

ORIGINAL RESEARCH

Weather radar data correlate to hail-induced mortality in grassland birds

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Abstract

Small-bodied terrestrial animals such as songbirds (Order Passeriformes) are especially vulnerable to hail-induced mortality; yet, hail events are challenging to predict, and they often occur in locations where populations are not being studied. Focusing on nesting grassland songbirds, we demonstrate a novel approach to estimate hail-induced mortality. We quantify the relationship between the probability of nests destroyed by hail and measured Level-III Next Generation Radar (NEXRAD) data, including atmospheric base reflectivity, maximum estimated size of hail and maximum estimated azimuthal wind shear. On 22 June 2014, a hailstorm in northern Colorado destroyed 102 out of 203 known nests within our research site. Lark bunting (*Calamospiza melanocorys*) nests comprised most of the sample ($n = 186$). Destroyed nests were more likely to be found in areas of higher storm intensity, and distributions of NEXRAD variables differed between failed and surviving nests. For 133 ground nests where nest-site vegetation was measured, we examined the ameliorative influence of woody vegetation, nest cover and vegetation density by comparing results for 13 different logistic regression models incorporating the independent and additive effects of weather and vegetation variables. The most parsimonious model used only the interactive effect of hail size and wind shear to predict the probability of nest survival, and the data provided no support for any of the models without this predictor. We conclude that vegetation structure may not mitigate mortality from severe hailstorms and that weather radar products can be used remotely to estimate potential for hail mortality of nesting grassland birds. These insights will improve the efficacy of grassland bird population models under predicted climate change scenarios.

Introduction

The damaging effect of large hail (≥ 2.5 cm diameter) is well documented in literature related to agriculture (Wille and Kleinkopf 1992; Vorst 1991) and commerce (e.g. Hohl et al. 2002; Das et al. 2009; Saa Requejo et al.

2011), but its contribution to wildlife mortality is understudied. This is due partly to economics and partly to the relative difficulty in measuring hail-induced animal mortality. Carcasses of hail victims may be difficult to detect or may be quickly scavenged after a severe hail event. This complicates measurement of hailstorm effects

on populations and requires researchers to act quickly after mass mortality events. The best-documented cases of mass mortality during hailstorms pertain to birds (Hall and Harvey 2007; Saunders et al. 2011; Diehl et al. 2014), suggesting that birds are highly vulnerable to hail. Small-bodied, non-avian taxa may be similarly vulnerable, but hail-induced mortality of avian species that form large flocks may be more obvious due to the unusual concentration of carcasses. Information derived from opportunistic studies on avian hail mortality are of limited utility to demographic modeling without spatially comprehensive hail incidence data across a population's range. Our study demonstrates the value of remotely sensed weather data for overcoming this obstacle.

Breeding birds are among the taxa most vulnerable to hail-related mortality because of their physical attributes and life history. Although skeletal hollowness in birds is offset by increased bone tissue density and tensile strength (Dumont 2010), most birds are small-bodied (Bokma 2004), making it unlikely that they could survive the impact of large hail. Even relatively large-bodied birds experience broken bones and other internal damage when hit by large hail (Heflebower and Klett 1980). A compounding factor is the rarity of shelter use by birds. Most species do not use burrows or cavities for nesting but rather build open-cup or scrape nests with little overhead structure (Collias 1997). Nest-monitoring studies have documented nest destruction by hail in both shorebirds (Graul 1975; Mabee and Estelle 2000; Saalfeld et al. 2011) and songbirds (La Rivers 1944; Conway and Johnson 2011). Nests may serve as a proxy for population-wide mortality. Relative to mobile adults, nests are easier to locate and monitor. Thus, it can be easier to measure the impact of hail on nests than on adults. High adult mortality concurrent with nest destruction (*ARC, personal observation*) suggests that bird mobility does not reduce hail risk in breeding areas. The correlation between hail-induced nest failure and adult mortality is unknown, but the density of destroyed nests could serve as an index of adult mortality.

The North American Great Plains is an ecoregion where relatively low annual precipitation and high evaporative potential (Rosenberg 1987), combined with cyclical grazing and fire (Fuhlendorf and Engle 2001; Derner et al. 2009), favor grasses over taller, woody vegetation. These environmental drivers generate a suite of unique ecological niches, and several bird species have evolved to breed only on the Great Plains (Knopf 1996). Populations of these species have declined due to habitat loss (Brennan and Kuvlesky 2005). As of 2004, 70% of the Great Plains had been converted to agriculture or other land cover types (Samson et al. 2004). Other environmental changes likely contribute to population declines, but may be more difficult to quantify than habitat loss. Developing metrics

of other sources of mortality is important for estimating demographic parameters for grassland bird populations, which in turn is key to predicting population change and assessing population viability.

