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Influence of habitat attributes on density of Virginia opossums (*Didelphis virginiana*) in agricultural ecosystems

William S. Beatty, James C. Beasley, Zachary H. Olson, and Olin E. Rhodes, Jr.

Abstract: In agriculturally fragmented ecosystems, mesopredators play dominant roles in food webs through scavenging. We examined the influence of habitat attributes associated with carrion on local Virginia opossum (*Didelphis virginiana* Kerr, 1792) density in an agricultural landscape. We conducted opossum mark–recapture in 25 forest patches from 2005 to 2010, which represented the most extensive sampling of opossums to date. We analyzed mark–recapture data with a closed robust design and evaluated effects of landscape features linked to carrion on opossum density and female opossum density with generalized linear mixed-effects models. We included landscape-level (1481.6 m buffer) and patch-level covariates linked to carrion in addition to other covariates associated with high opossum densities. We developed a set of 19 candidate models and examined model fit with Akaike's information criterion. The top model for opossum density included the density of adjoining roads, whereas the top model for female density included patch size, although the statistical null was a competing model in both cases. The long-distance dispersal capability and generalist diet of the opossum likely precluded us from detecting a definitive relationship between covariates and opossum density. The scale of effect for opossum density in agriculturally fragmented landscapes is likely larger than the spatial scales examined here.

Key words: agriculture, abundance, density, *Didelphis virginiana*, fragmentation, generalized linear mixed models, Indiana, Poisson distribution, robust design, Virginia opossum.

Résumé : Dans les écosystèmes fragmentés par l'agriculture, les mésoprédateurs jouent des rôles dominants dans les réseaux trophiques par l'entremise du comportement détritivore. Nous avons examiné l'influence d'attributs de l'habitat associés à la charogne sur la densité locale d'opossums de Virginie (*Didelphis virginiana* Kerr, 1792) dans un paysage agricole. Nous avons réalisé le marquage et la recapture d'opossums dans 25 parcelles boisées de 2005 à 2010, ce qui représente le plus important échantillonnage d'opossums à ce jour. Nous avons analysé les données de marquage-recapture en utilisant une conception robuste avec fermeture et évalué les effets d'éléments du paysage associés à la charogne sur la densité des opossums et la densité des opossums femelles à l'aide de modèles linéaires généralisés à effets mixtes. Nous avons inclus des covariables à l'échelle du paysage (zone tampon de 1481,6 m) et de la parcelle associées à la charogne, en plus d'autres covariables associées à de fortes densités d'opossums. Nous avons élaboré un ensemble de 19 modèles possibles et examiné leur calage à l'aide du critère d'information d'Akaike. Le meilleur modèle pour la densité d'opossums incorpore la densité de chemins environnants, alors que le meilleur modèle pour la densité des femelles inclut la taille de la parcelle, bien que l'hypothèse statistique nulle constitue un modèle concurrent dans les deux cas. La capacité de dispersion sur de longues distances et l'alimentation généraliste de l'opossum nous empêchent probablement de déceler une relation définitive entre les covariables et la densité d'opossums. L'échelle effective de la densité d'opossums dans les paysages fragmentés par l'agriculture est vraisemblablement plus grande que les échelles spatiales examinées dans le cadre de la présente étude. [Traduit par la Rédaction]

Mots-clés : agriculture, abondance, densité, *Didelphis virginiana*, fragmentation, modèles linéaires généralisés à effets mixtes, Indiana, loi de Poisson, conception robuste, opossum de Virginie.

Introduction

Anthropogenic land-use changes have significantly altered the composition and structure of Earth's ecological communities, creating a global land-use crisis characterized by extensive habitat loss and fragmentation (Foley et al. 2005; Jetz et al. 2007). Landscapes with high levels of habitat loss and fragmentation contain an increased number of smaller, isolated habitat patches, drastically altering the spatial configuration of remnant resources compared with historical distributions. Although wildlife responses to habitat loss and frag-

mentation may vary among species, environmental variables interact with a species' morphological, ecological, and behavioral characteristics to produce a local response to landscape disturbance (Henle et al. 2004; Pita et al. 2009; Červinka et al. 2013). Consequently, wildlife species may exhibit altered demographic characteristics to adapt to heterogeneous resource distributions associated with habitat fragmentation (Hokit and Branch 2003; Craul et al. 2009; Dharmarajan et al. 2009; Hostetler et al. 2009; Beasley et al. 2011).

Habitat loss and fragmentation is especially pervasive in agricultural ecosystems with landscapes characterized by numerous

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small, isolated forest remnants embedded within an agricultural matrix. Remnant forest patches in agriculturally fragmented landscapes vary in size, structure, quality, and landscape context, producing an environment that is conducive to spatial variation in density of resident wildlife (Craul et al. 2009; Hostetler et al. 2009; Beasley et al. 2011). To develop a thorough understanding of a species' response to habitat loss and fragmentation, multiscale analyses that evaluate environmental heterogeneity at different levels are essential in heterogeneous landscapes (Thornton et al. 2011).

Generalist mesopredators are often superabundant in agriculturally fragmented landscapes due to their ability to exploit anthropogenic food resources and (or) competitive release from apex predators (Prugh et al. 2009; Ritchie and Johnson 2009). In addition, generalist mesopredators are dominant scavengers and provide a vital link in energetic pathways in disturbed landscapes (Olson et al. 2012). In relatively intact ecosystems, local abundances of mesopredators and scavengers have been linked to availability of carrion. For example, in an intact forest in Europe, red fox (*Vulpes vulpes* (L., 1758)) relative abundance increased in areas with ungulate carcasses (Cortés-Avizanda et al. 2009). As a result, the spatio-temporal distribution and volume of carrion in an area may impact local abundance of scavengers in disturbed ecosystems (DeVault et al. 2011).

