# JOURNAL

## OF

# HERPETOLOGY

## Factors Influencing Occupancy Patterns of Eastern Newts across Vermont

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Abstract.—Of the threats facing amphibian populations today, habitat transformation resulting from land use is among the most pressing. Although conservation of pond-breeding salamanders clearly requires protection of breeding ponds and their surrounding habitat, little is known about the effects of land use and other factors on the occurrence of salamanders in the dispersal/terrestrial phase of their life cycle. To determine these effects, we surveyed populations of Eastern Newts (*Notophthalmus viridescens*) at 551 stations across Vermont and modeled salamander distribution as a function of environmental variables hypothesized to influence site occupancy. We developed a set of 12 models based on seven *a priori* hypotheses of site occupancy. We hypothesized that occupancy was influenced by (1) amounts of available habitat types, (2) arrangement of these habitat types, (3) geographic position, (4) housing density, (5) road density, (6) short-term changes in habitat distribution, or (7) habitat structure at the stand level. We used a single-season occupancy model to rank and compare the 12 models. A total of 232 Eastern Newts was detected at 82 of 551 stations. Of the 12 models, amount of habitat within 0.5 km of the survey station best represented the field data. Strong effects were indicated for developed land (−), open water (+), and forest (+) cover. Given a survey station with average forest and open water characteristics, stations with >5% developed land classes within a 0.5-km buffer had a very low probability of occupancy. Further research is needed to determine the direct role of development on occupancy patterns.

Many species of amphibians worldwide have declined markedly in abundance and extent in recent years (Collins and Storfer, 2003; Stuart and Chanson, 2004; Beebee and Griffiths, 2005) with some species becoming extinct (Houlahan et al., 2000; Alford et al., 2001). Amphibian declines have been linked to ultraviolet (UV) radiation, chemical pollution, climate change, disease, exotic species, and land-use practices (Collins and Storfer, 2003; Stuart et al., 2004, and references therein). Of these, land-use practices contribute either directly or indirectly to many of the proposed mechanisms of decline (Cushman, 2006) and are among the most significant threats to amphibian populations (Knutson et al., 1999; Carr and Fahrig, 2001; Hyde and Simons, 2001).

Changes in land use can affect amphibians by altering the relative amount (e.g., habitat loss) and spatial arrangement (e.g., habitat fragmentation) of habitat types and can alter the natural pattern of environmental disturbance (Mac et al., 1998). In New England, important contemporary threats include human population growth and the conversion of natural habitats to human-dominated cover types (Vermont Forum on Sprawl, 1999; Breunig, 2003). For example, between 1970 and 2003, >100,000 acres of natural land in Vermont have been developed—a 42% increase. Similar trends are occurring throughout the northern forest, prompting the Governor's Task Force on Northern Forest Lands to encourage large-scale political and legal strategies that curb or lessen development pressure (Harper et al., 1992). Such changes in land-use pattern can affect the abundance and distribution of amphibians in several ways, thereby influencing long-term population dynamics.

Of particular interest are those species whose habitat requirements vary depending on life stage (e.g., species that require ponds for breeding but upland terrestrial habitats for maturation and dispersal; pond-breeding sala-

manders). For example, the Eastern Newt (*Notophthalmus viridescens*) is an aquatic breeder with a relatively high dispersal capability (Petranka, 1998). Breeding adults occur in some deep ponds and lakes but are more generally associated with vegetated shallow-water habitats (Petranka, 1998). After an aquatic larval stage, Eastern Newts spend 2–7 yr as terrestrial efts before final metamorphosis into aquatic adults (Petranka, 1998). Efts have been tracked nearly 800 m from natal waters over a year of movement (Healy, 1975), meaning dispersal ranges could exceed several kilometers.

Because of the duality of breeding and nonbreeding habitat requirements, several factors might influence the occurrence of such species and amphibians in general. First, terrestrial salamander distribution is positively related to percentage of forest cover (Gibbs, 1998b; Guerry and Hunter, 2002; Herrmann et al., 2005) and negatively linked to ''urban'' cover types (Delis et al., 1996; Knutson et al., 1999). Second, the arrangement of breeding and nonbreeding habitat affects the probability of species occurrence. Salamander occurrence is greater where the distance between wetland and forest cover is small (Porej et al., 2004). In addition to distance, factors such as dryness and habitat contrasts are detrimental to forest salamander movements and abundance at habitat edges (Gibbs, 1998a; deMaynadier and Hunter, 2000; Marsh and Beckman, 2004; Marsh et al., 2005). Third, amphibians that migrate between upland and wetland habitats may be vulnerable to the deleterious effects of roads, which inhibit dispersal or directly contribute to mortality (Trombulak and Frissell, 2000; Carr and Fahrig, 2001; Marsh and Beckman, 2004; Marsh et al., 2005). Finally, housing development is often associated with increased road densities and also reduces natural cover and increases impervious surfaces. As with any land cover analysis, the importance of each of these factors on shaping salamander distribution may be scale dependent (i.e., the results differ depending on the size of the buffer used in analysis; Barr and Babbitt, 2002).