Hail is a common weather phenomenon in North America (Changnon 2008), and it can cause high bird mortality in areas where individuals are concentrated (e.g. Smith and Webster 1955; Johnson 1979; Diehl et al. 2014). Large-diameter hail regularly occurs on the Great Plains (Allen et al. 2015; Fig. 1). Further, the Great Plains breeding bird community is dominated by songbirds (Veech 2006), most of which construct open-cup nests (Collias 1997) that have little protection from hail. The frequency of hail mortality during grassland birds' evolutionary history may have been insufficient to drive an adaptive response. Increased hail frequency, as predicted under several climate change models (Trapp et al. 2007; Kapsch et al. 2012; Allen et al. 2015; Fischer and Knutti 2015), could lead to greater mortality in species that are not adapted to avoid hail impact. In combination with other threats such as habitat loss and fragmentation, higher frequency of severe hail could impair the ability of isolated populations to recover from these combined events (Saunders et al. 2011; McKechnie et al. 2012). Developing methods to quantify hail-induced bird mortality will be important for population monitoring if hail frequency increases.

Localized storm paths and intensity are randomly distributed (Morgan and Towery 1975) and not readily predicted. Thus, it would be challenging to design studies evaluating the impacts of naturally occurring extreme weather events; often the zone of highest intensity within a weather system may occur where populations are not under scientific observation. Quantifying the impact of hail on animal populations requires remote sensing technology that can be applied at large spatial scales and capture local variability in storm location and intensity. The metrics produced must distinguish between rain and hail, as well as between small and large hail, as these different hydrometeor classes are likely to cause very different outcomes for breeding birds.

Remote sensing technology that can provide metrics to quantify hailstorms is now available in the USA. The network of Next Generation Radars (NEXRAD) employed by the U.S. National Weather Service provides high-coverage data on atmospheric conditions. These stationary Doppler radars transmit pulses of electromagnetic radiation, and then coupled receiving sensors measure the intensity of returning radiation as decibels of reflectivity (dBZ). Output data are provided at fixed radial widths (measured in degrees) over five to fourteen elevations above the horizon, depending on operational mode (Lakshmanan et al. 2006). The base reflectivity (BR) represents the lowest elevational swath, with a beam centered 0.5° above the horizon and

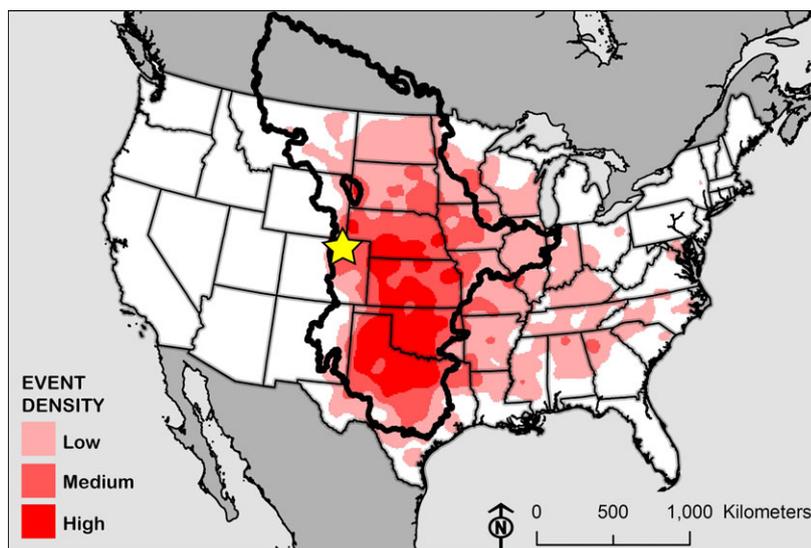


Figure 1. Distribution of United States large hail events in relation to The Great Plains ecoregion is indicated with the black polygon, derived from North America Level I ecoregion classification by the U.S. Environmental Protection Agency (<https://www.epa.gov/eco-research/ecoregions>). We obtained georeferenced records of U.S. hail events from the National Oceanic and Atmospheric Administration Storm Prediction Center Severe Weather GIS website (<http://www.spc.noaa.gov/gis/svrgis/>). This included 326 455 events documented in 1955–2015. We selected records with hail ≥ 2.5 cm, corresponding with the threshold for what is defined as damaging hail (Kapsch et al. 2012). This yielded 13 960 results. The region of highest large hail frequency (indicated in red) includes much of the Great Plains. The location of the study site is indicated with the yellow star.

measuring approximately $1^\circ \times 1^\circ$. Reflectivity is positively correlated with the density of precipitation and can be used to reliably distinguish between pure rain and rain mixed with hail (Kunz and Kugel 2015). Reflectivity and hail diameter, however, are not strongly correlated, although reflectivity readings in the upper end of the spectrum usually indicate large hail (Depue et al. 2007). NEXRAD also measures relative velocity of airborne objects, calculated from the Doppler shift within the reflected radar signal. Secondary products, such as the maximum estimated size of hail (MESH) (Witt et al. 1998; Stumpf et al. 2004) or maximum estimated azimuthal wind shear (AWS); (Smith and Elmore 2004), can then be extracted by applying algorithms to the reflectivity and relative velocity as part of the Warning Decision Support System – Integrated Information (WDSS-II; Lakshmanan et al. 2007). In this study, we demonstrate how these publicly accessible weather data (i.e. BR, MESH, and AWS) provide the means to estimate local storm intensity, which we relate to nest loss in a population of grassland-breeding birds.

