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Evaluating efficacy of fence markers in reducing greater sage-grouse collisions with fencing

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ABSTRACT

Anthropogenic infrastructure routinely interferes with wildlife movement, habitat use, and survival. Grouse in the family *Phasianidae* may be particularly susceptible to collisions with fences due to their morphology and life history. Because many *Phasianid* species are of conservation concern, managers often deploy markers on fences to reduce collision-associated mortality. However, scarce information on the effectiveness of different marker styles or the effects of local and landscape features on collision risk exists. Our objectives were to (1) determine the effectiveness of different marker styles in reducing collisions, (2) estimate the effects of local and landscape features on collision risk, and (3) evaluate an existing greater sage-grouse (*Centrocercus urophasianus*) collision risk model. We conducted greater sage-grouse collision surveys within Sublette County, Wyoming, USA in March and April of 2014 and 2015. Data were analyzed in a multi-scale occupancy model accounting for incomplete detection of collisions. We found substantial evidence for the ability of all markers to reduce collisions (~57% reduction), with little difference between the tested marker types. We found strong evidence for lower collision probabilities at fences with wood posts and on fences farther from leks. Our results also indicated a negative relationship between collision probabilities and the difference between fence and vegetation heights. We observed little evidence for differences in collision risk between areas defined as "high" or "moderate" risk in a pre-existing collision risk map. We recommend integrating fence marking into conservation practices requiring fencing, and prioritizing fence marking near leks in areas with greater fence exposure.

1. Introduction

Anthropogenic infrastructure such as fences routinely interferes in the movements, habitat use, and survival of a wide variety of wildlife species (Bevanger 1994; Drewitt and Langston 2008; Linnell 2016). Unfortunately, the installation of human infrastructures, including fences, typically witnessed across landscapes of high-income nations is now occurring in low-income countries as well (Bevanger 1994; Drewitt and Langston 2008). The broad-scale erection of fencing has continued due to civil and political unrest throughout the world (Bevanger and Henriksen 1996; Hayward and Kerley 2009; Linnell 2016), the need for maintaining domesticated livestock within an enclosed area (Hayter 1939), the need to exclude undesired animals from certain parcels (Bevanger and Henriksen 1996; Hayter 1939), or to maintain biodiversity (Hayward and Kerley 2009; Linnell et al. 2016).

Wildlife collisions with fencing represent a direct impact on the survival of individuals. Mortality associated with fence collisions has been well documented for numerous avian species, including the *Phasianids* which are thought to be susceptible to collisions with infrastructure due to their high wing loading, lekking behavior, and afoveal retina (Bevanger 1994; Lisney et al. 2012; Sillman 1973). In North America, Wolfe et al. (2007) found that 39.8% of lesser prairie-chicken (*Tympanuchus pallidicinctus*) mortality was caused by collision with fences and, based on a subset of the same data set, Patten et al. (2005) observed elevated mortality rates for female lesser prairie-chickens where habitats were more fragmented by fences, power lines, and roads. Similarly, greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) collisions with fencing have been observed in two studies in western North America (Christiansen, 2009, Stevens et al. 2012a). In Europe, collisions with fences and power lines have been observed for the western capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), red grouse (*Lagopus lagopus scoticus*), and ptarmigan (*Lagopus spp.*) (Baines and Summers 1997; Bevanger 1995; Catt et al. 1994). Although the impact of this collision-associated mortality on populations is not particularly well understood, there is some evidence indicating infrastructure collisions may contribute substantially

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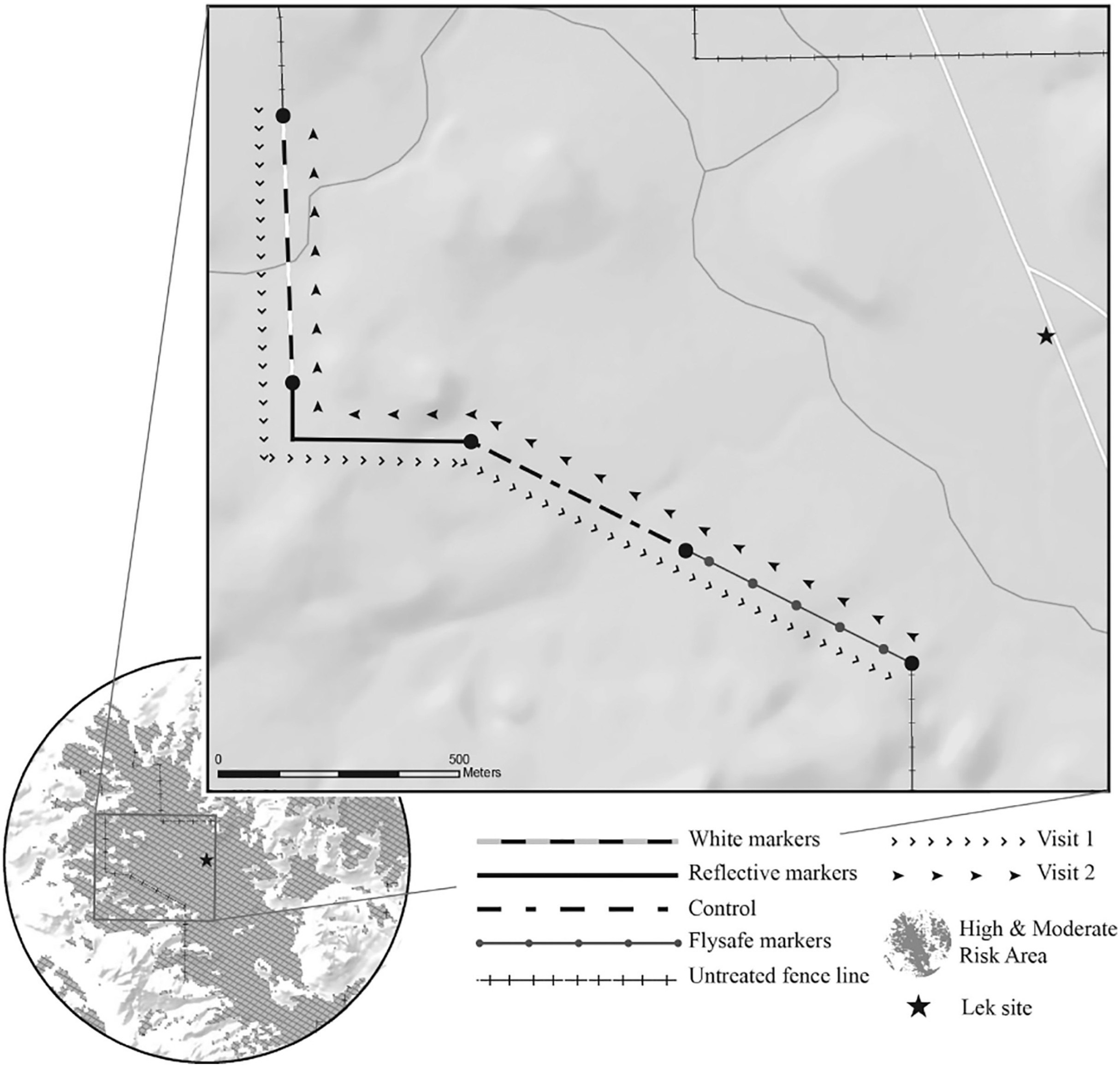

Fig. 1. Illustration of four treated segments of fence-line associated with a focal lek.

to population declines in some species (Baines and Andrew 2003; Bevanger 1995; Moss et al. 2000; Smith and Dwyer 2016).

The risk of wildlife collisions with fencing is likely impacted by a variety of site and landscape-scale factors (Stevens et al. 2012a). Site factors may include the density and height of local vegetation, fence height, type of fence, the type of fence posts, the distance between fence posts, the slope or ruggedness of the nearby landscape, and in the case of lekking species, the distance to surrounding leks and the number of individuals attending adjacent leks (Stevens et al. 2012a). Similarly, landscape-scale factors may include surrounding landcover types (Baines and Summers 1997), the density of individuals throughout the landscape (Baines and Andrew 2003), and movement corridors (including prominent ridges or other vegetative or topographic features that funnel animal movement) (Bevanger 1994; von Schweppenburg 1929).

Marking human infrastructure to increase its visibility is a common practice for reducing collisions for a variety of avian species (Luzenski et al. 2016), including *Phasianids* due to their predisposition for colliding with fences and the level of conservation concern regarding several species within this subfamily (Baines and Andrew 2003; Stevens et al. 2012b). The growing application of fence markers to reduce collisions has prompted government agencies and non-profit organizations to provide significant financial and personnel resources to install them at extensive scales (Natural Resources Conservation Service, 2015). This effort spurred one peer-reviewed study to evaluate the effectiveness of this practice. Stevens et al. (2012b) evaluated the effectiveness of fence markers in reducing greater sage-grouse collisions and found marked fences reduced collisions by 83%. Similarly, marking fences reduced black grouse (91%) and capercaillie (64%) collisions (Baines and Andrew 2003). Although these studies have shown that marking deer and stock fencing can reduce *Phasianid* collisions with fences, to date, no study has compared the efficacy of multiple marker types in reducing collisions, while accounting for imperfect detection, and considering site- and landscape-level factors that may influence collision rates. Durability concerns of marker types in Europe underscore the need for evaluating alternative marker styles (Baines and Andrew 2003). Additionally, few studies have empirically tested site- and landscape-scale factors that may influence the risk of grouse collisions with fencing.

