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# The effects of vegetation density and habitat disturbance on the spatial distribution of ixodid ticks (Acari: Ixodidae)

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**Abstract.** Larval, nymphal, and adult *Amblyomma americanum* (L.), and adult *Dermacentor variabilis* (Say) ticks were collected using timed dragging techniques, in an attempt to examine how different habitat variables affect models that describe the distribution of ticks in Virginia, USA. Tick count data were modeled using two approaches: (i) habitat and edge, and (ii) habitat, edge, vegetation density and levels of disturbance. Nymphs and adults tended to follow a forest edge distribution when analysed by habitat and edge. Using all variables, we detected a positive relationship with forest edges and negative associations with high-density vegetation. When larvae were modeled by habitat and edge, we failed to detect associations with the edges of habitats. When all variables were included in the larval analysis, disturbed meadow edges emerged as important in the first year, and the categories of disturbed and maturing habitat in the second year. Vegetation density and levels of disturbance were marginally important towards explaining the distribution of nymphs and adults; however, levels of disturbance were potentially more important to the distribution of larvae, than habitat types. Using the habitat and edge variables, and predicted mean encounter rates for all stages of *A. americanum* and adult *D. variabilis*, we successfully cross-validated our predictions of high, moderate and low tick densities in both years. The results for nymphs and adults were combined to develop a colour-coded threat assessment map. We estimated that the majority of ticks were located on ~ 20% of the landscape. The potential uses of geographical information system-based threat maps are discussed.

**Keywords:** ixodid ticks, geographical information system, habitat characterization, spatial distribution, predictive modeling.

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## Introduction

Upon completion of feeding, most ixodid ticks detach from their hosts, drop to the ground and eventually molt to the next stage. If these ticks happen to be gravid females, they will ultimately deposit eggs, which hatch into larvae. Whether completing a molt or hatching from an egg, there is much evidence suggesting that ticks seek hosts not far from their original locations on the landscape (Sonenshine et al., 1966, 1995; Wilson et al., 1972;

Daniels and Fish, 1990; Falco and Fish, 1991; Bunnell et al., 2003). In the interim, however, their survival depends on their ability to avoid desiccation, excessive moisture, and predators and parasites. Because ticks spend a small proportion of their lives attached to hosts (Norval, 1974; Sonenshine, 1993), the location of ticks in an ecosystem, indeed, where they survive, is a measure of habitat suitability (Estrada-Peña and Venzal, 2007).

The distribution of ticks on the landscape follows that of many organisms (Giles, 1978); higher densities are typically found along the edges or ecotones (Semtner et al., 1971b; Sonenshine, 1993). These ecotones are the confluence of two habitats, and are composed of both pioneer and older plant communities. Pioneer plant communities grow rapidly, often forming dense thickets that provide food and shelter for tick hosts, including, mammals, birds and

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reptiles. Some sections of these thickets act as permeable boundaries, impeding or allowing host movement to other habitats. Accordingly, if animal hosts spend more time in ecotones than other areas on the landscape (Leopold, 1933), and if there are permeable sections of these linear features of the landscape, then the numbers of detached and/or questing ticks should be concentrated in these zones.

In recent years, a number of researchers have modeled the intricate relationships among ixodid ticks, their hosts, and various aspects of their environment. These studies have been conducted along a continuum ranging from small scale, microhabitat-based models (Semtner et al., 1971a; Petney and Bull, 1984; Klomp and Bull, 1987; Chilton and Bull, 1993; Daniel and Dusbábek, 1994; Slowik and Lane, 2001) to large scale, landscape-based models (Semtner et al., 1971b; Semtner and Hair, 1973; Koch, 1984; Haile and Mount, 1987; Ostfeld et al., 1995, 1996a,b). For the latter, many of these include data that have been derived from remotely-sensed imagery (Glass et al., 1995; Nicholson and Mather, 1996; Bunnell et al., 2003). Developing small or large-scale vector population models is both difficult and labor-intensive. These difficulties span several disciplines and include field collections, habitat quantification (Daniel and Dusbábek, 1994), and validating models that have been developed from remotely-sensed images. Additional problems stem from the limitations of equipment, and data interpretation issues related to scale, habitat heterogeneity, and oftentimes, a paucity of data (Nicholson and Mather, 1996; Van Buskirk and Ostfeld, 1998; Kitron, 2000). Clearly, there is a critical need for developing modeling techniques that measure how tick populations respond to site specific factors, especially techniques that can be used for both small and large-scale predictions.