The Virginia opossum (*Didelphis virginiana* Kerr, 1792) is one example of a generalist mesopredator that has thrived in agricultural ecosystems and has recently expanded its range northward, possibly due to its ability to exploit carrion and anthropogenic resources (Gardner and Sunquist 2003; Kanda et al. 2009; Olson et al. 2012; Beatty et al. 2014). As a result, local opossum abundance in disturbed ecosystems may be linked to landscape features that generate predictable and abundant sources of carrion, which includes roads, forests, and wetlands (Glista et al. 2008). In addition, other local environmental variables such as the number of potential den sites, amount of developed land in the surrounding landscape, and patch size may influence local opossum abundance (Hossler et al. 1994; Kanda et al. 2009; Beasley et al. 2011). Although opossum density and abundance have been documented in the literature (Seidensticker et al. 1987; Kasparian et al. 2004), no research has been conducted to link opossum abundance and density to environmental variables.

In this study, we examined local abundances of the opossum in an agricultural landscape near its historical range boundary (Beatty et al. 2014) as a function of landscape- and patch-level covariates, which included variables that have been previously associated with carrion availability. We predicted increased opossum abundances within forest patches associated with abundant forest cover and high densities of roads and wetlands at multiple spatial scales. To test these predictions, we used a relatively long-term (6 year) capture–mark–recapture data set from 25 discrete forest patches in northern Indiana, USA, and examined the effects of environmental covariates associated with carrion on opossum density using two metrics. The first metric we included was overall opossum density to thoroughly model population trends in focal habitat patches. In addition to overall opossum density, we also examined the effects of resources linked to carrion on female opossum density. Opossums employ a promiscuous mating strategy and competition among opossum males for mates is likely intense, indicating that the number of females is a limiting factor in recruitment (Ryser 1992; Beasley et al. 2010). In addition, opossums are the definitive host for *Sarcocystis neurona*, which is a parasite that causes a debilitating neurological diseases in horses (equine protozoal myeloencephalitis (EPM); Dubey et al. 2001). Thus, wildlife managers could apply the results of our study to address local outbreaks of EPM and effectively address nuisance wildlife issues. In addition, opossums play a vital role in ecosystems as a scavenger that efficiently sequesters energy between trophic levels (DeVault et al. 2011; Olson et al. 2012). As a result, our research addresses basic and applied knowledge gaps regarding a dominant vertebrate scavenger.

Materials and methods

Our study area was located in the Upper Wabash River Basin (UWB), which included 1169 km² of primarily flat terrain in northern Indiana, USA. We used a geographic information system (GIS) developed from 1998 U.S. Geological Survey digital orthophotos of 1 m resolution to classify land cover in the study area into one of eight categories: agricultural areas, corridors, developed land, forest, grasslands, roads, shrub land, and open water (for detailed descriptions see Retamosa et al. 2008; Beatty et al. 2014). Ephemeral water sources, forested streams, and seasonal wetlands were difficult to definitively quantify based on aerial photos. Thus, we incorporated the U.S. Geological Survey National Hydrography data set and U.S. Fish and Wildlife Service National Wetland Inventory data set into the GIS to define two additional land-cover categories: streams and wetlands. Agriculture comprised approximately 66% of the study area, whereas 14% of the area was forested. Agricultural areas were dominated by row crops such as corn (*Zea mays* L.) and soybeans (*Glycine max* (L.) Merr.). Remnant forest consisted primarily of oak (genus *Quercus* L.) – hickory (genus *Carya* Nutt.) – maple (genus *Acer* L.) communities with a mean patch size of 7.3 ± 0.37 ha (range 0.01–252 ha). Wetlands and other lentic systems comprised approximately 4% of the study area, which included two large impoundments that totaled 2750 ha.

Virginia opossum trapping

Forested areas are important habitat for opossums inhabiting agriculturally fragmented landscapes because they provide denning resources (e.g., tree cavities, burrows) and cover throughout the year (Beatty et al. 2014). As a result, we selected 25 distinct forest patches distributed throughout the study area to concentrate opossum trapping efforts (Fig. 1). Sampled patches had not been recently managed and were spatially segregated to represent the range of resource heterogeneity within the study area (mean pairwise distance among patches = 16.4 ± 0.52 km). Opossums were captured from March to June (2005–2010) in the same 25 forest patches each year using box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA). Traps were set in a grid with 50 m spacing, prebaited with commercial cat food for 1–3 nights, and monitored for 10 consecutive nights. We saturated forest patches with traps up to a maximum of 30 traps per forest patch (mean = 19.4 traps, range = 4–30 traps). In our sample of 25 forest patches, mean patch size was 19.65 ha (range = 0.49–119.46 ha, SD = 30.52 ha). We used identical grids in each forest patch across years.

All newly captured opossums were ear-tagged, sexed, weighed, and sampled for tissue for genetic analysis prior to release (Beatty et al. 2012). Females were immobilized with a dosage of 5 mg·kg⁻¹ of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) to count and measure pouched young. Opossums with tags from a previous year were processed with the same methods as new individuals to obtain updated information. In northern Indiana, opossum young of the year from first litters begin travelling independently in late May, so we classified individuals as either young of the year or adults based on body mass (individuals <0.5 kg were young of the year) (Whitaker and Mumford 2008). All trapping and handling methods conformed to the American Society of Mammalogists' guidelines and Purdue University Animal Care and Use Committee Protocol 01-079 (Sikes et al. 2011).

