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Applications Of Bayesian Hierarchical Detection Models

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APPLICATIONS OF BAYESIAN HIERARCHICAL DETECTION MODELS

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ABSTRACT

Bayesian hierarchical detection models are useful for addressing uncertainty in datasets in the form of detection error and can be adapted to a variety of research questions. This dissertation uses three case studies to highlight advantages of Bayesian hierarchical detection models: 1) using prior information to model undetected species, 2) efficiently modeling a naturally hierarchical system, and 3) correcting for observation bias in two interconnected ecological metrics for effective disease management.

Detection error can bias ecological observations, especially when a species is never detected during sampling. In many communities, the probable identity of these species is known from previous research, but these data are rarely included in subsequent models. I present prior aggregation as a method to add information from external sources to Bayesian hierarchical detection models. Prior aggregation combines information from multiple prior distributions: in this case, an ecologically informative, species-level prior and an uninformative community-level prior. This approach adds external information into the model while retaining the advantage of modeling species in the context of the community. Using simulated data supplied to a multi-species occupancy model (MSOM), I demonstrated that prior aggregation improves estimates of metacommunity richness and environmental correlates of species occupancy. When applied to a dataset of Vermont small mammals, prior aggregation allowed the model to estimate occupancy correlates of the eastern cottontail, a species observed at several study sites but never captured.

Ectoparasites are exposed to a 'dual' environment: the individual host and the external environment. However, variation in the portion of the life cycle spent on-host leads to differences in selective pressures exerted by each environment. Parasites that spend most of the life cycle on-host face increased pressure to specialize, leading to differences in host specificity and occupancy patterns compared to ephemeral parasites which only contact the host to feed. Using data from small mammals and ectoparasites in Vermont, I used a multi-scale MSOM to 1) calculate the Bayesian R^2 at the site and host levels of the model to quantify explained variation in occupancy, and 2) compare number of host species and R^2 values across life history categories. Life history was significantly associated with host specificity and host-level R^2: parasites which spend more time on-host infested fewer hosts and had more variation explained by host traits than ephemeral parasites. However, there were no differences in site-level R^2 between categories, suggesting additional factors structure small mammal/ectoparasite communities.

Disease management requires accurate measurements of metrics such as population size and immunity rates. Raccoon rabies virus is managed through use of oral rabies vaccine bait distribution, and the efficacy of the strategy is evaluated by measuring population-level seroprevalence of rabies antibodies. Using data from the Burlington, VT area from 2015–2017, I modified a multinomial *N*-mixture model to 1) estimate raccoon abundance and seroprevalence while correcting for sampling error, and 2) evaluate the effects of management strategies, raccoon population characteristics, and other carnivore species on seroprevalence. Rabies seroprevalence was associated with traits of raccoon populations, increasing with average age and decreasing with population size. Seroprevalence also decreased with opossum captures, suggesting competition for baits. Management strategies did not affect seroprevalence within sampling sites, but there is evidence that baiting strategy affects seroprevalence at the regional level.

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COMPREHENSIVE LITERATURE REVIEW

Statistical reasoning typically follows two lines of thinking: frequentist statistics and Bayesian statistics. The latter, first proposed by Thomas Bayes in the late 18th century, has recently increased in use as a viable alternative to frequentist methods (Ellison 2004, McCarthy 2007). Bayesian logic reflects the process of scientific thinking: prior knowledge and new data are evaluated using a statistical model to produce a posterior conclusion (Eq. 1).

$$prior + data \xrightarrow{model} posterior \qquad \text{(Eq. 1)}$$

In addition to the intuitive logic of Bayesian thinking, Bayesian methods have three major advantages over their frequentist counterparts. One, frequentist methods make predictions about hypothetical replicates of datasets, whereas Bayesian methods make predictions about hypotheses (Berger and Berry 1988, McCarthy 2007, McElreath 2015): again mirroring scientific thinking. Two, Bayesian methods naturally incorporate prior information into a model, whereas frequentist methods are constrained to the information in a particular dataset (Ellison 2004, McCarthy and Masters 2005, McCarthy 2007, Low Choy et al. 2009). Finally, Bayesian methods can formally incorporate uncertainty, either by the inclusion of unknown but important model parameters (Wade 2000) or using Bayesian model averaging (Wintle et al. 2003, Hooten and Hobbs 2015).

Another method for incorporating uncertainty in Bayesian models is by explicitly accounting for observational error. Occurring during the data collection process, observation error can bias the data, masking important ecological patterns (Iknayan et al. 2014). A class of Bayesian models called hierarchical detection models account for

observational error by decoupling the ecological metric of interest and the detection process used to measure the metric (Iknayan et al. 2014, Kery and Royle 2015b, Kéry and Royle 2020). Using repeated data collection events, the model conceptualizes observation error as a probability that is conditional upon the underlying ecological state (Kery and Royle 2015b, Kéry and Royle 2020). Unlike other methods which correct for detection error, such as the Chao index (Chao 1984) or bootstrapping (Burnham and Overton 1979), hierarchical detection models can explicitly differentiate between a true absence of a species from a site and a non-detection event (MacKenzie et al. 2002, Dorazio and Royle 2005, Iknayan et al. 2014). Hierarchical detection models can also incorporate environmental covariates into the model and estimate their effects on the ecological metric, observational accuracy, or both (MacKenzie et al. 2002, Dorazio and Royle 2005, Iknayan et al. 2014). For these reasons, hierarchical detection models tend to be less biased and more precise than other methods (New and Handel 2015).

Despite their utility and flexibility, hierarchical detection models can only be applied to datasets which meet three key assumptions (Devarajan et al. 2020): first, the populations or communities surveyed must be closed during the duration of the sampling period (Kery and Royle 2015b). In other words, there cannot be births, deaths, immigration, or emigration during the repeated surveys, meaning the surveys must be completed in a short time period relative to the demographics of the study taxon. When populations or communities are not closed, the model tends to overestimate occupancy (Kery and Royle 2015b). Variations on base hierarchical detection models, such as the dynamic or multi-season model originally developed by MacKenzie et al. (2003), and

later adapted by others (e.g. Royle and Kéry 2007, Broms et al. 2016), allow for demographic changes between sampling periods, but not within them.

Second, sites at which the ecological metric is observed must be statistically independent. Non-independence tends to occur due to spatial autocorrelation between sites (Devarajan et al. 2020), which in turn tends to over-estimate the precision of model estimates (New and Handel 2015). Adequate study design, specifically ensuring that sites are sufficiently distant from one another based on the focal taxon's movement patterns, can help prevent violation of this assumption (Devarajan et al. 2020). The independence assumption can also be tested and corrected for statistically by modifying the detection portion of the model (Wright et al. 2016).

Third, hierarchical detection models assume accurate identification of species or individuals (Dorazio et al. 2011). Identification error can be due to a variety of factors, including improper marking methods for individuals (Link et al. 2010), similarity between different species (Simons et al. 2007, McClintock et al. 2010), or variation in the skill levels of observers (Genet and Sargent 2003, Iknayan et al. 2014). Violation of this assumption results in overestimation of species or individuals through overestimation of detection probability (Dorazio et al. 2011). Models which account for false positives as well as false negatives are useful for addressing this assumption in cases where misidentification is common (Royle and Link 2006).

A fourth assumption only applies to hierarchical detection models which estimate parameters for entire communities. Bayesian hierarchical detection models are able to jointly model all species in a community by assuming species can be described by a

common prior distribution (Link and Sauer 1996, Dorazio and Royle 2005, Iknayan et al. 2014). In other words, species are assumed to vary, but they share some common ecological characteristics. If species vary to the extent that they can no longer be described by a common prior, prediction error occurs as a result (Kery and Royle 2015b). Advantages and disadvantages to the common prior distribution are discussed in more detail in Chapter 1.

Despite these assumptions, and despite valid criticisms of hierarchical detection models (e.g. Lele and Dennis 2009), these models are highly flexible and can be adapted to most ecological sampling methods. Hierarchical detection models are useful in a variety of scenarios, from estimating site-occupancy (Iknayan et al. 2014) to understanding hierarchical processes (Cressie et al. 2009; Ogle 2009) to conservation decision-making (Wade 2000), to disease management (Davis et al. 2019b, 2019a). The straightforward logic of these models makes them a valuable addition to an ecologist's toolkit.

In this dissertation, I highlight three advantages of Bayesian hierarchical detection models by applying them to various ecological contexts. In my first chapter, I highlight how informative priors can be used to more accurately model species that are undetected during sampling but are known to occupy a region based on previous studies, natural history collections, indigenous knowledge, or observations by the researcher. I introduce a method called prior aggregation that combines information from multiple sources to more readily model these undetected species. In my second chapter, I take advantage of the inherent structure of hierarchical detection models to account for scale

in a host/ectoparasite system. I use the model to investigate how life history characteristics of ectoparasites influence the relative importance of site-level and host-level factors with regards to ectoparasite occupancy. Finally, hierarchical detection models are readily modifiable and can be easily applied to a wide variety of ecological questions. I take advantage of this flexibility in my third chapter, where I modify a type of hierarchical detection model to evaluate the efficacy of rabies management strategies in Burlington, Vermont.

Ecologically informed priors improve Bayesian model estimates of species richness and occupancy for undetected species

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Abstract

Detection error can bias observations of ecological processes, especially when some species are never detected during sampling. In many communities, the probable identity of these missing species is known from previous research and natural history collections, but this information is rarely incorporated into subsequent models. Here, I present prior aggregation as a method for including information from external sources in Bayesian hierarchical detection models. Prior aggregation combines information from multiple prior distributions— in this case, an ecologically informative, species-level prior and an uninformative community-level prior. This approach incorporates external information into the model without sacrificing the advantages of modeling species in the context of the community. Using simulated data supplied to a multi-species occupancy model, I demonstrated that prior aggregation improves estimates of 1) metacommunity richness and 2) environmental covariates correlated with species-specific occupancy probabilities. When applied to a dataset of small mammals in Vermont, prior aggregation allowed the model to estimate occupancy correlates of the eastern cottontail Sylvilagus floridanus, a species observed at several sites in the region but never captured. Prior aggregation can be used to improve the analysis of several important metrics in population and community ecology, including abundance, survivorship, and diversity.

Introduction

Estimates of biodiversity and other population and community metrics are often biased due to observer error. Biases or errors, especially detection error, can be introduced by characteristics of the target species, study design, or observer (Iknayan et al. 2014, Kellner and Swihart 2014). When species richness or species occupancy are of interest, detection error results in richness and occupancy estimates that are biased low (Iknayan et al. 2014, Benoit et al. 2018) and adds "noise" to the data in the form of false negatives, making it more difficult to evaluate the importance of environmental covariates (Gu and Swihart 2004). While good study design can reduce survey bias (Banks-Leite et al. 2014) and statistical methods such as the Chao index (Chao 1984) or bootstrapping (Burnham and Overton 1979) can correct species richness counts, optimal study design is not always feasible, and traditional statistical estimates are biased when detection rates vary spatially or when the community contains many rare species (New and Handel 2015).

More recent approaches to account for detection error include hierarchical occupancy models (MacKenzie et al. 2002), specifically the multi-species occupancy model (MSOM). MSOMs yield less biased estimates than traditional methods by jointly analyzing an ecological model of occurrence and an observation model of detection. This strategy allows the model to explicitly differentiate between the true state of the ecological metric and detection error (Dorazio and Royle 2005, Iknayan et al. 2014, New and Handel 2015). In a Bayesian framework, MSOMs are also able to efficiently model

data-poor species, either by assuming all species are ecologically comparable (Link and Sauer 1996) or by using informative priors with information drawn from sources such as previous studies or natural history collections (McCarthy and Masters 2005). However, the structure of MSOMs often renders these two approaches incompatible. This paper presents a method that combines the above approaches to model rare or undetected species with little to no associated data.

Unlike single-species models, MSOMs assume that all species-level parameters are drawn from a common prior distribution (Fig. 1a). In other words, all species are analyzed in the context of the full community. A community-level approach means that rare or hard-to-detect species, which may not yield sufficient data to model individually, can be analyzed by "borrowing" information from common species (Link and Sauer 1996, Ferrier and Guisan 2006). Although "borrowing" information can lead to estimates of rare species that are biased towards the community mean (Kéry and Schaub 2011, Iknayan et al. 2014), in general MSOMs yield more accurate and more precise estimates of rare species than single-species models.

The use of a community-level distributions in Bayesian MSOMs also implies that species that are known to occur in the study region, but were never detected during sampling, can be included in the model using a method called data augmentation (Royle et al. 2007, Royle and Dorazio 2012, Figure 1b), in which a series of zeroes are appended to the original data set to represent species in a community that may have been undetected (Royle et al. 2007). Data augmentation yields reliable community-level estimates when model assumptions are met and few species in the community were

missed (Guillera-Arroita et al. 2019). However, the lack of data for augmented species means that estimates of occupancy or covariate responses for undetected species are inevitably "pulled" towards the center of the community distribution (Link and Sauer 1996). In practice, this lack of data means the model doesn't have enough information to accurately estimate specific occupancy or detection probabilities for particular undetected species, so these species can only be used to calculate an asymptotic species richness estimate for the study region (Guillera-Arroita et al. 2019).

In a Bayesian framework, information needed to estimate specific parameters for particular undetected species can be readily incorporated by using an informative species-level prior. Using informative priors in ecological models tends to increase the confidence in conclusions (i.e., narrower credible intervals, McCarthy and Masters 2005). In the context of hierarchical detection models, other authors have demonstrated that "weakly informative" priors can be used to stabilize the model and prevent coefficients from taking extreme values (Northrup and Gerber 2018, Lemoine 2019), but the use of ecologically informative priors is much rarer. Ecologically informative priors may be rare in part because replacing the uninformative species-level prior with an informative prior means the species is no longer described by the community-level distribution, and the advantages of modeling species in the context of the community are lost.

A potential solution to this problem is prior aggregation. Originally used to combine multiple expert opinions (Genest et al. 1984), prior aggregation can be applied to MSOMs to combine the community prior and an ecologically informative prior

into a single prior distribution (Figure 1c). With an aggregated prior distribution, the model analyzes undetected species in the context of the community while allowing researchers to retain the identity of each undetected species and reduce the pull of the community prior. However, to my knowledge prior aggregation has never been used in the context of hierarchical occupancy models, and its effects on model performance remains unknown.

Using simulated data with known parameter values, I tested whether ecologically informative, aggregated priors for undetected species improve estimates of MSOMs. I compared the posterior estimates of metacommunity richness, local species richness, and species-level covariate responses from MSOMs with 1) uninformative priors, 2) informative priors, and 3) mis-specified priors. I also varied the relative contribution of the informative or mis-specified priors to the aggregated prior to determine if prior strength influenced model estimates. Finally, I applied prior aggregation to an empirical dataset of small mammal communities in Vermont to model occupancy correlates of an undetected species known to occur in the study region.

Methods

Data simulation. I simulated 50 metacommunities of $i = 22$ species which potentially occupy $j = 1$ to 30 sites. Species-level occupancy probabilities for the first 20 species in each metacommunity Ψ_i were drawn from a beta distribution $\Psi_i \sim Beta(\alpha=2, \beta=4)$, resulting in variable occupancy probabilities (95% interval 0.053–0.716). The remaining two species, which would represent undetected species, had species-level

occupancy probabilities that were fixed at 0.1 and 0.4, respectively, to facilitate comparison across simulations. These probabilities represent relatively rare species, which are more likely to be undetected during sampling due to their low occurrence (MacKenzie et al. 2005).

Site-level occupancy probability was a function of species-level occupancy probabilities and a continuous covariate (Eq. 2). Species in each metacommunity were assigned a coefficient of 0, 3, or -3, representing no response, a strong positive response, or a strong negative response to the environmental covariate. Coefficients were randomly assigned to the 20 detected species whereas responses for the undetected species were fixed at 0 and -3. For each metacommunity, the true occupancy state of each species Z_{ij}, denoted 1 if the species was present at the site and 0 if absent, was modeled as the outcome of a Bernoulli trial with the site-level occupancy probability as the probability of success (Eq. 3). Species that did not occupy any site in the initial simulation were assigned a value of 1 to the site with the highest occupancy probability to ensure there were 22 species in each metacommunity simulation.

$$logit(\Psi_{ij}) = a0_i + a1_i cov_j \quad \text{(Eq. 2)}$$

$$Z_{ij} \sim Bern(\Psi_{ij}) \quad \text{(Eq. 3)}$$

I simulated survey data by generating species-level detection probabilities p_i using a beta distribution $p_i \sim Beta(\alpha=2, \beta=8)$, resulting in low-to-moderate detection probabilities for the 20 detected species (95% interval 0.028–0.482). Undetected species were assigned a species-level probability of 0. Detection of a species during a survey was modeled as the outcome of a Bernoulli trial with the species-level detection probability as

the probability of success, conditional on the species being present at the site. If any of the 20 "detected" species were not detected during any survey, I assigned a value of 1 to the survey with the highest detection probability to ensure there were 20 detected and 2 undetected species in each simulation. Values for the beta distributions were chosen to create a scenario in which data augmentation is effective: when some observed species in the community have low occupancy and/or low detection probabilities, it is more reasonable to expect that some species were absent from all sampled sites or missed during all surveys (Guillera-Arroita et al. 2019).

Multi-species occupancy model. I analyzed the data using a single-season Bayesian MSOM (Dorazio and Royle 2005, Figure S1-1). This modeling framework consists of three levels; the first of which represents the true occupancy state w_i of all observed and potentially unobserved species i in the metacommunity (Eq. 4). The dataset of observed species n can be augmented by m all-zero encounter histories representing species that may or may not be present in the metacommunity. Choice of m is somewhat arbitrary, but should be large enough that the posterior distribution for estimated metacommunity richness N is not truncated but not so large as to be computationally prohibitive (Guillera-Arroita et al. 2019). The parameter w_i is then modeled as a Bernoulli trial such that $w_i = 0$ for species that were not present in the metacommunity and $w_i = 1$ for species that were either directly observed or were not observed but were likely available for sampling in the metacommunity (Dorazio and Royle 2005, Royle et al. 2007), in which the parameter Ω represents the probability of success. I augmented the

simulated dataset with 5 undetected species, of which two were present in the metacommunity.

The second level of the model represents the ecological quantity of interest; in this case, site-level occupancy. Site-level occupancy Z_{ij} takes the value of 1 when species *i* is present at site *j*, provided the species is available for sampling in the metacommunity. Occupancy is modeled as the outcome of a Bernoulli trial with the probability of success defined as the product of site-level occupancy probability Ψ_{ij} and the metacommunity parameter w_i (Eq. 5). Thus, a species cannot occupy a site if it is not available for sampling in the metacommunity.

In empirical datasets, site-level occupancy Z_{ij} is often imperfectly observed due to detection error associated with the sampling process. By sampling each site multiple times over a short period, the model can estimate the probability of detecting a species during a given survey and better estimate the true occupancy state (Dorazio and Royle 2005). Detection of a given species at a site during a given sampling period (x_{ijk}) is modeled as a Bernoulli process conditional on the species occupying the site (Eq. 6). Similar to the model for site occupancy, the probability of success is defined as the product of detection probability during a given sampling period pijk and the true occupancy state Z_{ij}— meaning a species cannot be detected at a site where it is not present.

$$w_i \sim Bernoulli(\Omega) \quad \text{(Eq. 4)}$$

$$Z_{ij}|w_i \sim Bernoulli(\Psi_{ij} * w_i) \quad \text{(Eq. 5)}$$

$$x_{ijk}|Z_{ij} \sim Bernoulli(p_{ijk} * Z_{ij}) \quad \text{(Eq. 6)}$$

Environmental covariates can be used to accurately estimate occupancy and detection probabilities using a logit link function. I used the simulated covariate in Eq. 2 to estimate site-level occupancy probability Ψ_{ij}.

Species-level values for model intercepts (*a0*, *b0*) and covariate coefficients (*a1*) for all detected species were modeled using uninformative priors (e.g. Eq. 7). The parameters of the community-level distribution from which species were drawn, called hyperparameters, were in turn drawn from a hyperprior distribution (Eq. 8):

$$a0_i \sim N(\mu_{a0}, \tau_{a0}) \qquad \text{(Eq. 7)}$$

$$\tau_{a0} \sim Gamma(0.1, 0.1) \qquad \text{(Eq. 8)}$$

The parameter tau (τ) in the equations above represents precision, and is used instead of standard deviation σ in the JAGS programming language (Plummer 2017).

Although the use of a hyperprior allows species with little or no data to be modeled in the context of the full community, model estimates for these species are often "pulled" to the center of the hyperprior distribution due to a lack of data. However, solely modeling these species using highly informative priors results in a loss of the advantages gained by modeling rare species in the context of the community. Prior aggregation is a promising tool for resisting the "pull" of the hyperprior when modeling undetected species, while also retaining the advantages from modeling undetected species in the context of the community. In brief, prior aggregation involves combining two or more prior distributions using a defined pooling method (Genest et al. 1984), typically as a way to account for multiple differing expert opinions. In the context of modeling undetected species, one can aggregate 1) the hyperprior distribution, towards the center of which

undetected species are pulled, and 2) a prior distribution based on information about the undetected species that is not present in the dataset.

I calculated aggregated priors for the two undetected species for the parameters a0 and a1 using logarithmic pooling for Gaussian distributions (de Carvalho et al. 2015, Eq. 9–11):

$$\boldsymbol{w}^* = \frac{\boldsymbol{\alpha}}{\boldsymbol{\sigma^2}} \qquad \text{(Eq. 9)}$$

$$\sigma^2_{pooled} = \frac{1}{\sum \boldsymbol{w}^*} \qquad \text{(Eq. 10)}$$

$$\mu_{pooled} = \sigma^2_{pooled} * \sum(\boldsymbol{w}^* * \boldsymbol{\mu}) \qquad \text{(Eq. 11)}$$

In which σ^2 is a vector of variances of the initial prior distributions, μ a vector of means, and α a vector of pooling weights (see below). The parameter *a0* was an aggregate of the community prior $N(\mu_{a0}, \tau_{a0})$ and an ecological prior $N(\mu_{True}, \tau_{True})$. For models with informative priors, μ_{True} was the true, simulated occupancy probability that were logit-transformed and rounded to the nearest integer; models with mis-specified priors used the opposite sign as the true value. Similarly, the parameter *a1* was an aggregate of the community prior and the ecological prior. Models with informative priors used the true value for the covariate response rounded to the nearest whole number as the mean of the distribution, whereas mis-specified models used a value with the opposite sign (or a value of -3 if the true covariate response was 0). The precision parameter τ was assigned a value of 0.5 for all ecological priors.

Pooling weights (Eq. 9) define the relative contribution of individual priors to the aggregated distribution. The weight assigned to each prior distribution represents the relative degree of confidence in the information it contains (Genest et al.

1984). Methods for systematically assigning prior weights have been developed (de Carvalho et al. 2015); however, these methods are typically used for aggregating multiple expert opinions, leaving weight assignment in other situations somewhat arbitrary (French 1983). I assigned the ecological priors for weakly informative models a weight of 0.15 relative to the hyperprior; for moderately informative models, a weight of 0.5; and for strongly informative models, a weight of 0.85. The vector of weights for each aggregated prior must sum to 1.

I compared models with possible prior combinations (informative/mis-specified x weakly/moderately/strongly) to one another and to a single model with uninformative priors, resulting in seven different models. I compared estimates of 1) regional species richness, 2) site-level species richness, and 3) species-level covariate responses across the seven models. I estimated all model parameters using a Bayesian analysis in the program JAGS (Plummer 2017) and the R package R2jags (Su and Yajima 2015, R Core Team 2020). I ran the model using three Markov chains and assessed convergence using the R-hat statistic, which compares between-chain and within-chain parameter estimates for each of the Markov chains (Gelman and Rubin 1992). Values for the length of the Markov chains, burn-in period, and thinning were chosen on a trial-and-error basis until model convergence was achieved. A tutorial of the prior aggregation method using R and JAGS can be found in Appendix S2; data and code associated with the analysis can be found at https://github.com/Beasley015/Beasley2021BayesianPriors.

Application to real data. In addition to the simulation analyses, I applied the prior aggregation method to an empirical dataset of small mammal trapping surveys

collected in Vermont from May–July 2019. Sampling occurred in 30 sites located in forests, uncultivated fields, and active farms (Figure S1-2). Trapping transects were 300 m long, with trap stations 10 m apart, with two traps per station placed to maximize capture efficiency (e.g. along fallen logs or rock ledges). Traps were baited with sunflower seeds and supplemented with batting and mealworms to reduce cold-related mortality (Do et al. 2013). Traps were opened in the evening and checked the following morning for a period of 3 consecutive days. I marked captured mammals with an ear tag, identified them to species, and released them unharmed at the point of capture.

I collected vegetation data at every 3rd trap station along each transect for a total of 10 samples per site. Vegetation metrics included 1) composition, measured as the proportion of each cover type in a 0.5 x 0.5 m grid, 2) vertical structure, measured using the point-touch method described in Wiens (1969), and 3) canopy cover, measured using a spherical convex densiometer. I reduced the dimensionality of the data using a Principal Components Analysis (PCA). I incorporated the first principal component as a covariate in the MSOM.

I examined how the use of informative priors affects estimates of real datasets in a similar manner to the procedure described in the previous section. The dataset was augmented with two all-zero encounter histories; with one representing the Eastern cottontail *Sylvilagus floridanus*, a species common in the study region and visually observed at some sampling sites, but with low catchability (and therefore detectability) in Sherman live traps.

I applied aggregated priors to the occupancy intercept $\alpha 0_i$ and the covariate response $\alpha 1_i$. Prior information was derived from the literature and field notes taken during sampling (Table 1). I ran one model with weakly informative priors and another with moderately informative priors using the relative weights defined in the previous section; these models were compared to a model with uninformative priors. I compared estimates of 1) regional species richness and 2) species-level covariate responses across these three models. Model specifications such as the number of Markov chains, model iterations, and evaluation of model convergence were determined in the manner described in the previous section.