Our research objectives were to 1) determine the effectiveness of different fence marker types, 2) estimate the effects of site and landscape features on collision risk and 3) evaluate an existing greater sage-grouse collision risk model. We evaluated the effectiveness of bright yellow FlySafe markers (FlySafe 2016), white markers with reflective

Fig. 2. Photographs of fence marker types deployed in our study. From left to right the above images represent the Flysafe, reflective, and white marker treatments.

tape and white markers without reflective tape compared to unmarked fence using a dataset collected in western Wyoming where sage-grouse densities are high and leks are abundant. Additionally, we investigated site and landscape features to identify areas with high collision risk and control for potentially confounding variables related to collision risk at multiple spatial scales. We evaluated an existing collision risk map (Stevens et al. 2013) to determine if observed sage-grouse collisions were correlated with areas predicted to have high or moderate collision risk.

2. Methods

2.1. Study area

Our study occurred on both private and public lands within Sublette County, Wyoming, USA. Sublette County contains some of the highest sage-grouse population indices within the occupied range (United States Fish and Wildlife Service, USFWS 2010). It lies within Management Zone II as identified by Stiver et al. (2006). The county covers approximately 3.2 million acres, of which, 80% is publicly owned. Elevations within Sublette County range from 6280 ft to 13,400 ft (Wyoming State Historical Society 2016). Lower elevations are largely characterized as sagebrush steppe habitat with riparian corridors along the Green River and its tributaries. Dominant vegetation within the lower elevation sagebrush steppe largely consists of Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis*) and basin big sagebrush (*Artemesia tridentate* ssp. *tridentata*). Fencing within our study area largely consisted of three to four metal strands with barbs on all wires. A small amount of fencing within our study area consisted of metal woven wire fencing in which the bottom half of the fence consisted of both vertical and horizontal metal strands without barbs and forming rectangles 9 cm by 12 cm. Above the woven wires were typically one or two single horizontal metal wire strands with barbs.

2.2. Sampling design

We developed the sampling frame for Sublette County, Wyoming, using the 3 km-radius collision risk polygons (Stevens et al. 2013) for sage-grouse leks represented in the Wyoming Game and Fish Department lek database (Christiansen 2012). We reclassified the high and moderate risk zones into a single collision risk category and omitted the low risk zone for each of the 308 lek polygons in Sublette County (Fig. 1) using a Geographic Information System (GIS; ArcGIS Version 10.0, ESRI 2011). Next, we intersected the combined high and moderate risk zones for the lek polygons with the Bureau of Land Management (BLM) fence database (Bureau of Land Management - Pinedale Field Office, GIS Staff 2013). The sampling frame consisted of 77 lek polygons containing a minimum of 2 km of fence within the combined high and moderate risk zone of the lek polygons. We defined the sampling unit as the lek, which was represented by the 3 km-radius collision risk polygon (Stevens et al. 2013).

We selected a spatially balanced sample of 26 lek polygons (hereafter, we refer to randomly selected leks as “focal leks”) using Generalized Random Tessellation Stratification (GRTS; Stevens and Olsen 2004). We determined land ownership from the Sublette County Assessor's Office and requested permission to access the sampling units in the rank order of the GRTS sample selection. When landowners denied permission, we selected the next highest rank order of the GRTS sample selection. A useful feature of the GRTS design is the spatially balanced property of the sample was maintained when private landowners denied permission to access the sampling units (Stevens and Olsen 2004).

2.3. Treatments

Each of the four treatments was randomly applied to 500 m stretches of fencing within the selected sample units. Treatments were defined as control (no marker), white (approximately 7.5 × 5 cm piece of white undersill vinyl siding), reflective (white markers with a 7.5 × 1.8 cm strip of lime-yellow Identi-Tape V97 high intensity reflective tape applied to each side), and Fly Safe markers (approximately 12 × 9 cm yellow plastic markers) (FlySafe 2016) (Fig. 2). We selected the marker treatments because they are representative of the gamut of treatments being implemented within the western U.S. to reduce sage-grouse and lesser prairie-chicken collisions with fencing. For the 500 m stretches receiving the white, reflective, or Fly Safe treatments, markers were spaced approximately 1 m from fence-posts and other markers on the top wire of the fencing to be consistent with fence marking recommendations (United States Department of Agriculture, USDA 2016). The design with all three treatments and the control employed at each sampling unit corresponds to a repeated measures design with random order of the treatments levels (Morrison et al. 2008).

2.4. Sampling methods

A total of four observers trained in sage-grouse feather identification and possessing extensive biological survey experience conducted field work throughout the two year study. Observers were intensively trained to ensure they possessed a complete understanding of field protocols, a sufficient ability to identify collision events, and could positively identify sage-grouse remains.

Surveys were conducted approximately biweekly in March and April of 2014 and 2015. A survey of a site entailed either two or four visits. The first visit consisted of an observer walking along the site's fence while scanning for evidence of animal collisions. The observer then crossed the fence and conducted the second visit by doubling back and walking to the starting point of the first visit (Fig. 1). A survey consisted of four visits when a second observer, surveying separately from the first observer, visited the same site on the same day. Observers did not discuss findings during the course of the surveys in order to avoid influencing detection rates.

Observers maintained a distance of 1-2 m from the fence during each visit. While surveying, observers primarily searched the wires of the fence for signs of a collision. Additionally, observers scanned the

Table 1
Covariates included in analyses of fence collisions by Greater Sage-Grouse in Wyoming, 2014–2015, and their expected effect on the parameter of interest (positive effect, +; negative effect, −). Parameters include large-scale occupancy (ψ), small-scale occupancy (θ), and detection probability (*p*). Means and ranges are shown for continuous covariates and levels and frequencies for the categorical covariates.

Covariate	Description	Parameter	Means (ranges) and levels (frequencies)	Expected effect
Occ Lek	Number of occupied leks within 3 km of the focal lek	ψ	1.51 (0–3)	+
Lek Ct	Sum of lek counts for leks within 3 km of focal lek	ψ	72.88 (0–265)	+
Year	Year in which survey was conducted	ψ,θ	2014 (26), 2015 (25)	N/A
Trt	Fence marker type	θ	Control (50), FlySafe (51), White (51), Reflective (50)	Risk of control > white > reflective > FlySafe
Mark	Fence marked or not	θ	Control (50), Marked (152)	Lower for marked
Angle	Angle (°) created by the triangle between the lek and end of fence segment	θ	16.34° (1°–120°)	+
Distance	Distance (km) between the midpoint of the fence segment and the nearest lek	θ	1.85 km (0.15 km–4.60 km)	−
Near Ct	Mean max male lek count for the nearest lek from 2014 to 2015	θ	54.63 (1–265)	+
Fence Exp	Mean difference (cm) between the top strand of a fence and the top of the surrounding vegetation	θ	67.69 cm (26.67 cm–96.10 cm)	+
Risk	Percentage of the fence segment in high risk areas based on Stevens et al. (2013)	θ	45.8% (0.0%–100.0%)	+
Post	Type of posts used in a fence segment	θ	Wood (138), T-post (4), both (62)	Risk of t-post > both > wood
Surv	Biweekly survey (primary) period in which survey was conducted	θ, *p*	1 (200), 2 (202), 3 (189), 4 (189), 5 (188), 6 (190), 7(186)	None
Visit	Visit (secondary period) in which survey took place	*p*	1 (1019), 2 (1014), 3 (114), 4(112)	None
Obs	Observer conducting the survey	*p*	A (432), B (226), C (525), D (1076)	None
Trap	"Trap effects" for the 2nd and 4th visits to account for potential lack of independence between visits by the same observer	*p*	1st/3rd (1133), 2nd/4th (1126)	Higher for 2nd/4th visits
Trap2	"Trap effects" accounting for whether a collision was detected or not on the 1st visit	*p*	Non-detection (1135), detection (1080)	Higher if previously detected
Cloud	Cloud cover (%)	*p*	46.1% (0.0%–100.0%)	−
Snow	Snow cover (%)	*p*	33.8% (0.0%–100.0%)	+

bushes and ground approximately 10 m out from either side of the fence for feathers or carcasses. Observers recorded ocular estimates of average snow and cloud cover (0–100%) during the course of each survey.

We considered a collision to have occurred when sage-grouse feathers were observed in the wires or barbs of a fence. We believe this represents a more accurate count of collisions as other experts have determined carcass recovery can be low due to scavenging (Stevens et al. 2011) and we believe wounded grouse may travel significant distances after striking fences before they expire. Collisions were recorded on each visit during which they were observed. In the event that feathers were found on the fence at multiple locations between two fence posts (the fencing between two fence-posts hereafter is referred to as a "panel"), the evidence was considered a single collision unless the largest gap between feathers on the wire exceeded the average wingspan of a sage-grouse (Sibley 2000). Analyses did not include any evidence in a fence that may have resulted from perching, prey plucking, or preening events, which were generally characterized by a small amount of feathers loosely affixed to the barbs of the fence and primarily distributed near a wooden post.

