Evaluation of infection risk of two endoparasites to moose (Alces alces) in the Adirondack Park of New York

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Abstract

Endoparasites *Parelaphastrongylus tenuis* and *Fascioloides magna* were attributed to 19% and 21% of mortalities in New York in 2015, respectively, and may be contributing factors to limiting moose (*Alces alces*) populations in the Adirondacks region. Field surveys were conducted to collect white-tailed deer (*Odocoileus virginianus*) fecal pellets under distance sampling protocol both to measure relative deer density and to diagnose the infection status of the pellets by *P. tenuis* and *F. magna*. Over the three years of data collection, 41.7% of fecal pellets collected ($N = 656$) contained *F. magna* eggs, and 34.7% of fecal pellets contained L1 *P. tenuis* larvae. We attempted to quantify the geospatial distribution of parasite infection using landscape variables such as habitat, geomorphon structure, elevation, and spatial trend, but goodness-of-fit tests indicated poor fit of the model structures we evaluated, whether assessed as continuous intensity of infection (Poisson, negative binomial, zero-inflated Poisson), or binary infection status (binomial). We conclude that the data are not extensive enough to quantify relationships between parasite infection in white-tailed deer fecal pellets and geospatial effects.

Introduction

Moose (*Alces alces*) populations are in decline in parts of their range in North America such as in Minnesota, Vermont, and New Hampshire in the United States of America and Nova Scotia, Alberta, Saskatchewan, Manitoba, and Ontario in Canada (Lankester 2018; Timmermann and Rodgers 2017). Some researchers point to parasite infection from liver fluke (*Fascioloides magna*) and/or brainworm (*Parelaphastrongylus tenuis*) as contributing factors to these declines (Murray et al. 2006; Lankester 2010, 2018; Wünschmann et al. 2015), although this claim is controversial (Lenarz 2009) and in some areas may coincide with other factors such as depredation or low reproduction rates that may disguise effects of parasite infection (Barber-Meyer and David Mech 2016; Kuzyk et al. 2018). Nevertheless, brain worm and liver fluke cause morbidity and mortality in moose populations and should be monitored.

Infections by *P. tenuis* are benign to white-tailed deer (*Odocoileus virginianus*), but cause severe neurological disorders in moose caused by migration of larvae through the central nervous system that often end in death (Pybus 2001; Lankester 2010). *Parelaphastrongylus tenuis* is acquired via ingestion of gastropod intermediate hosts, in which *P. tenuis* larvae have molt from L1 to L2, and L3 stages over approximately 4 weeks. Gastropods become infected by ingesting the mucuosal layer surrounding white-tailed deer fecal pellets, or from the soil over which the L1-stage larvae have been washed by precipitation.

Fascioloides magna infection damage manifests as lesions in the hepatic tissue due to migration of immature flukes or fibrous encapsulation of adult flukes (Pybus 2001). Again, moose are thought to become infected through ingestion of gastropod intermediate hosts. A major distinction is that the gastropod hosts are aquatic snails (typically within the genus *Lymnaea*) that become infected by free-swimming miracidia introduced to the water as eggs in white-tailed deer feces (Pybus 2001; Peterson et al. 2013; Malcicka 2015). The meracidia develop within the snail, ultimately generating cercariae that encyst as metacercariae on aquatic vegetation. Because moose select aquatic vegetation as a significant proportion of their diet, *F. magna* metacercariae are presumably commonly consumed by moose.

In the Adirondacks of New York, moose populations have increased since their extirpation in the late 19th century, but their populations have not seen the same growth during the 20th century as their New England counterparts (Timmermann and Rodgers 2017). Recent estimates of moose population size indicate that there are approximately 600 to 1000 moose in the Adirondacks (Wong, Fuller, and Royle, n.d.), a range which does not indicate substantial change from previous assertions of population size (Hickey 2008). Factors that may be limiting the population are not established, but the focal parasites *P. tenuis* and *F. magna* have been observed in moose necropsies with moderate frequency (REF Schuler and/or DEC).

The New York State Department of Environmental Conservation (DEC) has been gathering information on moose health from incidental mortalities (n = 117) since 2000 and the Animal Health Diagnostic Center (AHDC) started live moose testing in 2015. Moose in New York State appear to be substantially impacted

by several parasites excepting winter ticks, which are more common in New England states. Over 19% of mortalities were attributed to P. tenuis, 21% of moose carcasses examined were infected with liver flukes (Fascioloides magna). Migrating parasites cannot be detected in live moose, but were likely a problem as New York moose had 5-6x higher eosinophil (white blood cell) counts than New Hampshire or Maine moose.