Topography and site-level conditions can also influence salamander distributions. Microclimate change with elevation affects salamander relative abundance (Hyde and Simons, 2001; Barr and Babbitt, 2002; Ford et al., 2002). Additionally, UV-B radiation, implicated in amphibian declines (Kiesecker et al., 2001; Davidson et al., 2002; Kiesecker, 2002), is more intense at higher elevations (Diamond et al., 2005). At the site level, terrestrial salamander densities have been linked to stand age, ground cover, moisture, and coarse woody debris (Corn

and Bury, 1991; Hyde and Simons, 2001; Duguay and Wood, 2002; McKenny et al., 2006).

Although the literature suggests that many factors affect the distribution of species of pond-breeding salamanders, few have evaluated the relative strength of importance of each factor, which in turn would suggest the conservation efforts that would most greatly benefit populations. Furthermore, most studies of pond-breeding salamanders focus on conditions that affect the occurrence at breeding locations only (e.g., Semlitsch, 1998; Joly et al., 2001; Steen and Gibbs, 2005). However, because the terrestrial phase is long in duration (several years), understanding the conditions that affect the distribution of efts as well as breeding adults is critical (Gill, 1978).

With this goal, we surveyed populations of Eastern Newts in 2003 and 2004 at 551 random locations across Vermont and assessed salamander occurrence (mostly efts) as a function of environmental variables hypothesized to influence the probability of occupancy. We hypothesized that (1) the amount of forest, wetland, and water cover at a landscape level would have a positive effect on occupancy and that developed land cover would have a negative effect on occupancy, (2) increasing the interspersion and juxtaposition of breeding (wetland and water) and nonbreeding habitats (forest) at a landscape level would increase occupancy, (3) geographic position such as increased elevation would have negative effects on occupancy, (4) housing density would negatively affect occupancy, (5) road density would negatively influence occupancy, (6) current occupancy patterns are affected by the short-term (5-yr) changes in the amounts of breeding and nonbreeding habitat, and (7) forest stand structure variables that influence microclimate, such as litter depth, coarse-woody debris, and canopy coverage, would positively influence occupancy. We assessed the performance of these variables across two different landscape extents (0.5 km and 5 km for hypotheses 1, 2, and 4; 1 km and 5 km for hypothesis 5). For hypothesis 7, we assessed the effect of stand structure with two different models that described coarse woody debris. We used a single-season occupancy modeling framework (MacKenzie et al., 2002) to rank and compare the 12 models.

## MATERIALS AND METHODS

*Study Area.*—The study area included the entire state of Vermont (24,963 km$^2$). The Green Mountains run north-south through the state, and the low elevation, relatively temperate Champlain Valley comprises Vermont's northwestern boundary where the state borders Lake

**Legend**

· Vermont Study Sites

☐ Background

Non-habitat

Forest

Breeding habitat
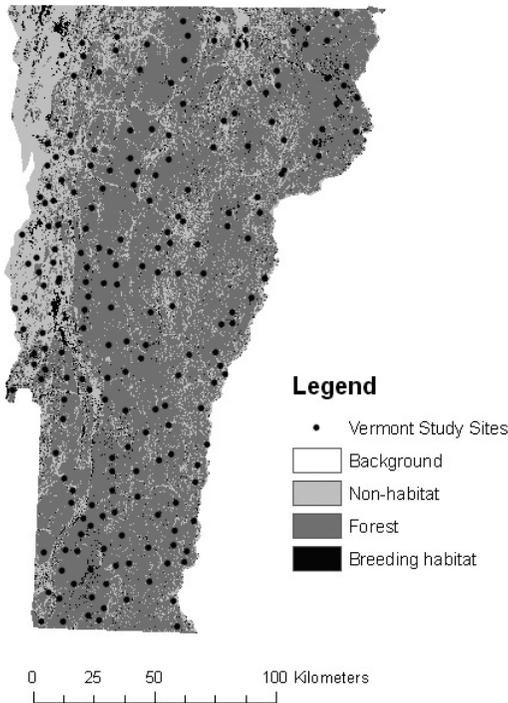
0   25   50        100 Kilometers

Fig. 1. Map of Vermont. Land-cover map of study area shows the distribution of nonhabitat (light grey), forested habitat (dark grey), and breeding habitat (black), derived from the National Land Cover Dataset (NLCD). Locations of the 143 study sites are depicted by black circles. Each site consisted of four survey stations, separated by 500 m, which were sampled with two methods: a time search of four, 2 × 12.6 m transects centered on the sampling station, and a timed area search within 25.2 m of the station centroid, exclusive of transects.