Virginia opossum abundance and density

A major assumption of capture–mark–recapture studies is tags are not lost, misread, or overlooked (Williams et al. 2001). We used a suite of 11 microsatellite loci with a nonexclusion probability of 3.9×10^{-14} to identify individuals with identical multilocus genotypes in the trapping data set using CERVUS (Kalinowski et al. 2007). Identical genotypes represented opossums that had lost

Fig. 1. Study area to examine the influence of environmental covariates on the abundance and density of Virginia opossums (*Didelphis virginiana*) in northern Indiana, USA, from 2005 to 2010. Trapping grids are displayed with black triangles.
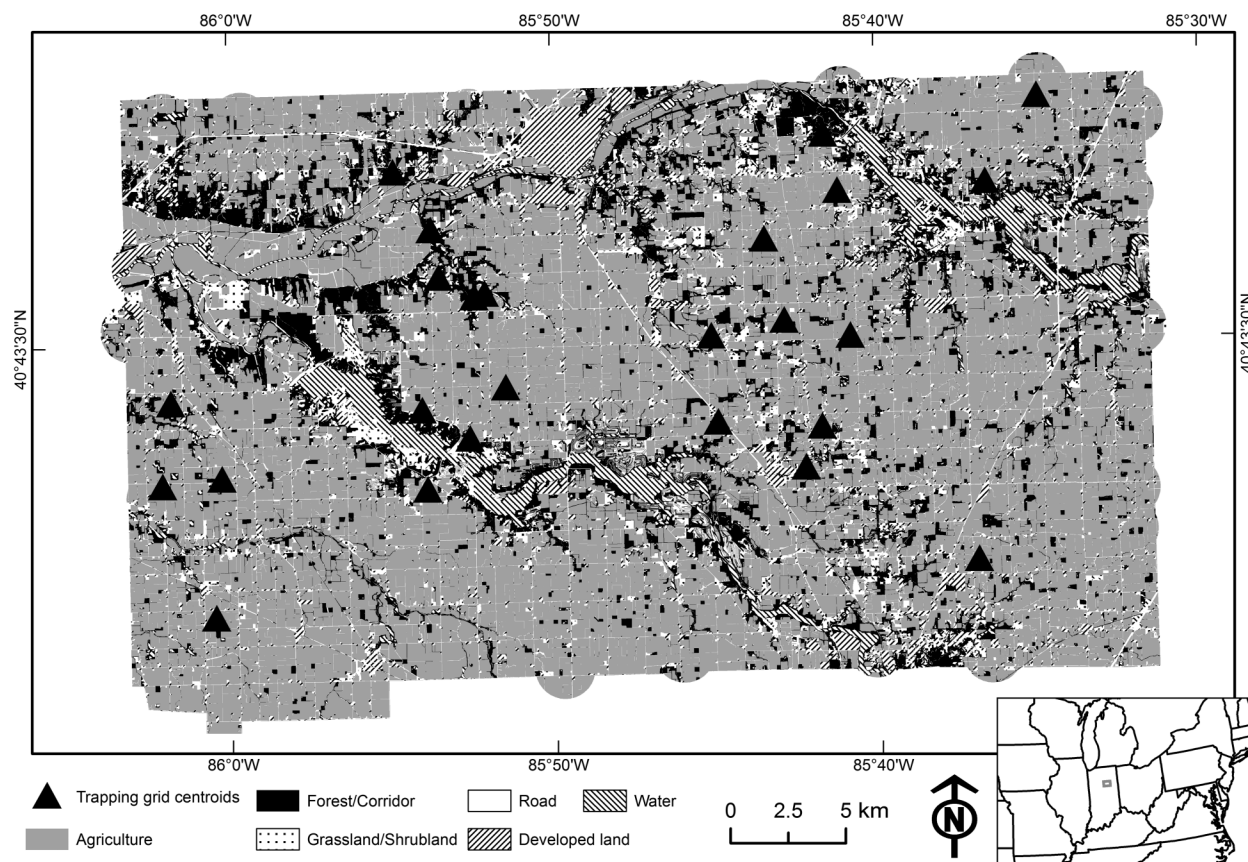
their initial tags and were subsequently tagged as new individuals upon recapture. We reevaluated all genotypes with ≤3 mismatching loci to confirm allele scores and examined demographic parameters for consistency. If necessary, we reanalyzed samples with newly extracted genomic DNA (for details see Beasley et al. 2010). Individuals with identical genotypes and different tag numbers were reconciled in the capture–mark–recapture data set.

We implemented a closed robust design to estimate opossum abundance in each forest patch (Pollock 1982; Kendall et al. 1995, 1997). The robust design incorporated a hierarchical structure consisting of two sampling levels: primary periods and secondary samples. Among primary periods, the population is considered open to additions and subtractions (e.g., births, deaths) to obtain estimates of apparent survival (Φ), temporary emigration (γ''), and immigration $(1 - \gamma')$ (Cormack 1964; Jolly 1965; Seber 1965). Secondary sampling occasions are nested within primary periods and are modeled with closed population models to estimate probability of capture (p), probability of recapture (c), and abundance (N). We considered each year to be a distinct primary sampling period to calculate apparent annual survival, immigration, and temporary emigration. Secondary samples were denoted as the 10 consecutive nights that comprised one annual trapping session. Thus, our closed robust design models included 6 primary periods (6 years) and 60 secondary sampling periods (6 years × 10 nights per year).