Results

Simulated data. Models with informative priors generally yielded more accurate estimates of metacommunity richness than models with uninformative or mis-specified priors (Figure 2). Specifically, models with strongly informative priors (i.e. the contribution of the ecologically informative distribution to the aggregate prior was high compared to the community distribution) typically yielded estimates that were closest to the true metacommunity richness of 22 species, whereas models with weakly mis-specified priors typically yielded estimates that were closest to the observed metacommunity richness of 20 species. Metacommunity estimates varied depending on the measure of centrality used to describe the posterior distribution from each model (Figure S1-3–S1-4).

At the site level, models with moderately and strongly informative priors yielded richness estimates that were closer to true values than models with uninformative priors (Figure 3). Models with weakly and moderately mis-specified priors generally estimated site-level richness as accurately as models with uninformative priors. Models with weakly informative and strongly mis-specified priors yielded richness estimates that deviated the most from the true values.

The model with uninformative priors correctly estimated a non-significant covariate response for one undetected species but failed to detect a significant covariate response for the second undetected species (Figure 4). Models with informative and mis-specified priors generally yielded more precise estimates of covariate responses for undetected species than models with uninformative priors (Figure 4). The models with weakly informative priors, weakly mis-specified priors, and moderately mis-specified priors yielded estimates qualitatively similar to the model with uninformed priors, and models with moderately and strongly informative priors correctly estimated covariate responses for both undetected species (Figure 4). The model with strongly mis-specified priors incorrectly estimated a positive covariate response for both undetected species (Figure 4). The improvement in covariate response estimates likely caused the improvement in site-level occupancy estimates for undetected species in models with informative priors (Fig. S1-5–S1-6).

Vermont small mammals. I captured 89 individuals representing 10 species. The most common species were the white-footed mouse *Peromyscus leucopus* with 33 individuals, the meadow jumping mouse *Zapus hudsonius* with 17 individuals,

and the woodland jumping mouse *Napaeozapus insignis* with 16 individuals. All other species were represented by fewer than 10 individuals.

The first principal component from the PCA of the vegetation data explained 82.4% of the variation in the data. This principal component was included in the model as an environmental covariate, capturing a gradient from mostly grassy cover (low PCA scores) to cover that is predominately leaf litter and other dead vegetation (high PCA scores; Figure S1-7).

The model with uninformed priors yielded a metacommunity richness estimate of 10 species, while models with informed priors yielded estimates of 11 species. At the species level, the augmented species S. floridanus was not predicted to have a covariate response significantly different from 0 in any model; however, the species-level estimate from models with informed priors were more precise than the model with uninformed priors (Figure 5).

Discussion

These results suggest that using prior aggregation to model undetected species improve estimates of multiple model parameters, provided the information supplied to the model is correct (Figures 2, 4). These findings align with previous work suggesting that informative priors in Bayesian models tends to improve model estimates (McCarthy and Masters 2005, Northrup and Gerber 2018, Lemoine 2019). In addition, prior aggregation tends to result in more ecologically meaningful conclusions for undetected species by reducing the pull of the community prior and retaining information

about species with particular characteristics rather than hypothetical species of unknown identity.

Species are more likely to be undetected when they are rare (McCarthy et al. 2013). Rare species are often of conservation concern (Fagan et al. 2002, Cunningham and Lindenmayer 2005, MacKenzie et al. 2005) and can drive site-level variation in metrics such as species richness, beta diversity, and functional diversity (Routledge 1977, Mao and Colwell 2005, Leitão et al. 2016, but see Lennon et al. 2004). A common strategy for addressing this problem is to use common, closely-related species as a proxy for rare relatives (Gaston and Kunin 1997). Modeling undetected species using uninformative priors is conceptually similar to using data from related species as a proxy, as estimates for undetected species are pulled towards the center of the community prior. However, rare and common species are often ecologically different (Kunin and Gaston 1993, Leitão et al. 2016), and accounting for these differences with ecologically informative priors can lead to more accurate estimates on which to base management decisions.

From a management perspective, estimates for specific sites may be just as important as regional or species-level estimates, especially for targeted management actions such as habitat restoration efforts or reserve design (Cabeza et al. 2004). My results suggest that prior aggregation does not improve site-level model estimates (Figure 3), and therefore prior aggregation may not be appropriate when characteristics of the site are of primary interest. However, the lack of improvement of site-level estimates may be due to characteristics of the simulated data and model structure rather than characteristics

of the priors. The simulated dataset included species with positive and negative covariate responses, which could be affecting the accuracy of site-level richness estimates compared to a covariate with more uniform effects, such as patch area. Models for the simulated and empirical datasets also assumed stochastic detection error. Detectability in real communities is often influenced by site-level or species-level characteristics (Iknayan et al. 2014), and accounting for site-level variation in detectability using model covariates tends to improve estimates (New and Handel 2015). In systems where detectability varies by site and is modeled using a covariate, the use of prior aggregation may improve site-level richness estimates compared to models with uninformative priors.

A key component of prior aggregation is assigning weights to each of the contributing priors. Weight choice determines how much of the ecologically informed prior contributes to the final aggregate and should reflect the reliability of the source of information (Genest et al. 1984). Defining the reliability of a source is difficult, and in practice the choice of prior weight is somewhat arbitrary (French 1983). That said, methods for choosing weights in a more meaningful way have been developed (Myung et al. 1996, Abbas 2009, Rufo et al. 2012a, 2012b) and a few of these also account for uncertainty about the weights (Poole and Raftery 2000, de Carvalho et al. 2015). A possible avenue for future research would include adapting these methods for use in MSOMs.

The concept of "borrowing" data from multiple sources is not new in ecology (MacKenzie et al. 2005), and pooling information across species within a dataset is a common practice in hierarchical detection models (Link and Sauer 1996, Iknayan et

al. 2014). Using prior aggregation to incorporate data from external sources such as previous studies or natural history collections to improve model accuracy is an extension of this concept. Although this work has focused on prior aggregation in the context of MSOMs, the flexibility of hierarchical detection models means that prior aggregation is not limited to questions of species richness or occupancy. Prior aggregation can potentially be used to add information about missing individuals in a population (Royle and Dorazio 2012) leading to more accurate estimates of abundance, survival rates, or diversity estimates. Despite the continuing challenges of choosing meaningful prior weights (Genest et al. 1984, de Carvalho et al. 2015) and prior selection in Bayesian ecological models in general (Northrup and Gerber 2018, Lemoine 2019, Banner et al. 2020), prior aggregation is a promising tool for using external data to generate more reasonable estimates in systems where non-detection is of ecological concern.

Acknowledgements

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other farmers and land managers. Methods were approved by the University of Vermont IACUC (Protocol #PROTO202000114).

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Tables

Table 1. Sources of ecologically informative priors for *S. floridanus*.

Parameter	Source	Description
α_0	Field notes	*S. floridanus* was visually observed at 20% of sites; the mean of the prior distribution was set at this value
α_1	Chapman et al. 1980, DeGraaf and Yamasaki 2001	Old fields and grasslands are preferred habitat in the northeastern United States, interpreted as a negative response to PC1. The mean of the prior distribution was set at -2.
	Field notes	All visual observations of this species occurred in old fields or active farms.

Figures

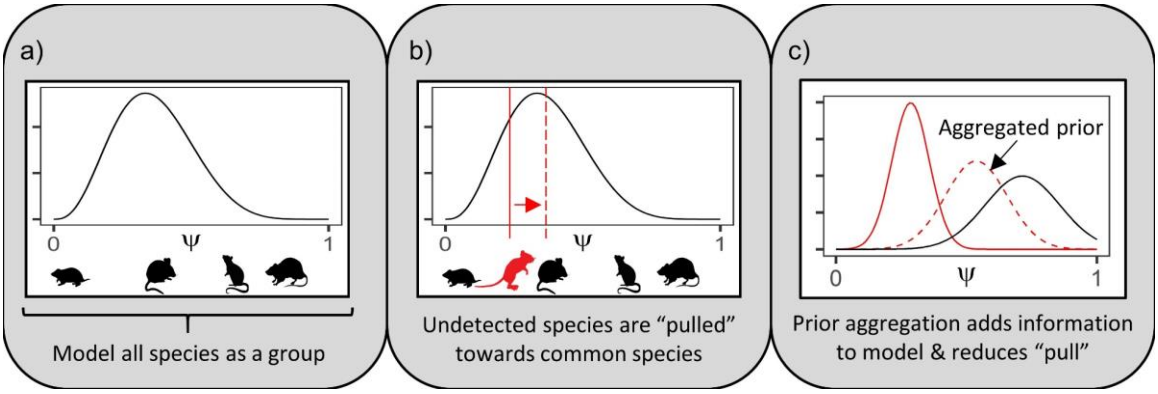

Figure 1. a) Community-based detection models account for rare or undetected species by assuming all species-level parameters, such as occupancy probability Ψ, are drawn from a common probability distribution called a hyperprior. b) Species that were never detected during sampling (red) can be analyzed by adding a set of zeroes to the data. However, a lack of data means the estimated parameters (dashed red line) are "pulled" to the center of the distribution and away from the true value (solid red line). c) When the identities of undetected species are known, the hyperprior (black line) can be combined with species-level information (solid red line) to form an aggregated prior (dashed red line) to reduce the "pull" of the hyperprior and more accurately model these species.

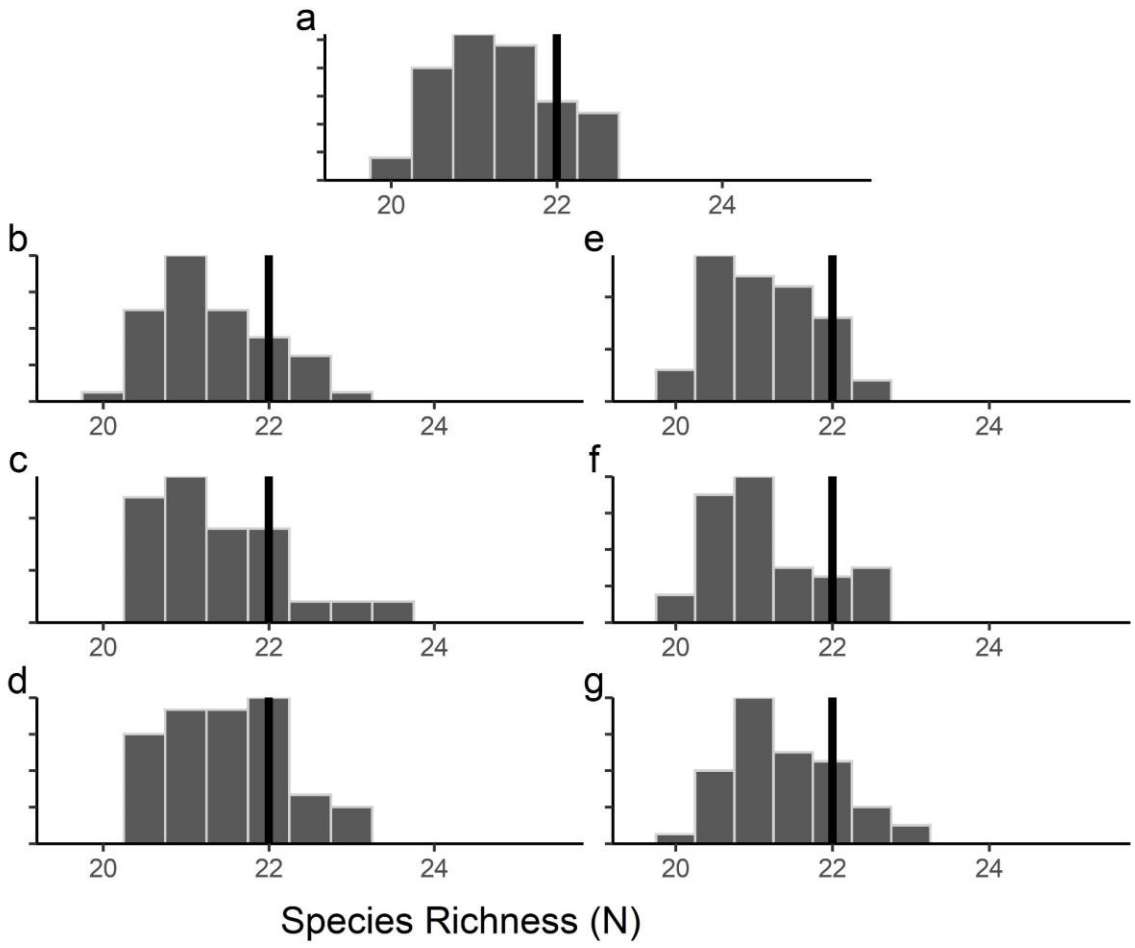

Figure 2. Distribution of estimated mean regional species richness (N) of the simulated datasets. Solid lines denote the true regional richness of 22 species. Models with uninformative priors (a) tended to yield an expected richness of 21 species. Models with weakly and moderately informative priors (b-c) yielded qualitatively similar estimates, as did models with moderately and strongly mis-specified priors (f-g). Models with weakly mis-specified priors tended to yield an expected richness of 20.5 species (e). Models with strongly informative priors yielded an expected richness of 22 species, the true regional richness of the simulated datasets.

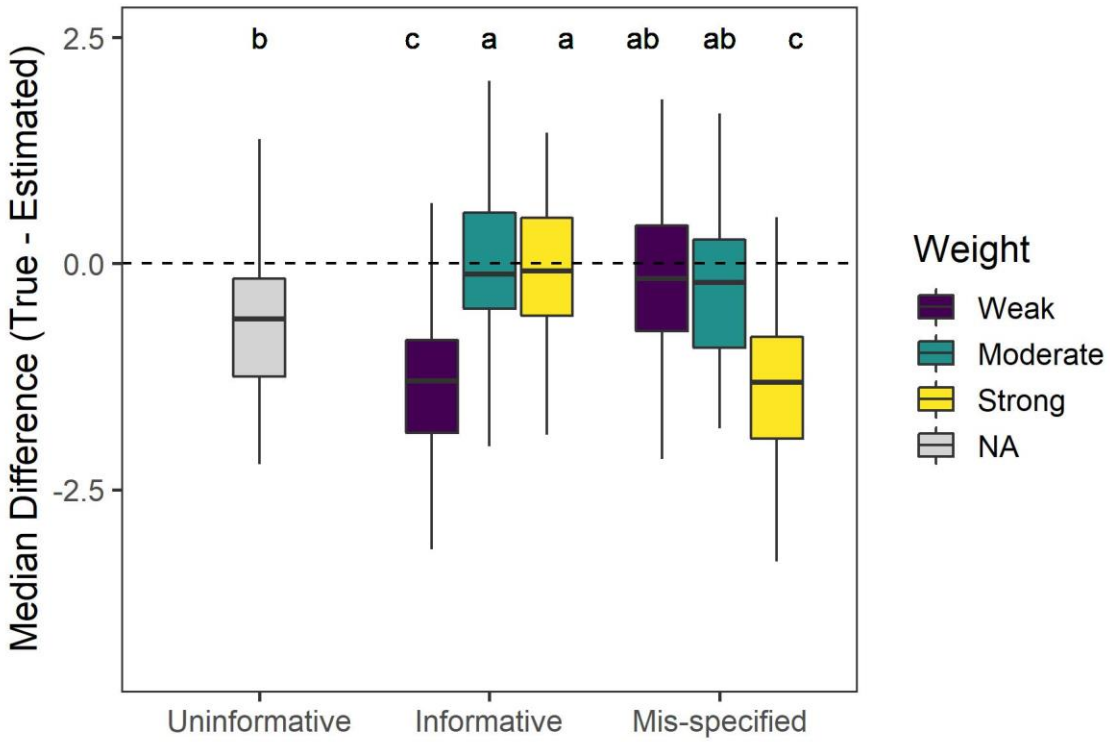

Figure 3. Median differences between true and estimated site-level richness of the simulated datasets. Models with moderately and strongly informative priors outperformed models with uninformative priors and strongly mis-specified priors. Models with weakly informative priors and strongly mis-specified priors performed less well than models with uninformative priors.

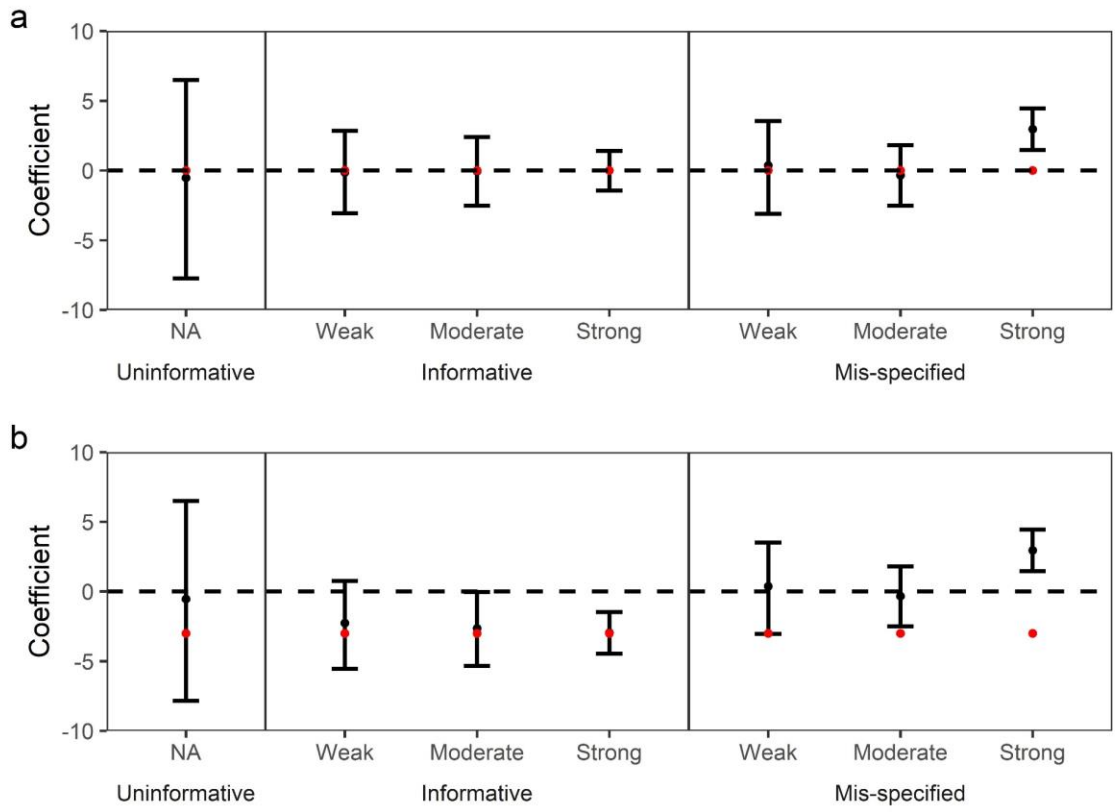

Figure 4. Estimated responses of two undetected species to simulated covariates. Error bars represent the 95% CI; error bars that did not overlap 0 (dashed line) were considered significant. Red dots represent the true value of the simulated coefficient. Increasing the relative weight of the species-level prior increased the precision of model estimates, regardless of the accuracy of the prior. The model correctly estimated a non-response to the covariate in all models except models with strongly mis-specified priors for the first undetected species (a). Models with moderately and strongly informative priors correctly estimated a significant, negative response to the covariate for the second undetected species (b).

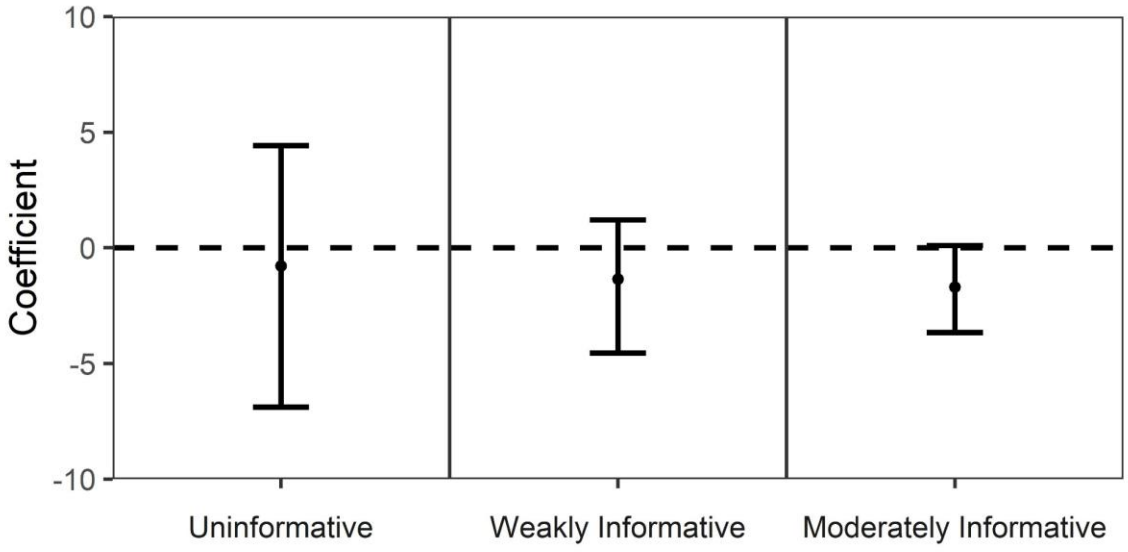

Figure 5. Species-specific responses to the vegetation covariate for the augmented species *Sylvilagus floridanus*. Error bars represent the 95% credible interval; bars that do not overlap 0 (dashed line) were considered significant and are marked with an asterisk (*).

Ectoparasite life history traits influence occupancy patterns at varying organizational scales

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Abstract

Ectoparasites are exposed to a 'dual' environment: the stable conditions on an individual host and a variable external environment. However, variation in ectoparasite life history traits, such as the portion of the life cycle spent on-host, leads to differences in selective pressure exerted by each environment. Parasites that spend most of the life cycle on-host are pressured to undergo increased host specialization, leading to differences in host specificity and occupancy patterns compared to ephemeral parasites which only contact the host to feed. Using data from small mammals and ectoparasites in Vermont, I used a multi-scale MSOM to 1) estimate ectoparasite occupancy on individual hosts nested within geographic sites, 2) calculate the Bayesian R2 at the site and host levels of the model to determine the variation in occupancy explained by each level, and 3) compared number of host species and the R2 values across different life history categories. Life history category was significantly associated with host specificity and host-level Bayesian R2: parasites which spend their full life cycle on the host parasitized fewer host species and had significantly more variation in occupancy explained by host-level covariates than ephemeral parasites. However, there were no significant differences in site-level R2 between life history categories, and no significant associations between site-

level R2 and host specificity, suggesting that additional factors may play a role in structuring small mammal/ectoparasite communities.

Introduction

Ecology is highly scale-dependent (Wiens 1989, Levin 1992, Schneider 2001, McGill 2010). The relative importance of ecological processes tends to vary across spatial, temporal, and organizational scales (Ellison and Gotelli 2021). For example, short term weather events and microclimates may influence local occupancy patterns of a species, but climate may be more important in limiting the extent of a species' range (Zuckerberg et al. 2011). Additionally, patterns at a coarser scale such as the landscape may emerge from processes occurring at a finer scale such as local sites (Ovadia and Schmitz 2002). The scale of observation can also influence which patterns can be detected in a system (Wiens 1989, McMahon and Diez 2007, Weiher et al. 2011). Observing and analyzing variables on multiple hierarchical levels is essential for understanding how ecological processes operate across scales.

Small mammals and their arthropod ectoparasites are useful for investigating the effects of scale because the organizational scales in the system are often clearly defined (Cardon et al. 2011). For example, host/parasite dynamics can be observed at the level of the individual host (i.e. host infra-community), across host individuals in a local population or community, or across a host species' geographic range (Krasnov et al. 2011b, 2015). Ectoparasites, unlike endoparasites such as helminths, are simultaneously exposed to multiple scales: specifically, the more localized environment of the host

individual and the broader environment of the host community or geographic locality (Cardon et al. 2011). Occupancy patterns of ectoparasites at various scales are determined by characteristics of this 'dual' environment of the host assemblage and external environment (Berkhout et al. 2020, Bolnick et al. 2020).

Although all ectoparasites are characterized by a dual environment, variation in ectoparasite life history and feeding mode leads to variation in the degree of exposure to the host environment relative to the external environment (Morand et al. 2007, van der Mescht et al. 2016). Ephemeral parasites such as ticks (order Ixodidae) are only in contact with the host during feeding and spend more time in the external environment (Kocan et al. 2015). By contrast, parasitic lice (order Psocodea) complete the full life cycle on the host (Kim 2006). Nest parasites such as certain mite (order Mesostigmata, Dowling 2006) or flea (Medvedev and Krasnov 2006) species, as well as species which associate with a host for a particular life stage (e.g. bot flies, order Diptera, Catts 1982, or fur fleas, (Medvedev and Krasnov 2006)), fall somewhere in between.

In addition to host contact, host specificity varies between ectoparasite species (Poulin and Mouillot 2003, Poulin 2007, Brown et al. 2022) and may influence the range of exposure to environmental pressures within an organizational scale: parasites specializing on one host species are exposed to less host-level variation than generalist parasites which may infest multiple host species. Differences in host contact and host specificity result in variation in the strength exerted by environmental pressures at each scale (Bolnick et al. 2020).

Differences in the relative strength of environmental pressures at different scales should result in observable differences in ectoparasite occupancy patterns. Specifically, I hypothesize that 1) the amount of host contact influences the relative strength of selective pressures at each environmental scale: parasite occupancy should be primarily driven by factors at the scale where the parasite spends most of its life cycle (Marshall 1981, Lareschi and Krasnov 2010, Sponchiado et al. 2017). Additionally, 2) host contact should also influence the selective pressure to specialize: parasites which spend a greater proportion of the life cycle on-host should parasitize fewer host species than parasites which spend less time on-host. Although associations between host contact and specialization have not been formally tested, host specificity has be found to be associated with other life history traits such as transmission mode (Pedersen et al. 2005, Poulin et al. 2006).