The geospatial distribution of infection risk to moose is a concern for management, and we attempt to quantify this by first assessing the spatial patterns in infection of white-tailed deer fecal matter.

Materials and Methods

Study area

We surveyed within the Adirondack Park of the state of New York. It is an area of approximately 24,000 km^2, composing approximately 17% of the state of New York. Elevation ranges from 100m - 1600m. The Adirondack Park contains primarily upland forest habitat dominated by such species as American beech (*Fagus grandifolia*), red spruce (*Picea rubens*), hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), striped maple (*Acer pensylvanicum*), and balsam fir (*Abies balsamea*). Approximately 20% of the park is composed of wetland habitats including open river corridors, floating bogs, and large open bogs dominated by conifers (Hickey 2008).

Field data collection

White-tailed deer fecal pellet groups were collected opportunistically during the years of 2016 and 2017 for the purpose of parasite quantification during a larger survey investigating the population size of moose in the park. The moose study surveyed triangular transects approximately 3 km long, selected by cluster random sampling. The clustering design of the transects were optimized for a spatial capture-recapture survey, including 3 transects per cluster separated by approximately 2-4 km.
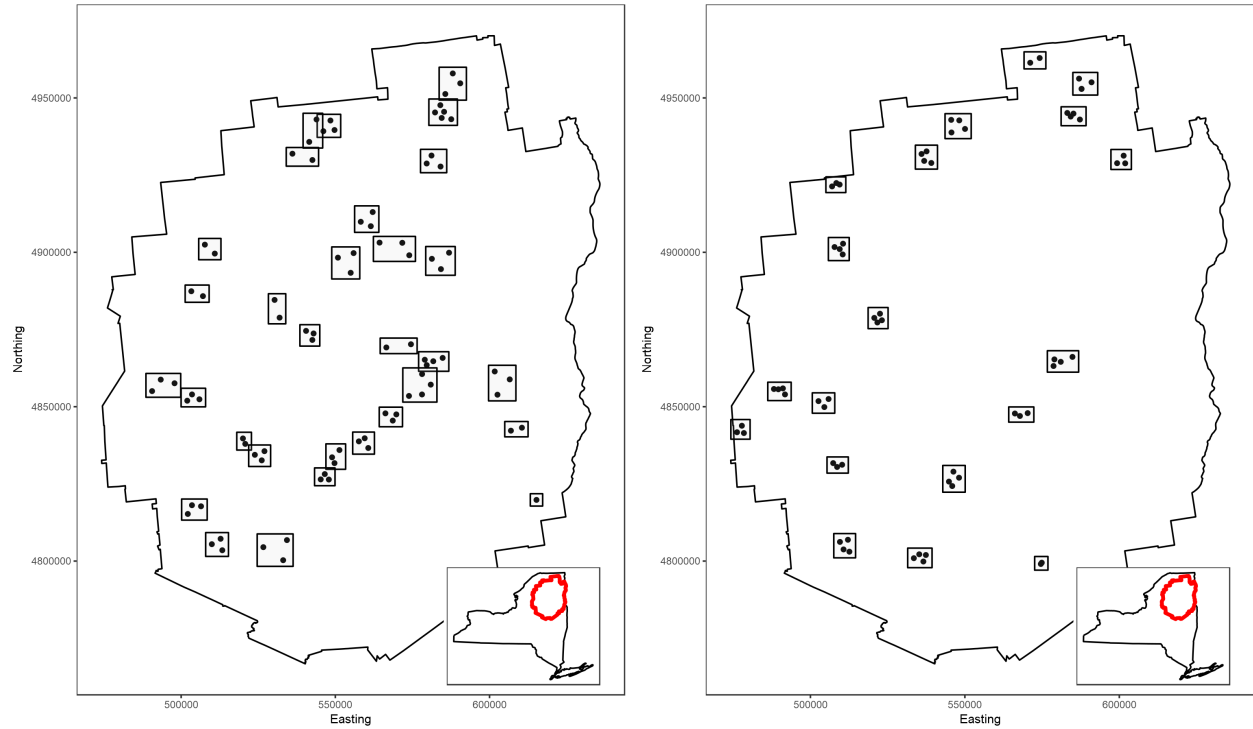
(a) Transect locations within the Adirondack Park for the 2016 survey.

(b) Transect locations within the Adirondack Park for the 2017 survey.

Figure 1: Transect locations within the Adirondack Park for the 2017 survey. Each dot represents the location of one transect, and each cluster of transects is bounded by a box. The inlaid plot indicates the extent of the Adirondack Park relative to the state of New York.