We developed a suite of candidate models to estimate local abundance of opossums and varied parameters at both primary and secondary levels. Among primary periods, we varied temporary emigration (γ'') and immigration $(1 - \gamma')$ to designate three types of movement models: no movement, random movement, and Markovian movement (Kendall 2012). We also developed model structures that permitted p and c to vary across years and

among forest patches. All candidate models were fit with two alternative survival parameter structures: (1) variation in survival across primary periods and (2) survival constant across primary periods.

At the level of secondary sampling occasions, we implemented Huggins closed capture models to obtain annual abundance estimates for each forest patch (Huggins 1991). In Huggins models, abundance (N) is a derived parameter and individual covariates (e.g., body mass, sex) can be incorporated to account for heterogeneity in capture and recapture probabilities. All model structures incorporating p and c at secondary and primary levels were run three separate times with the no movement, random movement, and Markovian movement emigration–immigration structures in program MARK (White and Burnham 1999). We ran all model structures without covariates and with all combinations of covariates (body mass, sex). Candidate models were ranked according to Akaike's information criterion adjusted for small sample sizes (AIC_c) and ΔAIC_c values were calculated for all candidate models (Burnham and Anderson 2002). Estimates of local opossum abundance (N) and apparent survival were based on the top model, which was >4.0 ΔAIC_c units from the next competing model (see Results) (Burnham and Anderson 2002). We also calculated female annual abundance (N_F) in each patch based on parameter estimates in the top model.

Abundance estimates derived from grid trapping should account for effective area trapped to estimate density (Williams et al. 2001). To estimate the effective area trapped, we applied a boundary strip (W) to each trapping grid equal to the radius of the median opossum home-range size (43.1 ha, $W = 370.4$ m) during the breeding season in our study area (Williams et al. 2001; Beatty 2012). We used median home-range size to minimize the effects of large observations in the home-range size data set and we specif-

ically applied the breeding season estimate because trapping was entirely concentrated within the breeding season (1 February to 20 June) (Beatty et al. 2014). Abundance estimates were then divided by effective area trapped to obtain density estimates for each forest patch in each year. Although spatial capture–recapture offers an alternative approach to estimating density (Royle et al. 2014), our study design was implemented in 2005 to focus on local abundance within forest patches. As a result, required information for spatial capture–recapture such as trap locations were not recorded during the first 5 years of the study.

Covariates

We measured a series of covariates at multiple spatial scales to examine variation in opossum density. At the patch scale, we measured covariates associated with or adjacent to each forest patch (denoted with -P). At the landscape scale, we measured covariates (denoted with -L) within a buffer equal to 4 × radius of the opossum breeding season median home-range size around each trapping-grid centroid (1481.6 m). We specifically used the multiplier 4 to measure landscape variables in an immediate area around each trapping grid while minimizing the influence of patch size in our landscape data. For example, multiples of 1 and 2 would primarily measure patch size, which we considered a patch-level variable rather than a landscape-level variable.

In agriculturally fragmented landscapes, forest patches provide natural refugia for wildlife and are associated with high rates of carrion on the landscape when they occur near roads (Roland 1993; Beasley et al. 2011; Beatty et al. 2014; Dharmarajan et al. 2014). For example, in a study conducted approximately 60 km from the UWB in a similar landscape, Glista et al. (2008) documented high rates of road-killed carrion availability near forest patches. As a result, we measured patch size (SIZE-P) and the percentage of forest (FOR-L) in the landscape surrounding each forest patch as indices of amount of forest near each study site. In addition to forest, carrion in agricultural landscapes may be correlated with streams and wetlands, which contain abundant amphibian populations and may be important resources for opossums as food and (or) water sources (Gardner and Sunquist 2003; Glista et al. 2008; Beatty et al. 2014). Thus, we measured the percentage of the surrounding landscape consisting of streams (STREAM-L) and wetlands and other lentic systems (WATER-L) for each forest patch. We also measured the percentage of each forest patch consisting of wetlands (WATER-P) and streams (STREAM-P) to measure these resources at a finer spatial scale. As our final proxies of carrion availability, we measured the density of roads (km·km^{-2}) within the landscape buffer surrounding each forest patch (ROADS-L). In addition, we measured the length of roads that adjoined each forest patch and standardized this value to patch size (ROADS-P). As a result, ROADS-P units are road kilometre per unit area of a forest patch (km·km^{-2}).

In addition to our measures of carrion availability, we measured several covariates that were not associated with high rates of road-killed carrion, but could also influence local opossum density. Specifically, den-site availability may affect local opossum density and reproduction (Hossler et al. 1994; Gardner and Sunquist 2003). We conducted den-site surveys from February to March 2009 prior to leaf emergence to quantify den-site density in each forest patch (DENS-P). We systematically surveyed the entire patch or a maximum area of 20 ha centered on the trapping grid, which was equal to the mean core-area size of opossums within the study area (Beatty 2012). Two researchers performed independent censuses of an area and compared counts to reach a consensus for the patch. Thus, we considered den-site surveys to represent a census of the surveyed area given our intensive search effort (Beasley et al. 2011). We recorded all dens as brush pile, ground den, hollow log, or tree cavity. Ground dens have been specifically identified as a limiting resource for opossum reproduction (Hossler et al. 1994; Gardner and Sunquist 2003). Thus, we

included the density of ground dens in each patch (GDENS-P) as an additional variable in analyses.