Champlain (Fig. 1). Elevation ranged from 30 m along the shores of Lake Champlain to 1,339 m at Mount Mansfield. Mean January temperatures ranged from $-10°C$ to $-5.5°C$ and mean July temperatures from 17.7°C to 21°C (Thompson and Sorenson, 2000). Annual precipitation ranged from about 75 cm in the Champlain Valley to more than 180 cm along the southern Green Mountain peaks (Thompson and Sorenson, 2000). Eleven frog and toad species and 12 salamander species are known to occur in Vermont (Andrews, 2002).

At the time of our study, most of Vermont was dominated by hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*), and American beech (*Fagus grandifolia*). The mid- and upper slopes of the Green Mountains supported montane stands of red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), and much of northeastern Vermont contained for-

ests of black spruce (*Picea mariana*), red spruce, balsam fir, paper birch, and white spruce (*Picea glauca*) (Thompson and Sorenson, 2000).

Human density varied from extremely rural areas in northeastern Essex County with 3.7 people per $km^2$, to Chittenden County, with 24% of the state's population and a human density of 91 people per $km^2$ (U.S. Census Bureau, 2001). Although mostly rural, the population of Vermont has grown at least 10% per decade since the 1960s (U.S. Census Bureau, 2001). Road density varied considerably from an average of about 0.53 $km/km^2$ in Essex County to over 1.55 $km/km^2$ in Chittenden County.

*Study Sites.*—We used a stratified sampling scheme to select 143 survey sites across the state of Vermont (Fig. 1). Sites were separated by at least 8 km. Stratified by development, agriculture, and forested land use (Long, 2006), sites were located in all major cover types, and across a broad gradient of human disturbance, forest fragmentation (i.e., highly heterogeneous landscape composition vs. homogeneously forested areas), ownership categories (e.g., public, private), elevation, and topographic complexity. Seventy-seven sites were surveyed in 2003 and 66 in 2004. Surveys were conducted in late May through mid-July in each year. Sites sampled in 2003 were characterized by more forest cover within 0.5 km of site centroid (mean = 89.9% vs. a 2004 mean of 57.5%) and lower percentages of developed land cover (mean = 0.6% vs. a 2004 mean of 10.2%).

*Salamander Sampling.*—Each site consisted of 3–4 sampling stations (geographic locations) spaced evenly around a geographic center point (hereafter referred to as the site centroid), with each station at least 500 m from other stations to ensure sampling independence. The station ($N$ = 551) was the basic statistical unit, sampled by (1) systematically searching four transects and (2) conducting a timed area search. Transects were 2 m wide, 12.56 m long, originated from the station centroid, and were oriented along the cardinal directions. Migratory efts that remain mobile for multiple years are expected to be found in leaf litter and debris (Healy, 1975). As such, each transect was searched for 5 min, and total detections per transect was recorded. The second survey per station consisted of a 10-min timed area search within a 25.22 m radius of the station centroid. For timed area searches, a single observer searched microhabitat features of known association with amphibians but not associated with transects and recorded the total number of salamanders detected. Because many amphibians are difficult to detect even when present (Bailey et al., 2004), destructive methods (e.g., logs over-

turned and broken apart, stones displaced) were used to locate salamanders under natural cover objects, leaf litter, and vegetation.

Resulting salamander data for each station were collapsed into a two-digit ''encounter history,'' the first digit representing the detection (1) or nondetection (0) of Eastern Newts on any of the four transects, and the second digit representing detection or nondetection of Eastern Newts associated with the area-search. For a survey with two occasions (transect search and area search), there were four possible encounter histories (11, 10, 01, 00).

In addition to documenting salamander occurrence, we collected vegetation data (see below), recorded precipitation within 24 h of each survey (i.e., 0 = no rain, 1 = rain), and measured air temperature (Enviro-safe® ''Easy Read'' Armor Case Thermometers −5°C to 50°C) at the station centroid at the time of each survey. These variables are known to affect detection probability of salamanders in Vermont (McKenny et al., 2006).

*Model Set Development*.—Based on a review of relevant literature, we identified 45 variables (potential model covariates) that we suspected could be associated with salamander occurrence. To minimize correlations of variables between and within models, we reduced the variable set by eliminating one of each pair of variables with Spearman's pairwise correlation (rho) greater than 0.55 or less than −0.55, except in the case of forest cover and development (rho = −0.61 at 500-m scale). The final models used combinations of 21 occupancy covariates (Table 1).