This study leveraged a rare opportunity to study ecological impacts after a severe weather event on 22 June 2014 passed over an ongoing grassland songbird nest-monitoring project at the Central Plains Experimental Range (CPER) – a shortgrass steppe grazing research facility in northeastern Colorado. Similar to previous studies of hail-induced mortality in birds, we quantified hail-related

mortality opportunistically, incidental to other research. However, unlike other studies, we went beyond anecdotal reporting and investigated the extent to which remotely sensed weather data could be used to predict the spatial distribution of nest destruction. Our specific objective was to assess the accuracy of NEXRAD data products in explaining the distribution of hail-induced nest mortality attributed to this single event. As part of this, we tested the hypothesis that the microhabitat at the nest site (i.e. surrounding vegetation) has an ameliorative factor in hail risk. We hypothesized that woody vegetation (shrubs and subshrubs) would shelter nests from hail impact and that vegetation cover directly over the nest bowl would be important to the probability of nest survival. We also hypothesized that vertical structure would be important to nest fate, since the buffering effect of vegetation against hail impact should increase with the height of the vegetation.

Materials and Methods

Study Area

We conducted this study at CPER, Weld County, Colorado, on the western edge of the Pawnee National Grassland. The climate is semi-arid, with most precipitation occurring in the summer months (Sala et al. 1992). Severe weather such as extreme rain and hail commonly

occurs during summer, but its spatiotemporal distribution is heterogeneous and unpredictable (Rosenberg 1987). Vegetation at CPER is dominated by C4 shortgrasses (primarily *Bouteloua gracilis* and *B. dactyloides*), with smaller proportions of cacti, midgrasses and forbs (Lauenroth and Sala 1992). The woody plant community includes both tall shrubs and low subshrubs (Lee and Lauenroth 1994). Plant community composition and structure at the study site are heterogeneous due to grazing treatments and topographic factors. Average vegetation height and percent cover by shrubs increase along a northeasterly axis. The CPER breeding bird community is primarily comprised of songbirds (Order Passeriformes). These small organisms are unlikely to survive the physical impact of large hail (i.e. ≥ 2.5 cm diameter), based on previous observations of mass mortality (Hall and Harvey 2007; Diehl et al. 2014). The dominant nest structure at CPER among these species is a partially recessed cup in the ground with little or no woody vegetation over the nest (ARC, *personal observation*). For ground-nesting species, nest-site vegetation may afford protection from wind, but the extent of overhead structure varies within and among species (With and Webb 1993).

Nest fates and measurements

From May to July 2014, we located nests by rope-dragging and completed high-frequency (2–4 day interval) nest checks as part of a larger study examining the relationship between nest survival and livestock grazing regime. As of 20 June 2014, we were monitoring 203 active nests, divided among species as follows: 186 lark bunting (*Calamospiza melanocorys*), seven horned lark (*Eremophila alpestris*), three Brewer's sparrow (*Spizella breweri*), two mourning dove (*Zenaidura macroura*), two McCown's longspur (*Rhynchophanes mccownii*), two grasshopper sparrow (*Ammodramus savannarum*) and one western meadowlark (*Sturnella neglecta*). Lark buntings construct an open-cup nest on the ground, similar to most other grassland-breeding species; so, we treated it as representative of grassland open-cup ground-nesters.

On 23 June, the day after the hail event, we checked all previously active nests and recorded the fate of each; nests were classified as 'failed' if all eggs were destroyed or all chicks were killed, and as 'survived' if at least one undamaged egg or living chick remained. After the storm, any failed nest was attributed to the storm, although the interval since the previous nest check was either 3 or 4 days for every nest. In most cases ($n = 74$), this assumption was supported by the presence of crushed eggs or dead chicks. In many cases, a dead parent bird was also found on or near the nest. We classified nests with live chicks, whole eggs and/or a live adult on the nest as still active.

As part of our larger project, we measured and identified vegetation at as many nest sites as possible. This provided us with vegetation data for 133 ground nests and three shrub nests within the hail-affected nest sample. We omitted shrub nests from subsequent analyses due to the small sample size. To quantify vegetation cover, we used a modified version of the line-point intercept (LPI) method (Canfield 1941). We centered a $0.5 \text{ m} \times 0.5 \text{ m}$ quadrat over the nest and took measurements within the quadrat at intersections of a 5×5 grid with 10-cm spacing. At each intersection, we aimed a laser beam at the ground directly beneath the point, and we recorded the number of contacts with any above-ground vegetation (by vegetation type), and whether the laser contacted bare ground, litter, or the basal portion of a plant at ground level. The laser projector, which was mounted on a tripod for stability, produced a 1.6 mm diameter beam (equivalent to the diameter of pin flags used by U.S. land management agencies for line-point intercept monitoring; Herrick et al. 2005). We quantified shrub cover as the number of intercepts by a shrub or subshrub. We quantified nest bowl cover as the number of intercepts by any vegetation type directly over the nest bowl. To quantify vertical structure, we used the Robel Pole method (Robel et al. 1970). We obtained low and high visual obstruction readings in each cardinal direction and calculated the means of low and high readings.

