

Title: Human activities and weather drive contact rates of wintering elk.

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Abstract:

1. Wildlife aggregation patterns can influence disease transmission. However, limited research evaluates the influence of anthropogenic and natural factors on aggregation.

Many managers would like to reduce wildlife contact rates, driven by aggregation, to limit disease transmission. We develop a novel analytical framework to quantify how management activities such as supplemental feeding and hunting versus weather drive contact rates while accounting for correlated contacts. We apply the framework to the National Elk Refuge (NER), Wyoming, USA, where the probable arrival of chronic wasting disease (CWD) has magnified concerns.

2. We used a daily proximity index to measure contact rates among 68 global positioning system collared elk from 2016 to 2019. We modelled contact rates as a function of abiotic weather-related effects, anthropogenic effects and aggregation from the prior day. The winter of 2017–2018 had greater natural forage availability and little snow, which led to a rare non-feeding year on the NER and provided a unique opportunity to evaluate the effect of feeding on contact rates relative to other conditions.

3. Supplemental feeding was the strongest predictor of aggregation, and contact rates were 2.6 times larger while feeding occurred compared to the baseline rate (0.34 and 0.13, respectively). Snow-covered area was the second strongest predictor of contact rates highlighting the importance of abiotic factors to elk aggregation, but this effect had half the strength of feeding. These results are the first to show, even in animals that congregate naturally, how greatly supplemental feeding amplifies aggregation. Contact rates were also 23% lower during times when elk hunting was active (0.10) compared to the baseline.

4. *Synthesis and applications.* Supplemental feeding increased contacts between elk well above the natural effects of weather, even after accounting for correlated movement expected in wintering ungulates. Similarly, differences in hunting season timing with adjacent areas led to an increase in contacts, suggesting an additional management option for reducing aggregation. The analytical framework presented supports the evaluation of temporally varying management actions that influence aggregation broadly and can be easily implemented whether the interest in changing aggregation is related to reduction of disease transmission, human–wildlife conflict or inter-species competition.

Keywords: adaptive management, aggregation, chronic wasting disease, contact rate, CWD, elk, supplemental feeding, transmission

Main text

Across taxonomic groups and around the world, large aggregations of wildlife often coincide with increased disease prevalence (Descamps et al., 2012; Rodríguez-Pastor et al., 2017; Venesky et al., 2011). Many different factors including predator presence and resource availability determine how wildlife use the landscape, creating aggregation patterns that influence both contact rates and local densities simultaneously and thus the likelihood of disease transmission (Figure 1). For directly transmitted pathogens, the contact rates between individuals determine disease spread and are often inextricably tied to the density of a population (i.e. density-dependent transmission; Begon et al., 2002). Density and the way aggregations occur also affect the extent and severity of environmental contamination and subsequently the indirect transmission of pathogens that can survive outside of a living host (Breban et al., 2009).

Research suggests that both natural and anthropogenic processes drive ungulate aggregation. In elk, *Cervus canadensis*, this behaviour is most notable during migration and in the winter months (Proffitt et al., 2012). Elk herds typically reach greatest densities during winter, in part because the challenges of foraging through snow and other conditions can lead to reduced areas conducive to foraging and reduced movement for conservation of energy. Many ungulates also naturally aggregate into herds for predator defence (Jarman, 1974). In terms of anthropogenic effects on aggregation, supplemental feeding has become ubiquitous from

backyard feeders and rubbish bins to the baiting of game species and feeding to meet population management goals (Murray et al., 2016). Previous studies often identify feeding as a factor driving increased aggregations, leading to increased contact rates between individuals and subsequent disease transmission (e.g. Cross et al., 2007); however, few explicitly measure the effect of feeding on contact rates or aggregation (see Cross et al., 2013) and we know of no studies comparing feeding to other environmental factors.