Covariates for the landscape-level models were derived through various GIS data sets. The basic data set was the 2001 National Land Cover Dataset (NLCD; Vogelmann et al., 2001). Landscape change variables were derived from the NOAA Coastal Change Analysis Program (C-CAP), an inventory land cover program that monitored changes in land cover from 1996–2001. The overall accuracy in land cover depiction is 85.1% with a range of 17% (Low Intensity Developed) to 99% (Water; http://www.csc.noaa.gov/crs/lca/ccap.html). Covariates for the stand-level habitat models were measured in the field by the survey teams as described below. All covariate values were standardized prior to analysis, and mean values were substituted for missing entries.

We developed 12 *a priori* models of salamander distribution in Vermont (Table 1). Models were named by the relevant hypothesis and the scale over which the variables were calculated (e.g., Amount 0.5 km). We assessed two models of the influence of habitat amount (Hypothesis 1) at the landscape scale: one at a spatial scale of 0.5 km and the other at 5 km (Table 1). Amount 0.5 km and Amount 5 km included covariates for percentage cover of forest (FOREST), wetland (WETLAND), open water (WATER), and human development (DEVELOPMENT; Table 1). These variables were based on pooling various NLCD land cover types. For example, deciduous, mixed, and coniferous forest types were combined as ''forest'' (FOREST). Forested uplands provide migratory, foraging, and overwintering habitat for newts. All palustrine wetland cover types were combined as ''wetland'' (WETLAND; note that this includes forested wetlands; hence a sample station could have substantial tree cover even if the FOREST value is low). WETLAND, along with surface water (WATER), represented a rough approximation of breeding habitat. All developed land cover classes were pooled as ''development'' (DEVELOPMENT; Table 1). Because remote sensing of wetlands is notoriously inaccurate, WETLAND is only an approximation of true wetland cover. In addition to wetlands, newts breed in small bodies of open water (Petranka, 1998), but small bodies of water are poorly represented by GIS data. Thus, the combined amount of WETLAND and WATER cover used here likely underestimated total breeding habitat.

The percentage of each land cover class was calculated within 0.5 km, 1 km, and 5 km radius buffers using FRAGSTATS (McGarigal and Marks, 1995) and a batch processor for ArcGIS (ESRI, Redlands, CA) developed by B. Mitchell (http://arcscripts.esri.com/details.asp?dbid=13839). The 0.5 and 1 km buffers were centered on stations, whereas 5 km buffers were centered on the site centroids. At the 0.5 km scale, FOREST was inversely correlated with DEVELOPMENT (rho = −0.61), indicating that as forest increased development decreased. The class for agricultural lands was not included in the model because of high correlation with for forest cover (|rho| > 0.76 at all scales).

We assessed the breeding and nonbreeding habitat arrangement hypothesis (Hypothesis 2) with models representing two spatial scales, 0.5 km and 5 km (Table 1), called Arrangement 0.5 km and Arrangement 5 km. We used FRAGSTATS and 2001 NLCD data to calculate a single variable that represented the interspersion and juxtaposition of breeding (WETLAND + WATER) and forest habitats (FOREST) surrounding stations. Any cover type other than FOREST, WETLAND, or WATER was considered nonhabitat. The arrangement metric was termed ARRANGEMENT (Table 1) and was the IJI index from the program FRAGSTATS (McGarigal and Marks, 1995).

TABLE 1. Description of seven model hypotheses to explain the probability of occurrence of Eastern Newts sampled in Vermont in 2003 and 2004. Each variable used in a given model is defined by its variable code and variable description. Hypotheses 1, 2, 4, 5, and 7 were evaluated at two spatial scales, resulting in a total of 12 models that were fit to the observed field data.

| Parameter of interest | Hypothesis | No. scales evaluated | Spatial scales evaluated | Variable code | Variables description | Data source |
|---|---|---|---|---|---|---|
| Occupancy | 1. Habitat amount | 2 | 0.5, 5 km | FOREST<br>WETLAND<br>WATER<br>DEVELOPMENT | % Forest cover<br>% Wetland cover<br>% Water cover<br>% Human development cover | NLCD 2001 |
| | 2. Habitat arrangement | 2 | 0.5, 5 km | ARRANGEMENT | Interspersion and juxtaposition index of breeding and upland habitat | NLCD 2001 |
| | 3. Abiotic | 1 | 0.5 km | ELEVATION<br>EAST<br>NORTH<br>ELEVATION × EAST<br>ELEVATION × NORTH | Elevation<br>UTM Easting<br>UTM Northing<br>Elevation × Easting<br>Elevation × Northing | NED |
| | 4. Housing | 2 | 0.5, 5 km | HOUSE | Total housing units | Theobald 2005 |
| | 5. Road | 2 | 1 km, 5 km | ROAD 1–2<br>ROAD 3–4 | Category 1–2 road density<br>Category 3–4 road density | VCGI |
| | 6. Habitat change | 1 | 5 km | WETLAND_loss<br>FOREST_loss | % Wetland cover lost between 1996 and 2001<br>% Forest cover lost between 1996 and 2001 | C-CAP 2001 |
| | 7. Stand structure | 2 | Station | V_CWD_more<br>V_CWD_less<br>LITTER<br>CANOPY<br>DENSITY<br>SAP<br>#_TREE<br>BA | Volume of more-decayed woody debris<br>Volume of less-decayed woody debris<br>Litter depth<br>Canopy extent<br>Understory density<br>Sapling density<br>No. trees selected by prism<br>Basal area of trees selected by prism | Field surveys |
| Detection probability | 1. Precipitation and temperature | | [All models] | PRECIPITATION<br>AIR TEMP | Precipitation within 24 h before survey (0,1)<br>Air temperature at time of survey | Field surveys |