In 2018, a single-observer distance sampling protocol was implemented to quantify deer fecal group abundance in addition to measuring parasite intensity. Along each moose transects, 6 distance sampling transects each 100m long were spaced 200m apart from each other. **INSERT FIGURE FOR DEER TRANSECTS** A total of 150 transects were sampled in 2018. At the specified start point, field technicians extended a 100m tape to serve as the center line, and made observations along its length. Any number of scat pellets were considered to constitute a fecal group, and the approximate number was recorded. When a fecal group was detected, its distance perpendicular from the center line, and parallel along the center line was recorded. The perpendicular distance is the focal variable of distance sampling, but the parallel distance provided highly precise location coordinates of the scats – because the start point of the transect was recorded with greater accuracy (due to longer GPS averaging time), the coordinates of the scats could be refined by translating the start point in space by the angle of the transect, and the parallel distance away from the start point.

Fifty-seven white-tailed deer fecal samples were collected in 2016, 391 samples were collected in 2017, and 174 samples were collected in 2018.

Parasitological analyses

The fecal samples were analyzed by the Cornell Animal Health and Diagnostic Center using several methods. For *F. magna*, Flukefinder, a modified Baermann technique, and fecal quantitative flotation were used. For *P. tenuis*, the modified Baermann, and fecal quantitative flotation methods were implemented. After 2016, the performant method for *F. magna* was determined to be Flukefinder, and for *P. tenuis* the performant method was the modified Baermann technique. This was assessed by **HOW? ASK KRYSTEN**, and validated post-hoc to have the greatest detection probability by an occupancy analysis.

Flukefinder

Needs to be updated by relevant members; Flukefinder methodology not in shared folder

Modified Baermann

Fecal flotation

Statistical Models

For analysis of relative risk of infection to moose, we implemented a hierarchical Bayesian modeling framework analyzed with the `R` package `INLA`, which uses integrated nested Laplace approximation to approximate the posterior distribution of model parameters.

Parasite intensity model

Let $\widehat{\lambda}(s)$ be the estimated per-fecal-group-sample abundance (or, intensity in the epidemiological sense). Let $S = \{s_i, i = 1, ..., n\} \subset \Omega$ be the n distinct locations where white-tailed deer fecal groups were observed within the observation region $\Omega \subseteq \mathbb{R}^2$, and let y_i be the observed parasite count within the fecal sample.

Parasites observed within each scat sample are ≥ 0, and due to the high prevalence of 0's, we considered a negative binomial distribution for the response in addition to the Poisson. On any bounded region $B \subseteq \Omega$, observations are thus modeled as follows:

$$y_i \sim \text{Poisson}(\mu_i)$$
$$\log(\mu_i) = \beta_0 + \beta_1 * x_1(s_i) + ... + \beta_p * x_p(s_i) + \Psi_1(s_i) \qquad (1)$$
$$\Psi_1(s_i) \sim GP(0, \Sigma)$$

Where, y_i represent the parasites observed per fecal group sample, μ_i is the mean function modeled dependent upon spatial covariates $x_j(s)$, and $\Psi_1(s)$ is a Gaussian process with mean 0 and covariance matrix Σ. The covariance function used is the Matern:

$$\text{cov}[\Psi(s), \Psi(s')] = \sigma_\Psi^2 \; \kappa ||s' - s|| \; \mathcal{K}_1(\kappa ||s' - s||)$$

where τ, κ are variance and range scaling parameters, respectively, $\sigma_\Psi^2 = 1/(4\pi\kappa^2\tau^2)$ is the marginal variance, and $\mathcal{K}_1$ is the modified Bessel function of the second kind and order 1 (See Lindgren and Rue (2015) for the specific representation and estimation of the spatial random effects within INLA). The spatial random field is optional and we test models with and without it to assess support for modeling unstructured spatial dependence.

Additionally, we assessed the fit of models treating the response as a binary random variable modeled under the binomial distribution and zero-inflated binomial distribution, with the same model of spatial dependence instead using a different link function.

Covariates on parasite intensity

In our model, we consider the following covariate effects on parasite intensity. Coordinate data (UTM Easting and Northing) are included to model broad-scale spatial trend. We considered a derived variable of precipitation representing the total accumulation of precipitation in the year prior to the data collection date, measured in inches. Precipitation affects the survival of *P. tenuis* and *F. magna* outside of a host (i.e. as L1 larvae, and eggs in feces, respectively), and so it is anticipated that deer would be more likely to be infected in areas of higher rainfall (Pybus 2001). Additionally, gastropod activity is inhibited by drought, and so

higher rainfall would suggest higher risk of infection due to a higher availability of gastropods to be ingested in the case of *P. tenuis* (Lankester 2018). We used the spatially interpolated PRISM dataset for precipitation (n.d.). We considered another derived variable for snowfall accumulation in the snowfall season prior to the data collection date (that is, from September until April prior to the date of survey). Similar to precipitation, we anticipate that areas that experience low snowfall in the year prior to the survey date will exhibit a higher parasite intensity due to increased parasite survival, and increased activity of gastropod intermediate hosts. The National Weather Service's National Snowfall Analysis dataset was used to obtain spatially-referenced snowfall amounts.