Over a century ago, encroachment on critical elk wintering habitat by the town of Jackson, WY, reduced elk survival and prompted the creation of a winter feeding programme and the National Elk Refuge (NER, Smith, 2001). Supplemental feeding of elk now occurs during winter months at 22 sites across the state of Wyoming (Cotterill et al., 2018; Cross et al., 2013). However, current densities of elk on the refuge are at greater levels resulting in increased risk for disease outbreaks, including chronic wasting disease (CWD, Galloway et al., 2017; U.S. Fish and Wildlife Service, 2019). CWD, a prion disease that causes extreme weight loss and neurological issues resulting in death (Williams et al., 2002), has spread rapidly across North America over the last two decades (Sutherland et al., 2018; U.S. Geological Survey, 2020). The transmission dynamics of CWD are multifaceted and still under investigation. Neither frequency nor density-dependent models alone capture the complexities of CWD transmission (Storm et al., 2013) and environmental transmission may play an important role in the spread of CWD (Almberg et al., 2011; Potapov et al., 2016).

This study focuses on the direct transmission pathway of CWD (Figure 1) to provide more information about the relationship between the rate of potentially infectious contacts and the mechanisms driving elk aggregation patterns. Elk wintering on the NER can reach densities of ~1,100 elk per km², which is over 70 times larger than densities in Colorado where CWD

prevalence is 13% (Monello et al., 2014). Modelling based on elk densities from the Jackson elk herd, which maintains a population of ~11,000 elk overall, suggests a greater likelihood of population decline at CWD prevalence as low as 7% (Galloway et al., 2017)

Concern about impending CWD transmission led managers of the NER in collaboration with Grand Teton National Park and Wyoming Game and Fish Department to develop a ‘Step Down Plan’ to reduce winter elk aggregations and thus contact rates between elk on the NER (U.S. Fish and Wildlife Service, 2019). The plan seeks to gradually reduce the elk conditioned behaviour and reliance on supplemental winter feeding. To guide implementation and measure the success of the ‘Step Down Plan’ managers need information not only about how feeding influences contact rates but also about other external factors (such as weather or hunting) which could amplify or negate the effects of feeding. Our overall objective was to test a general framework for quantifying the effect of influential factors on contact rates in wildlife. First, we measured the effect of supplemental feeding on elk contact rates on the NER over three winters. Feeding typically occurs on the NER each winter. However, the 2017–2018 winter was milder, and no feeding took place. This lapse in feeding created a unique scenario in this system to compare elk aggregation and contacts in fed and non-fed years. We then compared the relative effects of feeding to other anthropogenic and abiotic factors that contribute to winter elk contacts to inform managers about potential management options and to improve understanding about the context likely to influence their success in reducing disease risk.

Materials and Methods

Elk Collar Data

We examined elk location data from 2016 to 2019 for 73 adult female elk fitted with global positioning system (GPS) iridium collars (Telonics, Mesa, Arizona). The study periods

consisted of three distinct winter seasons each typically spanning from November to May of the following year. To provide a representative sample, elk capture operations were conducted by U.S. Fish and Wildlife Service and Wyoming Game and Fish Department staff across three feedgrounds within the National Elk Refuge (NER) in Wyoming, USA (43.4926 N, -110.7487 W). Collars recorded GPS locations at 1.5- hr intervals resulting in a maximum of 16 daily fixes per individual collared elk. We excluded 5 elk a priori from the study and subsequent analyses due to poor fix rate (i.e. mean daily fix success rate

Modeling Elk Interactions

To model contact rates, we used a proximity index, a measure of static interaction, referred to as Prox, to assess simultaneous joint space use between elk pairs (Long et al., 2014). Using the number of simultaneous fixes within a defined distance threshold, Prox represents the proportion of time two individuals are proximal in space during a period of interest (Long et al., 2014). For a given pair (individuals i and j):

$$Prox_{ij} = \frac{[Number\ of\ fixes\ within\ some\ distance\ during\ time\ t]_{ij}}{[Total\ fixes\ during\ time\ t]_{ij}} \quad (1)$$

where $Prox_{ij} = 1$ indicates complete attraction and $Prox_{ij} = 0$ indicates avoidance. We used a distance threshold of 500 meters and calculated pairwise daily Prox estimates for all elk. Other thresholds had the same pattern of change over time, but at 500m the variation was greatest while still relevant for a large herd of elk, thus maximizing our power to differentiate influences on contact rates. We derived a daily average Prox for the collared elk population, hereafter referred to as the contact rate.