Observers thoroughly documented all collisions found via photographs and written notes. Observers recorded collision locations with a hand-held Global Positioning System (GPS) unit. Additionally, observers recorded the following information pertaining to the collision evidence: the distance from the evidence on the fence to the nearest fence-post, the distance from the evidence on the fence to the nearest marker, the distance from the ground (or top of the snow layer, when applicable) to the highest evidence on the fence, and the strand of wire containing the collision evidence. Finally, the observers collected the following data to describe the collision site: the distance between the two fence-posts for the panel containing the evidence, the mean height of the vegetation along the fence panel containing the collision evidence, and the number of strands of wire on the panel of fencing containing the evidence. Photographs of feathers were sent to local experts if the field observers could not be sure of identification. Collision events were only included in analyses when species identification was possible (i.e., diagnostic feathers found).

2.5. Covariate data collection

We measured fence exposure by estimating the average height of woody vegetation and the height of the top strand of fencing in centimeters for each panel. We then subtracted the height of the woody vegetation from the height of the top wire of fencing to obtain a value of "fence exposure" in centimeters for the panel. If vegetation was taller than the fence, fence exposure had a negative value. We measured these values for six panels within each 500 m stretch. Values were calculated at the two panels representing the endpoints and systematically at four additional locations at 100 m intervals along each fence segment. The fence exposure values for each of the six panels per stretch were then averaged to derive a single mean fence exposure value for the 500 m stretch. With assistance from BLM personnel, we also noted whether posts within a fence segment were wood posts, metal t-posts, or a combination of the two.

Using ArcGIS 10.0 (ESRI) we calculated several covariates including: 1) the number of occupied sage-grouse leks within 3 km of the focal lek, 2) the sum of mean maximum male lek counts in 2014 and 2015 for all leks within 3 km of the fence segment midpoint, 3) the distance from the midpoint of each fence stretch to the nearest occupied sage-grouse lek and the mean maximum male count for that lek from 2014 to 2015, 4) the proportion of each fence stretch that fell within the high risk category of the collision risk map (Stevens et al. 2013), and 5) the angle of exposure for each stretch of fence (i.e., the angle created by the triangle between the ends of the fence segment and the associated lek).

Lastly, observers estimated cloud cover during each survey and percent of the ground covered by snow to the nearest 10%. In 2014 observers recorded a single value for the average snow cover values surrounding each of the four fence segments during a survey. In 2015 observers recorded a separate value for average percentage of snow cover along each fence segment. For analyses, we calculated the mean of the 2015 values for each survey to produce a single snow cover value consistent with the 2014 data. Table 1 summarizes all covariates included in our models.

2.6. Model justification and hypotheses

We used the method of working hypotheses (Chamberlin 1965) to evaluate alternate a priori hypotheses to understand how different marker types, site- and landscape-features and mapped collision zones affect sage-grouse fence collisions. We used the covariates in Table 1 to represent hypotheses for the objectives and translated the hypotheses into predictive models. We then used the predictive models to evaluate relative strength of evidence for the alternate hypotheses in a model selection framework (Burnham and Anderson 2002). We predicted detection of sage-grouse collisions at the fence segments would be incomplete, potentially biasing the measurement of effect sizes for the fence markers. Therefore, we evaluated several hypotheses for how observers and time occasions may influence the detectability of fence collisions. We predicted the detection of collisions would vary by observer (*Obs*), time of the biweekly surveys (*Surv*), and repeated visits (*Visits*, Table 1). We accounted for potential non-independence of detections when observers visited the fence segment twice on the same day using the *Trap2* covariate (Table 1). In addition, we hypothesized that snow cover (*Snow*) and cloud (*Cloud*) cover may interfere with the ability to detect the signs of collision (Table 1).

When evaluating the effectiveness of fence markers (objective 1), we predicted that collision risk would be lower on fence segments with markers than fence segments without markers (*Mark*, Table 1) since fence marking has been shown to reduce collision risk for grouse species (Stevens et al. 2013). In addition, we hypothesized that collision risk would be lowest on fence segments with yellow Fly Safe markers, intermediate on segments with white markers with reflective tape, and greatest on segments with white markers without reflective tape (*Trt,* Table 1). Because *Phasianid* species are known to see carotenoid-based colors (Mougeot et al. 2007), we predicted the bright yellow Fly Safe markers would be more effective than white markers with reflective tape. We predicted white markers with reflective tape would be more effective than white markers without reflective tape because reflective tape is thought to provide greater visibility for low light and snow background conditions (Stevens et al. 2013). In addition, we hypothesized that fence segments with wood posts would be more effective in reducing collisions than fence segments with iron t-posts and fence segments with both types (*Post*, Table 1) because wooden posts may be more conspicuous than iron t-posts (Stevens et al. 2012a) and sage-grouse are known to avoid areas with vertical woody structure (Stiver et al. 2006).

We evaluated site- and landscape features to identify areas with greater collision risk (objective 2) at multiple scales and to control for potentially confounding variables when evaluating the effectiveness of different marker types (Morrison et al. 2008). At the local scale, we hypothesized that collision risk would be higher on fence segments near active leks (*Distance*) and near leks with greater lek attendance (*Near Ct*, Table 1) as has been shown in previous research (Stevens et al. 2012b). In addition, we predicted that collision risk would be greater on fence segments with greater fence exposure above vegetation and on fence segments (*Fence Exp*) with a larger “exposure angle” in relation to the focal lek (*Angle*, Table 1). Stevens et al. (2012a) considered a variable for the height difference between the fence and the nearest lateral shrub, but did not find strong evidence for this variable. Nevertheless, we felt sage-grouse were more likely to fly above the vegetation than between it and greater fence exposure would therefore lead to greater collision risk. Given the positive association of collisions with lek counts and small lek distances, we hypothesized that birds needing to cross fencing to attend or leave a lek would have a higher risk of collision and used the *Angle* covariate to test this hypothesis. At the landscape scale, we hypothesized that collision risk would be greater in lek polygons with high numbers of occupied leks (*Occ Lek*) and with high lek counts (*Lek Ct*, Table 1). Stevens et al. (2012a, 2012b) measured the distance between fence segments and leks to show that distribution and abundance of leks was related to collision risk at the site-scale. We measured lek density and sage-grouse abundance within the 3-km^2 radius lek buffers (28 km^2) to evaluate the extent that lek distribution and abundance influenced collision risk of lek polygons at the landscape scale. Because sage-grouse are known to move between leks on the landscape (Emmons and Braun 1984), we predicted that lek polygons containing a greater number of leks and greater numbers of birds would also have greater collision risk. If landscape measures of lek distribution and abundance prove important, these covariates can be used to account for the dependence of the treatments within 3-km^2 radius lek polygons using the repeated measures design.

To evaluate an existing collision risk map by Stevens et al. (2013) (objective 3), we predicted that collision risk would be greater along fence segments in areas characterized by high risk than on fence characterized by moderate risk (*Risk*, Table 1). Because the collision risk map was based on terrain ruggedness and distance to nearest lek (Stevens et al. 2013), this hypothesis evaluates collision risk in response to moving farther from a lek with increasing topographic relief.

2.7. Statistical analyses

We developed a multi-scale occupancy model (Nichols et al. 2008) to estimate occupancy probabilities of collision evidence, and the factors influencing them at site- and fence-segment levels. The model allowed estimation of three parameters that corresponded to each level in the nested sampling design. We used repeat visits nested within each survey to estimate detection, repeat surveys of fence segments nested within a site (i.e., lek) to estimate small-scale occupancy (the probability of a collision occurring within a 500 m fence segment), and replicate leks nested within the study area to estimate large-scale occupancy (the probability of a collision occurring within any of the four fence segments associated with the focal lek). All analyses were conducted using Program MARK (version 8.0; White and Burnham 1999) via RMARK (version 2.1.14; Laake 2013). We defined our three general parameters as: (1) the probability that evidence of ≥ 1 new sage-grouse collision was present on ≥ 1 fence segment at site i during any of the surveys, ψ_i, (2) the probability that evidence of ≥ 1 new collision was present at a fence segment during survey j, θ_{ij}, and (3) the probability that a new collision was detected on visit k, given the fence segment was occupied during survey j and visit k, p_{ijk}. The multi-scale occupancy model is well suited for the repeated measures design by allowing the investigation of covariates influencing occupancy at the large-scale (i.e., collisions at any fence segment associated with a focal lek) as well as treatments effects on conditional occupancy at the small-scale (i.e., collisions at individual fence) while accounting for non-independence of fence segments within a lek. This is analogous to how variance is estimated in a mixed model with a random effect on the focal lek (Pavlacky et al. 2012). We assumed fence segments were closed to changes in occupancy within each survey and that new collisions were accurately identified and recorded. The fence segments were allowed to be open between surveys. This model also assumes that detections are independent; however, observers conducted the second visit on the opposite side of the fence immediately after the first visit. We attempted to account for this potential lack of independence by estimating separate detection probabilities for the first and second visits by the same observer during a survey period along with whether a collision was detected during the first visit.