To test these hypotheses, I will use a multi-scale, multi-species occupancy model (multi-scale MSOM) to 1) estimate ectoparasite occupancy in geographic sites and individual hosts within each site while correcting for detection error, 2) evaluate effects of site-level and host-level covariates on ectoparasite occupancy, and 3) calculate Bayesian R^2 to quantify the explanatory power of each level of the model. If host contact influences host specificity and occupancy patterns at each organizational scale, ectoparasite species that spend the majority of their life cycle on-host (e.g. lice, fur fleas) should parasitize fewer host species and have a larger host-level Bayesian R^2 than ectoparasites in other life history categories (Lareschi and Krasnov 2010). Ephemeral parasites which only contact the host during feeding (e.g. ticks) should display the

opposite trend, parasitizing many host species with a larger site-level Bayesian R^2 than other ectoparasites. Nest parasites (e.g. nest fleas, mesostigmatid mites) will likely fall somewhere in between.

Methods

Site-level environmental measurements. I sampled 10 sites located throughout Chittenden County, Vermont from May–August 2020. Four sites were located on active farms, three in old fields, and three in forested habitats. I sampled each site three times over the course of the study: the first sampling period was from May 26–June 14, the second from June 19–July 9, and the third from July 15–August 3. I set a 300 m linear sampling transect at each site. When possible, the transect began at the edge of the habitat patch and extended towards the center. Transects were sampled for a total of 3 consecutive trap days per sampling period for a total of 9 days per transect.

I measured site-level environmental variables on the first day of each trapping session at 30 m intervals along the sampling transect. I quantified site-level environmental variation by sampling vegetation cover, vertical structure, and canopy cover within a 0.5 m^2 quadrat. I quantified vegetation cover by recording the relative proportion of each cover type (e.g. grass, leaf litter) within the quadrat. Vertical structure was quantified using the point-touch method described in Wiens (1969). I measured canopy cover using a spherical convex densiometer. I repeated vegetation data collection once per sampling period and reduced the dimensionality of the data using a PCA. I ran

separate PCAs for vegetation composition variables, vertical structure variables, and all vegetation variables.

Small mammal trapping. To capture small mammal hosts, I placed trap stations every 10 m along the 300 m sampling transect. Each trap station consisted of two traps baited with sunflower seeds and 5 g dried mealworms and placed to maximize trapping efficiency (e.g. along fallen logs). I placed batting in each trap when night temperatures fell below 50°F (10°C) to reduce cold-related mortality (Do et al. 2013). Traps were set each evening and checked just after dawn the following morning for three consecutive trap days per sampling period.

Upon checking traps, captured mammals (excluding by-catch species) were transferred to a cloth handling bag. Rodents were marked with a unique ear tag and shrews were marked by clipping a patch of fur near the rump or shoulders, the location of which was used to identify individuals. Species, sex, mass, and standard external measurements (Hall 1962) were recorded for each mammalian host. I then searched for ectoparasites for a period of at least two minutes. Collected ectoparasites were stored in 70% ethanol. After handling, mammals were released at the point of capture. By-catch species (e.g. *Mustela* sp., *Glaucomys* sp.) were released at the point of capture without handling. Mammals found dead in the trap or euthanized due to poor body condition were prepared as museum specimens and deposited in the Zadock Thompson Natural History Collections at the University of Vermont. All handling procedures followed guidelines from the American Society of Mammalogists (Sikes and the Animal Care and Use

Committee of the American Society of Mammalogists 2016) and were approved by the University of Vermont IACUC (Protocol #PROTO202000114).

Parasite sampling. After collection, all ectoparasites were prepared for identification and permanent storage. Fleas and ticks were cleared of host blood and other soft tissues by making a small incision in the exoskeleton and suspending the parasite in 10% KOH for 12–24 hours. After clearing, fleas and ticks were returned to a 70% ethanol solution for 24 hours. All parasites were dehydrated by soaking for at least 24 hours in increasing concentrations of ethanol: 70%, 85%, and 95%. After dehydration, parasites were identified to the lowest possible taxonomic level and preserved in either 95% ethanol or slide mounted using synthetic Canada balsam medium. Fleas were identified to species using Benton (1983) and Lewis (2000, 2009); adult and nymph ticks were identified to species using Keirans & Litwak (1989), whereas larval ticks were identified to species using Coley (2015); mites were identified to order, and when possible family and genus, using Krantz & Walter (2009) and Allred & Beck (1966). All parasites were deposited in the Zadock Thompson Natural History Collections at the University of Vermont.

Analytical Methods. All analyses were completed in R 4.1.2 (R Core Team 2021) unless otherwise specified. Data and code are available at https://github.com/Beasley015/EctoLifeHistory.

I estimated ectoparasite occupancy at the site and host level using a multi-scale MSOM (Nichols et al. 2008, Szewczyk and McCain 2019). Like other hierarchical detection models, multi-scale MSOMs differentiate between an ecological metric of

interest (e.g. occupancy) and the survey process used to observe the ecological metric (e.g. small mammal trapping). Using data from repeated sampling events, hierarchical detection models can estimate the detection error in the sampling method and use it to generate more accurate estimates of the ecological metric (MacKenzie et al. 2002, Dorazio and Royle 2005, Iknayan et al. 2014). Multi-scale MSOMs differ from other hierarchical detection models by introducing multiple scales at which the ecological metric can be measured (Nichols et al. 2008). In the context of this study, ectoparasite species can occur at a geographic site and on small mammal hosts nested within the geographic site (Figure 6). Using repeated captures of each individual host, multi-scale MSOMs can more accurately estimate ectoparasite occupancy at each of these organizational scales.

Environmental covariates can be included at each level of the multi-scale MSOM to improve occupancy estimates and evaluate the effects of the covariates on occupancy. For the site-level model, I included vegetation covariates based on the results of the PCA. Covariates in the host-level model included host species, adjusted body mass, and host sex, each of which may affect ectoparasite occupancy patterns (Poulin and Mouillot 2003, Krasnov et al. 2012, Kamiya et al. 2014b). Host mass was scaled within each host species to better reflect body size variation of individuals within a species rather than across species. All other covariates were scaled to have a mean of 0 and a standard deviation of 1.

I analyzed the model using a Bayesian framework using JAGS 4.3.0 (Plummer 2017) with the R package R2jags (Su and Yajima 2015). I used uninformative priors for

all model parameters. Markov chain Monte Carlo sampling was completed using 3 chains of length 12,000 including a burn-in period of 5,000; thinned by 12 to reduce autocorrelation. Model convergence was assessed by visually examining the trace plots of the Markov chains and using the R-hat statistic (Gelman and Rubin 1992); an R-hat less than 1.1 was considered converged. Full model specifications are available in Appendix S2. Because larvae and nymphs of *Ixodes scapularis* vary in their ecology, particularly in phenology and host preferences (Levi et al. 2015, Kocan et al. 2015), I ran the model with *I. scapularis* individuals aggregated and with the life stages treated as separate species.

I calculated the variance explained by each level of the model using the Bayesian R^2 value proposed by Gelman et al. (2019). In the context of hierarchical models, Bayesian R^2 differs from classical R^2 definitions in two important ways: first, other measures of explained variance for hierarchical models are in comparison to a null model (Gelman and Pardoe 2006), whereas Gelman et al.'s (2019) definition of Bayesian R^2 summarizes the fit of each level within a single model. Second, there are certain instances in a Bayesian framework where the formula for classical R^2 (essentially, explained variance/total variance) can yield a result greater than 1 (Tjur 2009). Bayesian R^2 always yields a value between 0 and 1 (Eq. 12).

$$Bayesian\ R^2 = \frac{Explained\ variance}{Explained\ variance + residual\ variance} \quad \text{(Eq. 12)}$$

I calculated Bayesian R^2 for the site and host levels of the model based on Gelman et al. (2019). Further details of the analysis are available in Appendix S4.

I performed model selection using the Watanabe-Akaike Information Criterion (WAIC), an information criterion that performs better for hierarchical Bayesian models than traditional methods such as AIC (Hooten and Hobbs 2015). I performed model selection separately for the site and host levels of the model. In other words, when calculating the WAIC for each combination of model covariates for the site-level model, the host level model remained fixed with all covariates, and vice versa. Models with the lowest WAIC value were considered the best; models within two WAIC values of each other were considered equivalent.

To test the hypothesis that the amount of host contact influences ectoparasite occupancy patterns and host specificity, I assigned life history categories to each ectoparasite species based on the literature (Table S3-1). I compared site-level Bayesian R^2, host-level Bayesian R^2, and number of parasitized host species between categories using a Kruskal-Wallis test (Kruskal and Wallis 1952). Pair-wise comparisons were completed using a Dunn test (Dunn 1961). Life history categories with less than two species were not included in the analysis.

Because hosts and their parasites retain tight co-evolutionary links (Hafner and Nadler 1988, Poulin 2007), ectoparasite covariate responses are likely to mirror those of their hosts. To test this idea, I performed a MSOM on the host species using the same site-level covariates as the ectoparasite model. The structure of the host MSOM is similar to the ectoparasite MSOM, but the host MSOM only contains site occupancy as the ecological metric of interest. I analyzed the host MSOM using a Bayesian framework in JAGS 4.3.0 (Plummer 2017) and used uninformative priors for all model parameters.

Markov chain Monte Carlo sampling was completed using 3 chains of length 5,000 including a burn-in period of 1,000; thinned by 5 to reduce autocorrelation. Full specifications for the host MSOM can be found in Appendix S4.

To compare host and parasite covariate responses, I began by identifying the primary host species for each ectoparasite species. I used a method presented by Benton and Cerwonka (1960) to classify fleas based on host relationships and adapted it to identify the primary host for each ectoparasite species. For all ectoparasite species for which at least 5 individuals were collected, I visually inspected the distribution of abundances upon each host species (e.g. Figure S3-1). Because relative host abundance is likely to influence this distribution, I repeated the analysis using ectoparasite abundances that were adjusted for the relative abundance of each host. In cases where there was no clear preference between two or more host species (Benton and Cerwonka 1960), I included all potential primary host species in the analysis. Where possible, I verified the primary host species from previous studies (Table S3-2); in cases of conflict between the data and the literature, the primary host identified using the data was used because primary host identity may vary geographically (Benton and Cerwonka 1960, Krasnov et al. 2011a). Parasites for which fewer than 5 individuals were collected were also included in the analysis if there was a clear primary host based on the literature (Table S3-2).

After identifying primary hosts, I compared primary host and ectoparasite responses using a linear regression with the posterior mean of the host coefficient as the predictor variable and the posterior mean of the ectoparasite coefficient as the response variable. I repeated the regression for each vegetation covariate in the models.

Results

Data summary. The raw data consisted of 753 small mammal captures representing 11 species. Of these, two non-target species (*Tamiasciurus hudsonicus* and *Mustela* sp.) were removed from the dataset, along with 12 individuals that were found dead in the trap before the final day of sampling (2 *Microtus pennsylvanicus*, 1 *Sorex cinereus*, 9 *Blarina brevicauda*). The final dataset consisted of 417 individuals representing 8 species. The most common species was the white-fooded mouse *Peromyscus leucopus* with 222 individuals, followed by the meadow jumping mouse *Zapus hudsonius* with 78 individuals. The least abundant species was *Napaeozapus insignis* with 4 captured individuals (Figure S3-2).

I collected 410 ectoparasites representing 4 orders and 17 species from the captured small mammals. Prevalence averaged 0.465 across all host species and ranged from 0.105–0.788 among host species (Figure S3-3). Of hosts infested by at least one parasite, parasite load per capture event was typically 1 ectoparasite, with a range of 1–10 parasites (Figure S3-4).

Vegetation composition and vegetation height were highly correlated ($r = 0.844$) and the PCA with all vegetation data indicated that most of the variation in the data was explained by composition variables. Thus, results of the composition-only PCA were included in the model. The PCA yielded a first principal component that explained 92.5% of variation in the vegetation data and ranged from primarily grass and forb cover to primarily dead vegetation, specifically leaf litter (Figure S3-5). The second principal

component explained 7.2% of the variation in the data and ranged from primarily grass cover to primarily forb cover. The remaining principal components explained less than 5% of the variation in the data and were not included in the model.

Model Results. Model results with *I. scapularis* aggregated and disaggregated by life stage were qualitatively similar. The results below are from the model with disaggregated life stages.

Life history category was significantly associated with host specificity (χ^2 = 10.388, P = 0.006, η^2 = 0.645): fur parasites had fewer host species than ephemeral or nest parasites ($z_{ephemeral,fur}$ = -2.70, P = 0.007; $z_{fur,nest}$ = 2.65, P = 0.008, Figure 7). Associations between life history traits and site-level and host-level Bayesian R^2 values were generally non-significant (Site-level χ^2 = 4.601, P = 0.067, η^2 = 0.262; host-level χ^2 = 5.404, P = 0.100, η^2 = 0.200, Figure 7). However, there is some evidence for weak associations between the explanatory power of each level of the model and life history category. Despite being non-significant, the large effect size of the Kruskel-Wallace test indicates that site-level covariates may explain less variation in occupancy of nest parasites than fur or ephemeral parasites (Figure 8a). Additionally, a Dunn test yielded significant pair-wise differences in host-level Bayesian R^2 between fur and ephemeral parasites ($z_{fur,ephemeral}$ = 2.02, P = 0.044, Figure 8b). Host specificity is significantly associated with Bayesian R^2 values at the host level ($F_{1,15}$ = 16.59, P = 0.001, R^2 = 0.494, Figure 9b) but not the site level ($F_{1,15}$ = 1.924, P = 0.186, R^2 = 0.055 Figure 9a).

Model selection at the site level yielded a model with the Grass/Forb covariate as the best model; however, the full model containing both site-level covariates performed

equally well (Table 2). The best model at the host level was the model with all covariates. Models with the covariate for host species and either the covariate for mass or sex performed as well as the best model, indicating host species is likely the most important covariate for host-level occupancy (Table 2).

Primary host results were identical for raw counts and adjusted counts for all but two parasite species; therefore, the results using raw counts are discussed here. Results from the host MSOM indicated that hosts vary in their responses to PC1 (dead vegetation vs. grass/forb, Figure S3-6a) but not PC2 (grass vs. forb, Figure S3-6b). Thus, host and parasite covariate responses were only compared for PC1. Because host responses to PC1 behaved categorically (Figure S3-7), hosts were pooled based on habitat preference before comparing them to the parasite responses. Parasite covariate responses were not significantly associated with host habitat preferences; however, this may be an artifact of sample size ($t = 2.322$, $df = 1.84$, $P = 0.157$, $d = 1.52$, Figure 10)

Discussion

These results suggest that ectoparasite life history, specifically time spent in contact with the host, is associated with occupancy patterns and host specificity. Consistent with my predictions, fur fleas, which spend the greatest proportion of the life cycle on the host, parasitized fewer host species and had higher Bayesian R^2 values in the host-level model than ephemeral parasites which only contact the host to feed (Figures 7, 8b). Host-level Bayesian R^2 was negatively associated with host specificity (Figure 9b),

indicating that host traits explain less variation in occupancy for more generalist ectoparasite species. However, ephemeral and fur parasites did not differ in site-level Bayesian R^2 (Figure 8a), indicating that associations between life history, host specificity, and occupancy patterns may be more complex than my predictions would suggest.

Despite clear differences between life history categories at the host level, the explanatory power of the host model was very low (Figures 8b, 9b). Although this may seem counterintuitive given many ectoparasites retain strong phylogenetic associations with their host species (Brooks 1979, Hafner and Nadler 1988, Klassen 1992, Poulin 2007), the finding makes sense given the structure of the multi-scale MSOM. Because there is more variability in occupancy between host individuals than between host populations (i.e. more variability at the host than site levels), it is more difficult to predict ectoparasite occupancy on an individual host. Previous work has shown similar findings, in which parasite infra-communities (i.e. communities on an individual host) appear to be stochastically structured despite parasite communities displaying nonrandom structure at the host population level (Rynkiewicz et al. 2019). A null model analysis would be useful in determining whether infra-communities are structured stochastically (Gotelli 2001, Ulrich and Gotelli 2013), but such an analysis is beyond the scope of this paper.

The lack of differences in Bayesian R^2 at the site level may be due to the confounding effect of host habitat preferences: ectoparasites may be responding to host availability rather than characteristics of the geographic site. There is some support in the data for this conclusion: host species identity was in the best host models based on WAIC, and parasite site-level coefficients were weakly associated with host habitat

preferences. Anecdotally, host switches, in which ectoparasites not primarily associated with *P. leucopus* were collected from that species, tended to occur at sites where the primary host was present (Table S3-3). Host availability has been previously demonstrated to be a key driver of ectoparasite occupancy (Kamiya et al. 2014a, Johnson et al. 2016); and although there is some evidence that host availability is important in the context of these data, there is not enough support for a definitive conclusion.

Given the evidence above, it is possible that life history traits are not a primary driver of ectoparasite occupancy patterns. Rather, availability of the primary host species may be the main driver of ectoparasite occupancy, and life history traits influence a parasite's ability to switch to a non-preferred host. Parasite host switching is a common occurrence (Brooks and Hoberg 2007, Agosta et al. 2010), and parasite persistence on sub-optimal hosts is thought to be a stepping-stone for colonizing unrelated hosts (Araujo et al. 2015). Host availability as the primary variable influencing parasite occupancy has support in this dataset in that 1) host species identity was in the best models as selected by WAIC, and 2) generalist ectoparasites typically occurred on 1–2 preferred host species (Figure S3-8) and occupied secondary hosts at much lower rates. More work is needed to address whether life history traits influence host switches, as few studies have explored associations between host contact and host switching ability (but see Toit et al. 2013, Engelbrecht et al. 2016), and the dataset discussed here lacks control sites that *P. leucopus* did not occupy.

Alternatively, the lack of differences in site-level Bayesian R^2 between life history categories could be a result of different ecological processes affecting different

life history categories. As mentioned previously, ephemeral parasites such as ticks only contact the host to feed, and spend most of their life cycle in the external environment. As a result, it is likely that ticks truly respond to characteristics of the external environment, as demonstrated by previous studies (Ginsberg et al. 2017, Linske et al. 2019, Gallagher et al. 2022). By contrast, fur parasites such as fur fleas may be primarily influenced by host availability (Krasnov et al. 2002, 2019, Kamiya et al. 2014a, 2014b), and the high site-level R^2 may reflect host habitat preferences. Further work is needed to disentangle the effects of these two potential drivers of ectoparasite occupancy.

Multi-scale MSOMs are a useful framework for investigating host-ectoparasite communities, as the structure of the model reflects the hierarchical organization present in these systems (Nichols et al. 2008, Szewczyk and McCain 2019). MSOMs are also useful for reducing detection error, which may obscure patterns due to biased sampling methods or stochastic non-detection (Dorazio and Royle 2005, Iknayan et al. 2014). However, despite the modeling framework's utility for detecting patterns, MSOMs are limited in their ability to infer the mechanisms underlying said patterns. The associations between life history traits and occupancy patterns discussed in this paper could be a result of multiple different process which are not necessarily mutually exclusive, and further research is needed to differentiate between them.

In conclusion, this study demonstrates that host contact is associated with host specificity and the explanatory power of host-level variables on ectoparasite occupancy. However, host contact does not appear to be associated with the explanatory power of site-level variables. It is possible that host contact influences occupancy patterns

indirectly, such as by influencing a parasite species' ability to infest a non-primary host. More work is needed to disentangle the mechanisms by which ectoparasite life history traits such as host contact influence occupancy patterns across organizational scales.

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Tables

Table 2. Results of model selection using WAIC. The best model for each hierarchical level is indicated by a ΔWAIC of 0.00; models with a ΔWAIC less than 2 are considered equivalent to the best model.

Level	Model	WAIC	ΔWAIC
Site	Grass/Forb	79.43	0.00
	Grass/Forb + Dead Veg	79.64	0.21
	Intercept	81.95	2.52
	Dead Veg	83.56	4.13
Host	Species + Mass + Sex	83.86	0.00
	Species + Mass	84.40	0.54
	Species + Sex	85.82	1.96
	Species	89.28	5.42
	Intercept	91.64	7.78
	Sex	92.33	8.47
	Mass	93.88	10.02
	Sex + Mass	94.31	10.45

Figures

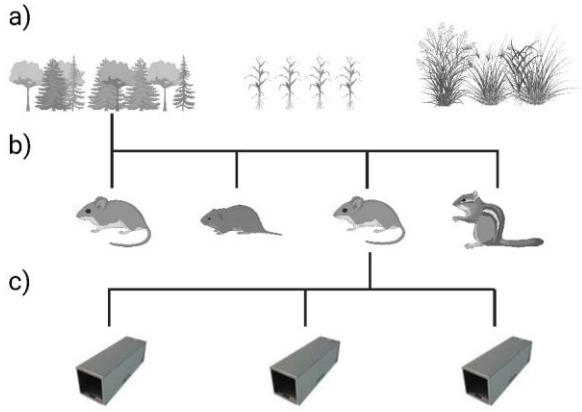

Figure 6. Conceptual diagram of the hierarchical system modeled using the multi-scale MSOM. Ectoparasite species may occupy a series of geographic sites (a), each with a suite of habitat characteristics. Each site contains small mammal hosts (b) that vary in characteristics such as species and body size. Each individual host is a sampling unit on which an ectoparasite may occur. By repeatedly sampling from each host over multiple captures (c), the MSOM can estimate the probability of detecting an ectoparasite species on a host given it is present.

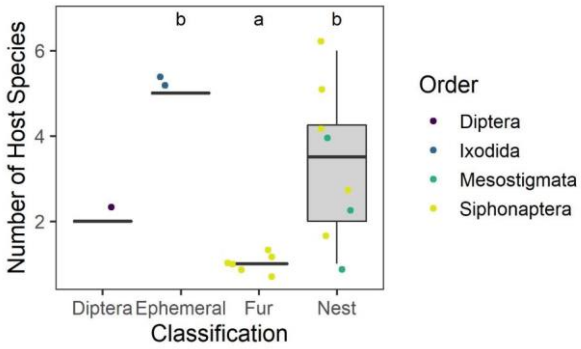

Figure 7. Number of host species parasitized by each ectoparasite species, separated by life history classification. Colors denote parasite order; letters indicate group assignments based on a Dunn test. Points are jittered for clarity. Fur parasites parasitized significantly fewer host species than nest parasites or ephemeral parasites (χ^2 = 10.388, P = 0.006, η^2 = 0.645). Bot flies (Diptera) are shown but were not included in the analysis due to small sample size.

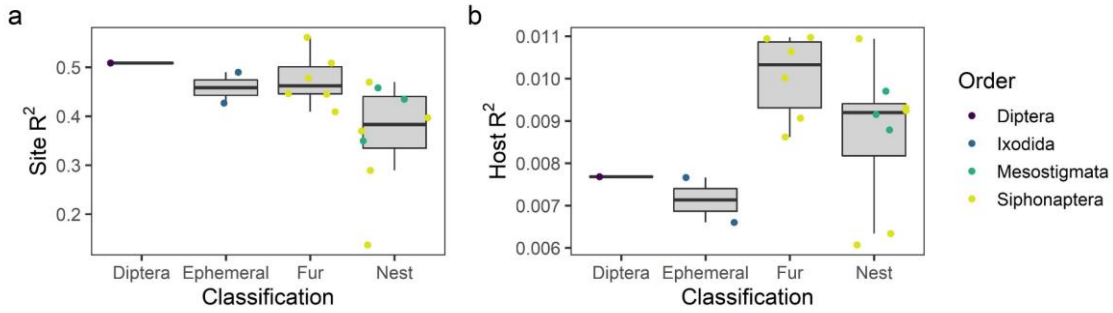

Figure 8. Bayesian R^2 values from the site model (a) and host model (b) for each ectoparasite species. Colors denote order; points are jittered for clarity. There were no significant differences in site-level R^2 between life history groups; however, the effect size (η^2) indicates nest parasites may have slightly less variation explained by site-level covariates than other groups (χ^2 = 4.601, P = 0.067, η^2 = 0.262). There were also no significant differences in host-level R^2 between groups (χ^2 = 5.404, P = 0.100, η^2 = 0.200), but pair-wise comparisons using a Dunn test yielded significant differences between ephemeral and fur parasites (P = 0.044). Bot flies (Diptera) are shown but were not included in the analysis due to small sample size.

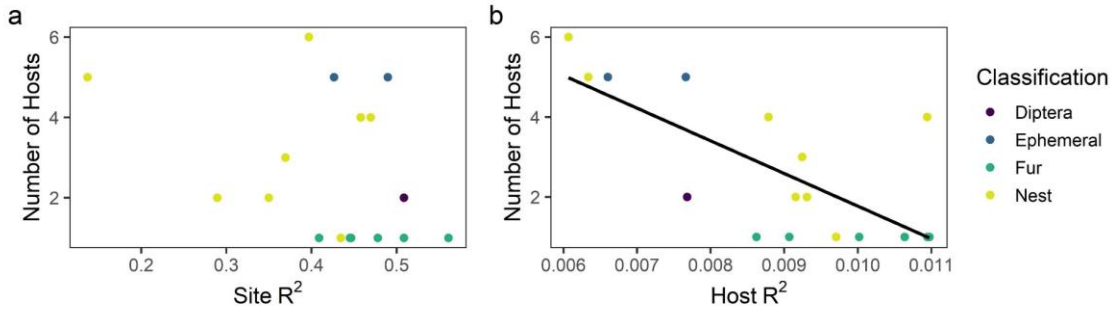

Figure 9. Associations between Bayesian R^2 from the site level (a) and host level (b) of the model and the number of host species parasitized by each ectoparasite species. Colors denote order. There was a significant, negative relationship between host-level R^2 and the number of hosts (b), indicating that host-level covariates tended to explain more variation in occupancy for more specialized parasites ($F_{1,15}$ = 16.59, P = 0.001, R^2 = 0.494, Figure 4b). There were no significant associations between site-level R^2 and number of parasitized host species ($F_{1,15}$ = 1.924, P = 0.186, R^2 = 0.055)

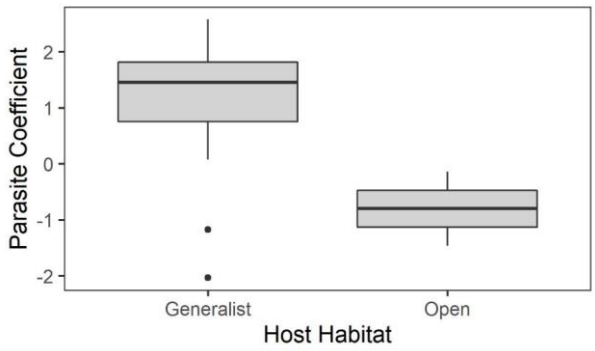

Figure 10. Coefficient values for the first covariate from the site-level model by host habitat preference. Negative coefficient values indicate habitats with more grass and forb ground cover; positive values indicate habitats with more leaf litter. Parasite habitat preferences were not significantly associated with ectoparasite habitat coefficients; however, the high Cohen's d value suggests that this may be an artifact of sample size. (t = 2.322, df = 1.84, P = 0.157, d = 1.52).