We restricted our contact rate calculations to days when at least 9 collared elk were present on the NER wintering area, which equates to a minimum of 36 unique pairs of elk with

possible contacts per day. When few elk pairs are present, contact rate values can be skewed towards zero or one. We calculated contact rates using the package `wildlifeDI` in the statistical computing environment R, which we used for all analyses (Long et al., 2014; R Core Team, 2019). To explore potential drivers of elk aggregation, we modelled the contact rate as a function of several explanatory variables using beta regression, which is suitable for response variables constrained between 0 and 1 (Cribari-Neto & Zeileis, 2010). We fit models to test our hypotheses in several stages. First, we screened variables using univariate models to remove those with no predictive power (based on effect size and variance) and ensure the spatial data layers represented the hypothesized biological relationships. We then separated screened variables into two subgroups. One group consisted of abiotic weather-related effects and the second included anthropogenic effects such as supplemental feeding and hunting pressure. We used likelihood ratio tests, comparing univariate and null models, to discern between and reduce duplication of variables representing the same biological process (Appendix 1, Bolker et al., 2009). We also included the daily sample size of collared elk (N) as a covariate on the precision portion of all beta regression models.

We tested for multicollinearity within each subgroup by comparing the variance inflation factor (VIF) of each explanatory variable (Appendix 1; Lüdecke et al., 2019; Marquardt, 1970). After checking for multicollinearity, we modelled all combinations of variables within subgroups and selected the best fitting combinations using Akaike's information criterion (AIC). We then compared top models for each subgroup against each other and a global model (all variables from both top models), again using AIC as our selection tool. Finally, we incorporated an additional covariate to account for the temporal autocorrelation present in the dataset. We used the previous day's contact rate ($t - 1$) as a predictor on contact rate (t). We added the

autocorrelation variable last to avoid masking the biological effects of interest during model selection. We also conducted a dominance analysis to determine the proportion of variance explained by each explanatory variable retained in the final model competition (Azen & Budescu, 2003, Navarrete & Soares, 2020).

Explanatory Variables

We formulated all explanatory variables daily to match the temporal resolution of elk relocations and contact rate calculations. To allow for direct comparison of effect sizes, we centred and scaled variables with mean zero and standard deviation of one. Abiotic variables comprised minimum temperature (°C) and seven snow related measures. We used the moving average of minimum temperature from the previous 5 days from the PRISM Climate Group (Hart & Bell, 2015). We examined three thresholds for daily snow events as binary variables: any snowfall, snowfall ≥ 3 inches and snowfall $\geq 10\%$ of current snow depth. We included fractional snow-covered area (fSCA), snow depth (linear and quadratic terms) to assess the effects of current snow condition on elk aggregation. To investigate the potential lag effects of snowfall events, we also incorporated net snow accumulation from the prior 2 days and the number of consecutive days with snow events which reset after each day without snowfall. The fSCA dataset is a 30-m resolution raster derived from MODIS and Landsat imagery (SNOWARP, Berman et al., 2018). We derived all other snow variables from the Snow Data Assimilation System (SNODAS), a 1-km resolution dataset (National Operational Hydrologic Remote Sensing Center, 2004).

Anthropogenic factors included hunter presence and supplemental feeding. We defined the effects of hunting in three ways: active elk hunting on the NER, elk hunting on districts surrounding the NER and active bison hunting on the NER. The presence of elk and bison

hunting on refuge was represented as binary variables. Off-refuge hunting was a continuous variable ranging from 0 to 3 depending on the number of hunting districts surrounding the NER with active elk hunting. Supplemental feeding was measured in 2 ways: the daily metric tonnes of feed placed on feed grounds (tons fed) and a binary version of feeding.

Wolf presence was the only natural biotic variable. We hypothesized that wolves might also affect elk aggregation, but because available data on GPS-tracked wolves did not fully match the temporal coverage of all other explanatory variables, we tested for a wolf effect with the smaller matching subset of the data (~90% of the original data). We used the best model from the initial model selection plus a covariate for wolf-elk distances (Appendix 2).

Results

Variable and Model Selection

After univariate variable screening (Appendix 1), abiotic and anthropogenic variable subgroups were reduced to four and two variables, respectively. Abiotic models included variables for snow depth (linear and quadratic terms), minimum temperature and fSCA. Anthropogenic models included variables for on-refuge elk hunting and supplemental feeding. We found no evidence of multicollinearity (all VIF < 2) within either the abiotic or anthropogenic set of explanatory variables (Zuur et al., 2010; Appendix 1; Table S4). Top models within each variable subgroup retained all variables from each subgroup based on AIC values (Table 2). Final model competition identified models including both anthropogenic and abiotic variables as the most parsimonious (Table 2).