Local terrain basins where water may collect were considered as a potentially important effect particularly for *F. magna*, as the life cycle of the parasite has a period during which metacercariae encyst on aquatic vegetation and once matured infect aquatic snail intermediate hosts. We hypothesized that intensity of infection for *F. magna* will be greater in basins than on slopes or peaks, and we assessed this by the geomorphon tool in QGIS, assessed at a resolution of 40km (1600 squared-kilometers). This resolution was selected because it maximized the variation in the geomorphon classification distribution relative to our sample locations.

INLA settings

Priors

We used default priors set by INLA for the covariate coefficients; that is:

$$\beta_p \sim \text{Normal}(0, 0.001)$$

where the second arguemnt of the Normal distribution is specified on the *precision* scale.

The priors for the Matern covariance parameters were specified using INLA's penalized complexity prior construction for the range parameter ρ and marginal variance σ.

Mesh

A mesh is required to fit Gaussian random effect models under the INLA framework. The tool `meshbuilder` was used to visually select settings that fulfilled the following criteria (see Figure \ref{fig:boundaries}):

- Relatively fine mesh resolution (< 1km) in the vicinity of sampled data
- Relatively low mesh resolution far from sampled data (>5km)

Model Specifications

Six models were applied using the covariates developed above upon response variables for both *F. magna* and *P. tenuis*.

Table 1: Model specifications and their covariates

| Model	Formula
Null Model	.
Full Model	Easting + Northing + Precipitation + Snow + Geomorphon + Elevation + Gaussian Process (GP)
Fixed Effects Model	Easting + Northing + Precipitation + Snow + Geomorphon + Elevation
Fixed Effects Parasite Survival Model	Precipitation + Snow + Geomorphon
Two-scale spatial model	Easting + Northing + GP
Two-scale spatial model and elevation	Easting + Northing + Elevation + GP
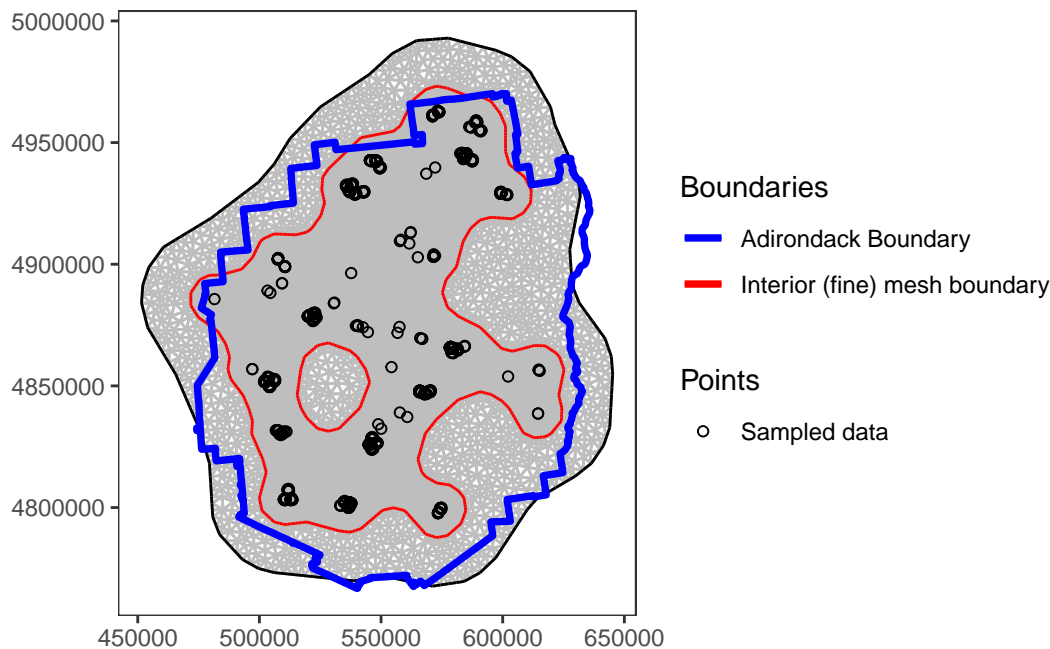
Figure 2: Boundary line of the Adirondack Park, as well as the mesh constructed for INLA.