Hail event and NEXRAD data

The severe thunderstorm for this analysis passed over the CPER area between ~1600 and 1900 MDT on 22 June 2014. It produced large hail as it crossed our study area on a southeasterly trajectory. It was part of a larger system of storms that day that produced hailstones with a maximum diameter in the range of 1.6–2.8 cm (SPC 2016). We obtained base reflectivity data from the Cheyenne, Wyoming NEXRAD station (KCYS) for the period from 2135 GMT on 22 June to 0051 GMT on 23 June from the NOAA Climate Data Online website (<https://www.ncdc.noaa.gov/cdo-web/>). This station was located 27–37 km from nests in the study area, and the data obtained represented 29 sweeps of the area; 18 intra-sweep intervals were 6 min long, four were 12 min long and three were 46 min long. These reflectivity files are provided in binary format. We used the NOAA Weather and Climate Toolkit (WCT; <http://www.ncdc.noaa.gov/wct/>) to convert these data to vector format. The WCT can be used to convert binary files directly to raster format, but reflectivity data are collected as polygons, so conversion into vector format preserves more information than conversion into raster. Furthermore, the WCT produces relatively coarse rasters. Export to vector format with the WCT, followed by conversion into raster (res:

0.0069°×0.0069°) with Esri ArcMap v10.2.2 resulted in better raster resolution and higher fidelity between the binary file and the resulting raster. We used the ArcMap Extract Values to Points tool to identify the maximum BR across all radar sweeps for each specific nest location. We downloaded additional NEXRAD weather radar data products associated with our focal severe hail event from the National Severe Storm Laboratory's (NSSL) WDSS-II portal (<http://ondemand.nssl.noaa.gov>). The WDSS-II system incorporates reflectivity data and relative velocity data from all available elevational sweeps of all available NEXRAD data and runs these through separate algorithms to calculate the MESH and the maximum azimuthal wind shear (AWS). The NSSL pre-calculates MESH data by first combining all available NEXRAD data onto a three-dimensional grid (i.e. latitude, longitude and height; Lakshmanan et al. 2006) and then applying a modified Hail Detection Algorithm to produce MESH patterns over the selected landscape at 60-sec intervals (Witt et al. 1998; Stumpf et al. 2004). The composite grid that we ultimately were able to download is based upon MESH data accumulated over successive radar sweeps to produce areal swaths of hailfall. Azimuthal wind shear, which is a metric of abrupt horizontal wind shifts (e.g. downdrafts or tornadoes), is pre-calculated by the NSSL through application of a linear least squares derivative filter on relative velocity data (Smith and Elmore 2004). The maximum value of shear, in units of per-seconds (s^{-1}), is calculated across multiple radars and the lower 2 km of the atmosphere and then assigned to georeferenced pixels measuring 0.005° for both latitude and longitude. We downloaded the georeferenced MESH and AWS rasters from the WDSS-II portal for a broad time span (15:00–23:00 MDT on June 22, 2014) which fully encompassed the period of severe weather passage over the CPER study site (~1800–MDT).

Statistical analyses

For all nests in our sample, we compared distributions for failed and surviving nests for each of the NEXRAD variables using a two-sample non-parametric Kolmogorov–Smirnov test (K-S Test), which tests for equality of continuous probability distributions for two samples of the same measurement variable. We selected the K-S test because it is non-parametric and does not assume the data conform to a specific distribution; it merely tests for equality of two empirically derived distributions. We used K-S tests for the subset of nests where vegetation was measured, to assess whether that subsample might be representative of the full sample. We also used a K-S test to compare the distributions of vegetation variables between failed and surviving nests.

For the subset of ground nests where vegetation was measured ($n = 133$), we fit a set of 21 logistic regression models to predict the probability of nest survival as functions of NEXRAD and vegetation variables. As part of the process of constructing these models, we evaluated the potential for collinearity among variables by estimating the absolute value of the pairwise correlation coefficient $|r|$. Because $|r|$ was greater than 0.59 for all pairs of NEXRAD variables, we did not consider any model that included these variables independently. Base reflectivity measures only atmospheric density, whereas maximum estimated size of hail and maximum estimated azimuthal wind shear are more advanced metrics of estimated hail size and angular velocity respectively. We therefore omitted base reflectivity as a covariate and considered only models with the effects of hail size, wind shear and the interaction between the two. Mean low and high visual obstruction readings were moderately correlated ($r = 0.58$); so, we considered only mean low visual obstruction reading in subsequent analyses. Correlation between other vegetation variables was low (range of $|r|$: 0.20–0.41). Because the NEXRAD data provided such strong separation between failed and surviving nests (quasi-complete separation), classical maximum likelihood estimators for logistic regression (e.g. function `glm` in R) did not converge. We therefore fit all models using the function `bayesglm` (package:arm; Gelman and Su 2015) in R ver. 3.2.3 (R Development Core Team 2015), specifying the binomial family to model the error distribution. This function uses the Estimation Maximization (EM) algorithm (rather than maximum likelihood) to fit the data, and we specified the default cauchy distribution as a vague prior (Gelman et al. 2008). To compare relative parsimony among models, we evaluated BIC values, associated weights of evidence, $w = e_i^{-\frac{1}{2}ABIC} / \sum_i e_i^{-\frac{1}{2}ABIC}$ and evidence $e. r. = \text{ratios } e^{\frac{1}{2}ABIC}$ to compare the relative support in the data for pairs of models.