2.8. Model set

To investigate our hypotheses regarding the factors influencing large- and small-scale occupancy and detection, the models in our

Table 2
Model set for models explaining variation in detection probabilities (p) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most general small- (θ) and large-scale (ψ) occupancy probability model structures. Because two covariates on each occupancy probability were different measures of similar hypotheses, we included both model structures on each of those parameters. Covariates included to explain variation in detection probabilities included: fixed visit effects (Visit), fixed survey effects (Surv), fixed observer effects (Obs), "trap effects" for the 2nd and 4th visits (Trap), "trap effects" accounting for whether a collision was detected or not on the 1st visit (Trap.2), cloud cover (Cloud), and snow cover (Snow). Model structure on small-scale occupancy included: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), an interaction between post type and marker type (Post × Trt), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). Model structures on large-scale occupancy included: Year and either the sum of lek counts at nearby leks (Lek Ct) or the number of nearby occupied leks (Occ Lek; indicated in ψ column). The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference between a model's AIC_c value and the minimum AIC_c value (ΔAIC_c), and AIC_c weights are also shown for models with $\Delta AIC_c \leq 10$.

ψ	p	npar	AIC_c	ΔAIC_c	Weight
Occ Lek	Null	25	415.082	0.000	0.582
Lek Ct	Null	25	416.051	0.969	0.358
Occ Lek	Snow	26	423.116	8.034	0.010
Occ Lek	Surv	26	423.388	8.306	0.009
Occ Lek	Cloud	26	423.572	8.490	0.008
Occ Lek	Trap.2	26	423.582	8.500	0.008
Lek Ct	snow	26	424.084	9.002	0.006
Lek Ct	surv	26	424.358	9.275	0.006
Lek Ct	cloud	26	424.541	9.459	0.005
Lek Ct	trap.2	26	424.551	9.469	0.005

model set consisted of various combinations of covariates on each parameter. We included 3 covariates on large-scale occupancy (ψ), 10 on small-scale occupancy (θ), and 7 on detection (p; Table 1). We also included interactions between post type and marker, as well as minimum distance to the nearest lek and maximum male count for that lek on θ. Because the model set was very large when considering all possible combinations of covariates, we used a sequential approach to model selection (Lebreton et al. 1992). We fit models that included all possible additive combinations of covariates on detection, while including additive effects for all covariates for large- (ψ) and small-scale (θ) occupancy. There were two covariates on large-scale occupancy that were different measures of the same hypothesis: (1) the number of occupied leks within 3 km of the focal lek (Occ Lek, Table 1) and (2) the sum of the lek counts for leks within 3 km of the focal lek (Lek Ct). We did not include both covariates in the same model. Therefore, we fit a global model containing all other additive combinations of covariates with Occ Lek and Lek Ct. separately, resulting in two global models. Then, using the most parsimonious detection structure(s), we evaluated hypotheses related to large-scale occupancy. Retaining the best large-scale occupancy model structure(s), we fit models that included all possible combinations of covariates thought to influence small-scale occupancy, including the two interaction terms.

We used an information-theoretic approach for model selection and used Akaike's Information Criterion (AIC) adjusted for sample size (AIC_c) for model comparison (Burnham and Anderson 2002). We used Akaike weights, w_i, as a measure of the relative amount of evidence for each model. Our model set for small-scale occupancy was not balanced because of the interaction terms and mutually exclusive covariates (i.e., Mark and Trt), so we used a modified version of cumulative weights based on the frequency of the covariate in the model set $[w_+(j)]$ (Doherty et al. 2012) to determine the relative importance of our covariates,

$$w_+(j) = \left[\frac{w}{1-w}\right] \Big/ \left[\frac{f}{1-f}\right],$$

where w is the cumulative Akaike weight (sum of Akaike weights for models containing the covariate) and f is the frequency of models containing the covariate in the model set. Weights ≫ 1 indicate support for the importance of that variable, weights near 1 are inconclusive, and weights ≪1 indicate little support for importance. We used the odds ratio to express the effect sizes (β) in terms of the percentage increase in the odds of collision.

3. Results

We found evidence of 64 confirmed fence collisions by sage-grouse during the study, with 15 detected in 2014 and 49 detected in 2015. Additionally, we observed 96 instances of possible or likely collisions which were not included in analyses. Over 60% of sites (16 of 26) and 26% of fence segments (27 of 104) contained evidence of ≥ 1 confirmed collision. Only two fence segments were constructed using t-posts exclusively, and no collisions were detected at those segments; therefore, we fixed small-scale occupancy (θ) of those segments to zero to assist with numerical convergence.

Our global models used in the sequential model selection, included year and either the number of nearby occupied leks or the sum of the lek counts at those leks effects on large-scale occupancy, ψ (Year + Occ Lek) or ψ (Year + Lek Ct); year, survey, treatment × post type, distance to nearest lek × count for nearest lek, fence angle to lek, proportion in high risk areas, and fence exposure effects on small-scale occupancy, θ (Year + Surv + Distance + Angle + Risk + Fence Exp + Post × Trt + Distance × Near Ct); and observer, cloud cover, snow cover, and visit effects on detection, p (Obs + Cloud + Snow + Visit).

3.1. Detection probabilities

Using these two global models, we explored 40 other detection structures, representing simplifications of our general detection structure (Tables 2 and A1). The most parsimonious model included a constant detection probability (w = 0.59), as did the 2nd best model, cumulatively accounting for 95.4% of the weight; thus, we retained this detection structure, p (.), in our subsequent models. We estimated the probability of detecting ≥ 1 collision at 0.935 (SE = 0.026).

3.2. Large-scale occupancy

Large-scale occupancy of collisions increased as the sum of nearby lek counts increased and was higher in 2015. However, the 95% confidence intervals for both of these effects included zero. Because of this uncertainty, the most parsimonious model for ψ was the constant model, which accounted for a majority of the AIC_c weight (w = 0.85) (Table 3). On average, large-scale occupancy was estimated to be 0.717

Table 3
Model set for models explaining variation in large-scale occupancy probabilities (ψ) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most parsimonious model on detection probabilities (i.e., null) and the global model structure on small-scale occupancy probabilities (θ). Model structures on large-scale occupancy included: Year and either the sum of counts at leks with 3 km (Lek Ct) or the number of occupied leks within 3 km (Occ Lek; indicated in ψ column). Model structure on small-scale occupancy included: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), an interaction between post type and marker type (Post × Trt), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). We also include the number of parameters (npar), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference between a model's AICc value and the minimum AICc value (ΔAIC_c), and AIC_c weights.

ψ	npar	AIC_c	ΔAIC_c	Weight
Null	23	402.913	0.000	0.852
Lek Ct	24	408.447	5.534	0.054
Year	24	408.498	5.585	0.052
Occ Lek	24	409.084	6.171	0.039
Year + Occ Lek	25	415.082	12.170	0.002
Year + Lek Ct	25	416.051	13.139	0.001

Table 4
Cumulative AIC_c model weights for variables thought to influence small-scale occupancy (θ) of greater sage-grouse fence collisions in Wyoming, 2014–2015. Cumulative weights were adjusted based on the frequency of the covariate in the model set (Doherty et al. 2012). Variables included in the model set are: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), wood post or wood and t-post (Post), marker type (Trt), whether a fence was marked or unmarked (regardless of marker type; Mark), the distance to the nearest occupied lek (Distance), the count at the nearest lek (Near Ct), an interaction between post type and marker type (Post × Trt), an interaction between post type and whether a fence was marked (Post × Mark), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). Modified cumulative model weights ≫ 1 suggest strong support for that variable, weights near 1 are ambiguous, and weights ≪ 1 suggest little support for that variable.

Variable	Cumulative weight
Post	12.797
Mark	4.188
Distance	3.349
Fence Exp	1.699
Year	1.261
Risk	1.246
Near Ct	1.078
Post × Mark	0.908
Surv	0.790
Distance × Near Ct	0.658
Angle	0.476
Trt	0.065
Post × Trt	0.001

(SE = 0.127).

3.3. Small-scale occupancy

We found strong evidence for effects of post type [w_+(Post) = 12.80], whether a fence was marked or not [irrespective or marker type, w_+(Mark) = 4.19], and distance to the nearest lek [w_+(Distance) = 3.35] on small-scale occupancy (Tables 4, 5, and A2). There was some support for the effects of fence exposure [w_+(Fence Exp) = 1.70], year [w_+(Year) = 1.26], the amount of fence segment within the high risk areas based on Stevens et al. (2013) [w_+(Risk) = 1.25], and the count at the nearest lek [w_+(Near Ct) = 1.08; Tables 4 and A2]. Consistent with our hypotheses, wood posts, fence marking, and increasing distance to nearest lek resulted in lower collision occupancy probabilities (Tables 6, A3, and A4 and Fig. 3). The amount of fence exposure and the proportion of fence in high risk areas increased the probability of a collision, as we predicted. Occupancy probabilities were higher in 2015 and as the count at the nearest lek increased, though these coefficients were not significant (Table 6). All marker types performed similarly [β = −0.843,(95% CI = −1.545, −0.141); odds ratio: 0.430, (0.128, 0.732)], with reflective [β = −1.018,(95% CI = −1.967, −0.068); odds ratio: 0.361, (0.018, 0.705)] and white markers [β = −0.808, (−1.703, 0.087); odds ratio: 0.446, (0.047, 0.857)] reducing occupancy probabilities slightly more than Fly Safe markers [β = −0.725, (−1.634, 0.184); odds ratio: 0.484, (0.044, 0.924)] based on the model including treatment and all other covariates with cumulative weights > 1.