Drivers of elk aggregation

Our analyses included 501 daily contact rate estimates. The mean daily contact rate across the collared elk population was 0.19 (SD = 0.1) and ranged from 0.004 to 0.63 during the three winter seasons (Figure 2). The effect of supplemental feeding was nearly twice that of the next strongest predictor of aggregation, fSCA (Table 3). During feeding, the mean daily contact rate was 0.34 (SD = 0.07), which is 2.6 times larger compared to the baseline rate when feeding and hunting was not taking place (0.13, SD = 0.04). Contact rates were 23% lower while hunting was active on the refuge (0.10, SD = 0.03) compared to the baseline contact rate. The effects of snow depth and minimum temperature on aggregation were minimal (Table 3). We also found a strong positive effect of temporal autocorrelation in the mean daily contact rate of the collared elk population (Table 3). The inclusion of the first-order autoregressive variable in the model (based on lag of 1 day) removed significant temporal autocorrelation (Appendix 3). Feeding and hunting account for 34% and 9% of the variation in contact rate after accounting for temporal autocorrelation. Snow-covered area, snow depth and temperature accounted for 28%, 23% and 6%, respectively, of the remaining variation. In the subset analysis which included an effect of wolves on elk aggregation we found no support for wolf-elk distances influencing elk contact rates (Appendix 2).

Overall, our model captures the major changes and trends in aggregation over the course of the winter season (see raw vs. modelled contact rates with and without accounting for temporal autocorrelation in Figure 2). However, we found considerable fine-scale variation in daily aggregation rates. The temporal autocorrelation variable we included helps account for some of these daily changes in aggregation though it is likely other unmeasured environmental variables contribute to this variation as well.

Discussion

We have demonstrated a framework for quantifying the relative effects of factors driving elk aggregation. Our findings echo previous research indicating elk aggregation is strongly regulated by winter severity (Proffitt et al., 2012) but notably our study is the first to examine the effect of supplemental feeding on aggregation relative to other environmental factors. Supplemental feeding has the largest positive effect on elk aggregation and is 1.8 times larger than the next strongest predictor of aggregation, fSCA (Table 3; Figure 2a,c). Feeding has an additive effect (Figure 3), above and beyond the abiotic conditions expected to influence degrees of congregation on winter range, and the response by elk to feeding occurs very quickly (Figure 2a,c). Importantly, we also found elk aggregate in response to increasing amounts of snow cover on the landscape. In the spring, current feeding continues after snow cover decreases (e.g. April 2019 in Figure 2c) suggesting feeding maintains greater elk aggregation when it would otherwise be declining. Ending feeding outright would have the largest effect in reducing elk aggregations. However, doing so could potentially reduce survival of elk by removing a conditioned winter food source without permitting time for elk to adjust to this resource loss. Our results suggest that ending feeding earlier during late winter would coincide more precisely with the abiotic cues elk respond to and allow for a structured reduction in aggregation during this time period.

Our analytical framework and findings set up a roadmap to evaluate aggregation of elk at the other 21 feedgrounds in the state of Wyoming. Furthermore, the novel methods we present can also be applied broadly to other systems where supplemental feeding and disease transmission are of concern. For example, supplemental feeding has been a regular tool in Europe to increase winter survival and reduce negative economic impacts due to bark-stripping in forest stands by red deer *Cervus elaphus* (Arnold et al., 2018; Putman & Staines, 2004). Red deer are also the main source of transmission of bovine tuberculosis (bTB) to domestic livestock

in areas such as Austria where management strategies include supplemental feeding, thereby promoting red deer aggregation (Fink et al., 2015). Research suggests prevalence of bTB in red deer is lower where feeding is not permitted or less common, such as in Italy and Switzerland (Chiari et al., 2014; Schöning et al., 2013). The variety of management approaches applied to red deer populations across Europe sets up a natural experiment that could benefit from the methods we present here and broaden understanding of the influence supplemental feeding has on red deer aggregations and bTB transmission. One key consideration when applying our approach across a broader spatial area is that the sampling distribution of collars across this wider area can have a large influence on the contact rate if not accounted for (e.g. determining the probability for contact between individuals using spatially distinct areas; Cross et al., 2012).