Results

Hail impact

Of the 203 monitored nests active at last check prior to the 22 June 2014 hailstorm, 102 (50.2%) appeared to have failed because of the storm, as evidenced by broken eggs and crushed chicks (Table 1). The average lark bunting nesting cycle (from the start of incubation to the fledging of young) is 19 days (Jehle et al. 2004), which is comparable to the nesting cycle durations for the horned lark (Verbeek 1967), McCown's longspur (Mickey 1943), Brewer's sparrow (Reynolds 1981) and grasshopper sparrow (Wray et al. 1982). Jehle et al. (2004) estimated

Table 1. Sample composition for nests located prior to the 22 June 2014 hailstorm, active at most recent nest check before storm, and checked the day after the storm.

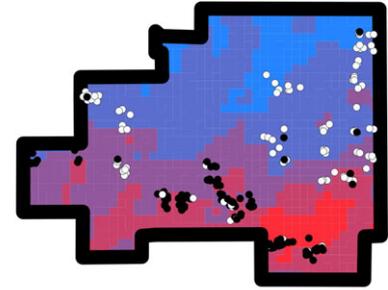
Species	All nests		Nests with vegetation data	
	Total sample	Failed	Total sample	Failed
LARB	186	94	123	49
HOLA	7	5	5	4
BRSP	3	1	2	1
MCLO	2	2	1	1
GRSP	2	0	2	0
MODO	2	0	1	0
WEME	1	0	1	0
Sum	203	102 (50.2%)	135	55 (40.7%)

LARB, lark bunting; HOLA, horned lark; BRSP, brewer's sparrow; MCLO, McCown's longspur; GRSP, grasshopper sparrow; MODO, mourning dove; WEME, western meadowlark; see Methods for scientific names.

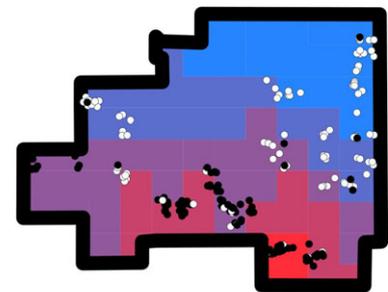
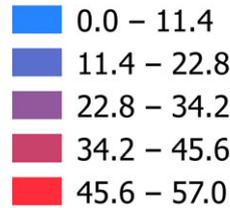
survival probability for lark bunting nests at three locations near our study site over the course of 3 years without severe hailstorms. Those estimates assumed a constant daily survival probability across nesting stages (i.e. nest survival probability did not vary between the egg and chick stages of nesting) and were fit using estimators in program MARK (Dinsmore et al. 2002). Average survival estimates for lark bunting nests for the entire nesting period ranged from 0.13 ± 0.05 to 0.45 ± 0.07 , yielding average daily survival ranging from 0.90 to 0.96. Assuming daily nest survival events are constant over time and independent, total nest survival probability for any interval can be estimated as the product of daily survival probabilities over that interval (Dinsmore et al. 2002). Using Jehle et al.'s (2004) minimum daily survival estimate of 0.90 over the maximum of 4 days between last nest check and the storm, the most conservative average background nest survival rate is 0.66; this translates to an expected 134 of 203 nests surviving the 4-day interval. We recorded 101 surviving nests over that interval. If the only process at work were background nest survival (i.e. no loss due to storm), we can use the binomial distribution to compute the probability of our result as follows: $Pr(X \leq k) = \sum_{i=0}^k \binom{n}{i} p^i (1-p)^{n-i}$, where $n = 203$, $k = 101$ and $P = 0.66$. The probability of 100 or fewer of 203 nests surviving 4 days if the true survival rate were 0.66 (the most conservative estimate for intervals without hailstorms) is $1.4 * 10^{-6}$. In other words, a conservative estimate of background nest loss represents an extremely improbable explanation for our data.

Mourning dove and western meadowlark nest cycles are comparatively longer (~29 days), such that under the same background daily survival probability, these species

dBZ (dB)



MESH (mm)



AWS (m s⁻¹)

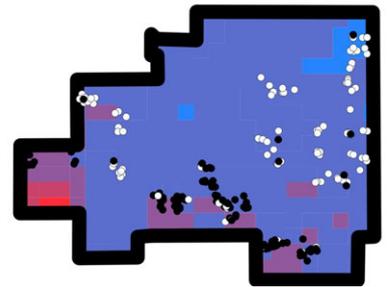


Figure 2. Distribution of nest fates at CPER relative to maximum NEXRAD BR, estimated size of hail (MESH) and AWS for the period of 21:35–00:51 GMT on June 22/23, 2014. Both BR and MESH rose from moderate levels in northwestern CPER (blue) to high levels in the area's southeast (red), which corresponded to an observed rise in nest mortality rates. Black dots represent nests that failed, and white dots represent nests that survived. AWS, azimuthal wind shear; BR, base reflectivity; CPER, Central Plains Experimental Range; MESH, maximum estimated size of hail.

would experience lower total nest survival probability. However, none of their nests failed, so elevated nest mortality cannot be attributed to including nests from these species in our dataset .