Herein we report on methods that classify a large, ecologically diverse area into a reduced number of quantifiable habitats, including their structure and ecological characteristics. This framework was then used to model and eventually predict the combined distributions and densities of the American dog tick

*Dermacentor variabilis* (Say), and the lone star tick *Amblyomma americanum* (L.). *D. variabilis* is a widely distributed vector of Rocky Mountain spotted fever (Sonenshine, 1993), human monocytic ehrlichiosis (Schulze et al., 2006) and has been implicated as the primary vector of tularemia (Hopla and Hopla, 1994). *A. americanum* is the primary vector of human monocytic ehrlichiosis (Lockhart et al., 1997), and is also a vector of tularemia (Hopla and Hopla, 1994). *A. americanum* has also been implicated in the transmission of southern tick-associated rash illness (STARI), that results in a clinical condition similar to Lyme disease, and is caused by *Borrelia lonestari* (Burkot et al., 2001; Childs and Paddock, 2003).

In Virginia, *A. americanum* nymphs and adults, and *D. variabilis* adults attain their maximum numbers in mid-summer. This season coincides with outdoor military training exercises, civilian recreational activities, and when personnel are most likely to encounter ticks. Although there exists a variety of measures for personnel to reduce exposure to ticks, compliance with these is poor (Gambel et al., 1998). We developed this research, in part, to develop methods for Fort Pickett Maneuver Training Center (Blackstone, Virginia, USA) personnel to identify areas with high threats from tick-borne diseases.

## Materials and methods

### *Site selection and characterization*

We conducted our study at Fort Pickett Maneuver Training Center, an 18,200 ha military training center near the town of Blackstone, Virginia. Fort Pickett lies on the Piedmont Plateau physiographic province and holds a variety of habitats. We condensed these into five categories: including, (i) forest, (ii) young woodland, (iii) meadow, (iv) wetland, and (v) thicket. The species of vegetation and the characteristics for each habitat category are detailed in Table 1. Forests consisted mostly of hickory (*Carya* spp.), oak (*Quercus* spp.) and maple (*Acer* spp.), and were characterised by the presence of a

Table 1. Vegetation classification at Fort Pickett, VA<sup>a</sup>, USA.

Habitat	Species
Forest	Canopy: hickory ( <i>Carya</i> spp.), northern red oaks ( <i>Quercus rubra</i> L.), sugar maple ( <i>Acer saccharum</i> Marsh.), sweet gum ( <i>Liquidambar styraciflua</i> L.), tuliptree ( <i>Liriodendron tulipifera</i> L.), white oak ( <i>Q. alba</i> L.); including loblolly pine ( <i>Pinus taeda</i> L.) and Virginia pine ( <i>Pinus virginiana</i> Mill.) when mixed forest. Understory: blueberry ( <i>Vaccinium corymbosum</i> L. and <i>V. angustifolium</i> Ait.), cherries ( <i>Prunus</i> spp.), dogwood ( <i>Cornus florida</i> L.), holly ( <i>Ilex</i> spp.), mountain laurel ( <i>Kalmia latifolia</i> L.).
Young woodlands	Sweetgum, tuliptree, red maple ( <i>Acer rubrum</i> L.), loblolly pines, sassafras ( <i>Sassafras albidum</i> Nutt.), oaks.
Meadows	Big bluestem ( <i>Andropogon gerardii</i> Vitman), little bluestem ( <i>Schizachyrium scoparium</i> Michx. (Nash)), bushy bluestem ( <i>A. glomeratus</i> Walt.), Virginia broomsedge ( <i>A. virginicus</i> L.), switchgrass ( <i>Panicum virgatum</i> L.), white clover ( <i>Trifolium repens</i> L.), goldenrod ( <i>Solidago</i> spp.), Lespedeza ( <i>Lespedeza bicolor</i> Turcz. and <i>L. cuneata</i> (Dumont)), spotted knapweed ( <i>Centaurea maculosa</i> Lam.).
Wetlands	Grasses and sedges, buttonbush ( <i>Cephalanthus occidentalis</i> L.), meadow beauty ( <i>Rhexia virginica</i> L.), smooth alder ( <i>Alnus serrulata</i> (Ait.) Willd.), sycamores ( <i>Platanus occidentalis</i> L.), various wetland asters ( <i>Eupatorium</i> spp.), willows ( <i>Salix</i> spp.).
Thickets	Brambles ( <i>Rubus</i> spp.), catbrier ( <i>Smilax</i> spp.), elderberry ( <i>Sambucus canadensis</i> L.), poison ivy ( <i>Toxicodendron radicans</i> (L.) Kuntze), Russian olive ( <i>Eleagnus angustifolia</i> (L.)), winged sumac ( <i>Rhus copallina</i> L.), blueberry, saplings, including: red maple, sweet gum, tuliptree, oak.
Ecotone/edge	Early-succession complexes of the above species that characterise thickets: brambles, catbrier, poison ivy and winged sumac.