In addition to dens, previous research has demonstrated that developed land (i.e., cities, homesteads, farm houses, barn yards, industrial properties) is an important habitat for opossums at northern latitudes because it has the potential to provide predictable and concentrated sources of food (Kanda et al. 2009; Beatty et al. 2014). Thus, we also measured the percentage of the landscape around each forest patch consisting of developed land (DEV-L). We measured GIS variables using the packages rgdal (Bivand et al. 2015), rgeos (Bivand and Rundel 2015), and sp (Bivand et al. 2013) in the program R (R Core Team 2015).

Statistical analysis

We developed a set of 19 candidate models to test the influence of our covariates associated with road-killed carrion on overall opossum density and female density. We first denoted a null model that included random terms for forest patch and year (model 1), which served as a base for the remaining 18 models (Table 1). Next, we included models to examine the effects of each of our covariates separately (models 2–12) and an additional model to examine the effects of den sites, which are important resources that provide shelter to opossums (model 13). We then developed models based on spatial scale and the expected relationship of covariates with carrion. In the first patch model, we included covariates that were not associated with carrion (model 14), whereas covariates associated with carrion were included in the second patch model (model 15). We then combined all patch-level variables to generate the final patch model (model 16). We developed landscape-level models with a similar approach. We included covariates associated with carrion in the first landscape-level model (model 17), whereas all landscape-level variables were included in another model (model 18). We then combined all variables associated with carrion into a final model (model 19). We used the same suite of candidate models for both opossum density and female density (Table 1).

We evaluated the influence of covariates associated with carrion on annual opossum density and female density in each forest patch with generalized linear mixed models (GLMMs). We modeled expected opossum abundance in each forest patch ($E(y_i)$) with a Poisson distribution (log-link) using k predictors and included logarithm of effective area trapped (A_i) as an offset term:

$$
\begin{aligned}
\log[E(y_i)] &= \beta_0 + \alpha_i + \gamma_j + x_{1,i}\beta_1 + \ldots + x_{k,i}\beta_k + \log(A_i) \\
\alpha &\sim \text{Normal}(0, \sigma^2_{\text{patch}}) \\
\gamma &\sim \text{Normal}(0, \sigma^2_{\text{year}})
\end{aligned}
$$
(1)

where β_0 is an intercept term, α_i is a random effect for forest patch with a mean of 0 and variance of σ^2_{patch}, γ_j is a random effect for year with a mean of 0 and variance of σ^2_{year}, $x_{1,i}$ represented the first predictor variable for the ith forest patch, and β_1 was the associated regression coefficient for the first predictor. The offset term from eq. 1 can be rearranged to aid interpretation:

$$\log[E(y_i)] - \log(A_i) = \beta_0 + \alpha_i + \gamma_j + x_{1,i}\beta_1 + \ldots + x_{k,i}\beta_k$$

$$\log\left[\frac{E(y_i)}{A_i}\right] = \beta_0 + \alpha_i + \gamma_j + x_{1,i}\beta_1 + \ldots + x_{k,i}\beta_k$$

which demonstrates that the modeled response variable was opossum density rather than abundance. Thus, we modeled expected opossum density in forest patch i ($E(d_i)$) with a Poisson distribution and log-link:

$$E(d_i) \sim \text{Poisson}(e^{\beta_0 + \alpha_i + \gamma_j + x_{1,i}\beta_1 + \ldots + x_{k,i}\beta_k})$$

Table 1. Candidate models used to examine variance in Virginia opossum (*Didelphis virginiana*) density and female density in 25 forest patches in northern Indiana, USA.

No.	Model	Description
1	Intercept + patch random effect + year random effect	Null model
2	DENS-P	Density of all den types (dens·km⁻²)
3	GDENS-P	Density of ground dens (dens·km⁻²)
4	ROADS-P	Density of roads that adjoin patch (km·km⁻²)
5	SIZE-P	Forest-patch area (km²)
6	STREAM-P	Percentage of forest patch consisting of lotic water
7	WATER-P	Percentage of forest patch consisting of lentic water
8	DEV-L	Percentage of surrounding landscape[a] consisting of developed land
9	FOR-L	Percentage of surrounding landscape consisting of forest
10	ROADS-L	Density of roads (km·km⁻²) within surrounding landscape
11	STREAM-L	Percentage of surrounding landscape consisting of lotic water
12	WATER-L	Percentage of surrounding landscape consisting of lentic water
13	DENS-P + GDENS-P	Shelter
14	DENS-P + GDENS-P + SIZE-P	Patch variables not associated with carrion
15	ROADS-P + STREAM-P + WATER-P	Patch variables associated with carrion
16	DENS-P + GDENS-P + SIZE-P + ROADS-P + STREAM-P + WATER-P	All patch variables
17	FOR-L + ROADS-L + STREAM-L + WATER-L	Landscape variables associated with carrion
18	DEV-L + FOR-L + ROADS-L + STREAM-L + WATER-L	All landscape variables
19	ROADS-P + STREAM-P + WATER-P + FOR-L + ROADS-L + STREAM-L + WATER-L	All variables associated with carrion

Note: Within the model column, -P is patch level and -L is landscape level.

[a]Surrounding landscape was defined as the area within a 1481.6 m buffer around the centroid of each trapping grid.

In all models, forest patch and year were denoted as random effects, whereas all other independent variables were denoted as fixed effects (Table 1).