Mortality and hail-related NEXRAD data values were each heterogeneously distributed across the study area (Fig. 2). For the full nest sample ($n = 203$), values for

estimated hail size and wind shear were not normally distributed and included multiple modes (Fig. 3). The distributions of values for MESH and AWS differed between failed and surviving nests (K-S test MESH: $D = 0.74$, $P < 0.001$; AWS: $D = 0.61$, $P < 0.001$). The distribution of estimated hail size at failed nest locations was to the right of that for locations with nests that survived, indicating that larger hail was estimated for locations where nests failed. The same comparative pattern was observed for wind shear; locations where nests failed experienced greater wind shear force than locations where nests

survived. Our sample of nests where vegetation was measured ($n = 133$) included 55 (41.3%) that had failed, and the comparative differences between distributions of weather variable values for failed and surviving nests were the same as for the full dataset.

Vegetation data

For the subset of nests where vegetation was measured ($n = 133$), distributions of values for shrub cover did not differ between failed and surviving nests (K-S test

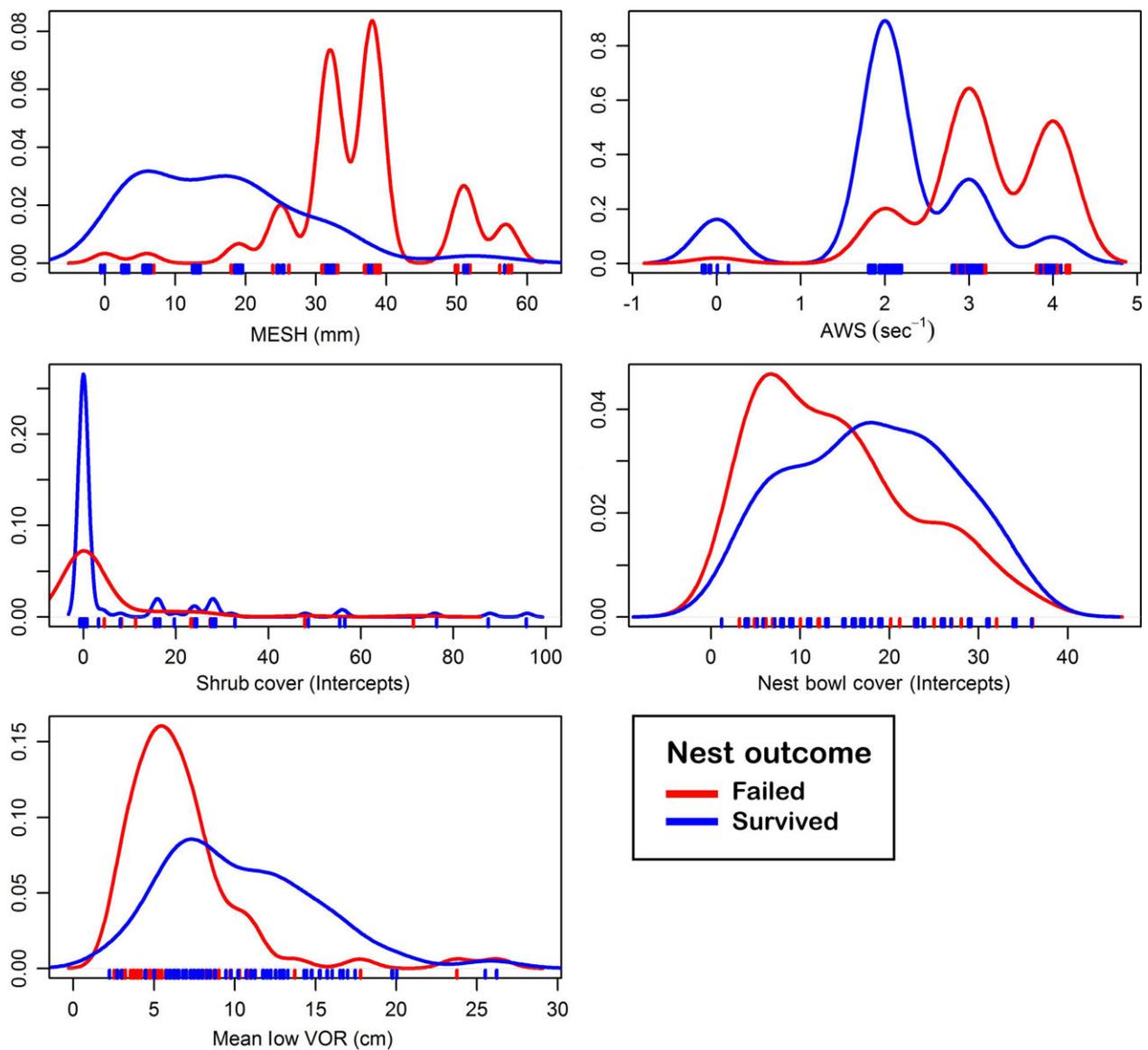


Figure 3. Density distribution of environmental covariates. Distributions of values for MESH and maximum estimated azimuthal wind shear differed between failed and surviving nests. Distributions of values for shrub abundance did not differ between failed and surviving nests, but distributions of nest cover and mean low visual obstruction reading (VOR) differed between failed and surviving nests. See text for test statistics. MESH, maximum estimated size of hail.