<sup>a</sup>Climax community at Fort Pickett consists of oak, hickory, and pine forests (Braun, 1950).

canopy and an understory. Young woodlands did not contain an understory but possessed the above species, including loblolly pine (*Pinus taeda* L.) and sweetgum (*Liquidambar styraciflua* L.). Meadows contained many species of vegetation and chief among these were bluestem grasses (*Andropogon gerardii* Vitman, *A. glomeratus* Walt., and *Schizachyrium scoparium* Michx. (Nash)), switchgrass (*Panicum virgatum* L.), clover (*Trifolium* spp.), goldenrod (*Solidago* spp.), Lespedeza (*Lespedeza* spp.) and knapweed (*Centaurea maculosa* Lam.). Wetlands possessed many grasses and sedges, asters (*Eupatorium* spp.), buttonbush (*Cephalanthus occidentalis* L.), smooth alder (*Alnus serrulata* (Ait.) Willd.), sycamores (*Platanus occidentalis* L.) and willows (*Salix* spp.). Thickets were a transitional stage for late successional meadows, with extensive numbers of brambles (*Rubus* spp.), catbrier (*Smilax* spp.), poison ivy (*Toxicodendron radicans* (L.) Kuntze), Russian olive (*Eleagnus angustifolia* (L.)), winged sumac (*Rhus copallina* L.) and various saplings, especially maples and sweetgum. Ecotones or edges consisted of many early-suc-

cessional complexes of the above species and many thicket species; including, brambles, catbrier, poison ivy and winged sumac.

For our study, we selected three primary habitats, three complementary ecotones and one wetland edge habitat (Table 2). We classified edges for each habitat based on noticeable changes in the composition of plant communities. Although each member of the edge pair can be variable in length, width and height, we reported the average ecotonal width used throughout our investigation (Table 2). As ticks are rarely found on aquatic and emergent wetland vegetation, we restricted our sampling to the shoreline. Likewise, we did not sample from the interior of thickets as we considered these impenetrable. During the first year of our investigation, we began to suspect that tick presence varied with (i) vegetation density, and (ii) levels of disturbance among habitats. Accordingly, we gradually introduced these two categories of data collection into our sampling sites during the first year. Since the first year of collecting involved a fixed number of sites, this procedure involved reclassifying all sites in mid-summer using the characteristics in Table 2.

Vegetation density categories (Table 2) are modified from Semtner et al. (1971b).

### *Tick collections and sampling methodology*

In both years, we visited Fort Pickett every three weeks, beginning in mid-May and through mid-September. During the first year of our study, we collected ticks from 21 fixed sites, three of which were eventually destroyed by bulldozers and other heavy vehicles. We visited each site ten times ( $n = 180$ ) and randomised collections among sites such that we did not follow the same site order with each visit. We collected ticks for three consecutive days using 1 m<sup>2</sup> white muslin tick drags and timed our walks for 10 min with a stopwatch. Within this period, an individual walking at a normal pace can easily cover the distance of ~ 0.75 - 1.0 km. We checked tick drags every 12-15 steps, and more fre-

quently when vegetation was dense. Upon capture, we placed ticks in coded vials for eventual identification in the laboratory. We removed ticks from clothing at the end of each timed collection and counted these in our study. When collectors were overwhelmed with large numbers of tick larvae, and occasionally, large numbers of nymphs, the specimens were rapidly removed from the tick drag with lint rollers (Evercare Inc., Waynesboro, GA, USA) and placed inside sealable plastic sandwich bags. We characterised habitats, identified plant species and the level of succession at each site, whether these locations were positive for ticks or not. We did not attempt to collect ticks when vegetation was wet from rain or heavy dew.