We centered and standardized all predictor variables using the mean and one standard deviation. We calculated variance inflation factors (VIFs) in the full model to screen predictor variables for evidence of collinearity and investigated variables with VIFs ≥ 5.0 (Kutner et al. 2005). To meet the assumptions of the Poisson model, we compared the sum of squared Pearson residuals to the residual degrees of freedom with a χ^2 distribution to obtain an estimate of overdispersion for all models for both overall and female opossum density. In both analyses (density and female density), we evaluated relative model fit with AIC_c (Burnham and Anderson 2002) and measured absolute fit with a pseudo-R^2 that quantified the amount of variance explained compared with the null model (model 1) (Nagelkerke 1991). We made inferences on the effects of our covariates on opossum density based on the top model according to AIC_c and considered all models with $\Delta AIC_c < 4.0$ to be competing models. In addition, we calculated 85% unconditional confidence intervals for all parameter estimates and assumed variables with confidence intervals that did not overlap zero significantly influenced the dependent variable. We used 85% confidence intervals rather than 95% confidence intervals because AIC_c model selection supports models with added variables at $p < 0.157$ (Arnold 2010). We performed all statistical analyses in R with the packages HH (Heiberger 2015), lme4 (Bates et al. 2015), and MuMIn (Barton 2015).

Results

Virginia opossum trapping

We captured a total of 750 adult opossums, including 407 females and 343 males, 1417 times over the course of the 6-year study. We captured six females in 2 consecutive years. No individuals were captured in 3 or more years. The mean number of individuals captured during the 10-day trapping period within each forest patch was 5.07 (range 0–12 individuals). Based on genetic analysis, only three opossums lost tags over the course of the study and were retagged as new individuals. Two of these opossums were trapped in consecutive years, whereas the other lost its tags within the 10-day trapping session. Raccoons (*Procyon lotor* (L., 1758)) were also frequently trapped over the course of the study

with local densities ranging from 0.0 to 40.4 raccoons·km⁻² (mean = 13.2, SD = 7.4) (Beasley et al. 2011, 2013).

Virginia opossum abundance and density

Analysis of candidate robust design models produced a single top model. The top model included a constant apparent survival rate across primary periods (Φ = 0.014, 95% CI = 0.007 to 0.029), no immigration and emigration, allowed p to vary among primary periods (years), and set $p = c$ within primary periods. Estimates of local opossum abundance were highly variable across years within forest patches (mean = 7.15, SD = 3.71, range = 0.00–17.67) as were estimates of female opossum abundance (mean = 3.35, SD = 2.16, range = 0.00–9.67). Corresponding density estimates also varied among forest patches and years for opossums (mean = 8.52 opossums·km⁻², SD = 4.10 opossums·km⁻², range = 0.00–20.95 opossums·km⁻²) and female opossums (mean = 3.59 female opossums·km⁻², SD = 2.22 female opossums·km⁻², range = 0.00–9.53 female opossums·km⁻²). Local estimates of the natural logarithm of opossum abundance and female abundance were only moderately correlated ($r = 0.52$); thus, we proceeded with separate analyses for overall and female opossum abundances.

Statistical analysis

Variance inflation factors for opossum density indicated independence of predictor variables in the full model (VIFs < 5.0). Analysis of Pearson residuals and residual degrees of freedom demonstrated that opossum density was not overdispersed in any candidate models. The top model (model 4) included density of adjoining roads (ROADS-P), which exhibited a consistently significant and positive relationship in all competing models (Fig. 2). However, the null was a competing model along with models 13, 2, 15, 16, 19, 12, and 9 with $\Delta AIC_c < 4.0$ (Table 2). In the competing model set, ground den-site density (GDENS-P), percentage of landscape consisting of forest (FOR-L), percentage of landscape consisting of streams (STREAMS-L), and percentage of landscape consisting of wetlands and water (WATER-L) exhibited significant and positive relationships with opossum density. In contrast, the density of dens with a forest patch (DENS-P) exhibited a significant and negative relationship with opossum density. However, pseudo-R^2 ranged from <0.01 to 0.10, indicating that models poorly ac-

Fig. 2. Predicted Virginia opossum (*Didelphis virginiana*) density (individuals·km⁻²) in a forest patch as a function of density of adjoining roads (km roads·km⁻² of forest). Gray lines represent 95% confidence intervals generated with the delta method (Oehlert 1992).
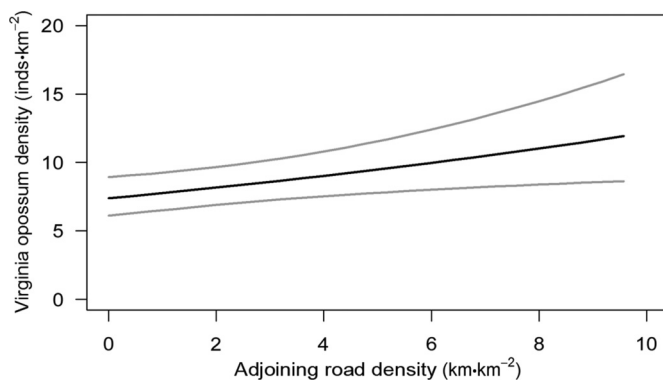
counted for variation in opossum density in our study area (Table 3).

Variance inflation factors for female opossum density models indicated that predicator variables were independent. Analysis of Pearson residuals and residual degrees of freedom demonstrated that female opossum density was not overdispersed in any candidate models. The top model for female opossum density included patch size (SIZE-P), which consistently exhibited a significant and positive relationship with female opossum density in all competing models. In the competing model set, ground den-site density and density of adjoining roads were significantly and positively associated with female opossum density. However, the null was also a competing model and pseudo-R^2 values ranged from <0.01 to 0.07, indicating that our models poorly accounted for variation in female opossum density in our study area (Table 3).