Hunting pressures on the NER disaggregate elk; but, hunting currently only occurs at the very beginning of the winter season (Figure 2). Following the end of the hunting season, elk aggregation generally increases (Figure 2a,b, less in 2c). However, offrefuge hunting continues after on-refuge hunting has ceased. Past research has shown that elk congregate on lands free of but adjacent to hunting (Mikle et al., 2019; Proffitt et al., 2010) and hunting pressure can strongly influence group size in elk (Gude et al., 2006; Proffitt et al., 2009). Elk may be driven onto the NER by off-refuge hunting once hunting on-refuge has ceased. Extending the hunting season on the NER may delay the movement of elk onto the refuge and decrease aggregation in early winter. However, increased hunting can directly increase mortality via harvest especially if CWD becomes established (Galloway et al., 2017) or indirectly reduce over-winter survival by interrupting seasonal acclimatization via increasing stress and forced movement during more severe winters (Arnold, 2020).

Snow can restrict elk movement and reduce forage availability, often in spatially variable ways. Both processes may alter the aggregation of elk in the winter. Sweeney and Sweeney (1984) found elk begin avoiding areas when snow depth reaches 40 cm and movement becomes increasingly limited with a critical maximum of 70 cm at which movement almost entirely stops. Although we considered multiple ways of describing snow conditions, including the commonly considered snow water equivalent (e.g. Proffitt et al., 2012), only depth and fractional snow-covered area were included in the most parsimonious model. Fractional snow-covered area was the second strongest predictor of elk aggregation with an effect size nearly four times larger than snow depth. Fractional snow-covered area indexes the pattern of increases in snow cover leading to less forage available and, in our study area, leads to increased aggregations in localized areas with less snow. This novel remotely sensed snow-cover data layer (Berman et al., 2018) provided fine resolution (30 m) snow information at daily time-scales across our entire study region. We expect this new index to be useful for many other winter wildlife questions.

We found little effect of distance between elk and wolf activity centres in driving elk aggregation. However, our analysis of the effect of wolves had several limitations: only a portion of wolves on the NER were collared, our inference is limited to when those wolves and elk are on the NER, and wolf-elk distances were summarized by day due to offsets in wolf versus elk fix timing. Previous research has shown elk group size decreases while wolves are present (Winnie Jr. & Creel, 2005), though it appears in our study that supplemental feeding may outweigh any predation effects at this scale. Furthermore, we examined interactions between wolves and prime-aged female elk, but research suggests wolves in our study region tend to feed predominantly on bulls, calves or older females (Woodruff & Jimenez, 2019; Wright et al., 2006). To better evaluate whether wolves affect contact rates in this region, a finer spatial and

temporal scale of analysis that includes other classes of elk would be needed (Brennan et al., 2015).

We also found that contact rates from 1 day were correlated with the contact rates on the next day (Table 3; Appendix 3). Accounting for this temporal autocorrelation reduced the effect sizes of the other explanatory variables in the model and described some substantial daily variation in contact rates that may be due to other environmental variables that we did not model. Pairs of elk rarely spent the entire day within 500 m of each other; these instances make up 4% of total observations ($N = 8533/218351$ elk-pair-days). Most contacts occurred in short bursts of interaction over a few hours to a few days. However, a few pairs of elk had consecutive days of contacts over longer time periods (up to 2 weeks) with the longest sustained contacts occurring in years when feeding took place (Figure 4; Appendix 3: Figures S2 and S3).

Future work on the drivers of winter elk aggregation would benefit from additional collared animals. For example, including bulls in the collared sample may be needed to better evaluate the role of wolves in elk aggregation and the role of male elk in CWD transmission. As the ‘Step Down Plan’ is implemented, to measure changes in aggregation, elk using areas adjacent to the NER will also need to be collared. This would also allow for a more comprehensive assessment of whether the responses we observed by elk on the NER are representative of elk more broadly across the region. Research across additional populations will also provide information about how or whether environmental factors differentially affect aggregation across the landscape. Changes in snowpack as the climate warms and as precipitation becomes more variable and changes seasonally may also influence the timing and location of elk aggregation and warrants consideration in subsequent studies. Our study focused on the direct transmission pathway for CWD by modelling drivers of contact rates among elk;

however, indirect transmission via environmental contamination is likely also important (Almberg et al., 2011; Potapov et al., 2016). Reducing aggregations of elk may also lessen the severity of contamination in heavily used areas but more research is needed on this subject. Subsequent studies on the role of aggregation in both direct and indirect transmission will be vital to provide decision-makers with the most thorough assessment of management tools for combating the spread of CWD.

