management Practices	• Improved riparian buffer protections	• Improved comprehensive planning for natural resources	• Financial assistance for habitat management	
0 (no threat)	15,264	50.5	x	x			
1 (low)	8508	28.2	x	x	x		
2 (moderate)	4911	16.2	x	x	x	x	
3 (high)	1086	3.6			x	x	x
4 (extreme)	461	1.5					x

protection network data is often difficult to obtain in part because local land trusts do not want to disseminate maps fearing that the public will see them as recreational lands when in fact they often have no recreational easements (Brewer, 2003). Yet, in our study, conservation lands data compiled by the Wells National Estuarine Reserve covered eight times more of the landscape than the more coarse-scale conservation lands layer provided by the U.S.G.S. used most often for conservation planning at an ecoregion scale. We concur with Theobald et al. (2000) and many others that through improved academic–NGO–local agency partnerships, fine-scale map data can become available for applied research, and that such partnerships provide an avenue for transferring research results to inform local, science-based conservation practices.

Reactive land purchases to conserve resources that are imminently threatened are often far more expensive than long-term strategies, as suggested by our conservation triage (Table 2). For example, a conservation fee purchase of only our top 1.5% high-value, high-threat habitat would require an enormous expenditure well out of balance with the resources of most conservation organizations, with the 461 ha of land in the highest threat level costing approximately $40 million based on current land values available from the state Planning Office. For comparison, this same dollar amount could purchase roughly 73,000 ha of remote, unsettled forest land elsewhere in the region. As a concurrent aspect of the overall strategy, we suggest that implementing aggressive, proactive conservation measures may be more cost efficient by preventing low to moderately threatened habitat from slipping to the highest threat status (Table 2). Nearly half of our study landscape is currently classified as under intermediate threat (levels 1–3), and loss or fragmentation of significant portions of this acreage might compromise the viability of pool-breeding amphibian populations in this region. Systematic planning and implementation of preventative measures could include improved regulations for small, isolated wetlands (Zedler, 2003), restrictions on development imposed by municipal zoning, and promulgation of voluntary best management practices (Calhoun et al., 2005) and conservation subdivision designs (Arendt, 1999; Milder, 2007) while simultaneously increasing efforts toward broad-scale environmental education (Calhoun and Reilly, 2008).

Conservation triage is controversial (Hobbs and Kristjanson, 2003; Lawler et al., 2003), but we believe it is a viable idea particularly in rapidly urbanizing landscapes. While we do not advocate abandoning high-value wetlands or wildlife habitat, we recognize that funding for conservation is limited, especially at the local scale and for ecosystems used by common animals. Small, isolated wetlands are particularly vulnerable and yet so locally abundant in some regions that guidance is needed to prioritize action – not only "where" to act and with what degree of urgency, but "what" to do with different areas of the landscape. Incipient amphibian declines necessitate identifying and protecting key habitats prior to the loss of those populations inhabiting them. Therefore, we recommend a strategic approach based on a spatially-explicit analysis of the relationship between modeled habitat for relative habitat specialists (e.g., pool-breeding amphibians) and estimated levels of landscape threat (e.g., exurban development in areas lacking conservation lands). Once vulnerable places are targeted by such analyses of threat, their ability to sustain amphibian populations should be assessed using spatially-explicit population viability models (e.g., Harper et al., 2008). Finally, conservation planners cannot rely on remotely-obtained geographic data alone. Regardless of scale, only rigorous field surveys will validate models and identify critical habitats. Ultimately, the most effective conservation strategy in urbanizing landscapes will arise from a union of geographic planning tools utilizing fine-scale habitat and threat data, on-the-ground biological surveys, and interactions with local stakeholders (Sanderson et al., 2002b).

Acknowledgements

Support for this research was provided by the University of Maine, Maine Department of Inland Fisheries and Wildlife (Non-game and Endangered Wildlife Fund), Maine Outdoor Heritage Fund, US Environmental Protection Agency, Maine Audubon Society, and the Robert and Patricia Switzer Foundation. The Wells National Estuarine Reserve provided a pleasant work environment and assistance with local-scale data. The model and manuscript were improved by critiques from K.P. Bell, E. Gallandt, W. Halteman, M. Schauffler, R. Seymour, N. Taylor, R. Freeman, S. Trombulak, and two anonymous reviewers. Finally, the authors are grateful to Aram J.K. Calhoun for her support and insights throughout the project.

References

Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30, 133–165.