We assessed the geographic position hypothesis (Hypothesis 3) with a single model representing one spatial scale, 0.5 km (Table 1). The model, Geographic Position 0.5 km, included variables for elevation (ELEVATION), latitudinal position (NORTH), longitudinal position (EAST; Table 1), and multiplicative terms for the interaction of elevation and geographic position (ELEVATION × EAST and ELEVATION × NORTH). UTM Easting (EAST) and UTM Northing (NORTH) were obtained directly from the 2001 NLCD data. Elevation was calculated from the U.S.G.S. National Elevation Dataset (URL: http://ned.usgs.gov) by averaging elevation within the 0.5-km buffer with ESRI ArcGIS Spatial Analyst. Note that these metrics were strongly correlated with the same metrics computed at a larger spatial extent (rho > 0.9 for each pair).

We assessed the housing density hypothesis (Hypothesis 4) with models representing two spatial scales, 0.5 km and 5 km (Table 1). The models, Housing 0.5 km and Housing 5 km, analyzed the effect on occupancy of the variable HOUSE, the mean housing units within either 0.5 km or 5 km, respectively (Table 1). HOUSE represented a certain type of development that is not well represented on the NLCD and is pertinent to the Vermont landscape because of an identified pattern of diffuse, nonurban residential development (Vermont Forum on Sprawl, 1999). Data were derived by Theobald (2005) and were based on population and housing from the U.S. Census Bureau's block group and block data for 2000. Maps of current housing density were generated using dasymetric mapping techniques described by Theobald (2001, 2003).

We assessed the road density hypothesis (Hypothesis 5) with models representing two spatial scales, 1 km and 5 km (Table 1), and called them Road 1 km and Road 5 km. Road density variables represented the mean density (km per km$^2$) of different road classes measured from 1:5000 GIS layer derived from multiple sources (VCGI: Long, 2006). Roads were reclassified from source data to conform to a single system of interstate highways (Category 1), state highways (Category 2), town roads (most unpaved; Category 3), and small roads (2- and 4-wheel drive, some impassable; Category 4). These categories were collapsed into two groups (ROAD 1–2 and ROAD 3–4), representing major and minor traffic volume (Table 1).

We assessed the habitat change hypothesis (Hypothesis 6) with a single model at the 5 km scale (Table 1). The Change 5 km model included two variables that included decreases in percent wetland and forest cover (WETLAND_loss and FOREST_loss) between 1996 and 2002 (Table 1). This model was evaluated at the 5 km scale around each station centroid and calculated the percent decrease in FOREST and WETLAND from 1996 to 2001.

We assessed the stand structure hypothesis (Hypothesis 7) with two models, Stand_more and Stand_less. The only difference between the models was that one included the volume of "more-decayed" coarse woody debris (CWD) and the other included the volume of "less-decayed" CWD. For each transect, we measured the decay class and diameter of any downed logs >10 cm in diameter at the point each intercepted the transect. Transect lengths for these variables were 25.22 m. The presence of sloughing bark put a log in the "more-decayed" class. At each station, we counted and measured the diameter at breast height (DBH) of all trees selected by a 10-factor prism. The number of trees selected by the prism (#_TREE) and their basal area (BA) were used in analyses (Table 1). Leaf litter depth (LITTER) was measured by inserting a ruler into the litter at nine points around each station: the station center and the middle and ends of each of the four transects. Because of logistical constraints, vegetation samples were not conducted at all stations. Mean values were substituted for missing values in the analysis.

*Statistical Analysis.*—We fit the 12 models (Table 1) to the detection/nondetection data using the single-season occupancy estimation option in the program PRESENCE (version 2; James E. Hines, Patuxent Wildlife Research Center, Laurel, MD). The single season occupancy model provides estimates of detection probability and occupancy probability (MacKenzie et al., 2002) within the same modeling framework. For all analyses, detection probability was estimated uniquely for each survey method (transect vs. area search). We included air temperature (AIR) and precipitation (PRECIP) as covariates for each survey method and assumed the influence of these covariates was independent of survey method. The models were ranked by their AIC$_c$ scores (Akaike's Information Criterion) and weighted (AIC$_c$ weight) as the probability of being the best model in the model set (Burnham and Anderson, 1998).