With respect to tick collection in the first year, we had three objectives:

- (i) to develop baseline data;
- (ii) to generate presence/absence models; and

Table 2. Habitat classification at Fort Pickett, VA, USA, including structure, characteristics, vegetation density and disturbance<sup>a</sup>.

Habitat/ecological zone	Structure and characteristics
Forest	Unfragmented, minimal disturbance, developed canopy and understory, pioneer communities absent, >8 m from edges of other habitats or road.
Forest edge	Fragmented, disturbed, barrier-like, pioneer communities present, contiguous with adjacent habitat edges, <8 m into forest.
Young woodlands	Unfragmented, saplings to medium size trees, no canopy or understory, grasses and forbs present, >4 m from edges of other habitats or road.
Young woodland edge	Fragmented, saplings to medium size trees, no canopy or understory, grasses and forbs present, contiguous with adjacent habitat edges, <4 m into young woodland.
Meadows	Unfragmented, grasses and forbs, saplings and thickets absent, >2.5 m from edges of other habitats or road.
Meadow edge	Fragmented, grasses and forbs, saplings and thickets present, contiguous with adjacent habitat edges, <2.5 m into meadow.
Wetland edge	Variable structure, wetland vegetation, <4.5 m from water, edges of other habitats and roads.
Vegetation density	
Low density	0 - <25% coverage: bare ground is apparent in all habitats, or covered with pine needles and leaf litter, few grasses, forbs and saplings.
Moderate density	25-75% coverage: bare ground is absent in all habitats, can walk through all habitats easily.
High density	>75% coverage: grasses, forbs, saplings and shrubs in all habitats; all habitats require much effort to walk through.
Disturbance	
Disturbed	Evidence of human-related disturbances, heavy deer use/browsing and storm damage.
Undisturbed	Few recent disturbances, appearance is characteristic for habitat, transitional vegetation is rare or absent.
Maturing	Transitional stage, most vegetation is early successional, almost ecotonal.
Near-pristine	Similar to undisturbed, with no observable disturbances.

<sup>a</sup>Climax community at Fort Pickett consists of oak, hickory and pine forests (Braun, 1950).

(iii) to develop tentative predictions for population densities.

The latter was of particular importance as we sought to model tick distribution as a function of habitat, vegetation density, and levels of disturbance as in Table 2. The primary objective for the second year collections was to cross-validate the count data predictions that we developed during the first year. Accordingly, the second year collections were unique insofar as we sampled each of 136 sites once, and spent 350 min in each of the seven habitat/edge categories listed in Table 2.

### *Modeling techniques*

We modeled all tick count data using generalized estimating equations (GEE) with the GENMOD procedure of SAS (SAS, 1998). Four indicator variables, including forest, young woodland, meadow and the primary (non-edge) aspects of the habitat, were used to model adults, nymphs and larvae by habitat/ecological zone. When these models, included vegetation density and levels of disturbance, the additional indicator variables consisted of high and low density and disturbed, undisturbed and maturing, respectively. We chose baseline values as follows: wetlands for habitat, edge for ecological zone, moderate for vegetation density, and near-pristine for level of disturbance. Because of the near similarity between the undisturbed and near-pristine levels of disturbance, we conducted an additional test after combining these categories as a separate baseline value. When the model coefficients were both significant and negative, this impacted the model by lowering the corresponding prediction.

Parameters having P-values greater than 0.10 were removed from the final model using a backwards variable selection method.

Adults and nymphs followed a Poisson distribution with a log link function. We modeled *A. americanum* larvae differently due to the large variability in larvae counts. When *A. americanum* larvae attach to a tick drag, they typically attach in clumps that number in the hundreds, minimally in the tens.