Discussion

Over the past century, the Virginia opossum has expanded its range northward due to its ability to exploit anthropogenic food resources and denning locations (Gardner and Sunquist 2003; Kanda et al. 2009; Beatty et al. 2014). One specific food resource that opossums may exploit in human-dominated landscapes is carrion, which is correlated with discrete landscape features such as forests, roads, and wetlands (Glista et al. 2008; Olson et al. 2012). For example, previous research that examined resource selection in an agriculturally fragmented landscape demonstrated that opossums frequently foraged proximate to roads, possibly to focus foraging efforts on carrion (Beatty et al. 2014). In addition, carrion likely comprises a significant portion of opossums' diet in agriculturally fragmented ecosystems (e.g., >40% volume) (Whitaker et al. 1977; Whitaker and Mumford 2008), although distinguishing between carrion and live prey is difficult in diet studies that analyze stomach contents. As a result, the recent northward range expansion of the opossum may also be attributed to its status as a dominant scavenger that efficiently exploits anthropogenic sources of carrion (i.e., road-killed). In this study, we predicted that local densities of opossums would be higher in areas with abundant forest and increased densities of roads and wetlands. However, our results only partially supported our prediction with null models included in competing models sets for both opossum density and female density. Nevertheless, we observed elevated mean opossum density estimates in our study area (8.52 opossums·km⁻²) compared with previous studies conducted in relatively intact landscapes (e.g., Seidensticker et al. 1987: 3.9 opossums·km⁻², Kasparian et al. 2004: 6.5 opossums·km⁻²).

The proficient dispersal ability of opossums, combined with their generalist diet, likely precluded us from detecting a definitive relationship between opossum density and our covariates associated with carrion (Beatty et al. 2012). Previous genetic studies on opossums conducted in our study area demonstrated limited to no site fidelity and a propensity to disperse long distances (Beatty 2012). For example, Beatty et al. (2012) estimated a median dispersal distance of approximately 6 km, whereas Hennessy et al (2015) estimated a median dispersal distance between 4 and 8 km for opossums. However, in a paternity analysis conducted within our study area, known opossum father–offspring pairs were documented up to 33 km apart (Beasley et al. 2010). Furthermore, both males and females disperse at similar rates within our study area (Beatty et al. 2012), which contrasts with observational studies conducted in relatively intact landscapes that documented male-biased dispersal (Wright 1989; Ryser 1995). In addition to their innate dispersal ability, female opossums can travel independently with young in the pouch, increasing their dispersal capacity compared with placental mammals (Gillette 1980; Hossler et al. 1994). Opossums may disperse from natal home ranges before reaching reproductive maturity and also disperse after reproducing within in an area. Thus, the limited site fidelity and proficient dispersal ability of opossums may limit our ability to link local opossum densities to local resources, indicating that opossums may be responding to environmental covariates at larger spatial scales than those examined in this study.

The spatial distribution of carrion in agriculturally fragmented landscapes is likely linked to areas with high vertebrate abundances such as forest patches (Houston 1979; Smith and Merrick 2001). However, the spatial distribution of road-killed carrion may be a function of a complex interaction of local habitat features, landscape factors, seasonal factors (e.g., rainfall, temperature), road densities, traffic volume, traffic speed, and local animal densities (Fahrig et al. 1995; Fahrig and Rytwinski 2009; D'Amico et al. 2015). For example, previous studies have found contrasting effects of traffic volume on road-killed carrion availability, likely due to an interaction with landscape factors (Jaeger et al. 2005; Coelho et al. 2008; van Langevelde et al. 2009). We did not account for traffic volume due to a lack of available data in our study area, and the specific effects of traffic volume on road-killed carrion availability may vary among patches. Thus, we feel that our indices of carrion availability on the landscape (forest, wetlands, roads) reflected the predominant trends in the spatial distribution of carrion in our study area, though we did not directly measure carrion availability.

Streams and riparian habitat are commonly associated with elevated densities of mesopredators in heterogeneous landscapes (Dijak and Thompson 2000; Gardner and Sunquist 2003). In our study area, forest patches with abundant riparian habitat were typically large patches with locally steep topography, which precluded agricultural production. Although the statistical null models were competing models for both overall and female opossum density, streams and wetlands were prominent variables in competing models for overall opossum density. Consequently, our results support a positive relationship between opossum density and riparian habitat, indicating that riparian habitat may provide concentrated resources such as water and potentially carrion to opossums in agriculturally fragmented ecosystems.

In robust design capture–mark–recapture models, permanent emigration and mortality are confounded. Consequently, survival estimates based on capture–mark–recapture studies are commonly reported as apparent survival to acknowledge uncertainty associated with permanent emigration and mortality (Lebreton et al. 1992; Gilroy et al. 2012). For species that disperse long distances or seasonally shift home ranges in response to resource heterogeneity, apparent survival estimates likely provide misleading and low estimates of survival. Opossums have relatively large home ranges, use multiple forest patches, and disperse long

Table 2. Model-selection results for generalized linear mixed-effects models (Poisson, log-link) to examine effects of patch-level (-P) and landscape-level (-L) variables on Virginia opossum (*Didelphis virginiana*) density in 25 forest patches in northern Indiana, USA, from 2005 to 2010.