Goodness-of-fit testing is necessary in occupancy modeling because models that do not "fit" the observed field data produce biased standard error estimates, thereby affecting inference. Goodness-of-fit testing for occupancy models consists of parametric bootstrap procedures to assess the adequacy of fit of a highly parameterized model in the model set (Burnham and Anderson, 1998; MacKenzie and Bailey, 2004).

TABLE 2. Model selection results of Eastern Newt probability of occurrence, depicting the fit of 12 alternative models to the observed field data collected in Vermont in 2003 and 2004.

| Model name | AICc | ΔAICc | AIC wgt | Model likelihood | No. par. |
|---|---|---|---|---|---|
| Amount 0.5 km | 569.63 | 0 | 0.9962 | 1 | 9 |
| Geographic position | 580.77 | 11.14 | 0.0038 | 0.0038 | 10 |
| Habitat change 5 km | 600.35 | 30.72 | 0 | 0 | 7 |
| Road 1 km | 603.57 | 33.94 | 0 | 0 | 7 |
| Housing 0.5 km | 612.82 | 43.19 | 0 | 0 | 6 |
| Arrangement 5 km | 615.96 | 46.33 | 0 | 0 | 6 |
| Road 5 km | 617.88 | 48.25 | 0 | 0 | 7 |
| Amount 5 km | 617.98 | 48.35 | 0 | 0 | 9 |
| Stand_less | 618.49 | 48.86 | 0 | 0 | 12 |
| Stand_more | 618.49 | 48.86 | 0 | 0 | 12 |
| Arrangement 0.5 km | 619.29 | 49.66 | 0 | 0 | 6 |
| Housing 5 km | 623.15 | 53.52 | 0 | 0 | 6 |

## RESULTS

*Salamander Surveys.*—A total of 232 Eastern Newts was detected at 82 of 551 stations. The ''naïve'' estimate of occupancy (the proportion of sites where salamanders were detected) was 0.14. Mean detections per station was 0.46. The highest count for a station was 34.

*Goodness of Fit.*—The bootstrap analysis indicated that the data fit the assumptions of single-season occupancy modeling (Burnham and Anderson, 1998; MacKenzie and Bailey, 2004; MacKenzie et al., 2006). The $X^2$ of the observed data was 1.01, and the mean $X^2$ of the bootstrap simulations was 2.81, resulting in an estimated overdispersion factor (''c-hat'') of 0.36. Given no evidence of overdispersion, we did not inflate the standard errors of parameter estimates in any analysis (Burnham and Anderson, 1998).

*Model Results.*—Of the 12 models, the top model was Amount 0.5 km with an AIC weight of 0.99 (Table 2). No other models were supported by the data ($\Delta$ AIC$_c$ > 10; Burnham and Anderson, 1998). Therefore, inferences about

which factors affected detection probability (the probability of detecting an Eastern Newt, given it was present on a site) and the probability that a station was occupied by an Eastern Newt were based only on results from the Amount 0.5 km model.

In terms of detection probability, the Amount 0.5 km model indicated that, given average air temperature and no rainfall, detection probability was 0.31 for area searches compared to 0.25 for transects. For both methods, detection increased as temperature increased, but precipitation within 24 h did not affect detection probability (Table 3).

In terms of station occupancy probability, the large degree of support for Amount 0.5 km indicated that habitat conditions surrounding a station were the best indicators of whether an Eastern Newt would be found at a randomly located station across Vermont. DEVELOPMENT and WATER had effects of great magnitude ($\beta_{DEVELOPMENT}$ = −7.38, $\beta_{WATER}$ = 4.41). FOREST also had a large, positive effect ($\beta_{FOREST}$ = 1.52, Table 3). WETLAND had a positive but relatively smaller effect ($\beta_{WETLAND}$

TABLE 3. Parameter estimates with corresponding standard errors (SE) and upper and lower confidence intervals from the model, Amount 0.5 km, obtained through maximum-likelihood analysis of Eastern Newt occupancy data collected in Vermont in 2003 and 2004. Cover types (percentage of habitat within 0.5 km of a survey station) represent forest (FOREST), wetland (WETLAND), open water (WATER), and development (DEVELOPMENT); percentages were transformed to standardized Z-scores for maximum-likelihood analysis.