Allen, C.R., Pearlstine, L.G., Kitchens, W.M., 2001. Modeling viable mammal populations in gap analysis. Biological Conservation 99, 135–144.

Arendt, R., 1999. Growing greener: putting conservation into local plans and ordinances. Island Press, Washington, DC.

Baldwin, R.F., Calhoun, A.J.K., deMaynadier, P.G., 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana sylvatica*. Journal of Herpetology 40, 443–454.

Bell, K.P., Irwin, E.G., 2002. Spatially explicit micro-level modelling of land-use change at the rural–urban interface. Agricultural Economics 27, 217–232.

Berven, K.A., Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution 44, 2047–2056.

Brewer, R., 2003. Conservancy: the land trust movement in America. Dartmouth College/University of Press of New England, Hanover, NH.

Burne, M.R., Lathrop Jr., R.G., 2008. Remote and field identification of vernal pools. In: Calhoun, A.J.K., deMaynadier, P.G. (Eds.), Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton, FL, pp. 55–68.

Calhoun, A.J.K., Reilly, P., 2008. Conserving vernal pool habitat through community based conservation. In: Calhoun, A.J.K., deMaynadier, P.G. (Eds.), Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton, FL, pp. 319–344.

Calhoun, A.J.K., Walls, T.E., Stockwell, S.S., McCollough, M.M., 2003. Evaluating vernal pools as a basis for conservation strategies: a Maine case study. Wetlands 23, 70–81.

Calhoun, A.J.K., Miller, C.I., Klemens, M.W., 2005. Conserving pool-breeding amphibians in human-dominated landscapes through local implementation of best development practices. Wetlands Ecology and Management 13, 291–304.

Carr, L.W., Fahrig, L., 2001. Effect of road traffic on two amphibian species of differing vagility. Conservation Biology 15, 1071–1078.

Clevenger, A.P., McIvor, M., McIvor, D., Chruszcz, B., Gunson, K., 2001. Tiger salamander, *Ambystoma tigrinum*, movements and mortality on the trans-Canada highway in southwestern Alberta. The Canadian Field Naturalist 115, 199–204.

Colburn, E.A., 2004. Vernal Pools: Natural History and Conservation. Woodward Publishing Company, Blacksburg, VA.

Compton, B.W., McGarigal, K., Cushman, S.A., Gamble, L.R., 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conservation Biology 21, 788–799.

Copenheaver, C.A., White, A.S., Patterson, W.A.I., 2000. Vegetation development in a southern Maine pitch pine-scrub barren. Journal of the Torrey Botanical Society 127, 19–32.

Dahl, T.E., 2000. Status and Trends of Wetlands of the Conterminous United States 1986–1997. US Department of the Interior, Fish and Wildlife Service, Washington, DC.

deMaynadier, P.G., Houlahan, J.E., 2008. Conserving vernal pool amphibians in managed forests. In: Calhoun, A.J.K., deMaynadier, P.G. (Eds.), Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton, FL, pp. 127–148.

deMaynadier, P.G., Hunter, M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3, 230–261.

deMaynadier, P.G., Hunter, M.L., 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12, 340–352.

deMaynadier, P.G., Hunter, M.L., 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management 63, 441–450.

deMaynadier, P.G., Hunter, M.L., 2000. Road effects on amphibian movements in a forested landscape. Natural Areas Journal 20, 56–65.