Accordingly, we categorized larvae in two groups; they were assigned a value of 1 if the count was  $\geq 1$ , otherwise they were assigned a 0. Larvae were modeled using a binomial distribution with a logit link. Wald chi-square tests were used to determine whether a parameter differed significantly from zero.

We used the FREQ procedure (SAS, 1998) to cross-validate the count data predictions for both years (Kleinbaum et al., 1998), basing our predictions on the numbers of ticks expected within a 10 min collection period. For nymphs and adults we set cut-off points as follows: 0-1 ticks = low; 2-4 ticks = moderate; and  $>4$  ticks = high. For larvae we used the following criteria: 0-1 ticks = low; 2-10 ticks = moderate; and  $>10$  ticks = high. Predictions for the adults and nymphs were calculated by raising  $e$  to the sum of the products of corresponding coefficients and indicator variables. Predictions for the larvae were calculated by setting the logit equal to the sum of the products of corresponding coefficients and indicator variables.

We report on two sets of results for count data predictions, and refer to these as predicting and conditional predicting. The former resulted from the correct matching of observed counts with the expected categories of low, moderate, and high. The latter included the correctly matched counts as above, and the values that resulted from predicting high, and observing low and moderate and predicting moderate, and then observing low. Conditional predicted values provide conservative estimates resulting in a "maximum" level of threat, albeit this threat level may be significantly higher than the actual surroundings. We used the chi-square test of independence and the likelihood ratio chi-square test (Agresti, 2002) to determine whether a relationship existed between the observed and expected categories (high, moderate and low).

### *Geographical information systems (GIS)*

Throughout this investigation, we wanted to develop criteria that made sense for personnel in the field, and accordingly, we did not test other cut-off points.

Our moderate thresholds for adults agree with mean encounter rates for *A. americanum* of 1.8 adults per 10 min (11 per hour) reported by Stromdahl et al. (2000). We used a digital orthophoto and a digital vegetation layer (Morton, 1998) for delineating all habitats. We also recorded habitat data on site with a global positioning system (GPS), to modify habitat categories that were either not included, or may have differed from the above database. We combined all significant habitat variables and count data predictions, and represented these as colour-coded threat polygons. All polygons were created within the GIS by a technique of buffering the boundaries between habitats based on distance (Table 2) using ArcGIS 9.1 (ESRI Inc., Redlands, CA, USA), with an onscreen display scale of 1:2000. The Arcview query function was used to estimate the area of each threat polygon as a percentage of the total map area.

## Results

We collected two tick species during our study, *A. americanum* and *D. variabilis*; larvae, nymphs and adults of the former, and adults of the latter. We analysed both adult species separately before combining our results in Tables 3 and 4. In 1998, the GEE model predicted high, moderate and low categories for *D. variabilis*. The same model only predicted the low category for *A. americanum* at all 18 sites, despite some counts in the moderate and high categories. When we combined both species the model correctly predicted high, moderate and low categories, in both years. The results in Table 3 describe tick models as a function of habitat and edge. The results presented in Table 4 contain these same variables and include the effects of vegetation density and disturbance.

In both years, forest edges were important to the distribution of adults and nymphs (Table 3), and several relationships emerged when vegetation density and disturbance were included in the model. Forests became the predominant habitat for adults and nymphs, and we detected significant negative relationships with high-density vegetation in three

of four analyses (Table 4), excepting adults in 1998. Edge remained a significant independent variable in all analyses, except for nymphs in 1999, when it was replaced by significant negative relationships with high-density vegetation, and both disturbed and undisturbed habitats (Table 4). Reciprocally, nymph distributions followed low-to-moderate density vegetation in maturing forests. The analyses for adults in 1999 revealed significant associations with all levels of disturbance, which suggest an equal distribution among these categories (Table 4). A summary of the results presented in Tables 3 and 4, suggests that nymphs and adults tend to “prefer” forest edges, and both “avoid” high-density vegetation.

Distributions of *A. americanum* larvae differed from those of the adults and nymphs. In both years, *A. americanum* larvae were significantly associated with the primary aspects of forests and meadows, including young woodlands in 1999 (Table 3). These results changed when all variables were included in the model (Table 4). We report significance for both years, the categories of meadow edge and disturbed in 1998, and disturbed and maturing in 1999.