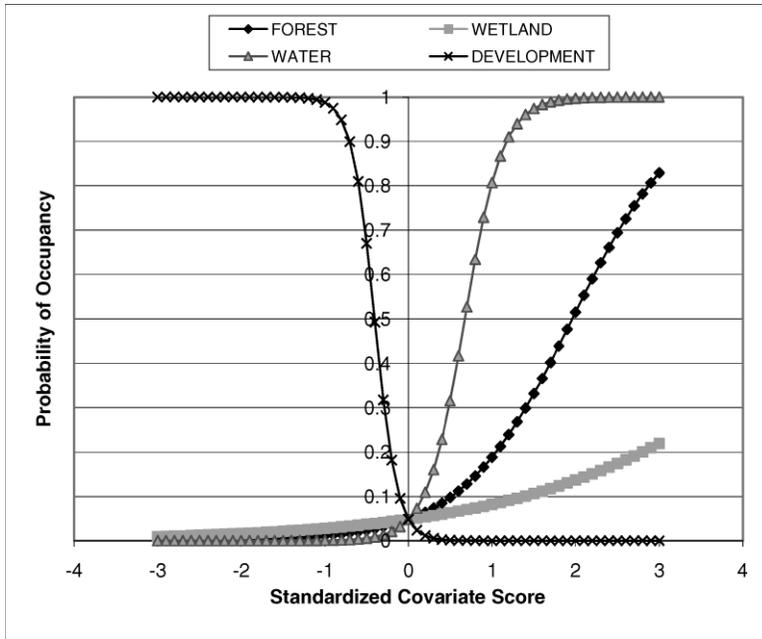| Parameter | β estimate | SE | UCI | LCI |
|---|---|---|---|---|
| Psi Intercept | −2.982 | 0.950 | −1.121 | −4.844 |
| FOREST_500 | 1.522 | 0.484 | 2.471 | 0.574 |
| WETLAND_500 | 0.570 | 0.285 | 1.128 | 0.012 |
| WATER_500 | 4.406 | 1.897 | 8.124 | 0.689 |
| DEVELOPMENT_500 | −7.383 | 3.288 | −0.938 | −13.827 |
| Intercept_AREA | −0.785 | 0.309 | −0.180 | −1.390 |
| Intercept_TRANSECT | −1.117 | 0.304 | −0.521 | −1.713 |
| PRECIPITATION | −0.122 | 0.301 | 0.468 | −0.712 |
| AIR TEMPERATURE | 0.487 | 0.163 | 0.807 | 0.167 |

Fig. 2. Independent effects of forest (FOREST), wetland (WETLAND), open water (WATER), and development (DEVELOPMENT) cover types on probability of occupancy based on parameter estimates from model Amount 0.5 km. Cover types values were percentages transformed to standardized Z-scores for maximum-likelihood analysis. The INT (intercept) line represents the ''average'' site, where all standardized covariates have $Z = 0$. The independent effects depict how a change in percent cover type will change probability of occupancy at a station when all other covariates exist at average station values.

$= 0.57$). In general, occupancy increased as FOREST, WETLAND, and WATER increased, and occupancy decreased as DEVELOPMENT increased (Fig. 2), suggesting that the amount of breeding and forest habitat within 500 m of a site is a factor controlling the distribution of this species at random locations across Vermont.

Although the analysis was conducted on standardized variables, one can use the mean and standard deviation of each variable (Table 4) to back-transform the Z-scores for more meaningful interpretation. In Vermont, the average percent forest (FOREST), wetland (WETLAND), open water (WATER), and development (DEVELOPMENT) across all survey stations was 75%, 2%, 1%, and 5%, respectively

(Table 4). With other landscape variables held constant at their average values, small increases in WATER (e.g., from 1–5%) resulted in a dramatic shift from 0.07–0.8 probability of occupancy, whereas small increases in WET-LAND (e.g., from 2–8%) resulted in a shift from 0.05 to 0.08 probability of occupancy. Thus, a relatively small amount of open water on the landscape appears to be needed for Eastern Newt occurrence.

Development had the opposite effect. With other landscape variables held constant at their average values, stations with ~5% DEVELOP-MENT had only a 0.05 probability of being occupied. Stations with higher levels of DE-VELOPMENT quickly led to zero probability of

TABLE 4. Summary statistics for variables in model Amount 0.5 km, including forest (FOREST), wetland (WETLAND), open water (WATER), and development (DEVELOPMENT) cover types within 0.5 km of a study site.

| | Mean | SD | Min | 1st quartile | Median | 3rd quartile | Max |
|---|---|---|---|---|---|---|---|
| FOREST | 75.05 | 32.95 | 0.00 | 56.82 | 93.24 | 98.85 | 100.00 |
| WETLAND | 2.24 | 5.92 | 0.00 | 0.00 | 0.00 | 1.83 | 60.94 |
| WATER | 0.74 | 4.13 | 0.00 | 0.00 | 0.00 | 0.00 | 63.57 |
| DEVELOPMENT | 4.98 | 14.72 | 0.00 | 0.00 | 0.00 | 0.86 | 97.71 |

occurrence. Thus, Eastern Newts appear to be very sensitive to any DEVELOPMENT within 0.5 km of a site.