4. Discussion

We adapted the multi-scale occupancy framework to investigate landscape- and local-scale features influencing the probability of fence collision, and our results support the anecdotal and limited empirical evidence for the threat of fences to sage-grouse (Christiansen 2009; Flake et al. 2010; Scott 1942; Stevens et al. 2012a, 2012b). Our study also provided insight into the factors influencing fence collisions at two spatial scales by using a multi-scale occupancy model. In addition to accounting for imperfect detection of collisions, this approach allowed us to account for the lack of independence between fence segments associated with a particular lek (Nichols et al. 2008; Pavlacky et al. 2012).

Studies regarding potential risk of collision with human-associated infrastructure have noted that risks to lekking species may be higher in close proximity to lek locations (Baines and Summers 1997; Bevanger 1994; Stevens et al. 2012a, 2012b). Therefore, we tested four hypotheses relating to the risk of collision in association to the number of leks, the number of individuals observed at nearby leks, the position of fencing (angle) in relation to a nearby lek, and the distance to the nearest lek. Unlike Stevens et al. (2012a), we found little evidence for an effect of the number of birds using nearby leks on collision probabilities and therefore failed to confirm our hypothesis. Similarly, there

Table 5
Model set for models explaining variation in small-scale occupancy probabilities (θ) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most parsimonious model on detection probabilities (i.e., null) and large-scale occupancy probabilities (i.e., null). Model structures on small-scale occupancy included: distance to nearest lek (Distance), the count at the nearest lek (Near Ct), fence exposure (Fence Exp), wood post or t-post (Post), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), marker type (Trt), marked or unmarked fence (regardless of marker type; Mark), Year, biweekly (primary) period (Surv), an interaction between Distance and Near Ct, and an interaction between Post and Mark or Trt. The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference between a model's AICc value and the minimum AICc value (ΔAIC_c), and AIC_c weights are also shown for the top 10 models.

θ	npar	AIC_c	ΔAIC_c	Weight
Fence Exp + Mark + Distance + Post + Risk + Near Ct	9	364.644	0.000	0.030
Fence Exp + Mark + Distance + Post + Risk + Year	9	364.756	0.111	0.028
Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct	10	364.903	0.259	0.026
Fence Exp + Mark + Post + Risk + Distance × Near Ct	10	365.270	0.626	0.022
Surv + Fence Exp + Mark + Distance + Post + Risk + Year	15	365.647	1.003	0.018
Fence Exp + Mark + Distance + Post + Near Ct	8	365.762	1.118	0.017
Fence Exp + Mark + Post + Risk + Year + Distance × Near Ct	11	365.794	1.150	0.017
Surv + Fence Exp + Mark + Distance + Post + Year	14	365.810	1.166	0.017
Fence Exp + Mark + Distance + Post + Year + Near Ct	9	365.998	1.354	0.015
Fence Exp + Mark + Distance + Post + Risk	8	366.015	1.371	0.015

Table 6
Coefficient estimates, standard errors (SE), and 95% confidence intervals (CI) for all variables explaining variation in small-scale occupancy (θ) probabilities of Greater Sage-Grouse fence collisioins in Wyoming, 2014–2015. Variables include fence exposure, whether a fence was marked (regardless of marker type; Mark), the distance to nearest lek (Distance), fences with wood and t-posts (wood and t-post), proportion of fence segment in high risk areas (Risk), year (2015), and the count at the nearest lek (Near Ct). The intercept represents an unmarked fence with wood posts in 2014 with all continuous variable values set to 0. Variables included had modified cumulative AIC_c weights > 1. Estimates from the third best model are reported because it is the best model including all variables with cumulative weights > 1. All significant coefficients (i.e., 95% CIs do no overlap 0) are indicated by an asterisk.

Parameter	Mean	SE	95% CI
Intercept*	−5.544	1.123	(−7.745, −3.342)
Fence Exp*	0.031	0.013	(0.005, 0.058)
Mark*	−0.843	0.358	(−1.545, −0.141)
Distance*	−0.586	0.192	(−0.962, −0.210)
Wood and T-post*	1.774	0.382	(1.025, 2.523)
Risk*	1.150	0.565	(0.042, 2.258)
2015	0.821	0.473	(−0.105, 1.747)
Near Ct	0.004	0.002	(−0.001, 0.009)

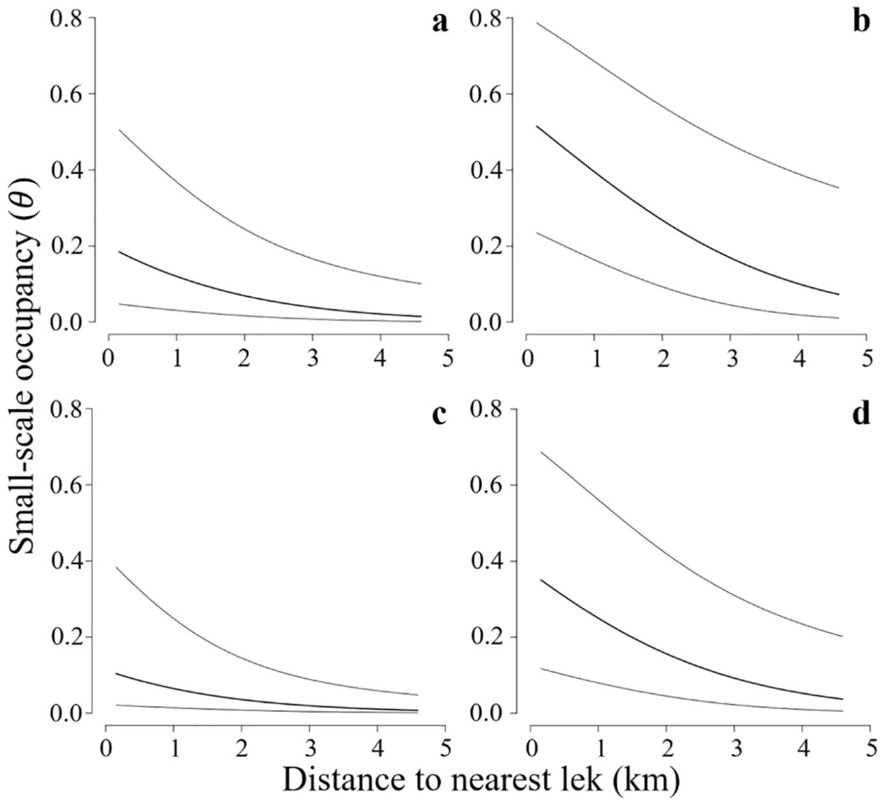

Fig. 3. Small-scale occupancy probability (θ, heavy lines) and associated 95% confidence intervals (light lines) as a function of distance to nearest lek for a) unmarked, wood post, b) unmarked, wood and t-post, c) marked, wood post, and d) marked, wood and t-post fence segments.

was no evidence to support an increased risk of collision near fencelines that are near multiple leks. Baines and Andrew (2003) similarly found no effect of lek indices on collision risk indicating that other factors may be more predicitive. Our findings may be partially due to using presence-absence data to detect differences among leks of various sizes, such that the probability of ≥ 1 collision is high for a fence near even a single smaller lek. Addtionally, lek counts have been criticized for their inability to accurately reflect abundance of sage-grouse (Beck and Braun 1980; Johnson and Rowland 2007; Walsh et al. 2004) but have been shown to be a reasonable index of the population of breeding males when standard survey protocols are followed (Jenni and Hartzler 1978; Emmons and Braun 1984; Walsh et al. 2004; Johnson and Rowland 2007). However, lek counts may not accurately represent the number of birds in the area surrounding a lek, and therefore, may be a poor indicator of the likelihood of a collision. We therefore recommend that future efforts to estimate or account for collision risk use estimated densities when possible.

Although there is an abundance of peer-reviewed work indicating that flight paths may greatly increase the risk of bird collisions with human infrastructure (Bevanger 1994; Bevanger 1998; Everaert and Stienen 2007; Henderson et al. 1996; Scott et al. 1972), we found no evidence for increased collision risk with an increased angle of fence exposure in relation to the lek which failed to confirm our hypothesis. It is possible this covariate was confounded with the distance to the nearest lek (closer distances having a larger angle) which we tested and describe in the following text. Nevertheless, we maintain that flight paths may be important in determining collision risk for some systems and species and encourage researchers to consider other potential vegetative, topographical, biological, and environmental factors that may influence or create flight paths in future studies.

We found the proximity of a fence segment to a lek influenced the probability of a collision (Distance); the average occupancy probability decreased by approximately 39% between distances of 153 m (i.e., smallest distance observed) and 1 km. This is consistent with the findings of Stevens et al. (2012a, 2012b) and confirmed our hypothesis. This relationship is likely due to increased encounters between birds and fences when a fence is closer to an area where birds congregate. We therefore recommend that marking efforts preferentially mark fence close to leks in the future. Additionally, we encourage future studies investigating risks of collisions with human-related infrastructure to consider accounting for water and/or food sources, geophagy sites, or other features that may lure large numbers of individuals into a localized area.