Results

We observed 41.7% positive diagnoses of *F. magna* over the three years of data collection ($N = 656$), with yearly positive results being 69% in 2016, ($N = 80$), 37.8% in 2017 ($N = 402$), and 38.5% in 2018 ($N = 174$). For *P. tenuis* we observed 34.6% infection prevalence among the fecal samples tested over all three years, with yearly positive results being 48.8% in 2016 ($N = 80$), 23.9% in 2017 ($N = 402$), and 52.6% in 2018 ($N = 174$) (Table 2).

Table 2: Raw frequencies and proportions of diagnoses performed on white-tailed deer fecal samples between 2016 and 2018.

Diagnosis	Species	Counts			Proportions		
		2016	2017	2018	2016	2017	2018
Positive	F. magna	55	152	67	0.688	0.378	0.385
	P. tenuis	39	95	92	0.488	0.239	0.526
Negative	F. magna	25	250	107	0.312	0.622	0.615
	P. tenuis	41	302	83	0.512	0.761	0.474

Model results

Model comparison was implemented by comparison of wAIC values produced by INLA. This information criterion is a measure of *relative* out-of-sample predictive accuracy, and lower wAIC values indicate greater relative performance.

F. magna

Among the models fit to the *F. magna* data, the best-supported model was the global model, followed by the second-best model with a delta-wAIC value of 27.97.

Model Name	wAIC
Full model	3052.38
Two-scale spatial model	3080.35
Two-scale spatial model and elevation	3083.11
Fixed effects model	3108.38
Fixed Effects Parasite Survival Model	3110.83
Null Model	3130.45

P. tenuis

Among the models fit to the *P. tenuis* data, the best-supported model was the reduced 'two-scale spatial model', which had only easting, northing, and the Gaussian process error model. The next best performing model followed with a delta-wAIC value of 8.7

Model Name	wAIC
Two-scale spatial model	2761.41
Two-scale spatial model and elevation	2770.12
Full model	2772.17
Fixed effects model	2795.64
Fixed Effects Parasite Survival Model	2823.92
Null Model	2824.85

Fixed effects parameter estimates

The parameter estimates for the models in general saw little agreement among the parameter estimates and/or wide plausible distributions.
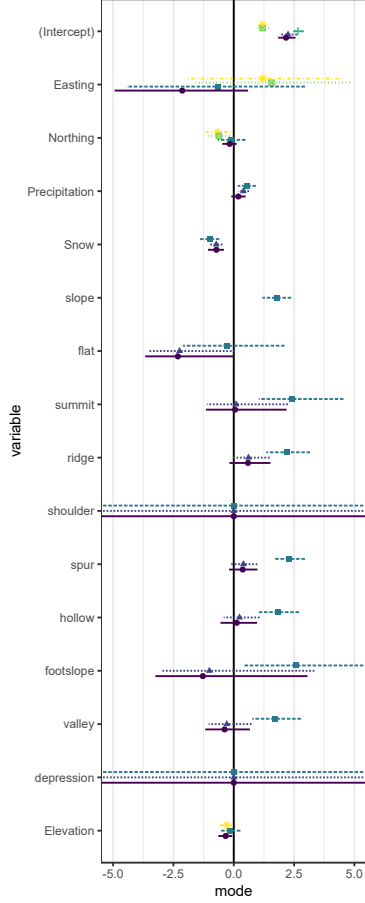
(a) *F. magna* model parameter estimates.
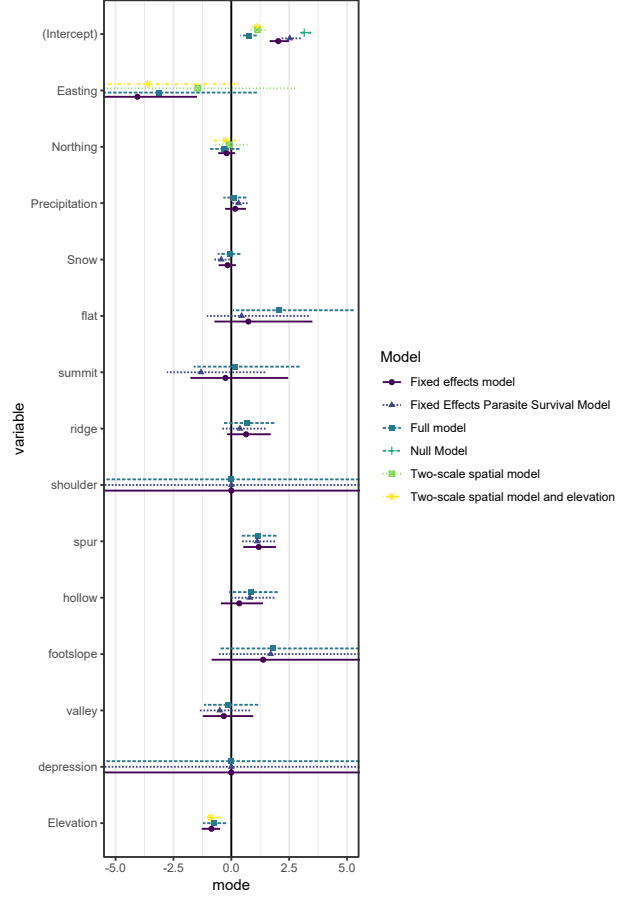
(b) *P. tenuis* model parameter estimates.