For the ticks collected in 1998, our observations matched the predictions for the categories of low, moderate and high, using the FREQ procedure as follows: for adults (69%), nymphs (67%) and larvae (43%). We obtained slightly different results using conditional predicting. All values increased, for adults (78%), nymphs (90%), and larvae (98%). For the ticks collected in 1999, our observations matched the categories of low, moderate and high; for adults (58%), nymphs (68%) and larvae (48%). When we included conditional predictions as above, all values increased for adults (78%), nymphs (95%) and larvae (98%). When we compared the observed and expected categories of high, moderate and low, the chi-square test of independence yielded significant results for all stages: adults (chi-square = 26.89; df = 4;  $P < 0.001$ ), nymphs (chi-square = 42.40; df = 4;  $P < 0.001$ ), and larvae (chi-square = 6.78; df = 4;  $P = 0.037$ ). Additional analyses using the likelihood ratio chi-square test produced similar, low P-values.

Combining the undisturbed and near-pristine levels of disturbance and then testing these as a single baseline value produced the following results. For the ticks collected in 1998, our observations

matched the predictions for the categories of low, moderate and high as follows: for adults (80%), nymphs (74%) and larvae (59%). We obtained mixed results using conditional predictions. The val-

Table 3. Significant values for all stages of *A. americanum* and adult *D. variabilis* ticks when modeled by habitat and ecological zone.

Year	Stage	Forest (SEM*)	P-value	Young woodland <sup>a</sup> (SEM*)	P-value	Meadow (SEM*)	P-value	Primary <sup>b</sup> (non-edge) (SEM*)	P-value
1998	Adults	0.858 (0.158)	<0.001					-0.741 (0.297)	0.013
	Nymphs	3.120 (0.757)	<0.001	-1.071 (0.403)	0.008	-0.666 (0.240)	0.006	-1.785 (0.898)	0.047
	Larvae	1.386 (0.437)	0.002			2.197 (0.786)	0.005		
1999	Adults	1.556 (0.169)	<0.001	0.953 (0.245)	<0.001	0.976 (0.215)	<0.001	-1.336 (0.284)	<0.001
	Nymphs	1.691 (0.195)	<0.001					-0.728 (0.308)	0.018
	Larvae	2.849 (0.481)	<0.001	1.981 (0.427)	<0.001	3.738 (0.810)	<0.001		

<sup>a</sup>An empty cell indicated that the parameter associated with this variable had a P-value larger than 0.10, and was removed from the final model; <sup>b</sup>negative coefficients indicate a non-preference for habitat and/or ecological zone; \*standard error of the mean.

Table 4. Significant values for all stages of *A. americanum* and adult *D. variabilis* ticks when modeled by habitat, ecological zone, vegetation density and level of disturbance.

Year	Stage	Variables <sup>a</sup>	Coefficients <sup>b</sup>	SEM*	P-value
1998	Adults	Forest	1.246	0.327	<0.001
		Primary (non-edge)	-1.061	0.424	0.012
	Nymphs	Forest	5.740	3.086	0.065
		Primary (non-edge)	-1.256	0.687	0.067
		High density	-1.986	0.939	0.035
	Larvae	Meadows	1.974	0.826	0.017
		Primary (non-edge)	-1.692	0.759	0.026
		Disturbed	2.187	0.578	<0.001
	1999	Adults	Forest	0.603	0.219
Primary (non-edge)			-1.327	0.271	<0.001
High density			-0.661	0.275	0.016
Disturbed			1.040	0.182	<0.001
Maturing			1.081	0.214	<0.001
Undisturbed			1.175	0.031	<0.001
Nymphs		Forest	3.681	0.272	<0.001
		High density	-2.164	0.536	<0.001
		Disturbed	-2.325	0.320	<0.001
		Undisturbed	-2.326	0.536	<0.001
Larvae		Disturbed	3.541	0.502	<0.001
		Maturing	2.32	0.367	<0.001

<sup>a</sup>Parameters and variables having a P-value larger than 0.10 were removed from the final model; <sup>b</sup>negative coefficients indicate a non-preference for habitat, ecological zone, density, or disturbance; \*standard error of the mean.

ues for adults were the same (80%), and the values for nymphs (89%) and larvae (100%) were higher. For the ticks collected in 1999, our observations matched the categories of low, moderate and high; for adults (62%), nymphs (76%) and larvae (39%). When we included conditional predictions as above, the values for adults were the same (62%), and those for nymphs (88%) and larvae (97%) were higher. The similarity between the test data (1999) and training data (1998) percentages, validates the models that were developed from both the near-pristine and undisturbed/near-pristine baselines.