As in Stevens et al. (2012a), our results suggest that fence post type has the largest effect on the occupancy probability of sage-grouse collisions, with the lowest occupancy probabilities for fence segments with wooden posts, which confirmed our hypothesis. Only two fence segments in our study had t-posts exclusively and neither of those segments had evidence of a collision on them; therefore, we were unable to estimate occupancy probabilities for segments with only t-posts. Unmarked fence segments with wooden posts had lower occupancy probabilities than segments with both wooden and t-posts and any of the fence markers; yet, collision rates for fence segments with wooden posts were reduced further by the use of fence markers. These results are consistent with those found by Summers and Dugan (2001), in which, they found full length paling (which resemble wooden posts) to be the most visible fence marker. As such, we recommend future marking efforts consider testing the effectiveness of wooden stays woven into the fencing. Additionally, preferentially marking fencing with t-posts or a mixture of wood and t-posts could maximize the reduction in potential *Phasianid* collisions with fencing as our results indicated fences without wooden posts may have high rates of collisions.

We found a small effect of the amount of exposed fencing on collision risk. As vegetation height near a fence decreased, the probability of a collision increased which supported our hypothesis. *Phasianids* are generally classified as "poor flyers" (Bevanger 1994; Rayner 1988) which characteristically engage in short flights (Viscor and Fuster 1987). These morphological constraints likely result in *Phasianids* engaging in proportionately more of their flight at low altitudes, often near the top of exposed vegetation, than many birds with lower wing loading. As the top of vegetation approaches or exceeds the top of human infrastructure there is thought to be less risk of collisions (Bevanger 1994). Although we observed a weak relationship between the amount of exposed fence and collision risk, we maintain areas with short vegetation may benefit more from the use of markers by making the fence more visible. Similarly, we suggest that taller "elk fences" in the western U.S. and "deer fences" in Europe may increase collision risk beyond that of stock fencing due to the potential for additional fence projection above the vegetation as well as a general increase in total fence area. This idea was not explicitly tested in our study and represents an area for future research.

Our study design was largely based on the collision risk map developed by Stevens et al. (2013) which predicted high risk of collisions in areas close to leks and with little topography. The authors acknowledged their range-wide model was created using data collected within a relatively small geographic area in Idaho. As such, they recommended additional validation efforts be conducted. Our findings suggested a slightly increased collision probability in high risk areas, but this effect was weak. Because we attempted to select fence-line segments within the high and moderate risk areas of this map, much of the fence-line included in our study fell within these areas. Therefore, low risk areas were not well represented in our study, precluding an evaluation of the low risk portions of the risk map. We recommend further investigation of the efficacy of the collision risk map in predicting collision risk, particularly to determine if greater slopes associated with topography do impact collision risk range-wide and to determine if low risk areas on the collision risk map have a lower number of associated fence collisions. Until the collision risk map can be evaluated further, we recommend that managers seeking to reduce sage-grouse collisions focus their fence-marking efforts on fence-lines in both the high and moderate risk zones which are both close to leks and possess local site characteristics which have been shown to increase collision risk in our study and/or in previous studies.

We estimated a detection rate of 0.94, suggesting a false absence rate of 6% in the raw collision data. Our detection rate was similar to the collision detection rate calculated by Baines and Andrew (2003) when they simulated collision events with grouse carcasses. This indicates that detection of collision events is likely quite high when conducting walking surveys, provided that evidence of the collision still persists on the landscape. Stevens et al. (2011) calculated much lower detection rates when conducting walking surveys within 15 m of bird carcasses which were placed in the field; however, their estimates accounted for both detectability and scavenging bias. We suspect the scavenging bias was the driving factor in the reduced detection rates; however, they also placed carcasses beyond the search window of both our study and that of Baines and Andrews (both, of which had an effective search strip width of approximately 5 m). Furthermore, Stevens et al. placed piles of feathers and the carcasses within the habitat whereas in the Baines and Andrews study the carcasses were "vigorously thrown at the fence to simulate flight collisions". Given that we regularly witnessed feathers widely strewn across areas of 30 m or more in our study, we feel the methods used by Stevens et al. (2011) may not have accurately created conditions similar to that of an actual collision event, ultimately underestimating detection probabilities of *Phasianid* collision evidence.

Our results suggest that all three types of fence markers employed in our research were effective at reducing collision probabilities and confirmed our hypothesis, with stretches of marked fence having a 57% (27% - 87%) lower probability of containing ≥ 1 collision. These results align with previous studies by Stevens et al. (2012b) and Baines and Andrew (2003) which found marking fences reduced *Phasianid* collisions with fencing. Our results provided weak evidence that reflective markers were the most effective marker type in our study, with a 64% (30%–98%) reduction in collision probability. Stevens et al. (2012b) saw an 83% reduction in sage-grouse collisions using reflective markers. The smaller effect observed in our study may be due in part to less resolution to detect covariate effects when using occupancy models compared to abundance measures because counts are summarized to presence or absence. In addition, the smaller effect observed in our study may be partially related to accounting for incomplete detection of sage-grouse collisions, despite detection being quite high. The collision reduction estimated in our study aligns well with the estimated 64% reduction for capercaillie, 91% reduction for black grouse, and 49% reduction for red grouse estimated by Baines and Andrew (2003).

Overall, we found little difference in the effectiveness of the three marker types, as models with a marker effect (for any marker type) had substantially more cumulative AIC_c weight than models with effects for all marker types individually. However, contrary to our hypothesis, Fly Safe markers were slightly less effective than both white and reflective markers. We estimated average per marker costs for white markers at \$0.14, reflective markers at \$0.71, and Fly Safe markers at \$0.40 (USD). Therefore, using the plain white markers without reflective tape, may represent the most cost-effective sage-grouse marking strategy of those we tested. In Europe, the only study to our knowledge, which investigated marker utility in preventing *Phasianid* collisions employed two strips of orange plastic netting on the fence (Baines and Andrew 2003). The authors acknowledged that, although effective in reducing collisions within woodlands, this marker style was not suitable for deployment in areas exposed to weather (i.e., open moorland), where red grouse densities may be high. We witnessed very little damage to the three types of markers we deployed and therefore recommend trials using these marker types in open habitats of Europe.

The effectiveness of the fence markers in reducing *Phasianid* collisions highlights the importance of integrating fence marking into ongoing conservation efforts. Prescribed grazing is often recommended to improve nesting and wintering habitat conditions for lekking-species of conservation concern such as the greater-sage-grouse (Monroe et al. in review) and lesser prairie-chicken (Hagen et al. 2016). Because the implementation of rotational grazing systems involves additional fencing to subdivide an area into several pastures (United States Fish and Wildlife Service, USFWS 2010), we recommend marking exposed fence near leks even in areas thought to have only moderate collision risk due to topography. We suggest fence marking may reduce the potential for ecological traps (Battin 2004) associated with conservation practices that require the creation of additional fencing.

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Appendix A

Table A1
Model set for models explaining variation in detection probabilities (*p*) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most general small- (θ) and large-scale (ψ) occupancy probability model structures. Because two covariates on each occupancy probability were different measures of similar hypotheses, we included both model structures on each of those parameters. Covariates included to explain variation in detection probabilities included: fixed visit effects (Visit), fixed survey effects (Surv), fixed observer effects (Obs), "trap effects" for the 2nd and 4th visits (Trap), "trap effects" accounting for whether a collision was detected or not on the 1st visit (Trap.2), cloud cover (Cloud), and snow cover (Snow). Model structure on small-scale occupancy included: fence exposure (Fence Exp), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), Year, biweekly (primary) period (Surv), an interaction between post type and marker type (Post × Trt), and an interaction between distance to nearest lek and the count at that lek (Distance × Near Ct). Model structures on large-scale occupancy included: Year and either the sum of lek counts at nearby leks (Lek Ct) or the number of nearby occupied leks (Occ Lek; indicated in ψ column). The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference between a model's AIC_c value and the minimum AIC_c value (ΔAIC_c), and AIC_c weights are included.