DEP, 2002. Wetlands Regulatory Program Overview. State of Maine Department of Environmental Protection, Augusta, ME, p. 14.
DEP, 2003. Mandatory Shoreland Zoning Act: Title 38 M.R.S.A. Maine Department of Environmental Protection, Augusta, ME (Sections 435–449).
Faccio, S.D., 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. Journal of Herpetology 37, 479–489.
Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D., Wegner, J.F., 1995. Effect of road traffic on amphibian density. Biological Conservation 73, 177–182.
Farnsworth, E., 2004. Forging research partnerships across the academic-agency divide. Conservation Biology 18, 291–293.
Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC.
Foster, D.R., 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80, 753–772.
Gamble, L.R., McGarigal, K., Jenkins, C.L., Timm, B.C., 2006. Limitations of regulated "buffer zones" for the conservation of marbled salamanders. Wetlands 26, 298–306.
Gamble, L.R., McGarigal, K., Compton, B.W., 2007. Fidelity and dispersal in the pond-breeding amphibian, Ambystoma opacum: implications for spatio-temporal population dynamics and conservation. Biological Conservation 139, 247–257.
Gibbs, J.P., 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands 13, 25–31.
Gibbs, J.P., 1998. Amphibian movements in response to forest edges, roads and streambeds in southern New England. Journal of Wildlife Management 62, 584–589.
Gibbs, J.P., 2000. Wetland loss and biodiversity conservation. Conservation Biology 14, 314–317.
Gibbs, J.P., Reed, J.M., 2008. Population and genetic linkages of vernal pool-associated amphibians. In: Calhoun, A.J.K., deMaynadier, P.G. (Eds.), Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton, FL, pp. 149–168.
Gordon, R.E., 1968. Terrestrial activity of the spotted salamander, *Ambystoma maculatum*. Copeia 1968, 879–880.
Groves, C., Kutner, L., Stoms, D., Murray, M., Scott, J., Schafale, M., Weakley, A., Pressey, R., 2000. Owning up to our responsibilities: who owns lands important to biodiversity? In: Stein, B.A., Kutner, L.S., Adams, J.S. (Eds.), Precious Heritage: the Status of Biodiversity in the United States. Oxford University Press, Oxford, UK, pp. 275–300.
Groves, C., Jensen, D., Valutis, L.L., Redford, K.H., Shaffer, M., Scott, J.M., Baumgartner, J.V., Higgins, J.V., Beck, M.W., Anderson, M.G., 2002. Planning for biodiversity conservation: putting conservation science into practice. Bioscience 52, 499–512.
Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., Jones, K., 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15, 1893–1905.
Harper, E.B., Rittenhouse, T.A.G., Semlitsch, R.D., 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. Conservation Biology 22, 1205–1215.
Hitchings, S.P., Beebee, T.J.C., 1998. Loss of genetic diversity and fitness in common toad (*Bufo bufo*) populations isolated by inimical habitat. Journal of Evolutionary Biology 11, 269–283.
Hobbs, R.J., Kristjanson, L.J., 2003. Triage: how do we prioritize health care for landscapes? Environmental Management and Restoration 4 (Suppl.), S39–S45.
Holland, C.C., Honea, J., Gwin, S.E., Kentula, M.E., 1995. Wetland degradation and loss in the rapidly urbanizing area of Portland, Oregon. Wetlands 15, 336–345.
Homan, R.N., Windmiller, B.S., Reed, J.M., 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications 14, 1547–1553.
Hunter, M.L., 1997. The biological landscape. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington DC, pp. 57–67.
Hunter, M.L., Calhoun, A.J.K., McCollough, M.M., 1999. Maine Amphibians and Reptiles. University of Maine Press, Orono, ME.
Kolozsvary, M.B., Swihart, R.K., 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates of farmland. Canadian Journal of Zoology 77, 1288–1299.
Krohn, W.B., Hepinstall, J.A., 2000. A Habitat-based Approach for Identifying Open-space Conservation Needs in Southern Maine. Maine Department of Inland Fisheries and Wildlife, Bangor, ME, p. 36.
Lawler, J.J., White, D., Master, L.L., 2003. Integrating representation and vulnerability: two approaches for prioritizing areas for conservation. Ecological Applications 13, 1762–1772.
Lehtinen, R.M., Galatowitsch, S.M., Tester, J.R., 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19, 1–12.
Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.
Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15, 40–49.
Marsh, D.M., Thakur, K.A., Bulka, K.C., Clarke, L.B., 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. Ecology 85, 3396–3405.
Marsh, D.M., Milam, G.S., Gorham, N.P., Beckman, N.G., 2005. Forest roads as partial barriers to terrestrial salamander movement. Conservation Biology 19, 2004–2008.
McDonough, C., Paton, P.W.C., 2007. Spotted salamander dispersal across a forested landscape fragmented by a golf course. Journal of Wildlife Management 71, 1163–1169.
Means, D.B., Palis, J.G., Baggett, M., 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology 10, 426–437.
MESPO, 2001. Forecast of Maine State/County/Town Populations. Maine State Planning Office, Augusta, ME.