$D = 0.14$, $P = 0.57$; Fig. 3). Shrubs were uncommon nest-site vegetation components: only 35 nests had any cover by shrubs. The distribution of nest bowl cover ($D = 0.36$, $P < 0.001$) and mean low visual obstruction reading ($D = 0.43$, $P < 0.001$) did differ between samples of failed and surviving nests. For both of these variables, the distribution at failed nest locations was to the left of that for locations with nests that survived, indicating more nest bowl cover and higher visual obstruction readings for surviving nests than failed nests.

Model fit

A model including the effects of MESH and AWS, and the interaction between the two covariates was best supported by the data (Table 2). The parameterized linear component for that model is $\sim 2.59 - 0.08 * \text{MESH} - 1.1 * \text{AWS} - 0.10 * \text{MESH} * \text{AWS}$. The coefficient for the interaction term in the fitted model was negative (-0.10) and non-zero (z -test for $H_0: X = 0$: $z = -4.1$, $P < 0.00001$). This indicates that as the product of hail size and wind shear increases (increase in either hail size, wind force or both), predicted failure probability increases (Fig. 4).

The second most parsimonious model added the effect of nest cover to the model above; the evidence against this second model as the one responsible for generating the data we observed was over 10 times greater than that for the top model. All models without the effects of MESH and AWS received no support from the data; the cumulative weight in favor of models including MESH and AWS was 100%.

Discussion

Severe storms can cause animal mortality through drowning or hail impact. Despite numerous other storms during our 2014 field season, each involving high-volume rainfall and small hail, no other storm caused perceptible mortality in nests under observation. No cases of birds drowning during severe storms have been recorded at our study site. Birds nesting near waterbodies may drown or abandon their nests (e.g. Sexson and Farley 2012), but there are no rivers or lakes in our study area. The apparent absence of drowning allowed us to focus on hail impact. Our focal storm was the only large-diameter (>2.5 cm) hail event in 2014. The apparent absence of mortality associated with small-diameter hail suggests estimation of hail incidence alone would be insufficient to gauge impact on breeding birds. Doppler weather data quantify various storm attributes, and our objective was to assess the accuracy of these data in predicting hail impact on breeding birds. We thought that combining multiple NEXRAD datasets might better explain nest mortality risk from hail. We further

Table 2. Models for the probability of nest survival as functions of NEXRAD and vegetation covariates were fit using Bayesian generalized linear models.

Model: Fate~	BIC	Δ BIC	Model weight	Evidence ratio
MESH*AWS	87.19	—	0.81	—
MESH*AWS + nest cover	91.85	4.66	0.08	10.26
MESH*AWS + VOR	91.86	4.67	0.08	10.30
MESH*AWS + shrubs	93.42	6.22	0.04	22.44
Global Model	99.28	12.08	0.00	420.47
MESH + VOR	102.81	15.61	0.00	$2.46 * 10^3$
MESH	103.49	16.30	0.00	$3.46 * 10^3$
MESH + cov	106.89	19.69	0.00	$1.89 * 10^4$
MESH + shrubs	108.38	21.19	0.00	$3.98 * 10^4$
VOR	164.13	76.93	0.00	$5.07 * 10^{16}$
Nest cover	172.49	85.30	0.00	$3.32 * 10^{18}$
Intercept only	182.42	95.23	0.00	$4.77 * 10^{20}$
Shrubs	183.76	96.57	0.00	$9.31 * 10^{20}$

Bayesian Information Criterion (BIC), a measure of model parsimony; Δ BIC is the difference between the BIC for a given model and that of the most parsimonious model and is used to quantify model selection uncertainty among models in the set; model weight (w) is the proportional support for each model in the total set (weights normalized so that they sum to 1 for the set); evidence ratio uses the ratio of Δ BIC to quantify relative degree of evidence against each model; for example, an evidence ratio of 10.26 indicates that the model is only one tenth as likely as the top model to have generated the data. All models including the MESH*AWS interaction term also included the main effect. MESH, maximum estimated size of hail; AWS, maximum estimated azimuthal wind shear; VOR, mean low visual obstruction reading; AWS, azimuthal wind shear

hypothesized that nest-site vegetation would have an ameliorative effect on mortality risk.

Efficacy of NEXRAD datasets

We observed high efficacy of NEXRAD BR, maximum estimated size of hail (MESH) and maximum estimated azimuthal wind shear (AWS) for predicting hail-related mortality. That is, distributions of values for each measure were generally distinct between failed and surviving nests. These three NEXRAD measurements covaried along a spatial gradient in the study area (Fig. 2). We attribute the resulting collinearity to parallel variance associated with storm cloud dynamics. We subsequently focused on the interactive effect of MESH and AWS on hail-related mortality risk. Strong support (as measured by w and the evidence ratios) for a nest failure model including the additive effect of MESH, AWS and the MESH*AWS interaction term indicates an important relationship between hail size and wind shear. It suggests that hailstones' potential for damage depends in large part on the force with which they strike the ground. This makes