Figure 3: Displayed are the mode and 95% credible interval for coefficients of fixed effects. See Appendix A for exact values.

Bayesian model checks

We checked the fit of the models using Bayesian predictive checks made available by the `INLA` package; specifically the conditional predictive ordinate (CPO) and the probability integral transform (PIT).

Conditional predictive ordinate

The conditional predictive ordinate (CPO) is a leave-one-out cross-validation measure, defined as

$$\text{CPO}_i = \pi(y_i^{\text{obs}}|y_{-i})$$

and describes the probability of observing of a particular observation when all of the data but observation i are used to fit to the model. Very small values indicate that the model is not likely to have predicted a particular observation and thus that model is not expected to generalize well.

All of our models exhibited poor performance with roughly half of the data points having low CPO values less than 0.1. In addition, the data points with low CPO values are strongly related to those points with the response > 0. In most models,

This indicates that the models overall fit the data poorly, having almost no predictive power to the domain of the response of interest.

Probability integral transform

Another goodness-of-fit measure that `INLA` provides is the probability integral transform value, which measures the probability of predicting a new observation less than or equal to the observed data value. More generally the probability integral transform states that the cumulative distribution function $\mathcal{F}$ of a random variable X evaluated at x_i for all i will have a random uniform distribution if the random values x_i are indeed generated by the same process as X. If we take $\mathcal{F}(X)$ to be predictions from a fitted model, departure from uniformity indicates that the observations x_i may not be well predicted by the model.

In the binary case, we observed reasonable CPO values, but

Discussion

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Appendices

Appendix A: Parameter estimates for the negative binomial model

Table 3: Fixed effect parameter estimates and distribution for *F. magna*

variable	mean	sd	0.025quant	0.5quant	0.975quant	mode
Null Model						
(Intercept)	2.670	0.116	2.450	2.668	2.905	2.663
Full model						
Easting	-0.710	1.878	-4.449	-0.696	2.950	-0.668
Northing	-0.099	0.289	-0.659	-0.103	0.483	-0.110
Precipitation	0.537	0.193	0.164	0.534	0.923	0.530
Snow	-1.013	0.219	-1.458	-1.008	-0.598	-0.997
slope	1.786	0.303	1.184	1.787	2.380	1.790
flat	-0.133	1.071	-2.109	-0.180	2.107	-0.277
summit	2.616	0.894	1.035	2.553	4.546	2.422
ridge	2.235	0.461	1.349	2.228	3.164	2.214
shoulder	0.000	31.623	-62.086	-0.001	62.034	0.000
spur	2.301	0.326	1.665	2.299	2.948	2.294
hollow	1.847	0.425	1.032	1.839	2.703	1.825
footslope	3.090	1.604	0.396	2.924	6.656	2.568
valley	1.736	0.511	0.770	1.722	2.781	1.694
depression	0.000	31.623	-62.086	-0.001	62.034	0.000
Elevation	-0.148	0.216	-0.576	-0.147	0.274	-0.145
Two-scale spatial model						
(Intercept)	1.204	0.131	0.948	1.202	1.471	1.200
Easting	1.591	1.617	-1.582	1.582	4.814	1.564
Northing	-0.606	0.285	-1.162	-0.609	-0.027	-0.615
Two-scale spatial model and elevation						
(Intercept)	1.177	0.126	0.928	1.176	1.432	1.175
Easting	1.248	1.624	-1.925	1.233	4.497	1.203
Northing	-0.662	0.276	-1.200	-0.665	-0.101	-0.671
Elevation	-0.288	0.201	-0.684	-0.289	0.107	-0.289
Fixed effects model						
(Intercept)	2.184	0.183	1.840	2.178	2.559	2.167
Easting	-2.154	1.408	-4.938	-2.148	0.594	-2.137
Northing	-0.173	0.152	-0.473	-0.173	0.123	-0.172