The impact of oral rabies vaccination targeting raccoons across a development intensity gradient in Burlington, Vermont, USA, 2015-2017

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Abstract

Management of the raccoon variant of rabies virus in the United States is primarily conducted using oral rabies vaccination (ORV). When a sufficient proportion of the population is vaccinated (~60%), the spread of rabies can be controlled and even eliminated. ORV has been successful at controlling and eliminating raccoon rabies in rural areas but there has been less success in urban areas. We studied the proportion of the raccoon population with rabies virus neutralizing antibodies (RVNA) during a 3-year

ONRAB ORV trial in urban areas of Burlington, Vermont. We used a modified *N*-mixture model to jointly estimate raccoon abundance, RVNA seroprevalence, and capture rates to examine factors that relate to ORV success to better inform management. We found that abundance was lower in less developed areas compared to more urban centers. Raccoon RVNA seroprevalence tended to decrease as population abundance increased yet increased with the average age of the population. Opossum captures correlated with a decrease in raccoon RVNA seroprevalence in low development areas, suggesting they may be competing for baits. The target bait density across the entire study area was 150 baits/km^2, but the hand baiting strategy was heavily concentrated on roads and resulted in uneven bait densities within sampling sites (ranging from 0 to 484 baits/km^2). Uneven bait distribution across the study area may explain low RVNA seroprevalence in some locations. Our results suggest that more even bait distribution across the study area may improve RVNA seroprevalence and support annual ORV to account for raccoon population turnover.

Introduction

Rabies virus remains a significant wildlife management and public health challenge in the United States (USDA 2017, Pieracci et al. 2020). Among meso-carnivores, a stable focus persists among populations of raccoons (*Procyon lotor*) in the eastern US (Gilbert 2018). The US Department of Agriculture (USDA), Wildlife Services, National Rabies Management Program (hereafter, NRMP) coordinates oral rabies vaccination (ORV) targeting meso-carnivore wildlife and annually distributes >9

million vaccine laden baits across diverse landscapes, with greatest emphasis in the region where raccoon rabies virus (RRV) is enzootic (Elmore et al. 2017).

Experimental ORV field trials to test the Ontario Rabies Vaccine Bait (ONRAB; Artemis Technologies Inc., an indirect, wholly-owned subsidiary of Ceva Sante Animale, S.A., Guelph, Ontario, Canada) targeting raccoons began during 2011 in West Virginia (Slate et al. 2014) and has since shown promise at achieving raccoon seroprevalence close to target levels needed for RRV elimination (60-80%; Rees et al. 2013, Reynolds et al. 2015). Average post-ORV seroprevalence using 75 baits/km^2 during three 3-year ONRAB trials was 52% in West Virginia (Slate et al. 2014, Johnson et al. 2021), 69% in the northeastern US (Gilbert et al. 2018b), and 58% in the St. Lawrence River region of New York (Pedersen et al. 2019a).

These trials and similar studies investigated how landscape composition impacts raccoon vaccine bait encounters, uptake, and rabies virus neutralizing antibody (RVNA) response in rural areas following ORV (e.g. Berentsen et al. 2013, Pedersen et al. 2019b). Fewer studies have focused on the success of ORV in urban/suburban raccoon populations. Recent studies in Long Island, New York reported lower raccoon RVNA seroconversion in medium and high intensity development areas and greater success with increasing distances from roads (Bigler et al. 2021a, 2021b). One study reported that the likelihood of RVNA seroconversion in raccoons following ORV with ONRAB was negatively impacted by the proportion of residential areas near the capture site (Mainguy et al. 2012). From 2012-2014, the NRMP conducted an ONRAB trial in urban/suburban areas near Cleveland, Ohio using 150 baits/km^2 in a ground bait area. The 3-year post-

ORV mean RVNA in raccoons was only 34% (n=1,464), suggesting challenges vaccinating populations in developed areas compared to rural areas (USDA 2017).

Urban challenges for ORV such as higher raccoon densities, smaller home ranges, and fragmented habitats are well documented and influenced by anthropogenic resources (Prange et al. 2003, 2004, Randa and Yunger 2006, Bozek et al. 2007, Rosatte et al. 2010, Berentsen et al. 2013, Slate et al. 2020). There also may be a greater abundance of nontarget bait competitors in urban areas (e.g., cats [*Felis catus*], dogs [*Canis lupus familiaris*], opossums [*Didelphis virginiana*]), which may impact ORV success targeting meso-carnivore populations. One NRMP goal is to eliminate RRV locally and nationally by moving ORV zones eastward over the next 30 years (Elmore et al. 2017). As ORV zones move east, more urban/suburban habitats will be encountered requiring a better understanding of effective strategies targeting raccoon populations in developed environments.

In this study, we estimate raccoon RVNA seroprevalence and determine the relative impacts of baiting strategies, raccoon population characteristics, and the landscape (e.g., development intensity and competitor abundance) on seroprevalence to inform rabies management.

Methods

Study area and habitat. The study area in Chittenden County, Vermont is within the urban/suburban ORV ground bait zone and encompasses portions of six townships: Burlington, Colchester, Essex, South Burlington, Williston, and Winooski. The hand

baiting zone was overlaid with 1-km^2 cells and the percent of habitat types was determined for each cell using the 2011 National Land Cover Database (NLCD; Homer et al. 2015). Using NLCD values 21 (Developed, Open Space), 22 (Developed, Low Intensity), 23 (Developed, Medium Intensity), and 24 (Developed, High Intensity), study area cells were classified into low, medium, or high intensity human development. Four non-adjacent sampling cells were randomly selected for each of the three development intensities, separated by at least 1 km (Figure 11A). Sampling cells had minimum spatial buffers of 1.2 km to the edge of the ground bait zone to limit raccoon movement in and out of the ORV zone. Mean percent development across cells in each of the three intensity classes was 45% for low (range 28-58%), 67% for medium (range 54-86%), and 92% for high (range 87-96%).

Oral rabies vaccine bait and distribution strategies. During August 2015-2017, approximately 25,000 ONRAB vaccine baits (Rosatte et al. 2009b) were distributed by hand throughout the study area at a target density of 150 baits/km^2. In urban/suburban areas, baits are hand distributed either by slow speed vehicles targeting hedgerows between properties, culverts under streets, dumpsters behind businesses or by walking sidewalks, railroad tracks, bike paths and placing baits in areas likely used by raccoons that are less likely to be encountered by people or pets. This is commonly referred to as "hand" or "ground" baiting (Gilbert and Chipman 2020). Baits were distributed annually in the hand bait zone across six grids that averaged 37 km^2 in size (Figure 11A). Field staff were assigned a number of baits per grid and recorded the location of baits distributed using push-button, screenless point of interest (POI) units (G-Log 760,

Transystem Inc., Miaoli, Taiwan). We mapped POI coordinates (dots) within sampling cells and used ArcMap 10.8 (ESRI 2011) to count the number of POI dots as a proxy for number of ONRAB baits distributed per cell.

Trapping, animal handling, and sampling. Sampling cells were trapped for 10 consecutive days in July (pre-ORV) and again in October (post-ORV) during 2015-2017. Each cell contained 25 live traps (model 608, Tomahawk Live Trap, LLC, Hazelhurst, Wisconsin, USA) baited with marshmallows and anise oil. Efforts were made to distribute traps evenly across cells given development and property access constraints. Traps were checked daily and moved within a cell every 2-3 days if no unique target animals had been captured.

Target animals (raccoons, striped skunks [*Mephitis mephitis*], gray and red foxes [*Urocyon cinereoargenteus* and *Vulpes vulpes*], and fishers [*Pekania pennanti*]) were anesthetized using a 5:1 ketamine:xylazine mixture via intramuscular injection (Kreeger 1999). Under anesthesia, animals were ear tagged with a unique identifier and the sex, reproductive status, relative age, weight, and general condition were recorded. A 5-7 ml blood sample was collected from the jugular vein and a first premolar tooth was extracted (when available). Target animals were released at the capture site after full recovery from anesthesia. All nontarget, as well as target animals recaptured within the same 10-day trapping session, were released immediately at the point of capture without sampling. Animals exhibiting abnormal behavior or with severe lesions were euthanized under heavy anesthesia with potassium chloride and a brainstem sample was collected postmortem.

RVNA determination and antigen testing. Serum samples were separated from whole blood and shipped frozen to the New York State Department of Health (NYSDOH) Rabies Laboratory where they determined RVNA titers by using a modified neutralization test (Trimarchi et al. 1996). Results were provided in IU/ml and samples ≥0.125 were considered RVNA positive. Brainstems were tested for rabies antigen by the Vermont Department of Health (VDH) Laboratory in Burlington, Vermont using the direct fluorescent antibody test (Center for Disease Control and Prevention and Prevention 2018).

Age determination. Teeth were shipped to Matson's Laboratory (Manhattan, Montana, USA) to determine age from cementum as described in Johnston et al. (1987); results were returned to the nearest year: 0 for young of the year juveniles and ≥1 for adults.

Population level analysis. We estimated raccoon abundance (N) and RVNA seroprevalence (S) post-ORV in 2015-2017 by modifying a multinomial N-mixture model with removal sampling (Kery and Royle 2015a, 2015b). This type of model estimates abundance by using daily counts of unmarked (unique) individuals to estimate the probability of detecting (or in our case capturing) an unmarked individual during a daily count. Capture probability is then used to generate abundance estimates. The model accounts for the decreasing probability of capturing a unique animal as individuals in the population are captured and marked (Kery and Royle 2015a). We modified the base model to include estimates of RVNA seroprevalence in each cell, i.e., to compare daily

counts of unmarked seropositive individuals to daily counts of all unmarked individuals to estimate cell-level seroprevalence (see Appendix S5 for more details).

We allowed abundance to vary with development intensity and capture rate to vary with trap availability (if traps were triggered by other species, they were not available to capture raccoons). We examined effects of habitat (human development level), population composition (raccoon abundance and average age), competition (numbers of other species caught), and management (ORV bait density and coverage). Bait coverage was calculated by drawing a 30m buffer (McClure et al. 2022) around each POI dot to represent the area of effect for each bait. We merged all buffers into a single polygon, then calculated coverage as the proportion of the study cell that intersected the buffer polygon. Model parameters were estimated using a Bayesian hierarchical model with uninformed priors in the programs JAGS (Plummer 2017) and R (R Core Team 2021). We evaluated covariate effects using the 75% credible interval (CI) as an exploratory metric and followed up with the appropriate frequentist analysis (e.g., linear regression, ANOVA, etc.) We used the Watanabe-Akaike Information Criterion (WAIC) to perform model selection (Watanabe 2010, Hooten and Hobbs 2015). We used posterior predictive checks to ensure the model was internally consistent (i.e. that model results made sense; Gelman et al. 1996, 2013) and post-hoc frequentist tests to complement the Bayesian analyses.

Results

Data summary. The number of ONRAB baits distributed within the greater Burlington area and the number of POI coordinates recorded as baits had minimal annual variation: 24,496 baits/24,111 POI dots in 2015 (-385 POI error), 24,298 baits/24,495 POI dots in 2016 (+197 POI error), and 24,459 baits/24,289 POI dots in 2017 (-170 POI error). The POI dots (proxy for number of baits distributed) in each sampling cell varied considerably by cell, development intensity, and year (Table 3).

During the 3-year field trial, 2,274 animals were trapped across 18,000 trap nights: 1,082 (48%) were target animals sampled for RVNA (902 raccoons, 164 skunks, 11 fishers, 4 gray fox, 1 red fox); 818 (36%) were nontargets released without sampling; and 374 (16%) were target animals recaptured during the same trapping session. Opossums totaled 275 among 818 (34%) nontarget captures during the trial (19% in low development, 31% in medium development, and 50% in high development).

Among 902 raccoons, 482 (53%) were sampled once and 174 individuals were sampled at least two times. Three target animals were found dead in a trap and nine were euthanized due to abnormal behavior or severe lesions. All were tested for rabies and one raccoon tested RRV positive, which was an adult lactating female found dead in a trap with a large open abdominal wound during the 2015 pre-ORV session. Most of the 902 raccoons sampled were captured in the medium development area (375) and the least were captured in the low development area (226), with 301 captured in the high development area. Of the 902 raccoons, an actual age was reported for 758 and sex was recorded for 900. Raccoons in the low development habitat had the highest proportion of

males (60%). In the medium development habitat, the proportion was slightly lower (58%) and the high development habitat had the lowest proportion of males (52%).

The RVNA seroprevalence rates and sample sizes for raccoons and skunks varied by year, sampling period, and development (Table 4). Regardless of development type, the 3-year mean RVNA among raccoons pre-ORV was 36.4% (n = 523, range: 16.8-46.5%) and 39.1% (n = 379, range: 28.8-44.4%) post-ORV.

Population level results. There was model uncertainty in the population level results (Table S6-1), suggesting that no single model was strongly supported over the set examined. There were no significant interaction terms based on the 75% CI and post-hoc analyses; therefore, we selected a model with all additive covariates.

The model corrected for the probability of capturing a unique raccoon decreasing when fewer traps were available to capture raccoons. Estimated raccoon abundance per cell by year ranged from 2-31, with a median of 10. Medium and high development cells had higher estimated raccoon abundance than low development cells (Figure S6-1). However, an ANOVA did not reveal differences between development categories (P = 0.257), likely due to high variability in raccoon abundance within medium development cells.

Estimated post-bait raccoon RVNA seroprevalence per cell ranged from 11.6-96.8% (median = 39.7%) and varied by year and development class (Figure 12). Medium development cells tended to have lower RVNA seroprevalence compared to low development (P = 0.077, η^2 = 0.144), possibly due to high variability observed in medium or high development cells.

Raccoon abundance did not affect seroprevalence based on the 75% CI; however, a linear model with estimated abundance as the predictor variable and estimated seroprevalence as the response demonstrated a negative relationship ($P = 0.020$, $R^2 = 0.124$, Figure 13A). Estimated raccoon seroprevalence increased as skunk captures increased ($P < 0.001$, $R^2=0.439$, Figure 13B), whereas opossum captures were not associated with seroprevalence based on the 75% CI or the results of a linear model ($P=0.385$, $R^2=-0.007$, Figure 13C). However, opossum captures explained 31% of the variation in seroprevalence in low development cells ($P = 0.036$, $R^2 = 0.305$).

Although the average age of captured raccoons did not impact raccoon RVNA seroprevalence based on the 75% CI, the results could be due to an influential outlier from a cell with a small sample size (Figure S6-2). Upon removing the outlier, results from a linear regression suggest that raccoon populations with a lower average age tend to have lower estimated RVNA seroprevalence ($P = 0.003$, $R^2 = 0.213$, Fig. 4).

The actual bait density and bait coverage within a cell did not impact RVNA seroprevalence based on the 75% CI or the results of linear models ($P = 0.054$, $R^2 = 0.078$; $P = 0.709$, $R^2 = -0.025$, Figure S6-3). There tended to be a weak positive relationship between the bait density and the seroprevalence, while the relationship between bait coverage within cells and seroprevalence was ambiguous.

Posterior predictive checks yielded no systemic discrepancies between the observed data and data generated by the model (Figure S6-4), but the distributions for the simulated data had slightly longer tails.

Discussion

The post-ORV raccoon RVNA seroprevalence was well below the target levels recommended for RRV elimination (60–80%; Rees et al. 2013, Reynolds et al. 2015) except for four cells that reached 60% estimated seroprevalence at least once during the study. Multiple environmental factors may contribute to raccoon RVNA seroprevalence in the greater Burlington area, where medium development sites had lower seroprevalence compared to low development sites, with no clear differences between sites comparing high development to low or medium development (Figure 12).

Characteristics of raccoon populations explain some of the variation in RVNA seroprevalence, as areas of greater raccoon abundance exhibited lower seroprevalence (Figure 13A). Furthermore, estimated raccoon abundance was lower across low development compared to medium or high development sites. Raccoons may thrive in moderate levels of human development, with residential areas and nearby forested areas (e.g., cemeteries and parks) close to the urban core where they can forage for anthropogenic food sources such as garbage, bird feeders, pet food, and vegetable gardens (McKinney 2002, Randa and Yunger 2006). Our classifications of low, medium, or high human development are all within the Burlington metropolitan area and even the low cells averaged 45% developed and should not be considered rural. Many studies have documented greater raccoon densities in urban/suburban compared to rural habitats (Schinner and Cauley 1974, Riley et al. 1998, Prange et al. 2003, Slate et al. 2020). Greater raccoon densities in urban areas may contribute to the lower RVNA

seroprevalence observed in the Burlington study area when compared to similar studies from rural areas.

Older raccoons had a higher probability of being RVNA seropositive than younger raccoons. This was expected as juvenile raccoons typically travel in family groups and may be inexperienced in foraging and encountering baits. During our post-bait sessions, juveniles had encountered only one baiting event, while adults had encountered at least two baiting events. Several studies have reported greater RVNA seroprevalence among adult compared to juvenile raccoons (Boulanger et al. 2008, Rosatte et al. 2009a, Horman et al. 2012, Mainguy et al. 2012, Slate et al. 2014, Pedersen et al. 2019a), where RVNA seroprevalence increases with animal age (Figure S6-1; Gilbert et al. 2018a, Johnson et al. 2021) and exposure to annual ORV baiting efforts. Overall, 45% of raccoons in our study were juveniles, similar to Mainguy et al. (2012) and Bigler et al. (2021a), but varied by development type (37% in low, 46% in medium, and 49% in high), which may relate to seroprevalence differences by development class. We concur with prior work suggesting that a pulse of susceptible juveniles entering the population each year underscores the need for annual ORV to maintain levels of population RVNA seroprevalence.

Skunks and opossums were more important factors affecting raccoon RVNA seroprevalence than expected. In low development areas, where the most opossums were captured, raccoon RVNA seroprevalence was lowest during the ORV trial. While this pattern only occurred in low development, it suggests potential bait competition between opossums and raccoons. Opossums made up one third of all nontargets captured during

our study and have been recognized as bait competitors with raccoons in previous studies (Olson and Werner 1999, Olson et al. 2000, Smyser et al. 2010).

Sites with greater skunk captures demonstrated higher raccoon RVNA seroprevalence. Except for one high development cell in 2015 with an unusually high number of unique skunks (25/km^2 during pre-bait and 19/km^2 during post-bait), skunk captures tended to be greatest in the low development cells, followed by medium development cells and least frequent in high development cells. Although skunks consume ORV baits, it's possible that their dependence on urban green spaces (Greenspan et al. 2018) reduces the likelihood of encountering baits distributed along roads. Additional research is needed to explain how interspecific encounters of target meso-carnivores may affect bait uptake and RVNA seroconversion in raccoons.

The target bait density for the Burlington ground zone was 150 baits/km^2, which is commonly used within urban areas with higher raccoon densities (Slate et al. 2020). Our baiting grids averaged 37 km^2 and 4,070 baits distributed per grid. Within sampling cells, the actual bait densities varied from 0-484 baits/km^2. There is a known number of baits per grid but, depending on habitats encountered while driving, distribution may be uneven or patchy within grids (Figure 11B-D). Additionally, concentrating delivery along roads may lead to bait distribution in suboptimal raccoon habitat (e.g., roadside ditches, under shrubs on front lawns), potentially reducing raccoon bait encounters (Bigler et al. 2021b). There was a slight positive association between actual bait density and raccoon RVNA seroprevalence, however, this was not a strong influence compared to other factors measured during the study. Within-cell bait coverage did not strongly influence

raccoon RVNA seroprevalence, perhaps because raccoon movements in developed areas may exceed the cell size (1 km^2). Prange et al. (2004) documented raccoon movements and home ranges in urban and suburban areas during the summer that exceeded the width and area of our cells.

There was some evidence that bait coverage at a scale larger than the 1 km^2 sampling cells was important, as a portion of the greater Burlington area was not baited during 2016 (Figure 11C) and raccoon RVNA seroprevalence rates were unusually low during 2017 (Figure S6-5B). There may be a cumulative effect of baiting (Sattler et al. 2009) for maintaining raccoon RVNA seroprevalence rates, considering the pulse of naive juveniles entering the population annually. A cumulative effect could explain the lower seroprevalence rates in medium development sites, as many of these sites were in or adjacent to the areas without baits. Future research should consider the potential benefit of reducing the size of baiting grids, which may result in fewer baiting gaps and increased raccoon RVNA seroprevalence.

There was considerable variability of raccoon RVNA seroprevalence estimates among cells. However, we observed a high probability of raccoon detection (capture) in our model, suggesting that this variability is not due to observation error. Detection-based models are useful in situations where bias or error in capture rates may introduce error in the observed data (Iknayan et al. 2014, Kellner and Swihart 2014). Our detection-model estimated relatively high capture rates, increasing our confidence that the seroprevalence estimates accurately represent the raccoon population in this area. The model also corrected for a decrease in raccoon captures as more traps are occupied, which is

important at sites with high numbers of recaptures or nontargets. The addition of seroprevalence to the base *N*-mixture model with removal sampling was also important for accurately modeling seroprevalence, as the model was able to jointly estimate abundance and seroprevalence, the former of which often affects the latter in wild populations (Mainguy et al. 2012).

The use of multiple analytical methods to support and expand upon the results of the *N*-mixture model shed additional light on the factors that may influence raccoon population RVNA seroprevalence associated with ORV. Evaluation of the 75% CI missed many important variables because of outliers (Figure S6-2) or because the pattern only held in one development class (Figure 13C). An individual-level analysis also supported the finding that seroprevalence was influenced by the average age of the population by providing an explanation for the pattern (i.e., that older raccoons are more likely to be seropositive; Figure S6-5A). Our consideration of multiple analytical approaches was useful for teasing apart complex relationships between biological and landscape factors in this urban environment.

During 2014 (prior to our study), there were 30 confirmed cases of RRV within our study area, declining to 7 and 1 case detected during 2015 and 2016, respectively. During 2017-2021, there were no cases of RRV in this area based upon consistent levels of surveillance each year. Despite the relatively low RVNA response in this study when compared to rural ONRAB studies, ORV led to case reduction and elimination during the study. For improved urban management of RRV using ORV, future research should focus

on a more comprehensive understanding of the interplay between RVNA seroprevalence for local and regional case reduction and elimination of RRV.

We identified several patterns impacting raccoon RVNA seroprevalence within the greater Burlington ORV area, but many questions remain. Future studies in developed areas should investigate potential factors among the ecological community of meso-carnivores and nontarget animals that may impact ORV effectiveness for raccoons (e.g., population densities, movements, home ranges, habitat use and selection, bait consumption). A comprehensive ecological understanding can inform refinement of baiting strategies for raccoons in urban/suburban environments. Bait stations require additional study such as incorporating them with hand baiting, locating them farther from roads to potentially bolster bait encounters as suggested by (Bigler et al. 2021b), and expand on work by Bjorklund et al. (Bjorklund et al. 2017) to improve specificity of access by raccoons. As the NRMP continues to work toward RRV elimination over the next 30 years and pushing the ORV zone eastward, an increasing number of urbanized areas will be encountered, and the challenges associated with ORV in urban areas will become more prominent. Continued investigation and research of ORV targeting raccoons in urban/suburban habitats is critical to successful elimination of RRV from the US and North America.

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Tables

Table 3. Mean ONRAB (Artemis Technologies Inc., an indirect, wholly-owned subsidiary of Ceva Sante Animale, S.A., Guelph, Ontario, Canada) bait density (per km^2) in cells of varying development intensities (low, medium, high) in the Burlington, Vermont, USA area, 2015-2107. Minimum and maximum bait densities are in parentheses. Each development intensity had four cells and target bait density was 150 baits/km^2.

Year	Low	Medium	High
2015	163 (18-394)	109 (45-260)	188 (73-386)
2016	268 (147-431)	142 (0-317)	175 (86-318)
2017	129 (85-205)	115 (49-184)	287 (164-484)

Table 4. Total percentage of rabies virus neutralizing antibodies for raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) sampled in cells with varying levels of human development before (pre) and after (post) oral rabies vaccination using ONRAB (Artemis Technologies, Inc., an indirect, wholly-owned subsidiary of Ceva Sante Animale, S.A., Guelph, Ontario, Canada) in the Burlington, Vermont, USA area, 2015-2017. Total sample sizes across four sampling cells for each development class and cumulatively (in total columns and rows) are in parentheses.