In summary, our approach compared the relative influence of several factors driving elk aggregation and results suggest changing feeding and hunting practices can be tools to reduce aggregation. This provides a framework to test the efficacy of the NER ‘Step Down Plan’ in the future. Two key components of the framework are location-based information of individuals which can be achieved via direct observation or remote sensing, and information on management activities and environmental factors at a temporal resolution relevant to disease transmission. This approach can also be more broadly applied to assess other systems where aggregation of ungulates or other wildlife is of concern and is not necessarily tied to scenarios where supplemental feeding is occurring. Other factors not examined here that may also influence the timing and magnitude of aggregation in wildlife include the phenology and productivity of forage, the spatial arrangement of resources which can be manipulated by habitat treatments, disturbance that moves animals around and overall population size (M'soka et al., 2017; Tosa et al., 2017).

Author Contributions

W.M.J. and T.A.G. identified the modelling framework with substantial input from co-authors (E.E.B., G.W.C., E.K.C., S.R.D., A.N.J. and P.C.C.) and wrote the initial draft; W.M.J. coded and fit all models; E.E.B. prepared snow-related remotely sensed data layers. All authors

contributed to paper revisions, application/interpretation of results, and feedback on graphics and figures. All authors gave final approval for publication.

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Data availability statement

Elk GPS data are available upon request via the National Elk Refuge and Grand Teton National Park. Wolf GPS data are considered sensitive by Wyoming Fish & Game and Grand Teton National Park and is not publicly available at this time.

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Figures & Tables

Table 1. Samples sizes for elk and recorded locations (1.5 hour fix interval) across three winter seasons on the National Elk Refuge, Wyoming, USA, 2016-2019. Changes in sample size occurred mid-winter when additional elk were collared (Collared During Season), collars dropped off as planned (Planned Collar Drops) or collars failed (Collar Failures).

Winter Season	Total Elk	Collared During Season	Mortalities	Planned Collar Drops	Collar Failures	Locations Recorded
2016-2017	46	29	3	0	1	62854
2017-2018	43	0	10	0	2	94287
2018-2019	54	18	3	14	1	70238

Table 2. Model selection results from competition of the abiotic and anthropogenic variable sub-groups, and results from the final model competition between both sub-group models and a combined model of elk contact rates on the National Elk Refuge, Wyoming, USA, 2016-2019.

Model Type	logLik	AIC	Δ AIC	weight
Abiotic Models (4 of 24 models)				
fSCA + Minimum Temperature + Snow Depth + Snow Depth ²	639.92	-1267.83	0.00	0.56
fSCA + Snow Depth + Snow Depth ²	645.86	-1267.37	0.46	0.44
fSCA + Snow Depth	633.24	-1237.31	30.55	0.00
fSCA + Minimum Temperature + Snow Depth	633.57	-1235.50	32.34	0.00
Anthropogenic Models (all models shown)				
Feeding + On Refuge Hunting	668.02	-1328.03	0.00	1.00
Feeding	653.04	-1300.10	27.94	0.00
On Refuge Hunting	457.12	-908.25	419.79	0.00
Final Model Competition				
Anthropogenic + Abiotic top models	767.10	-1518.29	0.00	1.00
Anthropogenic top model only	668.02	-1328.03	190.26	0.00
Abiotic top model only	639.92	-1267.83	250.46	0.00
Null (intercept only)	426.51	-849.03	669.26	0.00

Table 3. Coefficient table for parameters in final top model which included both abiotic and anthropogenic variables as well as a parameter accounting for temporal autocorrelation in elk aggregation on the National Elk Refuge, Wyoming, USA, 2016-2019. N is the daily sample size of collared elk which was modeled as a covariate on the precision portion of the beta regression models.