ψ	*p*	npar	AIC_c	ΔAIC_c	Weight
Occ Lek	Null	25	415.082	0.000	0.582
Lek Ct	Null	25	416.051	0.969	0.358
Occ Lek	Snow	26	423.116	8.034	0.010
Occ Lek	Surv	26	423.388	8.306	0.009
Occ Lek	Cloud	26	423.572	8.490	0.008
Occ Lek	Trap2	26	423.582	8.500	0.008
Lek Ct	Snow	26	424.084	9.002	0.006
Lek Ct	Surv	26	424.358	9.275	0.006
Lek Ct	Cloud	26	424.541	9.459	0.005
Lek Ct	Trap2	26	424.551	9.469	0.005
Occ Lek	Surv + Snow	27	432.197	17.115	< 0.001
Occ Lek	Cloud + Snow	27	432.347	17.265	< 0.001
Occ Lek	Snow + Trap2	27	432.355	17.273	< 0.001
Occ Lek	Surv + Cloud	27	432.568	17.486	< 0.001
Occ Lek	Surv + Trap2	27	432.627	17.545	< 0.001
Occ Lek	Trap	27	432.720	17.637	< 0.001
Occ Lek	Cloud + Trap2	27	432.811	17.729	< 0.001
Lek Ct	Surv + Snow	27	433.166	18.084	< 0.001
Lek Ct	Cloud + Snow	27	433.315	18.233	< 0.001
Lek Ct	Snow + Trap2	27	433.323	18.241	< 0.001
Lek Ct	Surv + Cloud	27	433.537	18.455	< 0.001
Lek Ct	Surv + Trap2	27	433.597	18.514	< 0.001
Lek Ct	Trap	27	433.688	18.606	< 0.001
Lek Ct	Cloud + Trap2	27	433.780	18.698	< 0.001
Occ Lek	Obs	28	439.208	24.126	< 0.001
Lek Ct	Obs	28	440.177	25.095	< 0.001
Occ Lek	Visit	28	440.748	25.665	< 0.001
Lek Ct	Visit	28	441.716	26.633	< 0.001
Occ Lek	Surv + Cloud + Snow	28	442.205	27.123	< 0.001
Occ Lek	Surv + Snow + Trap2	28	442.276	27.194	< 0.001
Occ Lek	Snow + Trap	28	442.373	27.290	< 0.001
Occ Lek	Cloud + Snow + Trap2	28	442.426	27.344	< 0.001
Occ Lek	Surv + Trap	28	442.621	27.538	< 0.001
Occ Lek	Surv + Cloud + Trap2	28	442.647	27.565	< 0.001
Occ Lek	Cloud + Trap	28	442.789	27.707	< 0.001
Lek Ct	Surv + Cloud + Snow	28	443.173	28.091	< 0.001
Lek Ct	Surv + Snow + Trap2	28	443.245	28.163	< 0.001
Lek Ct	Snow + Trap	28	443.342	28.260	< 0.001
Lek Ct	Cloud + Snow + Trap2	28	443.394	28.312	< 0.001
Lek Ct	Surv + Trap	28	443.589	28.507	< 0.001
Lek Ct	Surv + Cloud + Trap2	28	443.616	28.534	< 0.001
Lek Ct	Cloud + Trap	28	443.758	28.676	< 0.001
Occ Lek	Snow + Obs	29	449.910	34.828	< 0.001
Occ Lek	Cloud + Obs	29	450.240	35.158	< 0.001
Occ Lek	Surv + Obs	29	450.246	35.164	< 0.001
Lek Ct	Snow + Obs	29	450.877	35.795	< 0.001
Lek Ct	Cloud + Obs	29	451.208	36.126	< 0.001
Lek Ct	Surv + Obs	29	451.215	36.133	< 0.001
Occ Lek	Visit + Snow	29	451.315	36.233	< 0.001
Occ Lek	Visit + Surv	29	451.656	36.573	< 0.001
Occ Lek	Visit + Cloud	29	451.786	36.704	< 0.001
Occ Lek	Visit + Trap2	29	451.786	36.704	< 0.001
Lek Ct	Visit + Snow	29	452.283	37.200	< 0.001

Lek Ct	Visit + Surv	29	452.624	37.542	< 0.001
Lek Ct	Visit + Cloud	29	452.754	37.672	< 0.001
Lek Ct	Visit + Trap2	29	452.755	37.672	< 0.001
Occ Lek	Surv + Cloud + Snow + Trap2	29	453.244	38.162	< 0.001
Occ Lek	Surv + Snow + Trap	29	453.256	38.173	< 0.001
Occ Lek	Cloud + Snow + Trap	29	453.403	38.320	< 0.001
Occ Lek	Surv + Cloud + Trap	29	453.607	38.525	< 0.001
Lek Ct	Surv + Cloud + Snow + Trap2	29	454.212	39.130	< 0.001
Lek Ct	Surv + Snow + Trap	29	454.225	39.143	< 0.001
Lek Ct	Cloud + Snow + Trap	29	454.372	39.290	< 0.001
Lek Ct	Surv + Cloud + Trap	29	454.576	39.494	< 0.001
Occ Lek	Surv + Snow + Obs	30	462.022	46.940	< 0.001
Occ Lek	Cloud + Snow + Obs	30	462.034	46.951	< 0.001
Occ Lek	Surv + Cloud + Obs	30	462.383	47.300	< 0.001
Lek Ct	Surv + Snow + Obs	30	462.989	47.907	< 0.001
Lek Ct	Cloud + Snow + Obs	30	463.000	47.917	< 0.001
Lek Ct	Surv + Cloud + Obs	30	463.351	48.269	< 0.001
Occ Lek	Visit + Surv + Snow	30	463.354	48.271	< 0.001
Occ Lek	Visit + Cloud + Snow	30	463.458	48.376	< 0.001
Occ Lek	Visit + Snow + Trap2	30	463.458	48.376	< 0.001
Occ Lek	Visit + Trap	30	463.600	48.517	< 0.001
Occ Lek	Visit + Surv + Cloud	30	463.780	48.698	< 0.001
Occ Lek	Visit + Surv + Trap2	30	463.799	48.716	< 0.001
Occ Lek	Visit + Cloud + Trap2	30	463.929	48.847	< 0.001
Lek Ct	Visit + Surv + Snow	30	464.321	49.239	< 0.001
Lek Ct	Visit + Cloud + Snow	30	464.425	49.343	< 0.001
Lek Ct	Visit + Snow + Trap2	30	464.425	49.343	< 0.001
Lek Ct	Visit + Trap	30	464.567	49.485	< 0.001
Lek Ct	Visit + Surv + Cloud	30	464.748	49.666	< 0.001
Lek Ct	Visit + Surv + Trap2	30	464.767	49.685	< 0.001
Lek Ct	Visit + Cloud + Trap2	30	464.897	49.815	< 0.001
Occ Lek	Surv + Cloud + Snow + Trap	30	465.335	50.252	< 0.001
Lek Ct	Surv + Cloud + Snow + Trap	30	466.304	51.222	< 0.001
Occ Lek	Visit + Obs	31	474.083	59.000	< 0.001
Lek Ct	Visit + Obs	31	475.051	59.969	< 0.001
Occ Lek	Surv + Cloud + Snow + Obs	31	475.438	60.355	< 0.001
Lek Ct	Surv + Cloud + Snow + Obs	31	476.404	61.322	< 0.001
Occ Lek	Visit + Snow + Trap	31	476.629	61.547	< 0.001
Occ Lek	Visit + Surv + Cloud + Snow	31	476.755	61.673	< 0.001
Occ Lek	Visit + Surv + Snow + Trap2	31	476.775	61.692	< 0.001
Occ Lek	Visit + Cloud + Snow + Trap2	31	476.879	61.797	< 0.001
Occ Lek	Visit + Surv + Trap	31	476.984	61.902	< 0.001
Occ Lek	Visit + Cloud + Trap	31	477.020	61.938	< 0.001
Occ Lek	Visit + Surv + Cloud + Trap2	31	477.201	62.119	< 0.001
Lek Ct	Visit + Snow + Trap	31	477.597	62.515	< 0.001
Lek Ct	Visit + Surv + Cloud + Snow	31	477.723	62.641	< 0.001
Lek Ct	Visit + Surv + Snow + Trap2	31	477.742	62.660	< 0.001
Lek Ct	Visit + Cloud + Snow + Trap2	31	477.846	62.764	< 0.001
Lek Ct	Visit + Surv + Trap	31	477.952	62.870	< 0.001
Lek Ct	Visit + Cloud + Trap	31	477.988	62.906	< 0.001
Lek Ct	Visit + Surv + Cloud + Trap2	31	478.169	63.087	< 0.001
Occ Lek	Visit + Snow + Obs	32	488.636	73.554	< 0.001
Occ Lek	Visit + Cloud + Obs	32	488.987	73.905	< 0.001
Occ Lek	Visit + Surv + Obs	32	488.994	73.912	< 0.001
Lek Ct	Visit + Snow + Obs	32	489.603	74.521	< 0.001
Lek Ct	Visit + Cloud + Obs	32	489.955	74.873	< 0.001
Lek Ct	Visit + Surv + Obs	32	489.962	74.880	< 0.001
Occ Lek	Visit + Surv + Snow + Trap	32	491.496	76.413	< 0.001
Occ Lek	Visit + Cloud + Snow + Trap	32	491.542	76.459	< 0.001
Occ Lek	Visit + Surv + Cloud + Trap	32	491.893	76.811	< 0.001
Lek Ct	Visit + Surv + Snow + Trap	32	492.464	77.382	< 0.001
Lek Ct	Visit + Cloud + Snow + Trap	32	492.510	77.427	< 0.001
Lek Ct	Visit + Surv + Cloud + Trap	32	492.861	77.778	< 0.001
Occ Lek	Visit + Surv + Snow + Obs	33	505.266	90.184	< 0.001
Occ Lek	Visit + Cloud + Snow + Obs	33	505.279	90.197	< 0.001
Occ Lek	Visit + Surv + Cloud + Obs	33	505.653	90.571	< 0.001

Lek Ct	Visit + Surv + Snow + Obs	33	506.233	91.150	< 0.001
Lek Ct	Visit + Cloud + Snow + Obs	33	506.245	91.163	< 0.001
Lek Ct	Visit + Surv + Cloud + Obs	33	506.621	91.539	< 0.001

Table A2
Model set for models explaining variation in small-scale occupancy probabilities (θ) of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. We fit models using the most parsimonious model on detection probabilities (i.e., null) and large-scale occupancy probabilities (i.e., null). Model structures on small-scale occupancy included: distance to nearest lek (Distance), the count at the nearest lek (Near Ct), fence exposure (Fence Exp), wood post or t-post (Post), proportion of fence segment in high risk areas (Risk), angle of fence in relation to lek (Angle), marker type (Trt), marked or unmarked fence (regardless of marker type; Mark), Year, biweekly (primary) period (Surv), an interaction between Distance and Near Ct, and an interaction between Post and Mark or Trt. The number of parameters (npar), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference between a model's AICc value and the minimum AICc value (ΔAIC_c), and AIC_c weights are included for models with $\Delta AIC_c < 4$.