Species	Development	2015 Pre	2015 Post	2016 Pre	2016 Post	2017 Pre	2017 Post	Total Pre	Total Post
Raccoons	Low	48.4 (31)	46.4 (28)	52.5 (40)	55.6 (27)	17.9 (56)	38.6 (44)	36.2 (127)	45.5 (99)
	Medium	50.0 (64)	36.0 (50)	41.2 (51)	46.3 (41)	19.3 (109)	20.0 (60)	33.0 (224)	32.5 (151)
	High	40.0 (55)	52.2 (46)	47.4 (38)	34.1 (41)	12.7 (79)	31.0 (42)	29.1 (172)	39.5 (129)
	Total	46.0 (150)	44.4 (124)	46.5 (129)	44.0 (109)	16.8 (244)	28.8 (146)	32.5 (523)	38.3 (379)
Skunks	Low	0.0 (1)	38.9 (18)	20.0 (10)	41.7 (12)	8.3 (12)	0.0 (11)	13.0 (23)	29.3 (41)
	Medium	10.0 (10)	28.6 (7)	0.0 (4)	0.0 (2)	0.0 (3)	11.1 (9)	5.9 (17)	16.7 (18)
	High	14.8 (27)	30.8 (26)	0.0 (5)	n/a (0)	0.0 (3)	0.0 (4)	11.4 (35)	26.7 (30)
	Total	13.2 (38)	33.3 (51)	10.5 (19)	35.7 (14)	5.6 (18)	4.2 (24)	10.7 (75)	25.8 (89)

Figures

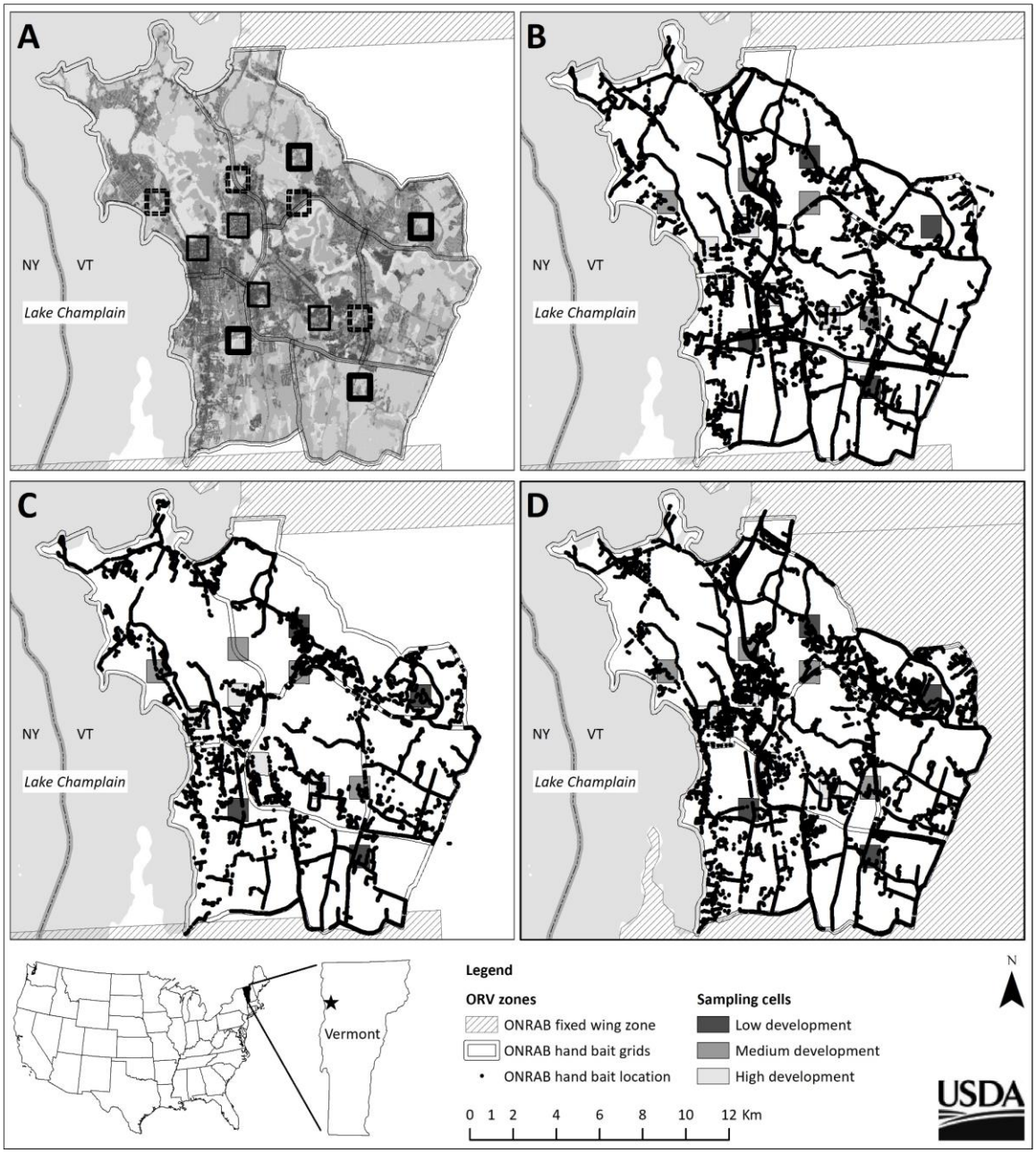

Figure 11. Study area where oral rabies vaccination using ONRAB (Artemis Technologies Inc., an indirect, wholly-owned subsidiary of Ceva Sante Animale, S.A., Guelph, Ontario, Canada) at 150 baits/km^2 was evaluated in the greater Burlington, Vermont, USA area (black star on state map). A) ONRAB hand bait zone grids (double black lines) with National Land Cover Database habitat; darker shades of gray indicate higher development intensities, while lighter shades include water, wetlands, forest, and agriculture. Sampling cells were 1 km^2: low (thicker black squares), medium (dashed

squares), and high development intensity (thinner black squares) in panel A. Panels B-D show the same hand bait grids and sampling cells (see legend) with ONRAB bait locations (black dots) for 2015 (B), 2016 (C), and 2017 (D).

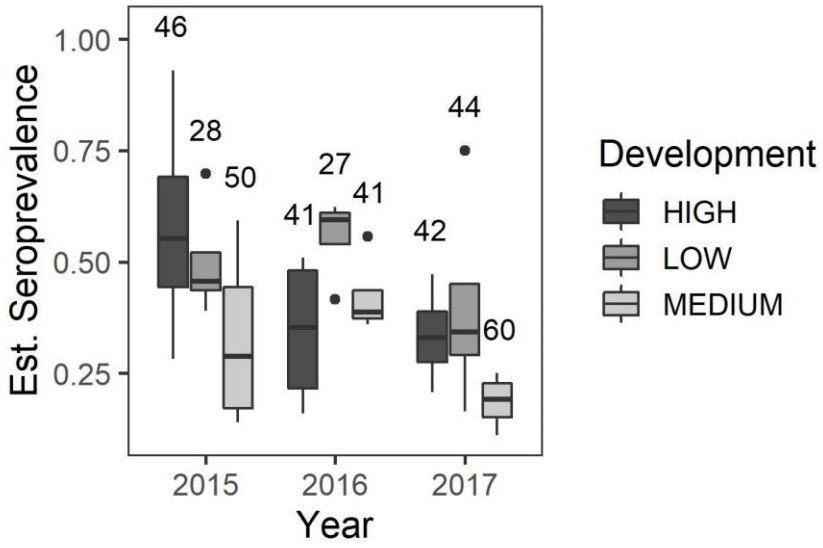

Figure 12. Estimated raccoon rabies virus neutralizing antibody seroprevalence across human development classifications, based on National Land Cover Database habitats, associated with a 3-year oral rabies vaccination trial with ONRAB (Artemis Technologies Inc., an indirect, wholly-owned subsidiary of Ceva Sante Animale, S.A., Guelph, Ontario, Canada) at 150 baits/km^2 in the greater Burlington, Vermont, USA area. Boxes represent quartiles, whiskers represent the 95% confidence interval, and dots represent outliers. Numbers denote sample sizes.

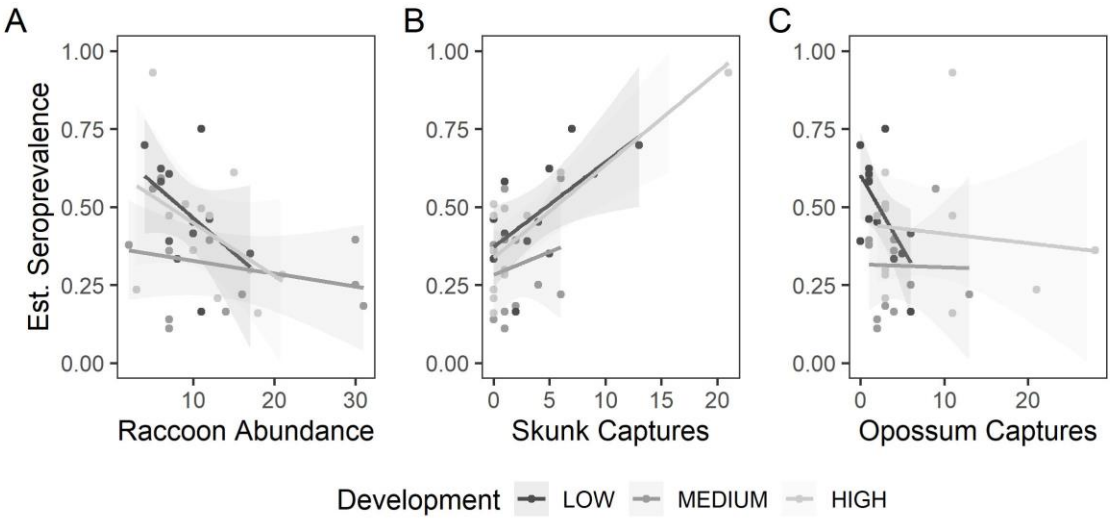

Figure 13. Estimated raccoon rabies virus neutralizing antibody (RVNA) seroprevalence tends to decrease with estimated raccoon abundance in the greater Burlington, Vermont, USA area (2015-2017) based on the results of a linear model (A; $F_{1,34} = 5.941$, $P = 0.020$, $R^2 = 0.124$), yet increase with skunk captures based on the results of a linear model (B; $F_{1,34} = 28.4$, $P < 0.001$, $R^2 = 0.439$). Estimated raccoon RVNA seroprevalence in cells classified as low development tended to decrease with increasing opossum captures (C; $F_{1,10} = 5.828$, $P = 0.036$, $R^2 = 0.305$). This association was not present in cells classified as medium and high development.

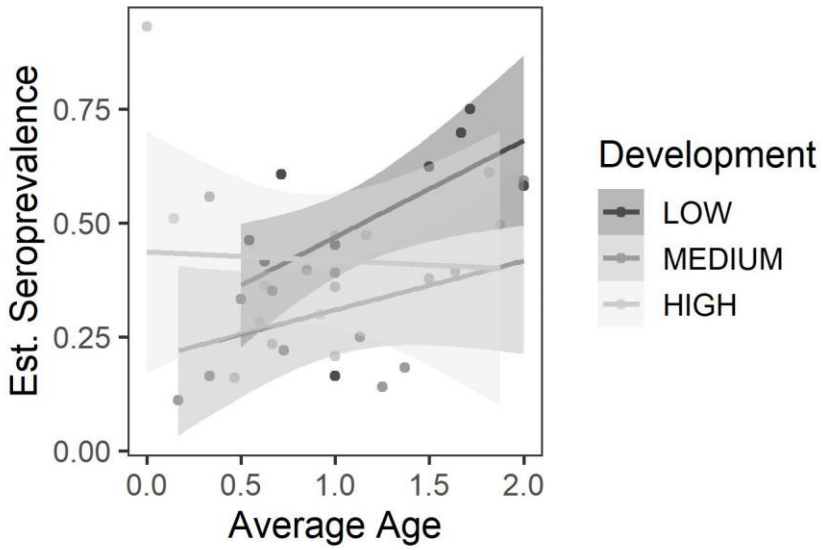

Figure 14. Study cells with a higher proportion of juvenile raccoons tended to have lower estimated rabies virus neutralizing antibody seroprevalence than cells with a higher proportion of adults for an oral rabies vaccination trial with ONRAB (Artemis Technologies Inc., an indirect, wholly-owned subsidiary of Ceva Sante Animale, S.A., Guelph, Ontario, Canada) at 150 baits/km^2 in the Burlington, Vermont, USA area, 2015-2017. Results are based on a linear regression after an influential outlier was removed ($F_{1,33}$ = 10.22, P = 0.003, R^2 = 0.213).

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Appendix S1: Supplemental Figures for Chapter 1

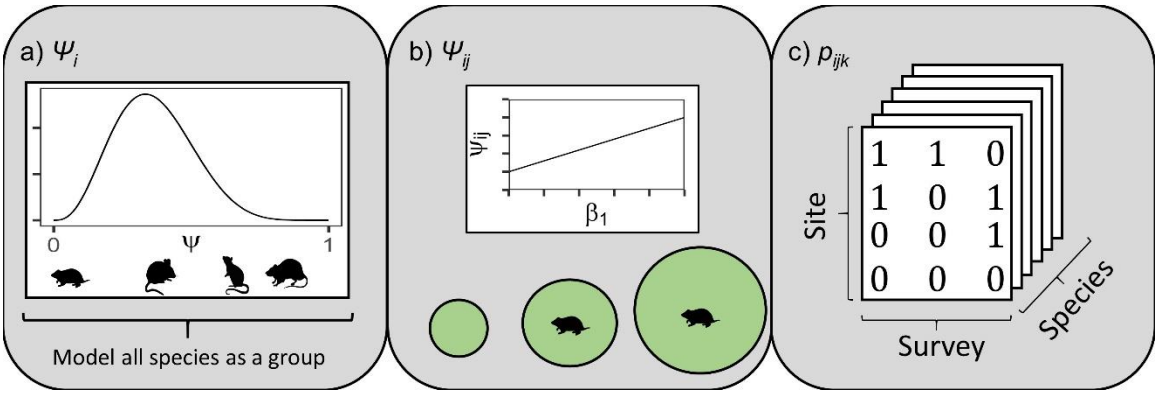

Figure S1-1. a) Multi-species occupancy models (MSOMs) have a hierarchical structure in which species-level parameters (such as occupancy probability Ψ_i) are drawn from a community-level probability distribution, allowing the model to evaluate all species in the context of the group. b) Site-level occupancy probability Ψ_{ij} is a function of species occupancy probability Ψ_i and site-level covariates such as patch area. c) Repeated sampling at each site yields estimates of detection probability p_{ijk} from encounter histories.

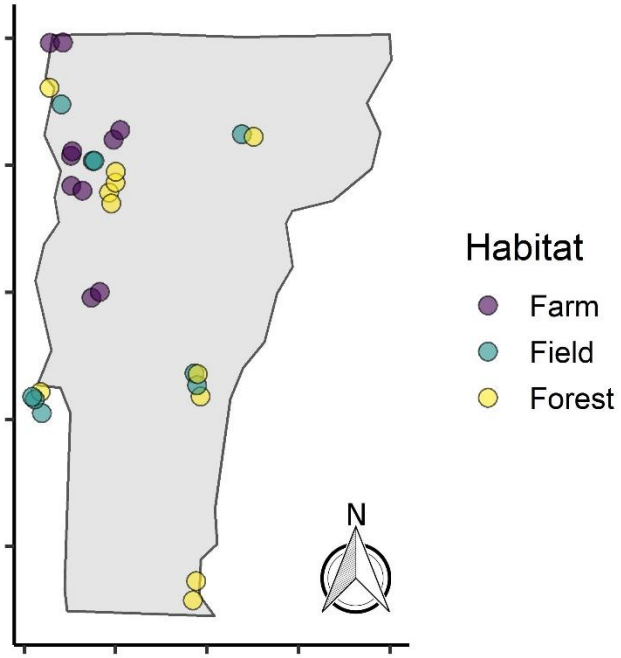

Figure S1-2. Map of trapping locations in Vermont. Points have been jittered for clarity. Colors denote habitat type.

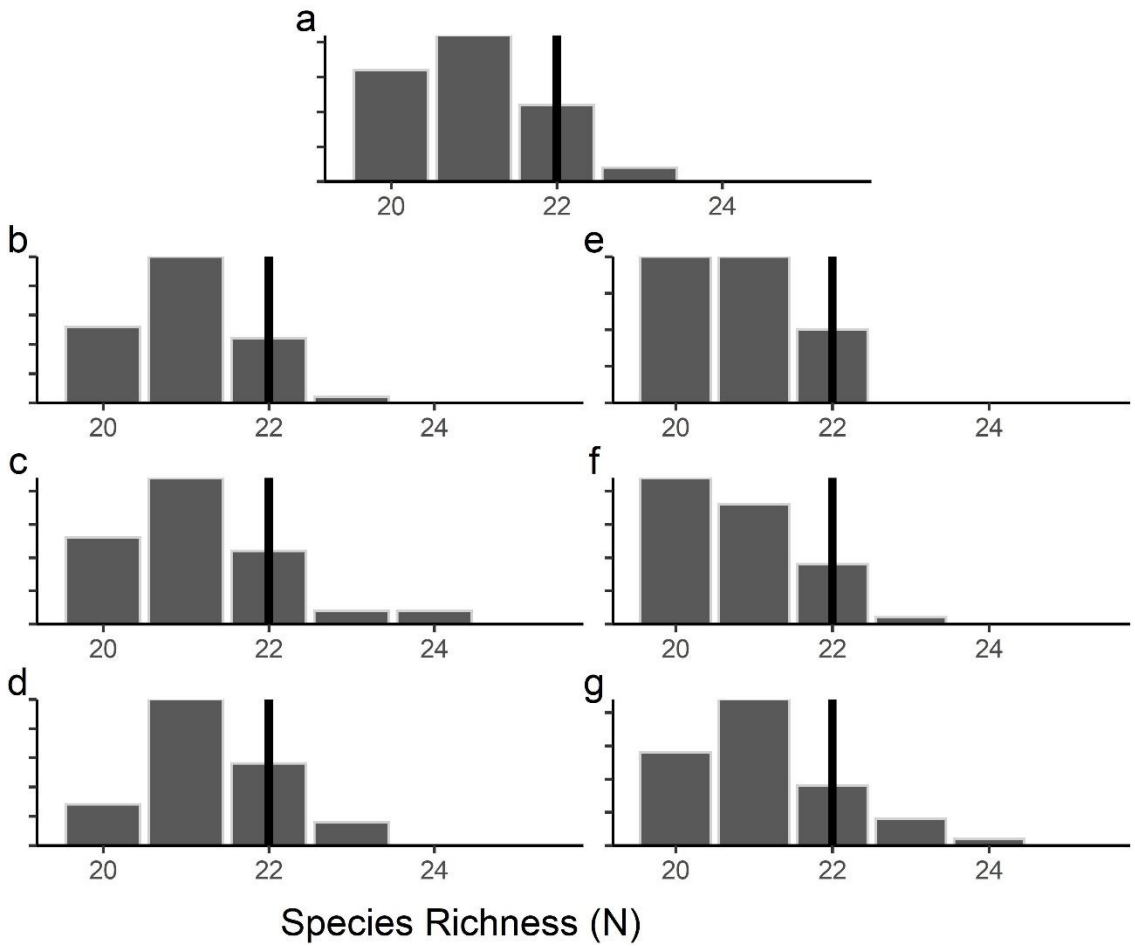

Figure S1-3. Distribution of estimated median regional species richness (*N*) of the simulated datasets. Solid lines denote the true regional richness of 22 species. Models with uninformative priors (a) tended to yield an expected richness of 21 species. Models with informative priors (b-d) yielded qualitatively similar estimates, as did models with strongly mis-specified priors (g). Models with weakly and moderately mis-specified priors tended to yield an expected richness of 20 species (e-f).

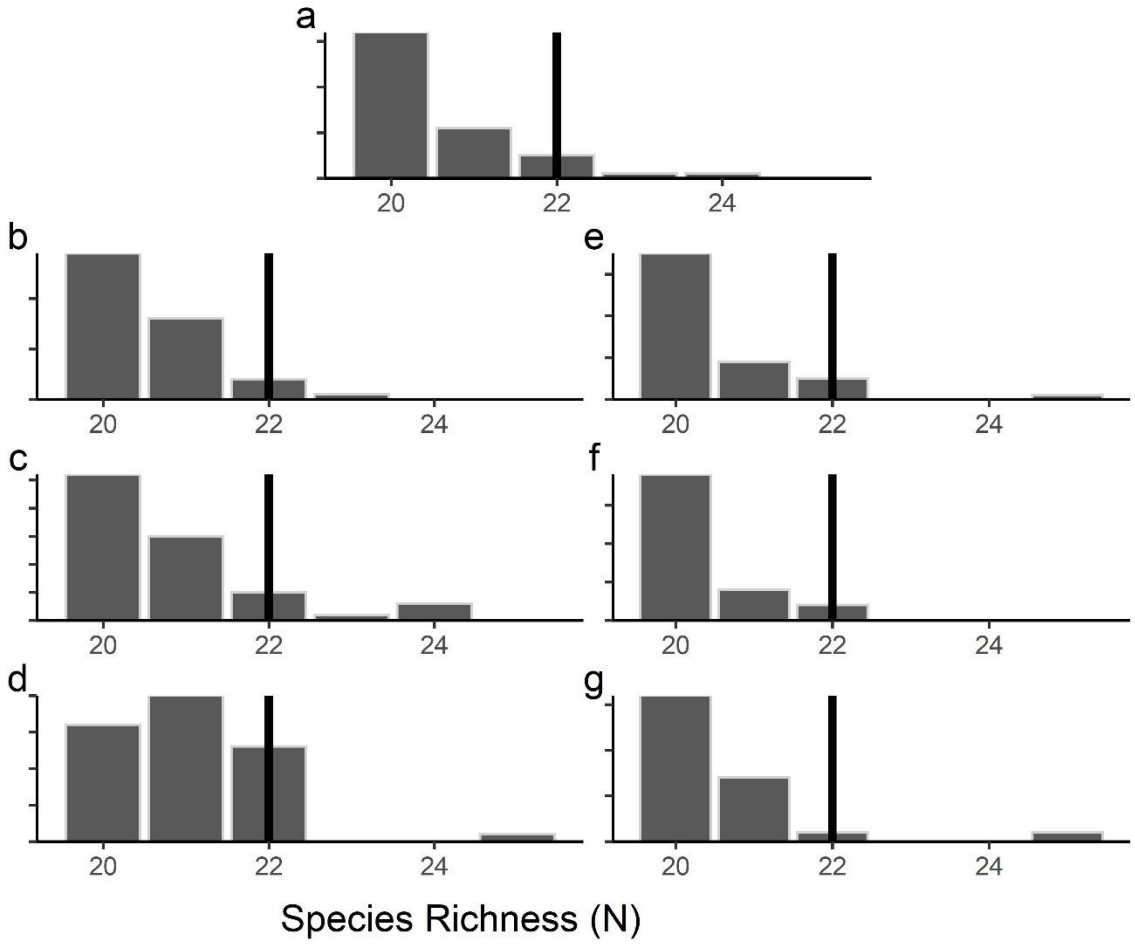

Figure S1-4. Distribution of estimated modal regional species richness (*N*) of the simulated datasets. Solid lines denote the true regional richness of 22 species. Models with uninformative priors (a) tended to yield an expected richness of 20 species. Models with strongly informative priors tended to yield an expected richness of 21 species (d). All other models were qualitatively similar to the model with uninformative priors.

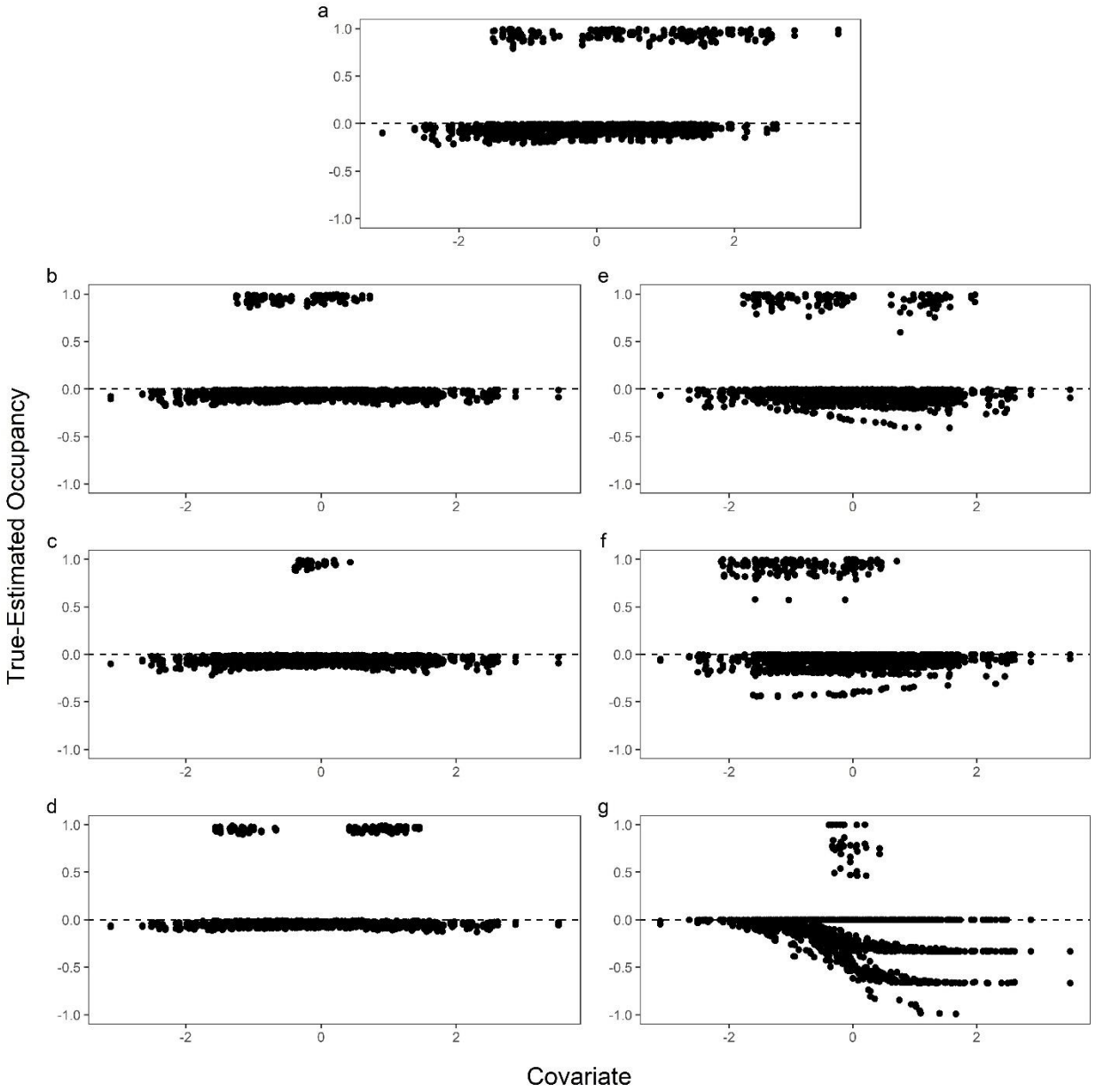

Figure S1-5. Comparison of true site-level occupancy and estimated occupancy probability for simulated species 21, which was undetected during sampling. Models with mis-specified priors (e–g) tended to over-estimate site occupancy, as shown by the increase in y-values closer to -1.