Explanatory Variables	Coefficient (SE)
Intercept	-1.66 (0.02)
Abiotic	
Fractional Snow-covered Area (fSCA)	0.19 (0.02)
Minimum Temperature (5-day mean)	0.01 (0.02)
Snow Depth (linear)	0.05 (0.03)
Snow Depth (quadratic)	-0.04 (0.01)
Anthropogenic	
Elk Hunting On Refuge	-0.12 (0.07)
Feeding (Yes/No)	0.34 (0.06)
Temporal Autocorrelation	0.43 (0.03)
Precision	
N (# of collared elk on refuge)	0.03 (0.01)

Figure 1. Conceptual diagram of disease transmission pathways when host aggregations are important in determining transmission mechanisms.

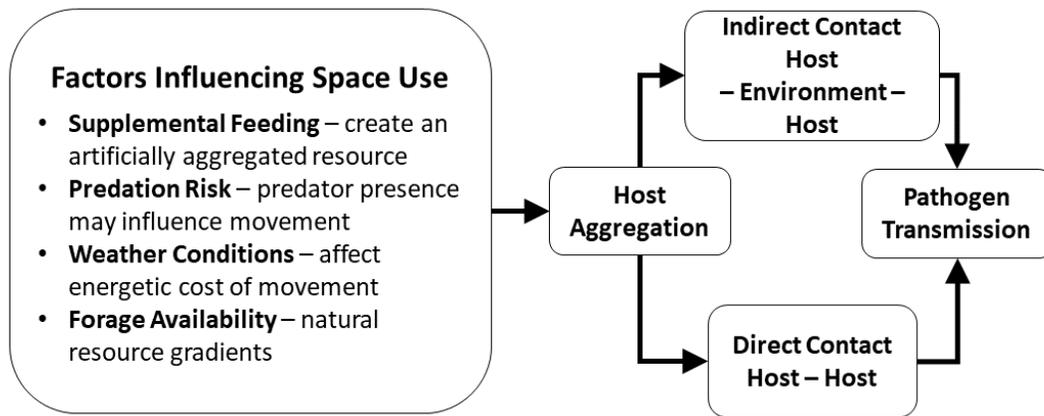


Figure 2. Comparison of raw daily contact rates to fitted contact rates, from models with and without the autoregressive parameter (AR), for elk on the National Elk Refuge, Wyoming, USA, 2016-2019. Contact rates are overlaid with timing of elk hunting and supplemental feeding, as well as fractional snow-covered area (fSCA). Data are shown for three winter seasons: 2016-2017 (1a), 2017-2018 (1b), 2018-2019 (1c).