MESPO, 2003. Housing Unit Forecast by Town to 2015. Maine State Planning Office, Augusta, ME.
Milder, J.C., 2007. A framework for understanding conservation development and its ecological implications. Bioscience 57, 757–768.
Montieth, K.E., Paton, P.W.C., 2006. Emigration behavior of spotted salamanders on golf courses in Southern Rhode Island. Journal of Herpetology 40, 195–205.
Moon, T.-Y., 2001. Choosing priority-conservation areas for vespine wasps by taxonomic rootedness, ecological niches and gap analysis. Korean Journal of Entomology 31, 169–175.
Morris, K.M., Maret, T.J., 2007. Effects of timber management on pond-breeding salamanders. The Journal of Wildlife Management 71, 1034–1041.
Patrick, D.A., Hunter Jr., M.L., Calhoun, A.J.K., 2006. Effects of experimental forestry treatments on a Maine amphibian community. Forest Ecology and Management 234, 323–332.
Petranka, J.W., 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC.
Plantinga, A.J., Mauldin, T., Alig, R.J., 1999. Land use in Maine: determinants of past trends and projections of future changes. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
Porej, D., Micacchion, M., Hetherington, T.E., 2004. Core terrestrial habitat for conservation of local populations of salamanders and wood frogs in agricultural landscapes. Biological Conservation 120, 399–409.
Regosin, J.V., Windmiller, B.S., Reed, J.M., 2003. Terrestrial habitat use and winter densities of the wood frog (*Rana sylvatica*). Journal of Herpetology 37, 390–394.
Reh, W., Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog, *Rana temporaria*. Biological Conservation 54, 239–249.
Rittenhouse, T.A.G., Semlitsch, R.D., 2007a. Postbreeding habitat use of wood frogs in a Missouri Oak-Hickory forest. Journal of Herpetology 41, 645–653.
Rittenhouse, T.A.G., Semlitsch, R.D., 2007b. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands 27, 153–161.
Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffman, M., King, B.B., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428, 640–643.
Rothermel, B.B., Semlitsch, R.D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology 16, 1324–1332.
Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002a. The human footprint and the last of the wild. Bioscience 52, 891–904.
Sanderson, E.W., Redford, K.H., Vedder, A., Coppolillo, P.B., Ward, S.E., 2002b. A conceptual model for conservation planning based on landscape species requirements. Landscape and Urban Planning 58, 41–56.
Scott, J.M., Davis, F., Csuti, F., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards, T.C.J., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 57, 5–41.
Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64, 615–631.
Semlitsch, R.D., 2002. Critical elements for biologically-based recovery plans for aquatic-breeding amphibians. Conservation Biology 16, 619–629.
Semlitsch, R.D., Bodie, J.R., 1998. Are small, isolated wetlands expendable? Conservation Biology 12, 1129–1133.
Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17, 1219–1228.
Semlitsch, R.D., Skelly, D.K., 2008. Ecology and conservation of pool-breeding amphibians. In: Calhoun, A.J.K., deMaynadier, P.G. (Eds.), Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton, FL, pp. 127–148.
Shoop, C.R., 1965. Orientation of *Ambystoma maculatum*: movements to and from breeding ponds. Science 149, 558–559.
Skidds, D.E., Golet, F.C., Paton, P., Mitchell, J.C., 2007. Habitat correlates of reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed. Journal of Herpetology 41, 439–450.
Stoms, D.M., 2000. GAP management status and regional indicators of threats to biodiversity. Landscape Ecology 15, 21–33.
Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science Express, 1–5.
Theobald, D.M., 2003. Targeting conservation action through assessment of protection and exurban threats. Conservation Biology 17, 1624–1637.
Theobald, D.M., 2004. Placing exurban land-use change in a human modification framework. Frontiers in Ecology and the Environment 2, 139–144.
Theobald, D.M., Hobbs, R.J., Bearly, T., Zack, J.A., Shenk, T., Riebsame, W.E., 2000. Incorporating biological information in local land-use decision-making:

designing a system for conservation planning. Landscape Ecology 15, 35–45.

Tiner, R.W., 1999. Wetland indicators: a guide to wetland identification, delineation, classification, and mapping. Lewis Publishers, Boca Raton, LA.

Windmiller, B.S., Calhoun, A.J.K., 2008. Conserving vernal pool wildlife in urbanizing landscapes. In: Calhoun, A.J.K., deMaynadier, P.G. (Eds.), Science and Conservation of Vernal Pools in Northeastern North America. CRC Press, Boca Raton, FL, pp. 233–252.

Woolmer, G., Trombulak, S.C., Ray, J.C., Doran, P.J., Anderson, M.G., Baldwin, R.F., Morgan, A., Sanderson, E.W., 2008. Rescaling the human footprint: a tool for conservation planning at an ecoregional scale. Landscape and Urban Planning 87, 42–53.

Zedler, P.H., 2003. Vernal pools and the concept of "isolated wetlands". Wetlands 23, 597–607.