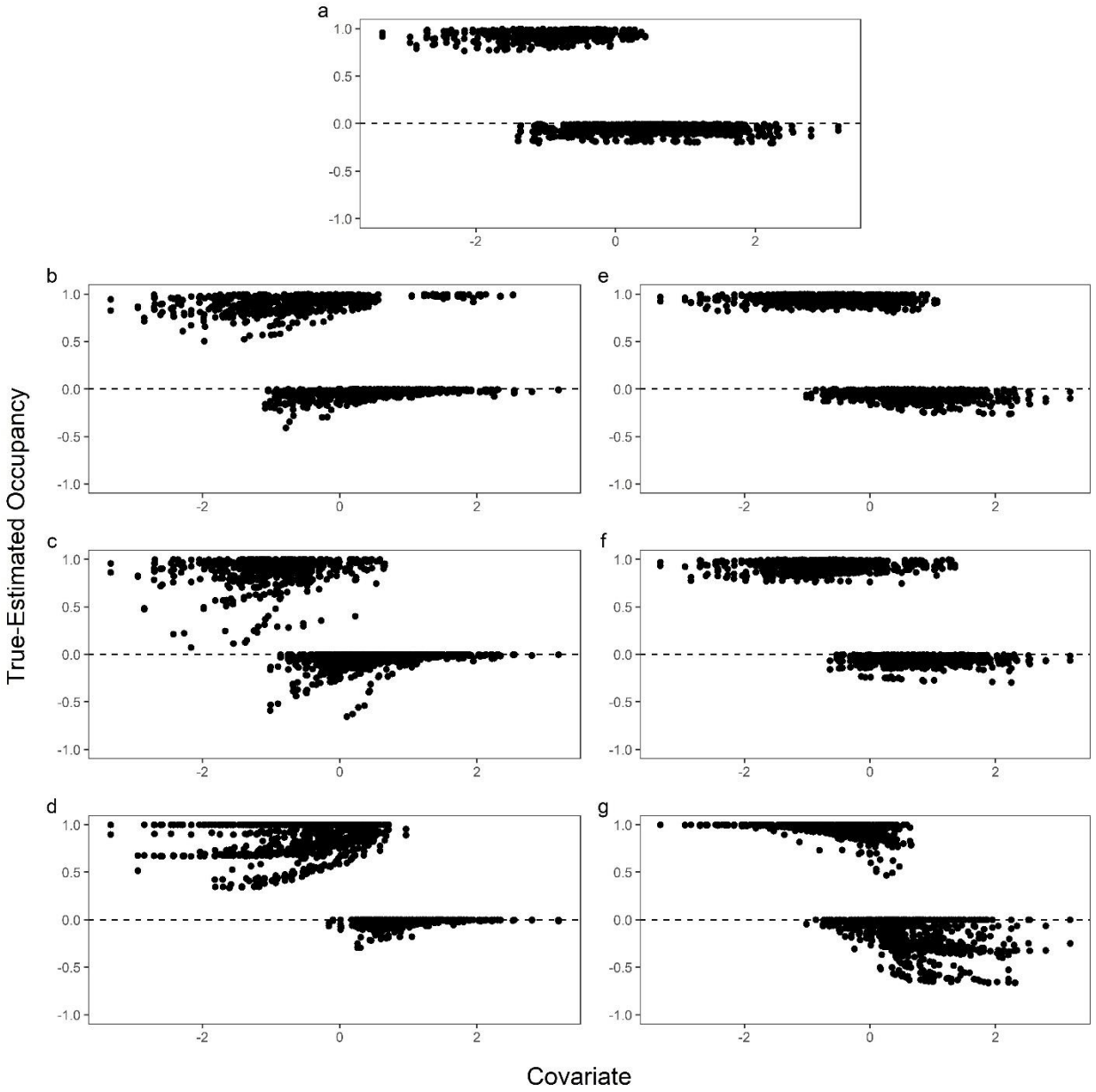

Figure S1-6. Comparison of true site-level occupancy and estimated occupancy probability for simulated species 22, which was undetected during sampling. Models with strongly mis-specified priors (e–g) tended to over-estimate site occupancy, as shown by the increase in y-values closer to -1.

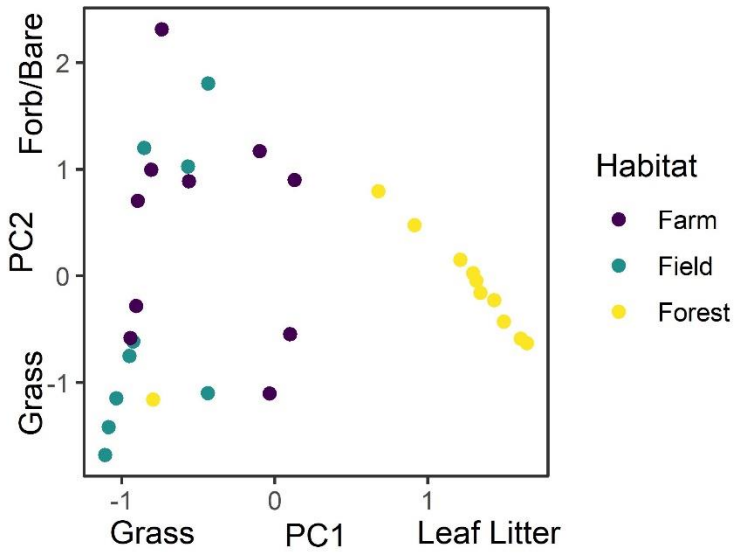

Figure S1-7. Results of the principal component analysis (PCA) on vegetation data. PC1 captured 82.4% of the variation in the data and captured a gradient from mostly grassy cover to mostly leaf litter. PC2 explained 10.5% of the variation in the data and captured a gradient from mostly grassy cover to a mix of forbs and bare ground.

Appendix S2: Tutorial for creating aggregated priors using R and JAGS

This appendix is a tutorial for using prior aggregation to include external sources of information in multi- species occupancy models (MSOMs). Running the code included in this tutorial requires the software JAGS, which can be downloaded here.

This tutorial does not include general information on Bayesian MSOMs or the use and selection of ecologically informed priors. For an introduction to Bayesian MSOMs, see Chapter 11 of *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS* by Royle and Kéry (2015). For a guide to Bayesian model selection, see Hooten and Hobbs (2015). For a guide to Bayesian model checking, see Conn et al. (2018). For more information on developing ecologically informed priors, see Low Choy et al. (2009), Banner et al. (2020), and citations therein.

This tutorial requires the following packages:

```
library(R2jags)
library(boot)
library(abind)
library(tidyverse)
library(ggnewscale)

# Set seed for reproducibility:
set.seed(23)
```

Simulate the community

We will begin by simulating a community consisting of 10 species. We will assume that we surveyed this community by sampling 20 sites over a period of 4 surveys each. We will also simulate a covariate that is correlated with the occupancy rates of some species:

half of the species in the community will respond negatively to the covariate, while the other half are not affected.

To simulate site-level occupancy, we will first draw species-level occupancy probabilities from a beta distribution: $\psi_i \sim Beta(\alpha = 2, \beta = 3)$. This distribution generates a wide range of occupancy probabilities (95% interval 0.067586 – 0.8058796), a situation in which data augmentation is known to work well. We will use a logit link function to account for covariate effects on site-level occupancy probability of each species. Finally, the true occupancy state for each species at each site will be the result of a Bernoulli trial with the site-level probability as the probability of success.

```
# Global variables
nspec <-10 # number of species
nsite <-20 # number of sites
nsurvey <-4 # surveys per site

Ks <- rep(nsurvey, nsite) # vector of surveys at each site

# Vector of covariate responses: half of species respond negatively
resp2cov <- c(rnorm(n =5,sd =0.25),

rnorm(n =5,mean =-3,sd =0.25))

resp2cov <- sample(resp2cov)

# Covariate values for sites
cov <- sort(rnorm(n =nsite))
```

Similarly to species-level occupancy probabilities, species-level detection probabilities will be drawn from a beta distribution p_i $Beta(\alpha = 2, \beta = 8)$. This will generate low-to-mid detection probabilities (95% interval 0.028145 – 0.4824965), another situation in which data augmentation performs well. Environmental or survey covariates that may influence detectability can be added using the logit link function;

however, for this example we will assume detectability does not vary across sites and surveys.

```
# Get probs from a beta distribution
sim.occ <- rbeta(n =nspec,shape1 =2,shape2 =3)

# Write function to simulate true occupancy state
tru.mats <- function(spec=nspec,site=nsite,
                     alpha1=resp2cov){

  #Get site-level psi to account for covariates
  alpha0 <- logit(sim.occ)

  #Create empty matrix to store occupancy probs
  logit.psi <- matrix(NA,nrow =spec,ncol =site)

  # Generate occupancy probs
  for(i in 1:spec){
    logit.psi[i,] <-alpha0[i] + alpha1[i]*cov
  }

  # Transform
  psi <- plogis(logit.psi)

  # Generate true occupancy state
  nlist<-list()
  for(a in 1:spec){
    nlist[[a]] <- rbinom(n =site,size =1,prob =psi[a,])
  }

  #Turn abundance vectors into abundance matrix
  ns<-do.call(rbind, nlist)

  return(ns)
}

# Get true occupancy states
tru <- tru.mats()
```

~

Simulated survey data will be the result of a Bernoulli trial with the species-level detection probability as the probability of encountering that species at a given site during a given survey.

```
# Generate mean detection probabilities from beta dist
mean.p <- rbeta(n =nspec,shape1 =2,shape2 =8)
mean.p <- sort(mean.p,decreasing =T)

# Generate detection histories
get.obs <- function(mat, specs){
#Detection intercept and cov responses
beta0<-logit(mean.p) #put it on logit scale

#Logit link function
logit.p <- array(NA,dim = c(nsite, nsurvey, specs))
for(i in 1:specs){
  for(j in 1:nsite){
    for(k in 1:nsurvey){
      logit.p[j,,i] <-beta0[i] # Add covariates here
    }
  }
}

p <- plogis(logit.p)

#Simulate observation data
L<-list()

for(b in 1:specs){
  y<-matrix(NA,ncol =nsite,nrow =nsurvey)
  for(a in 1:nsurvey){
    y[a,]<-rbinom(n =nsite,size =1,prob =p[,,b]*mat[,b] }
    L[[b]]<-t(y)
  }

  #Smash it into array
  obs<-array(as.numeric(unlist(L)),
               dim=c(nsite, nsurvey, specs))

  return(obs)
}

obs.data <- get.obs(mat =tru,specs =nspec)

# Look at observed occurrence
maxobs <- apply(obs.data, c(1,3), max)
```

By calculating the column sums, we can see that one species went undetected in the simulated survey:

```
colSums(maxobs) # One species was not observed
## [1] 4 4 1 5 2 7 2 0 1 1
```

To make the JAGS script easier to write and the figures more readable, the undetected species was moved to the last column in the observed data.

Define the informed prior

Next, we will define the informed species-level prior distribution for the undetected species. Although the priors can be defined in the main model text, writing them separately allows you to more easily to adjust the variance, relative weights, etc. of different prior combinations. Running models with different priors is recommended as a test for prior sensitivity.

Most Bayesian MSOMs use normally-distributed priors, but other distributions can be used. Code for aggregating non-normal distributions can be found in de Carvalho et al. (2015). We will define the mean ofinformed species-level prior using the true value of the simulated covariate. We know the true value of the covariate is:

```
# Get true covariate value
resp2cov[10]


## [1] -2.745199
```

We will round this value to -3 as the mean of the informed prior distribution. We will also assign a variance of 0.5 (standard deviation of approximately 0.7). This value is

somewhat arbitrary, but in general large standard deviations (> 2) are not recommended, as they can yield bimodal posterior distributions (Northrup and Gerber 2018).

We will use the Markov chain Monte Carlo (MCMC) sampler JAGS to analyze the model. JAGS is compatible with most operating systems and the language is similar to R. The package R2jags will allow us to call JAGS directly from R.

In order for JAGS to analyze the model, we have to write a text file to send to JAGS. Begin by writing a character object that defines the mean and variance of the informed prior distribution:

```
# Write script for priors in JAGS language
priors <-"#Info for species-level prior distribution
          inf.mean <- -3 #mean of distribution
          inf.var <- 0.5 #variance of distribution"
```

Next, define the relative weights of the community-level hyperprior and the informed species-level prior. The weight is a value between 0 and 1 that determines the relative contribution of each prior to the aggregated prior (weights of each prior must sum to 1). To assign weights, create a vector with the weight of the community-level prior as the first element and the species-level prior as the second:

```
priors <- paste(priors,
         "#Define prior weights: how much each distribution
         #contributes to the final aggregate
         #Hyperprior first, then informed
           weights <- c(0.5, 0.5) #these are equal weights")
```

Next, pool the distributions. For normal distributions, the pooled mean μ_{pooled} is:

$$\mu_{pooled} = \sum(\boldsymbol{w}\mu) * v_{pooled}$$

where μ is a vector of raw means and v_{pooled} the pooled variance. The pooled variance v_{pooled} is:

$$v_{pooled} = \frac{1}{\sum \boldsymbol{w}}$$

The term **w** is defined as **w** = α/**v**, where α is the vector of weights and **v** is a vector of raw variances.

Because **w** typically represents the regional occupancy of a species in MSOM notation, we will use the term 'lb' to calculate the pooled mean and variance. The terms 'a1.mean' and '1/tau.a1' are the mean and variance, respectively, of the community-level hyperprior, which we will define later.

```
priors <- paste(priors,
           "#Pool the distributions

           lb[1] <- weights[1]/(1/tau.a1)

           #1/tau.a0 is the variation of
           hyperprior lb[2] <-
           weights[2]/inf.var

           pooled.var <- 1/sum(lb)

           pooled.mean <- sum(lb*c(a1.mean,inf.mean))

             *pooled.var")
```

Finally, we will use the pooled mean and variance of the aggregated prior above when we define species-level priors:

```
priors <- paste(priors,
              "for(i in 1:spec){

                #Create priors from hyperpriors/aggregated prior

                w[i] ~ dbern(omega)

                #w=1 means species was available for sampling

                a0[i] ~ dnorm(a0.mean, tau.a0) #a0 is the occupancy
                intercept


                a1[i] ~ dnorm(ifelse(i==10,pooled.mean,a1.mean),
                         ifelse(i==10,(1/pooled.var),tau.a1))

                #Use ifelse() here because detected species #are still
                drawn from hyperprior


                b0[i] ~ dnorm(b0.mean, tau.b0) #b0 is detection
                intercept")
```

Write the JAGS script

Next, we write the full model script in the JAGS language:

```
# Function to create text file
write.model <- function(priors){
  mod <- paste("
    model{
    # Define hyperprior distributions: intercepts
    omega ~ dunif(0,1)

    mean.a0 ~ dunif(0,1)
    a0.mean <- log(mean.a0)-log(1-mean.a0) tau.a0 ~ dgamma(0.1, 0.1)

    mean.a1 ~ dunif(0,1)
    a1.mean <- log(mean.a0)-log(1-mean.a0) tau.a1 ~ dgamma(0.1, 0.1)

    mean.b0 ~ dunif(0,1)
    b0.mean <- log(mean.b0)-log(1-mean.b0) tau.b0 ~ dgamma(0.1, 0.1)

    ",priors,"

      #Estimate occupancy of species i at point j for (j in 1:J){
        logit(psi[j,i]) <- a0[i] + a1[i]*cov[j]
             Z[j,i] ~ dbern(psi[j,i]*w[i])
             #Estimate detection of i at point j during survey k for(k
             in 1:K[j]){
             logit(p[j,k,i]) <-
             b0[i] obs[j,k,i] ~ dbern(p[j,k,i]*Z[j,i])
             }
        }
    }

      #Estimate total richness by adding observed and
      unobserved species

      n0<-sum(w[spec])

      N<-(spec-1)+n0

    }
    "
    )
  writeLines(mod,"samplemod.txt")
}
```

Run model

Before running the model, we need to send some information to JAGS, including our data, the parameters we want JAGS to return, and the initial values for the Markov chains.

```
# List of data to send to model
datalist <- list(J =nsite,K =Ks,obs =obs.aug, spec =nspec,cov =cov)

# Parameters to save after model is analyzed
parms <- c('N', 'a0', 'b0', 'a1', 'Z', 'a1.mean','tau.a1',
           'pooled.mean', 'pooled.var')

# Initial values for the Markov chains
init.values<-function(){
  maxobs <- apply(obs.aug, c(1,3), max)
  inits <- list(w = rep(1,nspec),
                a0 = rnorm(n =nspec),
                a1 = rnorm(n =nspec),
                b0 = rnorm(n =nspec),
                Z =maxobs)
}
```

Finally, run the model in JAGS:

```
# Send model to JAGS
model <- jags(model.file = 'samplemod.txt', data =datalist,
              n.chains =3,parameters.to.save =parms,
              inits =init.values,n.burnin =1000, n.iter =5000,
              n.thin =3)
```

Creating Figures

We can check if prior aggregation worked by comparing the posterior distribution (i.e. the model result) to the aggregated prior, and the aggregated prior to its parent distributions. If prior aggregation was successful, the aggregated prior should be somewhere in between the informed species-level prior and the community-level

hyperprior. The posterior distribution should resemble the aggregated prior more than the two parent distributions.

We will start by extracting the mean and standard deviation of each prior from the model. Note that model parameters are either variance or precision (tau); these need to be converted to standard deviation.

```
# Get values from aggregated prior
pooled.mean <- median(model$BUGSoutput$sims.list$pooled.mean)
pooled.sd <- median(sqrt(model$BUGSoutput$sims.list$pooled.var))
# Medians used because posterior is asymmetrical

# Create objects from informed values used in priors
inf.mean <--3

inf.sd <- sqrt(1/0.5)

# Pull community distribution priors from model
comm.mean <- median(model$BUGSoutput$sims.list$a1.mean)
comm.sd <- median(sqrt(1/model$BUGSoutput$sims.list$tau.a1))
# These are symmetrical but using median for consistency

# Pull posteriors from model
post.mean <- mean(model$BUGSoutput$sims.list$a1[,10])

post.sd <- sd(model$BUGSoutput$sims.list$a1[,10])
```

We will compare the distributions using ggplot:

```
# Plot the distributions
ggplot()+
  stat_function(fun =dnorm,n =1000,
                args = list(mean =pooled.mean,sd =pooled.sd),
                size =1, aes(linetype ="Aggregated",color ="Prior"))+
  stat_function(fun =dnorm,n =1000,
                args = list(mean =inf.mean,sd =inf.sd),
                size =1, aes(linetype ="Informed",color ="Prior"))+
  stat_function(fun =dnorm,n =1000,
                args = list(mean =comm.mean,sd =comm.sd),
                size =1, aes(linetype ="Community",color ="Prior"))+
  stat_function(fun =dnorm,n =1000,
                 args = list(mean =post.mean,sd =post.sd),
                 size =1,
                 aes(linetype ="Aggregated",color ="Posterior"))+
  xlim(c(-6,5))+
  scale_linetype_manual(breaks = c("Aggregated","Informed","Community"),
                 values = c(1,3,5),name ="Prior")+
  scale_color_manual(breaks = c("Prior","Posterior"),
                 values = c("black","red"),name ="")+
  labs(y ="Density") +
  theme_bw(base_size =16) +
  theme(panel.grid = element_blank(), axis.title.x = element_blank())
```

Based on this figure (Figure S2-1), prior aggregation was successful. The posterior distribution (red) is most similar to the aggregated prior (solid black line). Note that the posterior has been pulled slightly towards the center of the community-level prior (dashed black line): this is normal, and occurs as a result of modeling all species in the context of the community.

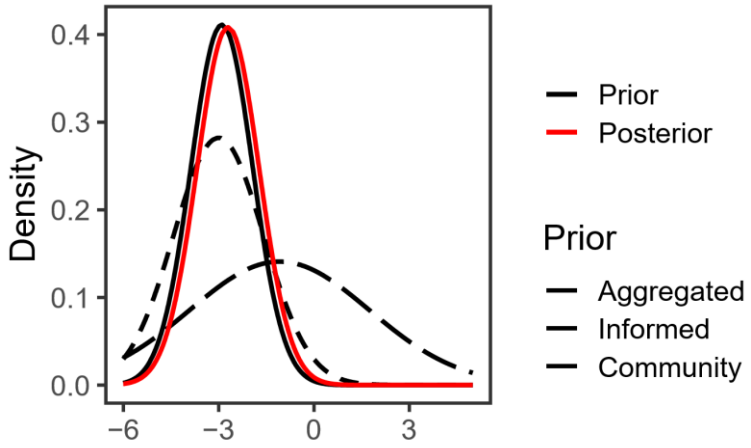

Figure S2-1: Comparison of the posterior distribution of the undetected species (red line) and the priors (black lines). The aggregated prior (solid black line) should fall somewhere in between the informed species-level prior (dotted black line) and uninformed community-level prior (dashed black line).

Next, we will evaluate whether the model successfully accounted for the regional occurrence of the undetected species. First we will extract the posterior

```
# Extract regional species richness N from model
Ns <- as.vector(model$BUGSoutput$sims.list$N)

# Create table of counts for each estimate
Ns %>%
  table() %>%
  data.frame() %>%
  {. ->>ns.frame}
colnames(ns.frame) <- c("N_Species","Freq")

# Look at mean and median estimates
median(Ns)
```

distribution of the parameter N, or regional species richness, from the model. To determine whether the model accounted for the missing species, you can use a measure of centrality such as the median:

```
## [1] 10
```

Or, more commonly, the expected value for the parameter (i.e. the peak of the posterior probability distribution, Figure 2). For our simulated data, the expected value and median estimates agree on a regional richness estimate of 10 species.

```
# Check it graphically
Ns.median <- median(Ns)
ggplot(data =ns.frame, aes(x = as.integer(as.character(N_Species)),
                           y =Freq)) +
  geom_col(width =0.95,color ='lightgray')+
  scale_x_discrete(limits = c(9,10))+
  labs(x ="Estimated Richness (N)",y ="Frequency")    +
  scale_y_continuous(expand = c(0,0))+
  theme_classic(base_size =14) +
  theme(axis.text.y = element_blank(), axis.title.y = element_blank(),
        legend.key.height = unit(40,units =      'pt'), aspect.ratio
        =1/1))
```

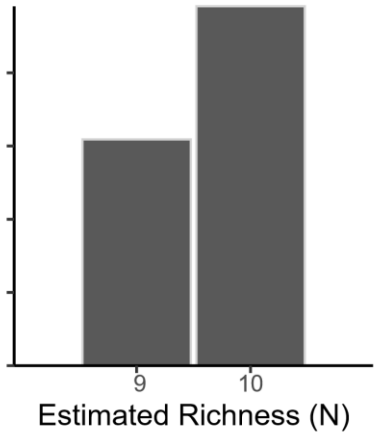

Figure 2: Posterior distribution of estimated regional species richness. The expected regional richness value, or the peak of the distribution, is 10 species, meaning the model successfully accounted for the undetected species.

To examine individual species' responses to the environmental covariate, we begin by extracting the parameter from the JAGS object and adding labels denoting species IDs:

```
# Extract covariate estimates from jags object
a1s <-model $BUGSoutput$sims.list$a1

a1s <- as.data.frame(a1s)

# Create a vector of species names
specnames <- logical()
for(i in 1:nspec){
  specnames[i] <- paste("Spec", i,sep ="")

}

colnames(a1s) <-specnames
```

Next, pivot the data from wide to long format for easier plotting, and calculate summary statistics. Usually, the best method for evaluating species' responses is by viewing the 95% credible interval (CI) and using the mean as the measure of centrality:

```
# Pivot data frame for plotting
a1.long <-a1s %>%
  pivot_longer(cols =
               everything(),names_to
               ="Spec", values_to ="a1")

a1.long$Spec <- factor(a1.long$Spec,levels =specnames)

# Get summary stats
a1.stat <-a1.long %>%
  group_by(Spec) %>%
  summarise(mean = mean(a1),lo =  quantile(a1,0.025), hi =
            quantile(a1,0.975)) %>%
  mutate(tru.resp =resp2cov)
```

Create the plot using ggplot:

```
# Make interval plot
ggplot(data =a1.stat, aes(x =Spec,y =mean))     +
      geom_point(size =1.5) +
      geom_errorbar(ymin =a1.stat $lo,ymax =a1.stat$hi, size =1,
                    width =0.2)  +
      geom_point(aes(y =tru.resp),color ="red",size =1.5) +
      geom_hline(yintercept =0,linetype ="dashed",size =1) +
      scale_y_continuous(limits = c(-25,20)) +
      labs(x ="Species",y ="Coefficient") +
      theme_bw(base_size =14) + theme(panel.grid = element_blank())
```

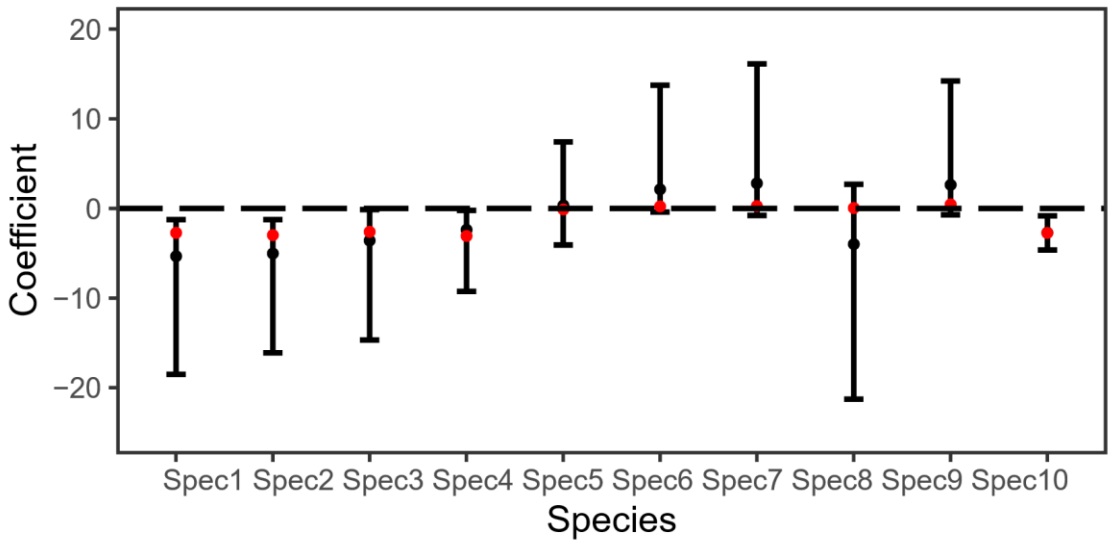

Figure 3: Estimated species-level responses to the simulated covariate. Mean estimates are denoted by black dots, whereas the true, simulated values are denoted with red dots. Error bars represent the 95% credible interval (CI); a CI which does not overlap 0 is usually considered significant.