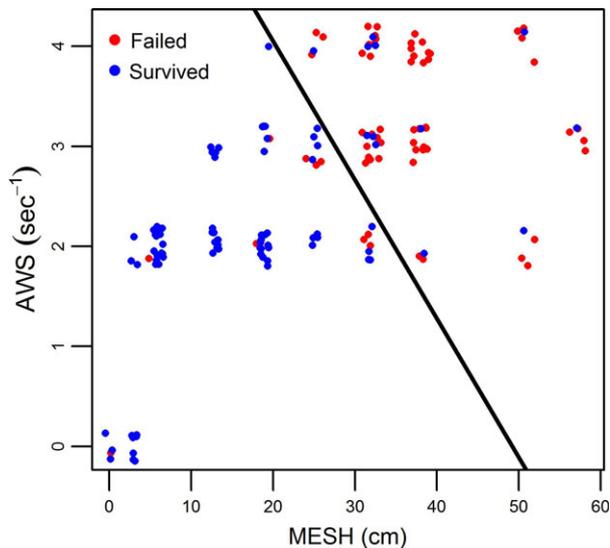


Figure 4. Effect of MESH and AWS on nest survival, based on the best supported logistic regression model. As maximum estimated AWS and MESH increased, hail-induced nest mortality became likely. The strong support for the model including only the additive and interactive effects of MESH and AWS ($w = 0.81$) indicates that wind shear augmented the impact of hail, inducing greater impact than would have been predicted based on hail size alone. AWS, azimuthal wind shear; MESH, maximum estimated size of hail.

intuitive sense, but to the best of our knowledge, we are the first to demonstrate the accuracy of Level-III data through a study on known wildlife mortality. This is a powerful indication that, given the knowledge of animal distributions and life histories, NEXRAD data can inform population modeling at large spatiotemporal scales.

Ameliorative effect of nest environment

We quantified the impact of shrub cover, subshrub cover, vegetation cover directly over the nest bowl and vertical vegetation structure on hail-related mortality risk. None of these variables strongly influenced mortality risk. Shrub cover was rare in our nest sample, and the distribution of values did not differ between failed and surviving nests. Models including shrub cover were not well-supported by the data. Partial nest bowl cover by vegetation was ubiquitous, and there was a difference between distributions of this variable for failed and surviving nests; nests that failed tended to have less cover than those that survived. However, models including this variable received little support from the data, suggesting that nest bowl cover did not mitigate the impacts of hail size and wind shear on the probability of nest survival. There was a similar difference in vertical vegetation structure between failed and surviving nests but effectively no support for models including this variable. These observed differences in nest

bowl cover and vertical structure between failed and surviving nests probably reflect the study site's gradient in vegetation height and density, which both increased along the same axis as increasing storm intensity (Fig. 2).

Nest-site vegetation associations vary with species life history (e.g. Cody 1981; Martin 1993; Powell and Steidl 2000), and the vegetation used by some species would likely play a larger role in offsetting risk of hail impact. On the other hand, in areas of less frequent severe hail-storm occurrence (Fig. 1), the biological community may lack protective behavior [e.g. shielding clutches (Thompson 1934; Johnson 1966), nest placement (Hadley 1969), sheltering in dense vegetation (Rockwell 1909), or physical attributes, e.g. egg shell thickness (Rahn and Paganelli 1989)]. We expect that hail-induced mortality likely affects open-cup nesters differently than birds that use other nest types, and warrants further examination across guilds.

Ecological implications

Large hail occurs more frequently on the Great Plains than in most other U.S. ecoregions, and our study site is located in one of the areas of highest frequency (Fig. 1). Hail may have particularly strong effects on grassland bird population viability because a single event not only destroys nests but also kills breeding adults. A nest failure rate of 50% is not extreme for grassland birds. Lark buntings, which dominated our sample, typically lose >40% of nests to predation (Jehle et al. 2004; Skagen et al. 2005). However, the heterogeneous distribution of mortality (Fig. 2) was highly atypical, as was the widespread adult mortality observed in this event. All species in this study have the capacity to re-nest, so nests destroyed by hail may be replaced by surviving adults within the same season if sufficient breeding opportunity remains following a severe hail event. However, even in the absence of additional storms, the probability of reproductive failure remains moderate to high due to increased nest predation pressure in grassland ecosystems (Vickery et al. 1992; Pietz and Granfors 2000; Murray 2015). Multiple severe hailstorms within the same season could prevent adults from re-nesting successfully, and the loss of breeding adults could depress population productivity for multiple seasons. For demographically marginal populations, this could result in extirpation.

Conservation implications

Our study supports the utility of Doppler weather radar data for estimating the impact of hail events on nesting birds across a larger area than that typically encompassed by direct monitoring efforts. The frequency of days conducive to severe storm formation is projected to increase (Kapsch et al. 2012). Remotely sensed weather radar data

make it possible to estimate the extent and severity of severe hail impacts for nesting birds and, as such, can serve as an important tool in monitoring bird populations. Combined with known ranges of breeding birds, it should be possible to estimate hail-induced mortality at a regional or local scale. Further, based on climate models and the expected increase in hail frequency, adding hail threats to population viability projections should allow us to generate more accurate estimates across possible management scenarios. Although the incidence of large hail cannot be controlled, estimating its prevalence and contribution to mortality may help prioritize actions, especially pertaining to land use, to offset the effect of hail on nesting bird populations. These estimates can help identify potential changes to management practices that will most benefit the conservation of bird populations.

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