Table 3: Fixed effect parameter estimates and distribution for *F. magna (continued)*

variable	mean	sd	0.025quant	0.5quant	0.975quant	mode
Precipitation	0.191	0.151	-0.102	0.191	0.489	0.189
Snow	-0.730	0.168	-1.069	-0.727	-0.408	-0.721
flat	-2.058	0.936	-3.670	-2.142	0.000	-2.318
summit	0.305	0.854	-1.154	0.225	2.189	0.055
ridge	0.632	0.432	-0.180	0.618	1.521	0.591
shoulder	0.000	31.623	-62.086	-0.001	62.034	0.000
spur	0.383	0.300	-0.194	0.379	0.983	0.371
hollow	0.168	0.385	-0.549	0.153	0.965	0.125
footslope	-0.618	1.619	-3.247	-0.821	3.056	-1.281
valley	-0.315	0.471	-1.181	-0.336	0.669	-0.379
depression	0.000	31.623	-62.086	-0.001	62.034	0.000
Elevation	-0.343	0.147	-0.639	-0.340	-0.062	-0.335
Fixed Effects Parasite Survival Model						
(Intercept)	2.267	0.172	1.945	2.262	2.620	2.251
Precipitation	0.406	0.114	0.186	0.404	0.634	0.402
Snow	-0.733	0.137	-1.008	-0.730	-0.470	-0.726
flat	-1.980	0.922	-3.558	-2.066	0.054	-2.248
summit	0.349	0.858	-1.115	0.268	2.244	0.096
ridge	0.656	0.400	-0.087	0.640	1.487	0.609
shoulder	0.000	31.623	-62.086	-0.001	62.034	0.000
spur	0.410	0.285	-0.137	0.406	0.980	0.398
hollow	0.284	0.378	-0.417	0.269	1.070	0.239
footslope	-0.340	1.622	-2.969	-0.545	3.342	-1.011
valley	-0.218	0.453	-1.043	-0.242	0.738	-0.289
depression	0.000	31.623	-62.086	-0.001	62.034	0.000

Table 4: Fixed effect parameter estimates and distribution for *P. tenuis*

variable	mean	sd	0.025quant	0.5quant	0.975quant	mode
Null Model						
(Intercept)	3.163	0.141	2.897	3.160	3.452	3.152
Full model						
(Intercept)	0.761	0.181	0.391	0.767	1.103	0.780
Easting	-3.072	2.099	-7.194	-3.085	1.109	-3.116
Northing	-0.291	0.320	-0.915	-0.295	0.355	-0.302
Precipitation	0.141	0.254	-0.345	0.136	0.652	0.128
Snow	-0.083	0.251	-0.594	-0.078	0.396	-0.067
flat	2.390	1.335	0.065	2.286	5.289	2.065
summit	0.422	1.167	-1.629	0.334	2.953	0.150
ridge	0.713	0.567	-0.376	0.704	1.856	0.686
shoulder	0.000	31.623	-62.086	-0.001	62.034	0.000
spur	1.155	0.402	0.372	1.153	1.951	1.148
hollow	0.910	0.537	-0.101	0.895	2.007	0.865
footslope	2.570	1.903	-0.539	2.340	6.872	1.821
valley	-0.070	0.596	-1.180	-0.091	1.164	-0.135
depression	0.000	31.623	-62.086	-0.001	62.034	0.000
Elevation	-0.739	0.256	-1.229	-0.744	-0.221	-0.755
Two-scale spatial model						

Table 4: Fixed effect parameter estimates and distribution for *P. tenuis (continued)*