The model correctly estimated significant negative covariate responses for detected species 1–4 and the undetected species 10 (Figure 3). Based on the position of the mean (black dots) relative to the 95% CI, we can also deduce that the posterior distributions for the detected species are highly skewed, with long tails extending away from zero. By contrast, the "stabilizing" effect of informed priors is clear in the model estimate for species 10, which has a more symmetrical and precise posterior distribution.

Additional literature cited

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Appendix 3: Supplemental Tables and Figures for Chapter 2

Table S3-1. Life history classifications of sampled ectoparasite species with associated literature. The bot fly *Cuterebra fontinella* was not included in comparisons of life history categories because it was the only species in its category. Asterisks indicate opposing views in the literature.

Ectoparasite	Order	Classification	Literature
Orchopeas leucopus	Siphonaptera	Nest	Traub 1972, Jackson and DeFoliart 1976; Haas et al. 1973*
Ixodes scapularis (larva)	Ixodida	Ephemeral	Kocan et al. 2015
Megabothris quirini	Siphonaptera	Nest	Benton and Cerwonka 1960
Hyperlaelaps sp.	Mesostigmata	Nest	Dowling 2006
I. scapularis (nymph)	Ixodida	Ephemeral	Kocan et al. 2015
Ctenophthalmus pseudagyrtes	Siphonaptera	Nest	Benton and Kelly 1969
M. acerbus	Siphonaptera	Fur	Amin and Sewell 1977; Lewis 2009*
Cuterebra fontinella	Diptera	Diptera	Catts 1982
M. asio	Siphonaptera	Nest	Benton and Cerwonka 1960, Quackenbush 1971
Unknown Mesostigmata	Mesostigmata	Nest	Dowling 2006
Peromyscopsylla hesperomys	Siphonaptera	Fur	Traub 1972
Epitedia wenmanni	Siphonaptera	Nest	Benton 1955, Traub 1972
Androlaelaps sp.	Mesostigmata	Nest	Dowling 2006
Doratopsylla blarinae	Siphonaptera	Fur	Traub 1972
Monopsyllus vison	Siphonaptera	Fur	Haas et al. 1973
O. howardi	Siphonaptera	Fur	Traub 1972, Amin and Sewell 1977
P. scotti	Siphonaptera	Fur	Traub 1972

Table S3-2. Abundance and preferred host species of sampled ectoparasites. Parasite species for which fewer than 5 individuals were not assigned a primary host. An asterisk (*) in the literature column indicates a difference in preferred host between the literature and the dataset; in these cases, the primary host from the literature is also listed.

Ectoparasite	Abundance	Preferred host	Literature
Orchopeas leucopus	193	*Peromyscus leucopus*	Benton and Cerwonka 1960
Ixodes scapularis (larva)	87	*P. leucopus*	Schmidt et al. 1999
Megabothris quirini	55	*Zapus hudsonius*	Lewis 2009; Benton and Cerwonka 1960, Osgood 1964, Benton and Kelly 1975 (*Myodes gapperi**)
Hyperlaelaps sp.	14	*Microtus pennsylvanicus*	
I. scapularis (nymph)	12	*P. leucopus*	Kollars et al. 1999, Schmidt et al. 1999 (*Tamias striatus**)
Ctenophthalmus pseudagyrtes	11	*P. leucopus; Tamias striatus*	Benton and Cerwonka 1960, Osgood 1964, Miller and Benton 1973 (no host preference*)
M. acerbus	8	*T. striatus*	Benton and Cerwonka 1960, Miller and Benton 1973, Benton and Kelly 1975
Cuterebra fontinella	7	*P. leucopus*	Catts 1982
M. asio	6	*M. pennsylvanicus*	Benton and Cerwonka 1960, Osgood 1964, Miller and Benton 1973, Benton and Kelly 1975

Table S3-2. Abundance and preferred host species of sampled ectoparasites. Parasite species for which fewer than 5 individuals were not assigned a primary host. An asterisk (*) in the literature column indicates a difference in preferred host between the literature and the dataset; in these cases, the primary host from the literature is also listed.

Ectoparasite	Abundance	Preferred host	Literature
Unknown Mesostigmata	6	*P. leucopus*	
Peromyscopsylla hesperomys	4		Benton and Cerwonka 1960, Miller and Benton 1973, Benton and Kelly 1975, Eckerlin and Gardner 2021 (*P. leucopus*)
Epitedia wenmanni	2		Benton and Kelly 1975 (*Peromyscus*)
Androlaelaps sp.	1		
Doratopsylla blarinae	1		Benton and Cerwonka 1960, Osgood 1964, Miller and Benton 1973, Benton and Kelly 1975, Eckerlin and Gardner 2021 (*Blarina brevicauda*)
Monopsyllus vison	1		Benton and Cerwonka 1960, Osgood 1964, Miller and Benton 1973, Benton and Kelly 1975 (*Tamiasciurus hodsonicus*)
O. howardi	1		Benton and Cerwonka 1960, Miller and Benton 1973, Benton and Kelly 1975, Eckerlin and Gardner 2021 (*Sciurus carolinensis*)
P. scotti	1		Miller and Benton 1973, Benton and Kelly 1975 (*P. leucopus*)

Table S3-3. Parasite occurrences on the small mammal *Peromyscus leucopus* for which the primary host is a different species. These ectoparasites tended to occur on *P. leucopus* at sites where the primary host had also been captured.

Parasite Species	Primary Host	Geographic Site	Primary host present?
Megabothris quirini	*Zapus hudsonius*	Audubon 2	No
		Intervale 1	Yes
		Intervale 2	Yes
		St. Mike's 1	Yes
		St. Mike's 2	Yes
Hyperlaelaps sp.	*Microtus pennsylvanicus*	Jericho 1	No
M. asio	*M. pennsylvanicus*	St. Mike's 1	Yes
Orchopeas howardi	*Tamiasciurus hudsonicus*	Jericho 1	Yes

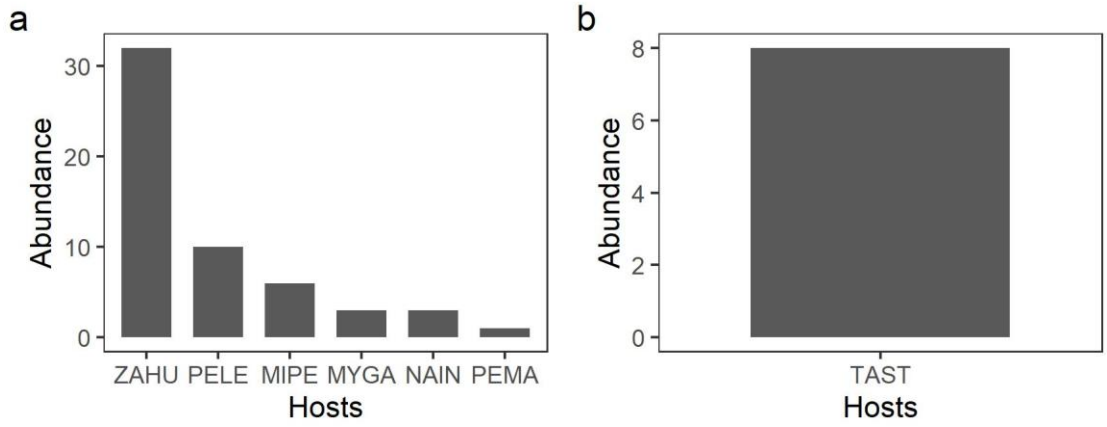

Figure S3-1. Abundances of a) *Megabothris quirini* and b) *M. acerbus* on host species upon which they were collected. The flea *M. quirini* represents a Class 4 parasite based on Benton and Cerwonka (1960), which is able to infest several host species but shows a clear preference. The flea *M. acerbus* is a Class 1 parasite due to the clear primary host and no to incidental infestation of other species. Host abbreviations are as follows: ZAHU = *Zapus hudsonius*, MIPE = *Microtus pennsylvanicus*, PELE = *Peromyscus leucopus*, NAIN = *Napaeozapus insignis*, MYGA = *Myodes gapperi*, PEMA = *Peromyscus maniculatus*, TAST = *Tamias striatus.*

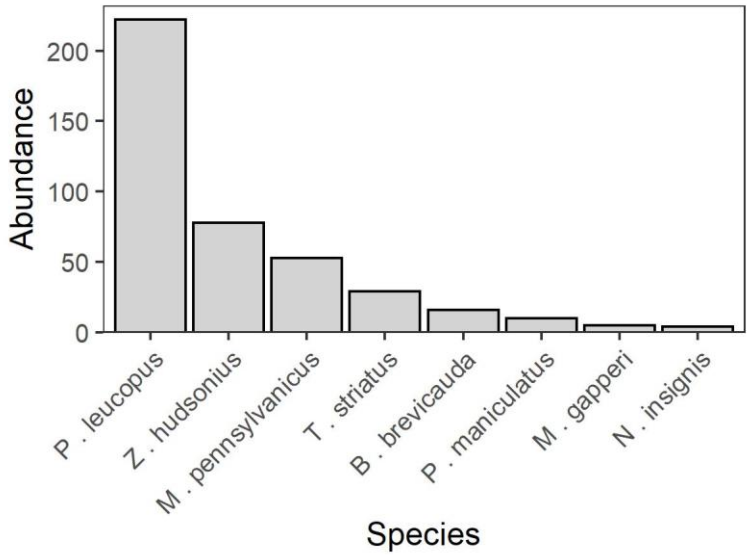

Figure S3-2. Abundances of small mammal hosts captured in Chittenden County, VT in summer 2020. The most common species was the white-fooded mouse *Peromyscus leucopus* with 222 individuals, followed by the meadow jumping mouse *Zapus hudsonius* with 78 individuals. The least abundant species was *Napaeozapus insignis* with 4 captured individuals.

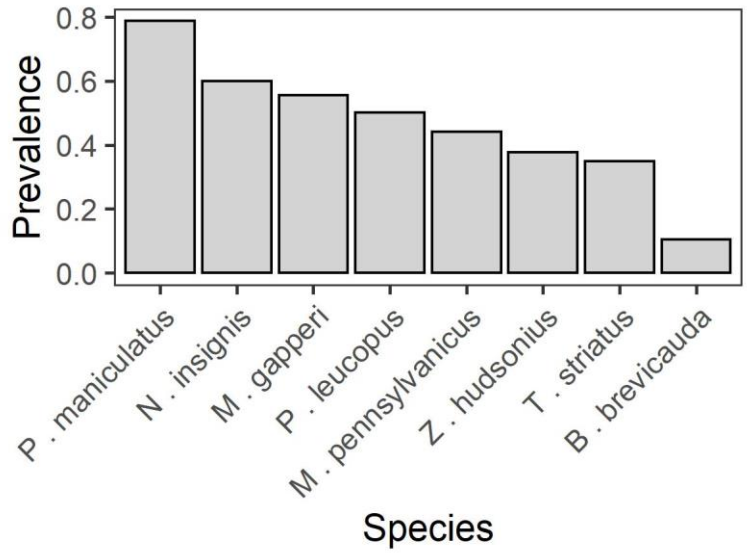

Figure S3-3. Ectoparasite prevalence, or the proportion of hosts infected by at least one ectoparasite, per mammalian host species. Prevalence averaged 0.465 across all host species and ranged from 0.105–0.788 among host species.

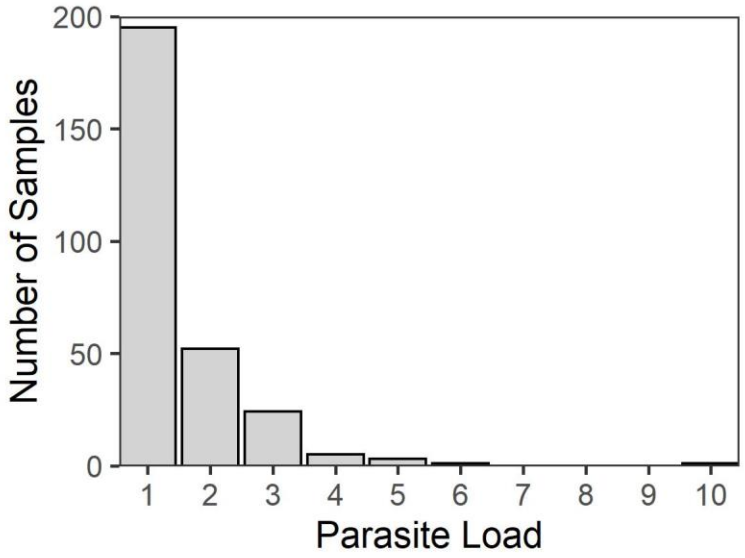

Figure S3-4. Parasite load (i.e. abundance per host) per capture event in which at least 1 ectoparasite was collected. Small mammal hosts, if infested, were typically only infested with 1 ectoparasite, with a range of 1–10 ectoparasites per sample.

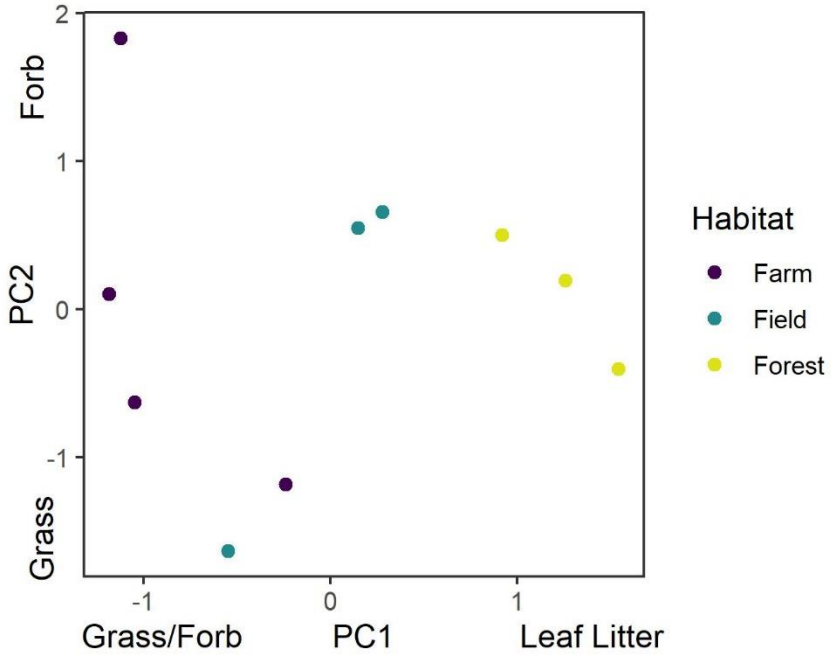

Figure S3-5. Results of the principal component analysis on vegetation composition data. PC1 explained 92.5% of the variation in the data and ranged from mostly grass/forb cover to mostly leaf litter. PC2 explained 7.2% of the variation in the data and ranged from grass cover to forb cover. Colors denote habitat designation of each site.

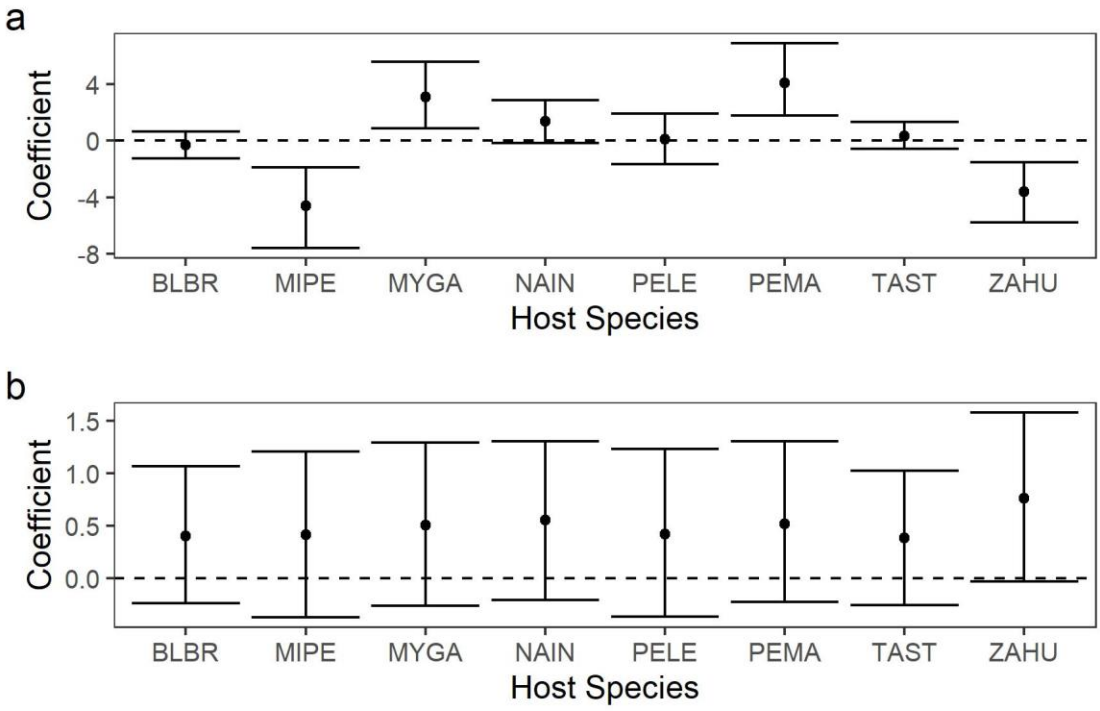

Figure S3-6. Responses of small mammal hosts to model coefficients for a) leaf litter cover and b) grass and forb cover. Points denote the mean of the posterior distribution. Error bars denote the 95% credible interval of the posterior; bars which do not overlap 0 (dashed line) are considered significant. A positive response to leaf litter cover (a) corresponds to a preference for forested habitats, whereas a negative response corresponds to a preference for open habitats. Positive responses to the grass/forb coefficient (b) correspond to a preference for habitats with more forb cover. Species abbreviations are as follows: BLBR = *Blarina brevicauda*, MIPE = *Microtus pennsylvanicus*, MYGA = *Myodes gapperi*, NAIN = *Napaeozapus insignis*, PELE = *Peromyscus leucopus*, PEMA = *Peromyscus maniculatus*, TAST = *Tamias striatus*, ZAHU = *Zapus hudsonius*.

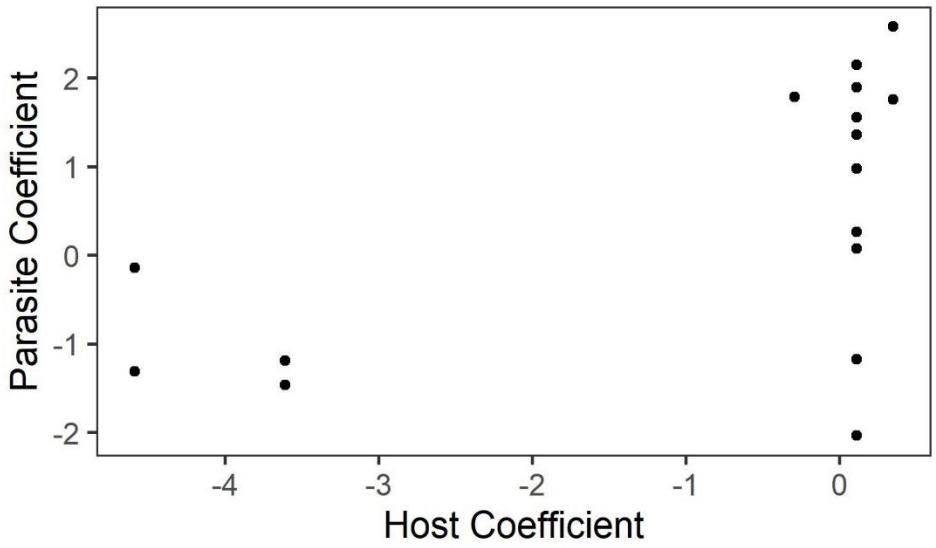

Figure S3-7. Small mammal host and ectoparasite coefficients for the PC1 (dead vegetation) covariate in the multi-scale model. Negative values indicate a preference for open habitat, values near 0 indicate no habitat preference, and positive values indicate a preference for forested habitats. Host coefficient values tend to behave categorically rather than linearly.

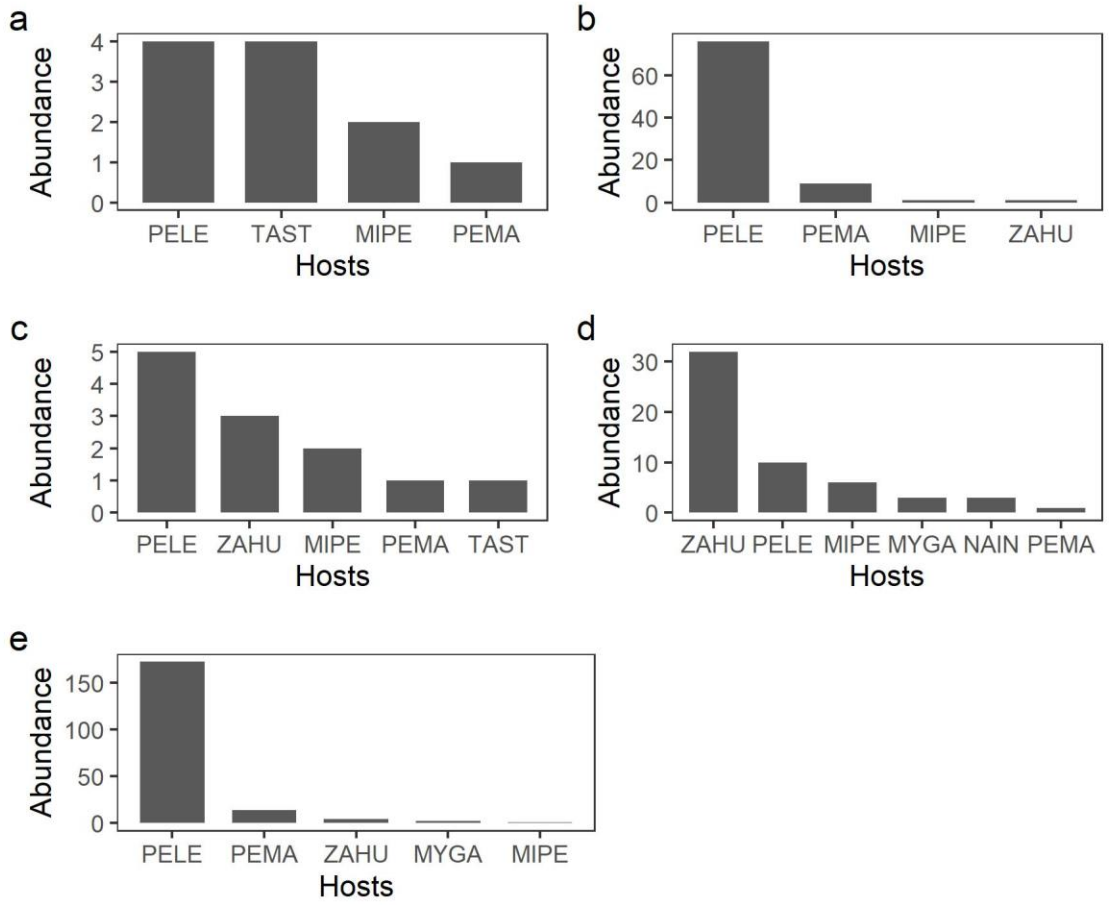

Figure S3-8. Abundance distributions on small mammal hosts of parasites infesting at least four host species: a) *Ctenophthalmus pseudagyrtes*, b) *Ixodes scapularis* (larvae), c) *I. scapularis* (nymph), d) *Megabothris quirini*, and e) *Orchopeas leucopus*. Most species demonstrated a clear preference for 1–2 host species.

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Appendix S4: Expanded Analytical Methods for Chapter 2

Multi-scale MSOM. Multi-scale, multi-species occupancy models (multi-scale MSOMs) are an extension of the MSOM developed by Dorazio and Royle (2005). MSOMs yield less biased estimates of occupancy than traditional methods by decoupling an ecological metric (e.g. occupancy) from the observation process that can introduce bias or error into the data (e.g. small mammal trapping, avian point counts, Iknayan et al. 2014). The ecological metric and observation process are then jointly modeled, with the observation process conditional on the true state of the ecological metric. The multi-scale MSOM is an extension of this framework, in which additional levels can be added to the model to account for multiple observation methods (Nichols et al. 2008) or multiple scales at which the ecological metric can be observed (Szewczyk and McCain 2019).

I used a multi-scale MSOM to estimate occupancy of ectoparasite species on 1) geographic sites and 2) individual small mammal hosts inhabiting each geographic site while accounting for detection error. Occupancy at geographic sites Z_{ij} takes the value of 1 when the ectoparasite species i is present at site j on at least one host individual k. Occupancy is modeled as the outcome of a Bernoulli trial in which the probability of success defined as Ψ_{ij} (Eq. S4-1). Occupancy of an ectoparasite species on a small mammal host within a geographic site z_{ijk} is the product of a Bernoulli trial in which the probability of success θ_{ijk} is conditional on the ectoparasite's presence at the geographic site (Eq. S4-2).