The above analyses for nymphs and adults were depicted as threat polygons in a 24 ha region of Fort Pickett, known as the Twin Lakes area (Fig. 1). We did not attempt to map larvae since the results were not consistent between analyses. Queries for each edge polygon produced the following results that were expressed as percentages: high threat forest edge (red) 14.4%; moderate threat meadow edge (orange) 3.6%; and low threat wetland edge (yellow) 1.5%. When combined, these polygons represent 20% of the mapped area.

## Discussion

The spatial distributions that we report for *A. americanum* and *D. variabilis* nymphs and adults are consistent with the body of literature (Semtner et al., 1971b; Sonenshine and Levy, 1972; Campbell and Mackay, 1979). In addition, Semtner et al. (1971b) suggested that tick distributions were largely influenced by movements of white-tailed deer *Odocoileus virginianus* Zimmerman, the primary host for all stages of *A. americanum* among different geographical locations (Patrick and Hair, 1979; Bloemer et al., 1988). It has been reported that deer spend much of their time associated with ecotones (Bartlett, 1938), although radio-telemetry studies involving deer have subsequently revealed daily and seasonal variation among regional populations.

There exists a working hypothesis that movements of vertebrate hosts, determine the distribution of ticks (Estrada-Peña, 2002; Bunnell et al., 2003).

Semtner and Hair (1973) reported that the locations where engorged *A. americanum* females and nymphs have detached from deer in the spring and early summer will determine the distribution of larvae later that summer and adults the following spring. It is not as easy to comprehend the distribution of *D. variabilis* as a function of host movements, since it has several principal hosts, including mice, voles, chipmunks and rabbits. The edge-related ecology of these mammals has been well-studied, and one can envision much interaction with the edges of meadows, forests and wetlands. In the absence of distribution studies, however, it seems reasonable to suggest that the locations where ticks detach from their hosts or deposit their eggs is random within host-occupied areas, thus, proportional to the area of each habitat type.

Our attempts to identify additional relationships by including vegetation density and disturbance in our model produced mixed results and consistent patterns were not apparent. The significant negative relationship with high-density vegetation for nymphs and adults in three of four analyses indicates that, perhaps, tick hosts did not frequently use these areas, or these areas were not conducive to survival. For nymphs in 1999 (Table 3), our findings suggest that densities in maturing habitats were similar to densities in ecotonal or edge-like habitats, or those habitats in a transitional stage (Table 2). So, for this analysis, the maturing category may be equivalent with edge. Although the inclusion of the above variables revealed additional relationships or probable trends, these may be of minimal importance to the population. The most apparent changes observed in this study concerned distributions of *A. americanum* larvae. The replacement of primary habitats with the categories of edge and disturbed in 1998, and disturbed and maturing in 1999, suggests that disturbed and maturing habitats are potentially more important to the distribution of larvae than the primary aspects of habitats. Thus, habitats having these qualities must be related to either larval survival or attraction to the host of adult treks (e.g. deer) on which the adults feed, and then lay eggs from which larvae hatch.





Fig. 1. The spatial distribution of nymph and adult *A. americanum* and adult *D. variabilis* based on models and cross-validated count models over a 2-year period. Colours indicate the following tick densities: red - forest edge, high density; orange - meadow edge, moderate density; yellow - wetland edge, low density. Total area for predictions is 24 ha with an onscreen resolution of 1:2000.