variable	mean	sd	0.025quant	0.5quant	0.975quant	mode
(Intercept)	1.127	0.178	0.773	1.127	1.477	1.130
Easting	-1.465	2.147	-5.716	-1.460	2.756	-1.450
Northing	-0.066	0.374	-0.781	-0.074	0.699	-0.090
Two-scale spatial model and elevation						
(Intercept)	1.085	0.146	0.781	1.093	1.352	1.115
Easting	-3.503	1.889	-7.133	-3.538	0.330	-3.609
Northing	-0.222	0.278	-0.756	-0.229	0.351	-0.239
Elevation	-0.856	0.246	-1.317	-0.865	-0.347	-0.884
Fixed effects model						
(Intercept)	2.053	0.212	1.656	2.046	2.491	2.031
Easting	-4.080	1.336	-6.730	-4.071	-1.481	-4.054
Northing	-0.200	0.187	-0.565	-0.200	0.167	-0.201
Precipitation	0.176	0.231	-0.272	0.174	0.635	0.170
Snow	-0.168	0.190	-0.546	-0.166	0.200	-0.162
flat	1.091	1.084	-0.729	0.979	3.504	0.738
summit	0.071	1.079	-1.768	-0.033	2.456	-0.252
ridge	0.703	0.481	-0.184	0.681	1.707	0.639
shoulder	0.000	31.623	-62.086	-0.001	62.034	0.000
spur	1.204	0.358	0.519	1.198	1.927	1.186
hollow	0.405	0.463	-0.448	0.385	1.371	0.345
footslope	2.225	1.922	-0.850	1.970	6.613	1.376
valley	-0.228	0.555	-1.232	-0.259	0.948	-0.321
depression	0.000	31.623	-62.086	-0.001	62.034	0.000
Elevation	-0.869	0.202	-1.279	-0.865	-0.486	-0.855
Fixed Effects Parasite Survival Model						
(Intercept)	2.550	0.216	2.148	2.542	2.999	2.526
Precipitation	0.321	0.194	-0.056	0.320	0.706	0.317
Snow	-0.433	0.190	-0.807	-0.433	-0.061	-0.432
flat	0.830	1.129	-1.056	0.710	3.350	0.449
summit	-0.956	1.088	-2.784	-1.069	1.464	-1.311
ridge	0.445	0.494	-0.460	0.422	1.482	0.374
shoulder	0.000	31.623	-62.086	-0.001	62.034	0.000
spur	1.143	0.369	0.439	1.135	1.888	1.121
hollow	0.868	0.474	0.000	0.845	1.862	0.800
footslope	2.610	1.997	-0.567	2.338	7.177	1.703
valley	-0.390	0.563	-1.399	-0.425	0.813	-0.496
depression	0.000	31.623	-62.086	-0.001	62.034	0.000

Table 5: Random effect parameter estimates and distribution for *F. magna*

variable	mean	sd	0.025quant	0.5quant	0.975quant	mode
Null Model						
nbinomial disp. par.	0.122	0.008	0.106	0.121	0.139	0.121
Full model						
nbinomial disp. par.	0.166	0.014	0.140	0.165	0.195	0.165
Range for i	5515.167	2213.500	2331.133	5143.199	10895.930	4451.775
Stdev for i	1.207	0.215	0.825	1.195	1.668	1.174

Table 5: Random effect parameter estimates and distribution for *F. magna (continued)*

variable	mean	sd	0.025quant	0.5quant	0.975quant	mode
Two-scale spatial model						
nbinomial disp. par.	0.150	0.012	0.127	0.150	0.175	0.149
Range for i	11526.408	7173.748	3244.258	9764.533	30171.243	7078.406
Stdev for i	1.103	0.222	0.722	1.084	1.590	1.051
Two-scale spatial model and elevation						
nbinomial disp. par.	0.149	0.012	0.126	0.149	0.174	0.148
Range for i	11060.536	7649.846	2720.299	9077.986	31174.637	6192.311
Stdev for i	1.027	0.228	0.630	1.012	1.522	0.985
Fixed effects model						
nbinomial disp. par.	0.133	0.009	0.115	0.133	0.152	0.132
Fixed Effects Parasite Survival Model						
nbinomial disp. par.	0.131	0.009	0.114	0.131	0.150	0.130

Table 6: Random effect parameter estimates and distribution for *P. tenuis*

variable	mean	sd	0.025quant	0.5quant	0.975quant	mode
Null Model						
nbinomial disp. par.	0.081	0.006	0.070	0.081	0.093	0.081
Full model						
nbinomial disp. par.	0.105	0.010	0.085	0.106	0.125	0.107
Range for i	5458.300	3432.441	1742.839	4543.395	14497.705	3322.667
Stdev for i	0.987	0.335	0.471	0.942	1.770	0.854
Two-scale spatial model						
nbinomial disp. par.	0.108	0.010	0.090	0.108	0.128	0.107
Range for i	10451.968	5610.929	3792.004	9088.597	24976.959	7069.275
Stdev for i	1.499	0.276	1.016	1.480	2.093	1.447
Two-scale spatial model and elevation						
nbinomial disp. par.	0.103	0.009	0.085	0.103	0.122	0.103
Range for i	6021.166	3800.863	1839.593	5028.645	15973.662	3666.118
Stdev for i	0.990	0.306	0.468	0.970	1.650	0.921
Fixed effects model						
nbinomial disp. par.	0.093	0.007	0.080	0.092	0.107	0.092
Fixed Effects Parasite Survival Model						
nbinomial disp. par.	0.084	0.006	0.073	0.084	0.097	0.084