DISCUSSION

The strongest effect on newt occupancy was from development and was negative. This is a useful finding from a conservation perspective. The relative imprecision of this estimate is caused by the low overall values of this variable across Vermont. Even at these low values, proximity to developed land cover essentially precluded newt occupancy. Most development in Vermont is currently taking place in agricultural and open lands. There was a moderate negative correlation between DEVELOPMENT and FOREST (rho = −0.61 at 0.5 km). DEVELOPMENT and agricultural lands (crops, orchards, hayfields, and pasture) were moderately correlated (rho = 0.55). Agricultural cover was not included in any models because of strong negative correlations with FOREST cover (|rho| > 0.76) and ELEVATION (rho = −0.67).

Interpretation of the effect of DEVELOPMENT and FOREST must include consideration that forest cover is largely the alternative to agricultural and open cover in Vermont. The positive effect of FOREST indicates open areas are inhospitable to newts. The effect of DEVELOPMENT could reflect the presence of otherwise open areas that might not have supported high newt occupancy regardless of the level of development. Nevertheless, land use and development by humans generally means creation of land cover types expected to be inhospitable to newts and the effects of this on the landscape of Vermont can only be expected to increase over time.

Although the model beta was large, the impact of increasing FOREST on probability of occupancy is not dramatic (Fig. 2). Two factors could account for this pattern. First, the study area was largely forested; hence, FOREST values vary little across occupied and unoccupied sites, diluting its effect in the analysis. The median value of FOREST was 93%, the median values of the other variables was 0% (Table 4), and FOREST varied the least of all variables (Table 4; Coefficient of Variation of FOREST = 0.44). Second, FOREST is not an exhaustive description of tree cover because WETLAND includes forested wetlands and other wetlands. It is possible that forested wetlands are a particularly important land cover type for Eastern Newts and that this effect is subsumed by the broader WETLAND category.

The effect of WATER was strong and positive. The vast majority of the newts sampled in this study were terrestrial efts. Open water bodies nearby could be breeding sources for the migratory efts that formed the majority of the sample. The models of arrangement of breeding and nonbreeding habitats, which evaluated the juxtaposition and interspersion of breeding and forest habitat, were not supported by the data. The prolonged duration of the eft phase allows efts to radiate widely, weakening a close link between detection location and natal waters, especially at this scale. Even so, increasing the amount of water (WATER) and wetlands (WETLAND) within 500 m of a station increased the probability of occupancy, regardless of how it is arranged with forest habitat in the landscape.

Measurements of changes in land cover between 1996 and 2001 did not predict occupancy. This is likely because Vermont experienced little change in breeding and nonbreeding habitat at our sampling locations between 1996 and 2001. Although urban and residential development is increasing in Vermont, the effect to date has been localized, with most of the change involving conversion of farmland to development land uses (Vermont Forum on Sprawl, 1999), a pattern unlikely to affect newts.

Forest stand metrics were not as important as in McKenny et al. (2006). Their study employed identical protocols to test the effects of forestry practice on the abundance of Eastern Red-Backed Salamanders (*Plethodon cinereus*) and was conducted in higher elevation, contiguous forests in northern Vermont. Their study sites were located within managed forests, resulting in little variation across sites other than stand-level attributes. Species-specific ecological differences could also account for these different results. Although Eastern Newts exploit many of the same conditions as Eastern Red-Backed Salamanders, the latter are more extensively subterranean and, therefore, could benefit more from subsurface conditions correlated to the stand conditions measured in that study. Eastern Red-Backed Salamanders are not toxic, and stand conditions may also provide cover from predators. Additionally, Eastern Red-Backed Salamanders do not require wetland/water for reproduction and are less likely than Eastern Newts to migrate or disperse long distances to carry out their water-dependent life cycle.

Eastern Newts appear common and widely distributed, but they go undetected by large-scale monitoring programs focused on vernal pools and call surveys. To better understand the landscape ecology of Eastern Newts in Vermont, a clearer picture of their true breeding habitat is required. This species is a good candidate for studying the effects of landscape-level processes on long-term metapopulation

dynamics (Cushman, 2006). Some subset of breeding sites likely supplies recruits for a larger area, but additional research will be necessary to determine whether breeding sites or terrestrial habitat that provides foraging sites, overwintering sites, and migratory linkages are more critical for determining distribution throughout the landscape. Eastern Newts appear to be adapted to shifting aquatic habitats such as beaver impoundments (Gill, 1978). The processes affecting breeding site productivity and how such productivity is related to surface water availability, distribution, and persistence (e.g., fewer beavers, more artificial ponds) may offer some insight into key processes affecting newt distribution. Further occupancy studies of Eastern Newts in Vermont could allow the measurement of patterns of colonization and abandonment. Such information would help to elucidate key processes and increase our understanding of the impacts of future land-use change on this species.

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