In attempting to predict the presence of ticks on the landscape, we hypothesized that where we failed to collect ticks, hosts had never used these areas or tick mortality was very high. Koch (1984) reported that *A. americanum* eggs did not survive in meadows and that larval mortality was greatest in these areas. In Virginia, Sonenshine et al. (1966) compared the distribution of *A. americanum* among four vegetation classifications, and reported that tick densities were lowest in meadow habitats. Similarly, Semtner et al. (1971a) reported that tick survival was lowest in meadow habitats, and attributed the causes to high night-time humidity and low daytime humidity. These reports are convincing, and could suggest that the egg and larval stages of ticks are more affected by microclimatic factors than are nymphs and adults. Once these regulating factors have exerted their influence on the population, then suitable microhabitats would determine survival for the population. Perhaps in time, the population of nymphs and adults would give the appearance of

migrating toward edges, when in fact there is a change in proportionate abundance with greatest losses occurring in the least favorable habitats. Surviving ticks would be located in edges or in disturbed or transitional-type patches that possess optimal microclimatic conditions.

In addition to the above, our significant cross-validation of models that predict high, moderate and low counts of ticks by habitat characteristics and time extend those of the literature. Bunnell et al. (2003) predicted presence of *Ixodes scapularis* Say within 86% of their study locations in five states, and Estrada-Peña (2002) predicted varying patch densities for *I. ricinus* in Spain. Our study demonstrated that a significant part of the tick population occupies ~ 20% of the map area, with the highest predicted counts for nymphs and adults associated with forest edges, an area comprising 14.4% of the total map area. These percentages agree with those reported by Goddard (1997). Although some part of the population exists away from the edges, we believe that the

high threat zones possess important qualities for maintaining the population.

Although our predicted counts were not exact, the results were significantly similar between years, and between types and edges. We also observed similar, even slightly better results after combining the two levels of disturbance into a single baseline value. These results suggest that minor visible differences among levels of disturbance can effect the predictions of a model. Accordingly, we believe that our methods present a useful approach for developing similar models that involve ticks or other disease vectors on the landscape. Threat maps (Fig. 1) have several potential uses, chief of which includes identifying high threat zones for the judicious application of acaricides. The benefits of precisely targeting insecticides are well-known, especially, reducing costs and toxic substances in the environment. Threat maps could also serve as a guide for landscape management. In this case, certain areas on the landscape could be modified such that they would not be conducive to tick survival (Haile and Mount, 1987; Mount et al., 1999). Finally, we believe that these maps could serve as a guide for people to avoid tick-infested areas. In various parks across the United States, and on numerous military installations, personnel have access to brochures or training aids that assist with identifying poisonous plants, snakes and insects. Viewing, printing and distributing a graphic such as our threat map has the potential to serve as a similar, personnel protection aid.

In the present study, we demonstrated the effects of including vegetation density and levels of disturbance in predictive models that describe tick distributions. The former was marginally important to the distribution of nymphs and adults. However, the latter clearly illustrated that levels of disturbance, or stages of succession, are potentially more important to the larval population than is the vegetation community. Vegetation maps are increasingly being used by personnel on public-use and military lands, and vegetation density is one of the factors that can be rapidly extracted from georeferenced databases. Levels of disturbance are a qualitative measurement

that can be assessed on site, and thus, need to be implemented both systematically and consistently, as was done throughout this investigation. Future vector population modeling investigations will probably include other qualitative categories that, *a priori*, might seem unimportant to the vector or the host population. Perhaps these remain undetected because of the problems that arise from scale or habitat heterogeneity, as well as the tendency for statistically significant parameters to mask their effects. More complex sampling procedures and analytical techniques than those used in this study will probably result in our ability to predict tick densities among habitat patches that vary in quality. Accordingly, we need to focus on the movements of ticks during each life stage, the movements and behaviour of their mammalian hosts and develop better tick sampling methodology. Campbell and Mackay (1979) have suggested using a combination of techniques, including radio-telemetry of mammals, and radioisotope tagging of ticks (Sonenshine, 1993). These techniques are labor intensive, and one can easily imagine the difficulties involved with data interpretation; however, the data resulting from tick and host movements are critical for determining patch size. When this information is combined with newer, high-resolution remotely-sensed images and recent vegetation/habitat maps, we will then have the capacity to develop threat and risk maps that accurately predict the probable locations of vectors and the diseases that they transmit.

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