Occupancy in empirical datasets is often imperfectly observed. However, by capturing hosts multiple times over a short period, the model can estimate the probability

of detecting an ectoparasite species during a host capture event (MacKenzie et al. 2002, Iknayan et al. 2014). The estimated detection probability is used to generate more accurate estimates of the true occupancy states. Detection of an ectoparasite species during capture event *l* (x_{ijkl}) is modeled as a Bernoulli trial with a probability of success p_{ijkl} (Eq. S4-3). Detection probability is conditional on the ectoparasite species occupancy the individual host: an ectoparasite species cannot be detected on a host individual if it is not present.

$$Z_{ij} \sim Bernoulli(\Psi_{ij}) \qquad \text{(Eq. S4-1)}$$

$$z_{ijk}|Z_{ij} \sim Bernoulli(\theta_{ijk} * Z_{ij}) \qquad \text{(Eq. S4-2)}$$

$$x_{ijkl}|z_{ijk} \sim Bernoulli(p_{ijkl} * z_{ijk}) \qquad \text{(Eq. S4-3)}$$

Environmental covariates can be included in the models to increase the accuracy of occupancy and detection probability estimates (Dorazio and Royle 2005, Iknayan et al. 2014). I included covariates in all levels of the model using the logit link function (Eq. S4-4-6). Covariates PC1 and PC2 in the site model represent the first and second principal components of the vegetation data, respectively (Eq. S4-4). The host model contained covariates for host species identity, mass standardized by host species, and sex (Eq. S4-5); the detection model contained covariates for Julian date and capture number of the host (Eq. S4-6).

$$logit(\Psi_{ij}) = a0_i + a1_i PC1_j + a2_i PC2_j \qquad \text{(Eq. S4-4)}$$

$$logit(\theta_{ijk}) = \beta0_i + \beta1_i Species_j + \beta2_i Mass_j + \beta3_i Sex_j \text{ (Eq. S4-5)}$$

$$logit(p_{ijkl}) = \gamma0_i + \gamma1_i Date_j + \gamma2_i Capture_j \qquad \text{(Eq. S4-6)}$$

Priors for model intercepts and covariate coefficients for each ectoparasite species were drawn from a common distribution, the hyperparameters of which were in turn drawn from a hyperprior distribution (example in Eq. S4-7–8). By assuming each ectoparasite is drawn from a common distribution, the model can "borrow" information from common species to supplement estimates for species with limited data (Link and Sauer 1996). This allows rare or poorly detected species to be modeled in the context of the ectoparasite community, rather than attempting to model each species individually.

$$\alpha 0_i \sim N(\mu_{a0}, \tau_{a0}) \qquad \text{(Eq. S4-7)}$$

$$\tau_{a0} \sim Gamma(0.1, 0.1) \qquad \text{(Eq. S4-8)}$$

The hyperparameter tau (τ) in the equations above represents precision and is used in lieu of standard deviation (σ) in the JAGS programming language (Plummer 2017).

I analyzed the model using a Bayesian framework using JAGS 4.3.0 (Plummer 2017) with the R package R2jags (Su and Yajima 2015). Markov chain Monte Carlo sampling was completed using 3 chains of length 12,000 including a burn-in period of 5,000; thinned by 12 to reduce autocorrelation. Model convergence was assessed by visually examining the trace plots of the Markov chains and using the R-hat statistic (Gelman and Rubin 1992); an R-hat less than 1.1 was considered converged.

Bayesian R^2

Bayesian R^2 as proposed by Gelman et al. (2019) is defined as (Eq. S4-9):

$$R^2 = \frac{Var_\mu}{Var_\mu + Var_{res}} \qquad \text{(Eq. S9)}$$

In which Var_{μ} represents modelled predicted means and Var_{res} modelled residual variance. Both of these values are calculated from the posterior distributions of the model.

The modelled predicted means are essentially the estimated occupancy probability for each ectoparasite species at the site and host levels of the model (Ψ_{ij} and θ_{ijk}, respectively); thus Var_{μ} is the calculated variance of the posterior distributions. For logistic regression, Var_{res} is defined following Tjur (2009, Eq. S4-10):

$$Var_{res} = \frac{1}{N}\sum_{n=1}^{N}[\pi_n(1-\pi_n)] \qquad \text{(Eq. S4-10)}$$

In which π_n are predicted probabilities.

Small Mammal MSOM

The structure of the MSOM estimating occupancy for small mammal hosts is similar to the multi-scale MSOM for parasites, with the exception that occupancy is only observed at the level of the geographic site. Thus, the probability of detecting a small mammal during a given survey is conditional on the small mammal species occupying the geographic site (Eq. S4-11).

$$x_{ijk}|Z_{ij} \sim Bernoulli(p_{ijk} * Z_{ij}) \qquad \text{(Eq. S4-11)}$$

I used the same site-level covariates in the host model as in the parasite model to facilitate comparisons between coefficients (Eq. S4-4). The detection model for small mammal hosts was similar to the detection model for ectoparasites (Eq. S4-6) but did not include a covariate for capture number.

I analyzed the host MSOM using a Bayesian framework in JAGS 4.3.0 (Plummer 2017) and specified priors using the same methods as the ectoparasite model (Eq. S7–S8. Markov chain Monte Carlo sampling was completed using 3 chains of length 5,000 including a burn-in period of 1,000; thinned by 5 to reduce autocorrelation.

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Appendix S5: Expanded Methods for Chapter 3

Tetracycline Analysis. To determine evidence of ONRAB bait consumption by raccoons, we shipped premolar teeth to Matson's Laboratory (Manhattan, Montana, USA) to determine the presence of tetracycline (TTCC) biomarker. Using the same cross section cut for age determination, teeth were microscopically examined for the presence of TTCC, seen as yellow fluorescence using an ultraviolet filter (Johnston et al. 1987). When possible, the lab provided biomarker presence results indicated by one or more tetracycline depositions, potentially indicating one or more ONRAB baits consumed, but biomarker in our database was simply recorded as binary presence or absence. We used a one-tailed z-score test with significance set at $p<0.05$ for calculating TTCC presence between pre- and post-oral rabies vaccination (ORV).

Of the 902 raccoons sampled for rabies virus neutralizing antibody (RVNA), 773 had a result for TTCC biomarker (presence or absence). Raccoons were significantly more likely to have biomarker present post-ONRAB than pre- (pre- 17.0% [n=454], post- 32.0% [n=319], $p<0.00001$). That trend was true in all three development types as well: low pre- 19.8% [n=111], post- 42.7% [n=82], $p=0.00029$; medium pre- 14.6% [n=192], post- 23.8% [n=122], $p=0.0197$; high pre- 17.9% [n=151], post- 33.0% [n=115], $p=0.00219$).

Population-level analysis. We estimated raccoon abundance (N_{it}) in each cell during each year as a random draw from the expected abundance λ_{it}; which, based on the literature, we expected to vary with the intensity of human development (Eq. S5-1; Šálek

et al. 2015). We assume the true abundance to be close to the expected abundance, but stochastic variation might result in a true abundance value that is different than the expected value (Eq. S5-2).

$$log(\lambda_{it}) = \beta 0_{it} + \beta 1 * Dev_i \qquad \text{(Eq. S5-1)}$$

$$N_{it} \sim Pois(\lambda_{it}) \text{(Eq. S5-2)}$$

In addition to the abundance model, we estimated raccoon RVNA seroprevalence S_{it} in cell I in year t in a model similar to the abundance model. However, we used a logit link function instead of a log link function, which is more appropriate for estimating values that are bound between 0 and 1 (Eq. S5-3). We were particularly interested in determining if the density of baits or the geographic coverage of baits impacted the raccoon RVNA seroprevalence estimates, as this would help inform management strategies (these were termed "Density" and "Cover", respectively). We were also interested in whether characteristics of raccoon populations were associated with RVNA seroprevalence, specifically estimated raccoon abundance and the relative proportion of juveniles to adults in the population ("Abund" and "Age", respectively). We also examined the impact of other environmental factors, such as urban development intensity in the sampling cells (low, medium, and high; termed "Dev"), and the abundance of potential competitors such as skunks and opossums, as these factors may affect raccoon behavior and influence ORV bait uptake (Prange and Gehrt 2004, Stark et al. 2020). To estimate the proportion of the population that is RVNA seropositive we modeled the number of seropositive raccoons captured per day (pos_{itj}) as a proportion of the total daily captures (n_{itj}, Eq. S5-4).

$$logit(S_{it}) = \alpha 0_{it} + \alpha 1 * Density_{it} + \alpha 2 * Cover_{it} + \alpha 3 * Dev_i + \alpha 4 * Abund_{it} + a5 * Age_{it} + a6 * Opossums_{it} + a7 * Skunks_{it} \quad \text{(Eq. S5-3)}$$

$$pos_{itj} \sim Bin(S_{it}, n_{itj}) \quad \text{(Eq. S5-4)}$$

The detection model for abundance is a multinomial mixture model with removal sampling. In this model, multinomial categories correspond to unique encounter histories, and multinomial cell probabilities are functions of the probability *p* of those encounter histories occurring within the sampled n_{it} individuals (Kéry and Royle 2016). For example, consider a population of animals captured and removed over three consecutive sampling periods. Individuals captured on the first day will have an encounter history 1 -- --, individuals on the second day 0 1 --, and so on. By assigning probabilities to unique encounter histories, the model is able to account for the decreasing probability of encountering a unique individual as the proportion of tagged individuals in the population increases.

Environmental and survey factors that may affect detection (capture) probability can be incorporated as covariates using a logit link function, which converts linear relationships to a probability scale that is bound between zero and one. Our detection model included a covariate for the number of closed traps (due to recaptures, captures of nontarget species, or triggered traps with no capture) on trap day *j*, as decreasing the number of available traps may reduce the likelihood of capturing an unmarked individual (Eq. S5-5). We did not include an explicit detection model for seroprevalence as we assumed RVNA testing error was negligible compared to error in capture rates.

$$logit(p_{itj}) = w0_{it} + w1_{it} * ClosedTrap_j \quad \text{(Eq. S5-5)}$$

To aid in estimation and comparison, all continuous covariates were scaled to have a mean of 0 and a standard deviation of 1. Model parameters were estimated using a Bayesian hierarchical model with uninformative priors in the programs JAGS (Plummer 2017) and R (R Core Team 2021). We chose a Bayesian approach because it is a flexible tool to jointly estimate multiple variables of interest, in this case abundance, seroprevalence, and detection (capture). We fit the model using three Markov chains for 7500 iterations with a burn-in period of 1000; posterior chains were thinned by 5 to reduce autocorrelation. We assessed model convergence visually and using the $\hat{R}$ statistic (Gelman and Rubin 1992); values less than 1.1 were considered converged.

Covariate significance was evaluated using the 95% and 75% credible interval (CI). Credible intervals that did not overlap 0 indicated a significant covariate. After evaluating a model with all independent covariates, we analyzed additional models that each included one interaction term. For all independent covariates and significant interaction terms (based on the 75% CI), we followed up with an appropriate frequentist test (usually an ANOVA or linear regression) to supplement the conclusions made based on the CI's.

After evaluating covariate significance, we used model selection to determine which covariates had the most explanatory power. We used the Watanabe-Akaike Information Criterion (WAIC) to perform model selection because it tends to perform better than methods such as the Akaike Information Criterion or Bayesian Information Criterion when applied to hierarchical models (Hooten and Hobbs 2015). If WAIC results

were inconclusive, we presented the results from the model that included all independent covariates and any significant interaction terms.

To ensure the model is internally consistent (i.e., the model makes sense given the observed data) we assessed model fit using posterior predictive checks, which involves comparing simulated data generated from the fitted model to the observed data (Gelman et al. 1996, Gelman and Hill 2006, Gelman et al. 2013). We evaluated model fit by graphically comparing the distributions of simulated abundance and seroprevalence to the corresponding distributions of the observed data; systematic differences in the shapes of the distributions are typically an indicator of poor model fit. Although posterior predictive checks are more conservative methods such as cross-validation (Sinharay and Stern 2003, Conn et al. 2018), posterior predictive checks are sufficient for detecting large deficiencies in model fit.

Individual level analysis

We studied the probability an individual would seroconvert by conducting a logistic regression where the response was the RVNA status of the individual. We examined individual effects (age and sex), development class (high, medium, or low), sampling period (pre- or post-baiting), and year. We also examined the interactions between year and sampling period and year and development type. Models were compared using the second order Akaike Information Criterion (AICc; Burnham and Anderson 2004). To compare the relative strength of different factors we examined the cumulative covariate weights associated with each covariate corrected by the number of

models each covariate was in within the model set (Doherty et al. 2012). Higher cumulative covariate weights show more support and values above 0.5 are considered important. Model averaging was used to estimate parameters when model uncertainty existed.

We were interested in which factors were most influential in determining an individual raccoon's RVNA seroprevalence status. We found that age of the raccoon was most strongly associated with an individual's probability of being RVNA seropositive (cumulative covariate weight = 1.00), followed by an interaction between sampling period and year (cumulative covariate weight = 1.00). Development type and sex were not strongly related to the probability an individual would be seropositive (cumulative covariate weights of 0.17 and 0.33 respectively).

Age was the most important factor, with the probability of being RVNA seropositive increasing with age (β_{age} = 0.2, SE= 0.05). The probability of being RVNA seropositive was 26% for a juvenile, 52% for a 5-year old, and 76% for a 10-year old raccoon (Fig. S6-5A; these estimates are based on an individual in the low development area, pre-bait, in 2015).

There was a significant interaction between sampling period and year. An individual raccoon who was caught during 2015 or 2016 had a higher probability of being RVNA seropositive than an individual caught during 2017 (Fig. S6-5B). There was not a difference in the pre-bait vs. post-bait probability of being seropositive during 2015 or 2016. In contrast, during 2017 the probability an individual would be RVNA seropositive increased post-baiting compared to pre-baiting (Fig. S6-5B).

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Appendix S6: Supplemental Tables and Figures for Chapter 3

Table S6-1. Results of model selection with WAIC. The best model is shown at the top. A ΔWAIC value less than 2 indicates the model explains the data as well as the best model. With the exception of the full model (all covariates), models with 3 or more covariates are not shown.

Model	WAIC	ΔWAIC
Intercept	45.25	0.00
Density	45.30	0.05
Skunks	45.38	0.12
Density + Skunks	45.40	0.15
Opossums	45.47	0.22
Opossums + Skunks	45.65	0.40
Coverage + Skunks	45.68	0.43
Development	45.71	0.46
Coverage	45.83	0.58
Age + Skunks	45.84	0.59
Raccoons + Skunks	45.97	0.72
Age + Opossums	46.02	0.77
Raccoons	46.05	0.80
Opossums + Raccoons	46.05	0.80
Coverage + Age	46.06	0.81
Coverage + Opossums	46.06	0.81
Skunks + Development	46.06	0.81
Age	46.09	0.84
Opossums + Development	46.13	0.88
Density + Coverage	46.16	0.91
Density + Opossums	46.17	0.92
Density + Development	46.23	0.98
Density + Raccoons	46.23	0.98
Density + Age	46.28	1.03
Coverage + Development	46.28	1.03
Raccoons + Development	46.30	1.04
Coverage + Raccoons	46.31	1.06
Age + Raccoons	46.39	1.14
Age + Development	46.44	1.19
Full	47.95	2.69

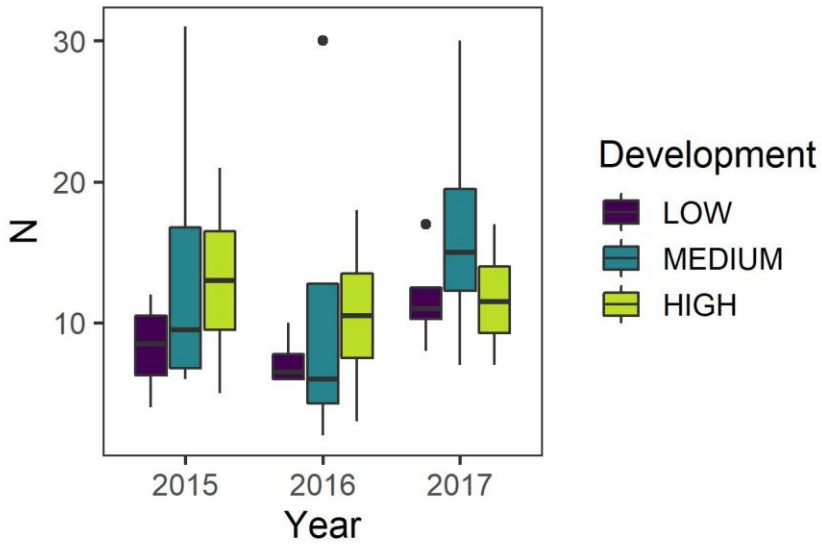

Figure S6-1. Estimated raccoon abundance (N) across urban development classes in the greater Burlington, Vermont, USA area, 2015–2017. Boxes represent quartiles, lines the 95% confidence interval, and dots are outliers. The model estimated that raccoon abundance was higher in sites classified as medium and high development than sites classified as low development based on the 75% credible interval; however, an ANOVA did not support this finding ($F_{2,33}$ = 1.415, P = 0.257).

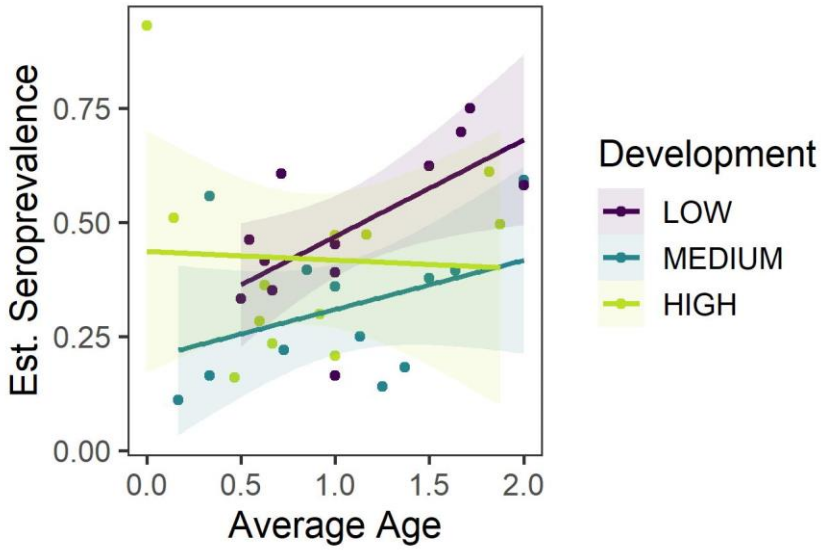

Figure S6-2. Relationship between average raccoon age (in years) and estimated rabies virus neutralizing antibody seroprevalence when an influential outlier is included. The outlier was excluded from the analysis due to an unusually small sample size at the site. There is no significant association between average age and estimated seroprevalence when this outlier is present ($F_{1,34}$ = 2.477, P = 0.125, R^2 = 0.041).

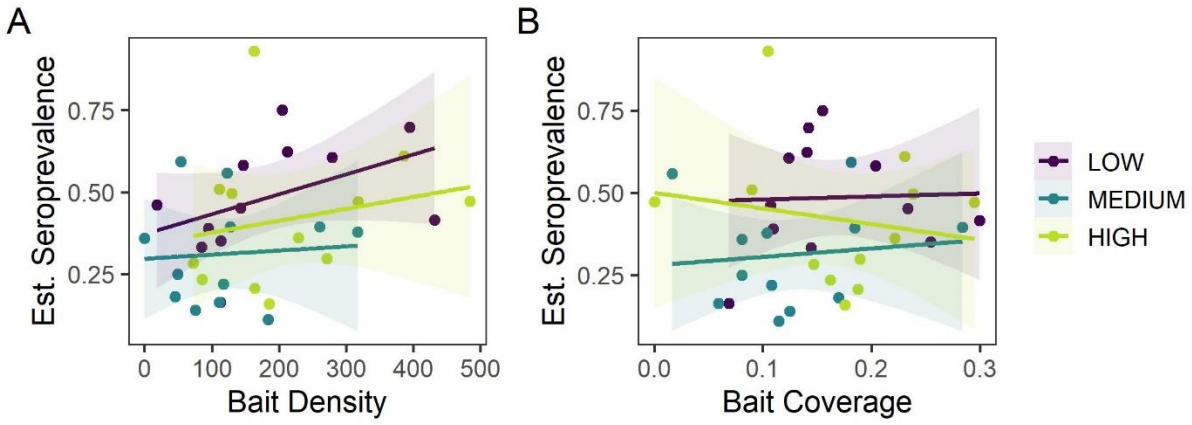

Figure S6-3. Relationships between estimated raccoon rabies virus neutralizing antibody seroprevalence and A) bait density (i.e., baits per km^2) and B) bait coverage (a measure of spatial evenness) across urban development classes. There were no significant associations between bait density ($F_{1,34}$ = 3.974, P = 0.054, R^2 = 0.078) or bait coverage ($F_{1,34}$ = 0.141, P = 0.709, R^2 = -0.025) and seroprevalence.

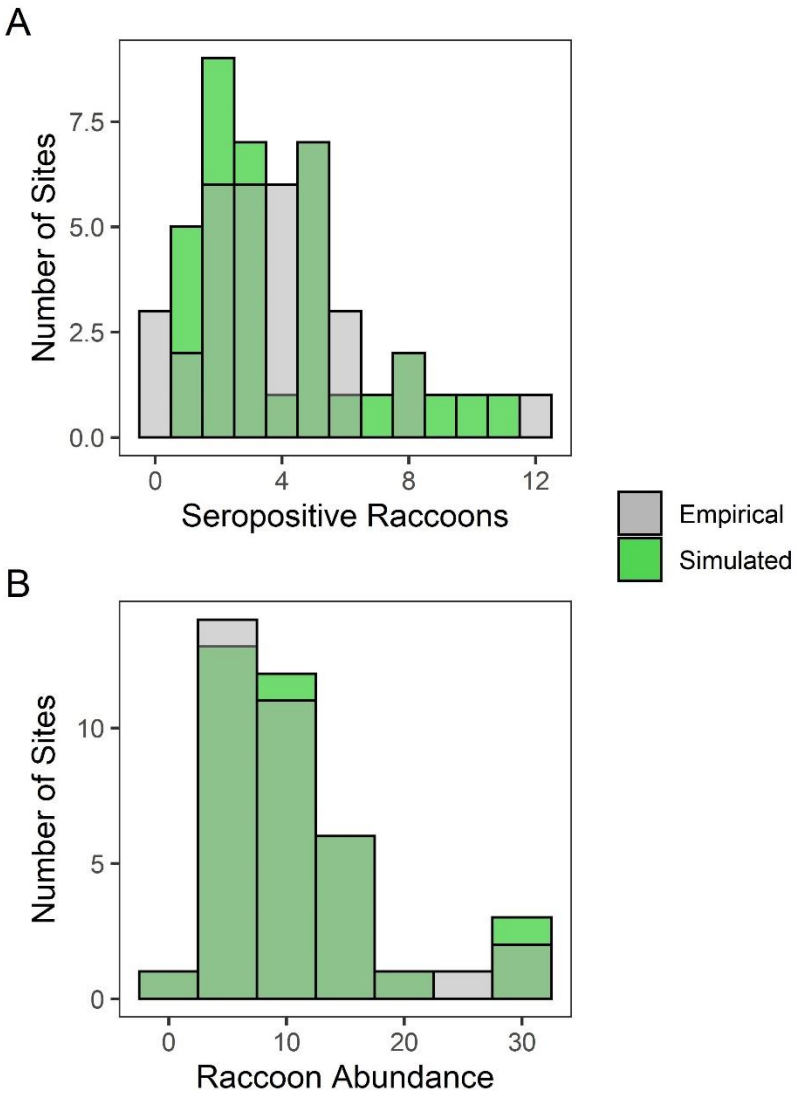

Figure S6-4. Comparison of the distributions of empirical data and simulated data predicted by the model for A) the number of rabies virus neutralizing antibody seropositive raccoons per site and B) total raccoon abundance at each site. Large differences in the shape of the empirical and simulated distributions would indicate the model is not internally consistent.

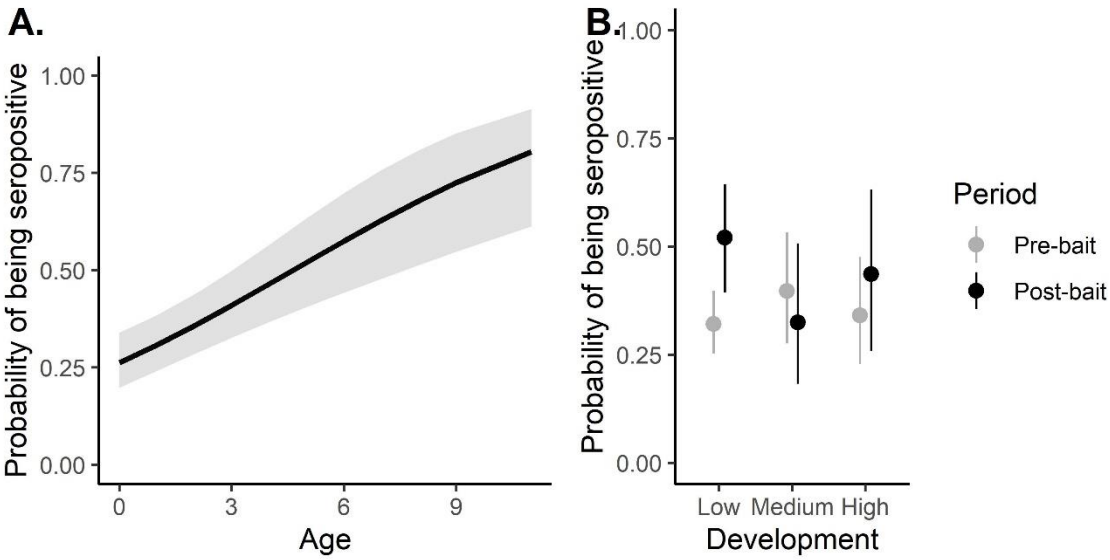

Figure S6-5. The probability an individual raccoon will be rabies virus neutralizing antibody seropositive based on the age (A) and the year and sampling period (B). Uncertainties are 95% confidence intervals shown either as a shaded region (A) or vertical line (B).