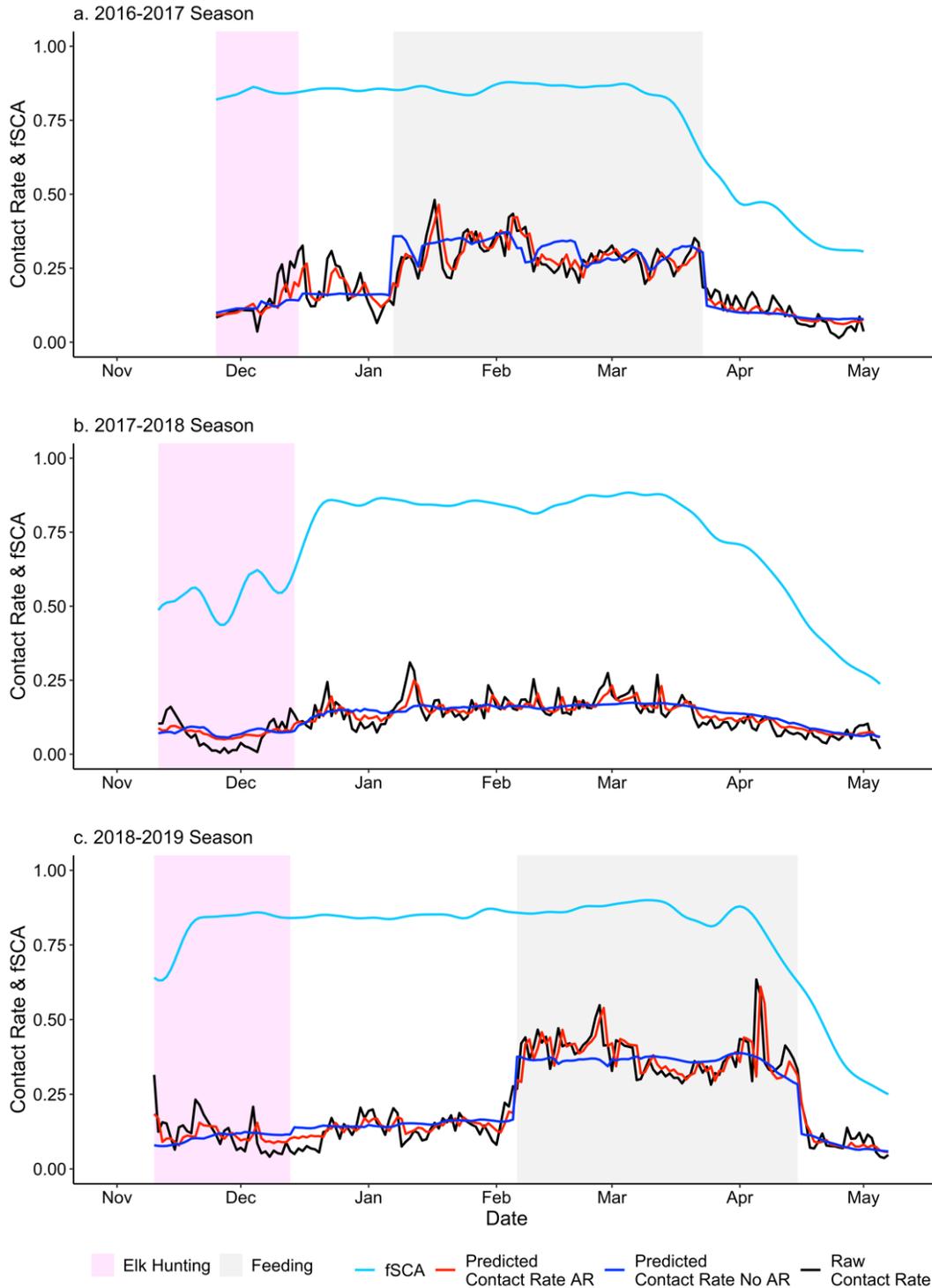


Figure 3. Predicted mean contact rate for elk on the National Elk Refuge, Wyoming, USA, 2016-2019. Contact rate shown with and without supplemental feeding and as a function of fractional snow-covered area (fSCA). Shaded regions represent the 95% confidence intervals.

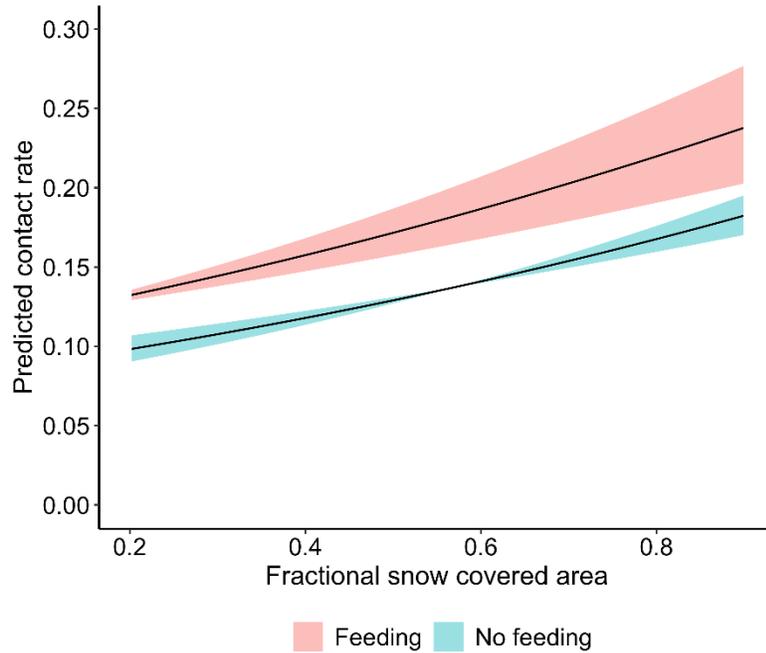


Figure 4. Histogram of the number of consecutive days of any contact between all pairs of elk on the National Elk Refuge, Wyoming, USA, 2016-2019. During the non-feeding portion of the winter season, few pairs of elk were in contact for longer than 4 days and none beyond 7 days.