Model	Intercept	DENS-P	GDENS-P	ROADS-P	SIZE-P	STREAMS-P	WATER-P	DEV-L	FOR-L	ROADS-L	STREAMS-L	WATER-L	ΔAIC$_c$	w_i	R^2
4	−2.50*			0.12*									0.00	0.30	0.04
13	−2.50*	−0.14*	0.09*										2.94	0.07	0.03
2	−2.50*	−0.09*											2.95	0.07	0.02
15	−2.50*			0.12*		−0.01	−0.05						2.97	0.07	0.05
16	−2.50*	−0.11*	0.07	0.12*	0.05	−0.04	−0.05						3.04	0.07	0.09
19	−2.50*			0.12*		−0.04	−0.03		−0.06	0.05	0.11*	0.12*	3.23	0.06	0.10
12	−2.50*											0.08*	3.27	0.06	0.02
1	−2.50*												3.88	0.04	—
9	−2.50*								0.07*				3.95	0.04	0.01
11	−2.50*										0.07		4.18	0.04	0.01
17	−2.50*								−0.03	0.05	0.11*	0.12*	4.67	0.03	0.05
5	−2.50*				0.05								4.74	0.03	0.01
14	−2.50*	−0.13*	0.09		0.02								4.91	0.03	0.04
10	−2.50*									0.05			4.99	0.02	0.01
8	−2.50*							0.05					5.00	0.02	0.01
7	−2.50*						−0.05						5.09	0.02	0.01
6	−2.50*					0.03							5.74	0.02	<0.01
3	−2.50*		0.01										5.95	0.02	<0.01
18	−2.50*							0.01	−0.03	0.04	0.10*	0.12*	6.84	0.01	0.05

Note: For definitions of patch-level and landscape-level variables refer to Table 1. ΔAIC$_c$, difference in Akaike's information criterion adjusted for small sample size; w_i, Akaike weight.

*Significant at $p = 0.15$.

Table 3. Model-selection results for generalized linear mixed-effects models (Poisson, log-link) to examine effects of patch-level (-P) and landscape-level (-L) variables on female Virginia opossum (*Didelphis virginiana*) density in 25 forest patches in northern Indiana, USA, from 2005 to 2010.

Model	Intercept	DENS-P	GDENS-P	ROADS-P	SIZE-P	STREAMS-P	WATER-P	DEV-L	FOR-L	ROADS-L	STREAMS-L	WATER-L	ΔAIC$_c$	w_i	R^2
5	−3.37				0.10*								0.00	0.18	0.02
1	−3.37												0.98	0.11	—
3	−3.37		0.09*										1.11	0.10	0.01
4	−3.37			0.07									1.81	0.07	0.01
14	−3.37	0.02	0.08		0.10*								1.94	0.07	0.04
11	−3.37										0.07		2.01	0.07	0.01
9	−3.37								0.05				2.32	0.06	0.01
10	−3.37									0.04			2.59	0.05	<0.01
2	−3.37	0.03											2.86	0.04	<0.01
8	−3.37							0.03					2.88	0.04	<0.01
6	−3.37					0.03							2.91	0.04	<0.01
12	−3.37											0.02	2.94	0.04	<0.01
7	−3.37						−0.02						3.01	0.04	<0.01
13	−3.37	−0.03	0.11*										3.10	0.04	0.01
16	−3.37	0.10	0.05	0.12*	0.16*	0.07	0.02						3.60	0.03	0.07
15	−3.37			0.07		0.01	−0.02						6.02	0.01	0.01
17	−3.37								0.00	0.03	0.07	0.05	7.81	0.00	0.01
18	−3.37							−0.02	−0.01	0.04	0.08	0.05	9.97	0.00	0.01
19	−3.37			0.06		−0.02	0.01		−0.01	0.04	0.07	0.05	13.55	0.00	0.02

Note: For definitions of patch-level and landscape-level variables refer to Table 1. ΔAIC$_c$, difference in Akaike's information criterion adjusted for small sample size; w_i, Akaike weight.

*Significant at $p = 0.15$.

distances in agriculturally fragmented landscapes (Beasley et al. 2010; Beatty 2012; Beatty et al. 2012, 2014). Thus, our estimate of apparent annual survival ($\Phi = 0.01$) likely underestimated true annual survival of opossums in agriculturally fragmented landscapes, as previous estimates of annual survival for opossums have ranged from 0.17 to 0.25 (Gipson and Kamler 2001). Indeed, preliminary results from a radiotelemetry study indicated that mean annual opossum survival in our study area was approximately 0.45 (range = 0.30–0.59) (W.S. Beatty, unpublished data). Although potential opossum predators such as coyotes (*Canis latrans* Say, 1823) and red fox were present within the study area, vehicle collisions, human conflicts, and winter stress are likely the primary causes of opossum mortality at northern latitudes (i.e., our study area) (Whitaker and Mumford 2008).

The scale of effect is defined as the spatial scale at which landscape covariates efficiently explain an ecological response of interest for a species (Jackson and Fahrig 2012). Simulation studies have demonstrated that the scale of effect is likely dependent on species traits such as body size (Brown et al. 1993), home-range size, dispersal distance (Bowman et al. 2002; Ricci et al. 2013), and reproductive rate (Jackson and Fahrig 2015). However, home-range size varies extensively within species and is likely linked to habitat productivity (McNab 1963; Edwards et al. 2009; Bjørneraas et al. 2012). As a result, the scale of effect could vary within a species according to landscape context (Jackson and Fahrig 2015). In this study, we did not detect a definitive relationship between opossum density and landscape- and patch-level covariates. Thus, the scale of effect for opossum density within our human-dominated

study area is likely larger than measured in this study due to the dispersal ability of the opossum and its generalist diet.

Acknowledgements

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