θ	npar	AIC_c	ΔAIC_c	weight
Fence Exp + Mark + Distance + Post + Risk + Near Ct	9	364.644	0.000	0.030
Fence Exp + Mark + Distance + Post + Risk + Year	9	364.756	0.111	0.028
Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct	10	364.903	0.259	0.026
Fence Exp + Mark + Post + Risk + Distance × Near Ct	10	365.270	0.626	0.022
Surv + Fence Exp + Mark + Distance + Post + Risk + Year	15	365.647	1.003	0.018
Fence Exp + Mark + Distance + Post + Near Ct	8	365.762	1.118	0.017
Fence Exp + Mark + Post + Risk + Year + Distance × Near Ct	11	365.794	1.150	0.017
Surv + Fence Exp + Mark + Distance + Post + Year	14	365.810	1.166	0.017
Fence Exp + Mark + Distance + Post + Year + Near Ct	9	365.998	1.354	0.015
Fence Exp + Mark + Distance + Post + Risk	8	366.015	1.371	0.015
Fence Exp + Mark + Distance + Post + Year	8	366.230	1.586	0.014
Surv + Mark + Distance + Post + Year	13	366.584	1.940	0.011
Surv + Fence Exp + Distance + Post + Risk + Year	14	366.689	2.045	0.011
Surv + Fence Exp + Mark + Distance + Post + Risk	14	366.791	2.147	0.010
Surv + Fence Exp + Mark + Distance + Post + Near Ct	14	366.803	2.159	0.010
Surv + Fence Exp + Mark + Distance + Post + Risk + Near Ct	15	366.871	2.227	0.010
Surv + Fence Exp + Distance + Post + Year	13	366.883	2.239	0.010
Surv + Mark + Distance + Post + Risk + Year	14	366.897	2.253	0.010
Fence Exp + Distance + Post + Risk + Year	8	366.926	2.282	0.010
Surv + Distance + Post + Risk + Year	13	366.997	2.353	0.009
Surv + Distance + Post + Year	12	367.005	2.361	0.009
Angle + Surv + Post + Year	12	367.072	2.428	0.009
Surv + Fence Exp + Mark + Distance + Post	13	367.177	2.533	0.008
Fence Exp + Distance + Post + Risk + Year + Near Ct	9	367.183	2.538	0.008
Angle + Surv + Distance + Post + Year	13	367.336	2.692	0.008
Surv + Fence Exp + Mark + Distance + Post + Year + Near Ct	15	367.365	2.721	0.008
Angle + Surv + Mark + Post + Year	13	367.420	2.776	0.007
Fence Exp + Distance + Risk + Near Ct + Post × Mark	10	367.457	2.813	0.007
Mark + Distance + Post + Risk + Year + Near Ct	9	367.459	2.815	0.007
Fence Exp + Distance + Risk + Year + Post × Mark	10	367.587	2.942	0.007
Fence Exp + Mark + Distance + Post	7	367.590	2.946	0.007
Surv + Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct	16	367.591	2.946	0.007
Fence Exp + Distance + Risk + Year + Near Ct + Post × Mark	11	367.717	3.073	0.006
Angle + Fence Exp + Mark + Distance + Post + Risk + Near Ct	10	367.748	3.104	0.006
Angle + Fence Exp + Mark + Distance + Post + Risk + Year	10	367.821	3.177	0.006
Mark + Distance + Post + Risk + Year	8	367.882	3.238	0.006
Angle + Surv + Mark + Post	12	367.902	3.258	0.006
Mark + Distance + Post + Risk + Near Ct	8	367.992	3.348	0.006
Angle + Surv + Mark + Post + Near Ct	13	368.029	3.385	0.006
Fence Exp + Distance + Post + Risk + Near Ct	8	368.075	3.431	0.005
Surv + Mark + Distance + Post + Year + Near Ct	14	368.076	3.432	0.005
Angle + Surv + Post	11	368.076	3.432	0.005
Fence Exp + Distance + Post + Year + Near Ct	8	368.107	3.463	0.005
Angle + Fence Exp + Mark + Distance + Post + Risk + Year + Near Ct	11	368.160	3.516	0.005
Fence Exp + Distance + Post + Year	7	368.210	3.566	0.005
Mark + Distance + Post + Year + Near Ct	8	368.239	3.595	0.005
Angle + Surv + Mark + Distance + Post + Year	14	368.255	3.611	0.005
Surv + Distance + Post + Year + Near Ct	13	368.264	3.620	0.005
Fence Exp + Mark + Post + Distance × Near Ct	9	368.276	3.632	0.005
Fence Exp + Risk + Post × Mark + Distance × Near Ct	11	368.284	3.640	0.005
Surv + Mark + Distance + Post + Near Ct	13	368.308	3.664	0.005
Surv + Distance + Post + Risk + Year + Near Ct	14	368.328	3.684	0.005
Angle + Fence Exp + Mark + Post + Risk + Distance × Near Ct	11	368.379	3.735	0.005
Angle + Surv + Post + Near Ct	12	368.397	3.753	0.005

Surv + Mark + Distance + Post + Risk + Year + Near Ct	15	368.414	3.770	0.005
Surv + Fence Exp + Distance + Post + Year + Near Ct	14	368.431	3.787	0.005
Distance + Post + Risk + Year + Near Ct	8	368.445	3.801	0.004
Angle + Fence Exp + Mark + Distance + Post + Near Ct	9	368.449	3.805	0.004
Angle + Fence Exp + Mark + Distance + Post + Year	9	368.468	3.824	0.004
Fence Exp + Post + Risk + Year + Distance × Near Ct	10	368.499	3.855	0.004
Fence Exp + Distance + Near Ct + Post × Mark	9	368.531	3.886	0.004
Mark + Distance + Post + Year	7	368.550	3.906	0.004
Surv + Fence Exp + Distance + Post + Risk + Year + Near Ct	15	368.591	3.947	0.004
Mark + Distance + Post + Near Ct	7	368.623	3.979	0.004

Table A3
Coefficient estimates, standard errors (SE), and 95% confidence intervals (CI) for all variables from the best model explaining variation in small-scale occupancy (θ) probabilities of Greater Sage-Grouse fence collisions in Wyoming, 2014–2015. Variables include fence exposure (Fence Exp), whether a fence was marked (regardless of marker type; Mark), the distance to nearest lek (Distance), fences with wood and t-posts (wood and t-post), proportion of fence segment in high risk areas (Risk), and the count at the nearest lek (Near Ct). The intercept represents an unmarked fence with wood posts with all continuous variable values set to 0. All significant coefficients (i.e., 95% CIs do no overlap 0) are indicated by an asterisk.

Parameter	Mean	SE	95% CI
Intercept*	− 5.104	1.068	(− 7.197, − 3.012)
Fence Exp*	0.033	0.013	(0.007, 0.059)
Mark*	− 0.922	0.359	(− 1.623, − 0.217)
Distance*	− 0.500	0.197	(− 0.886, − 0.113)
Wood and T-post*	1.783	0.387	(1.025, 2.541)
Risk*	1.128	0.565	(0.020, 2.235)
Near Ct	0.005	0.002	(0.000, 0.010)

Table A4
Coefficient estimates, standard errors (SE), and 95% confidence intervals (CI) for all variables from the second best model explaining variation in small-scale occupancy (θ) probabilities of Greater Sage-Grouse fence collisioins in Wyoming, 2014–2015. Variables include fence exposure (Fence Exp), whether a fence was marked (regardless of marker type; Mark), the distance to nearest lek (Distance), fences with wood and t-posts (wood and t-post), proportion of fence segment in high risk areas (Risk), and the count at the nearest lek (Near Ct). The intercept represents an unmarked fence with wood posts with all continuous variable values set to 0. All significant coefficients (i.e., 95% CIs do no overlap 0) are indicated by an asterisk.

Parameter	Mean	SE	95% CI
Intercept*	− 5.181	1.090	(− 7.317, − 3.046)
Fence Exp*	0.032	0.013	(0.006, 0.058)
Mark*	− 0.818	0.356	(− 1.515, − 0.121)
Distance*	− 0.650	0.186	(− 1.015, − 0.285)
Wood and T-post*	1.685	0.374	(0.952, 2.418)
Risk*	1.161	0.557	(0.069, 2.253)
2015*	0.875	0.431	(0.030, 1.720)

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