



Management and Conservation

Nest Success and Cause-Specific Nest Failure of Grassland Passerines Breeding in Prairie Grazed by Livestock

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ABSTRACT Livestock grazing is a widespread source of habitat modification, and may affect populations of ground-nesting grassland birds by influencing rates of nest failure. Nesting attempts can fail for various reasons, and determining risk of failure from specific causes associated with livestock grazing would enhance development of range management practices in areas managed for threatened grassland bird populations. Domestic livestock may influence nest failure by affecting vegetation structure, numerical or functional responses of predators, or directly by trampling nests. We hypothesized stocking rate may influence nest fate because it affects the amount and distribution of remaining vegetation, and the number of large herbivores to which nests are exposed. In 2007 and 2008, we evaluated nest fates for savannah sparrows and horned larks under 4 stocking rates experimentally applied in 40-ha paddocks in northeastern Oregon, USA. In addition to stocking rate, we evaluated variables such as vegetation structure and predator abundance and activity to help clarify mechanisms responsible for nest failure. We used a discrete competing risks framework to estimate daily probability of nest survival and failure from specific causes. These algorithms, implemented in a stand-alone graphical user interface-driven model, allow incorporation of covariates within an information theoretic approach to model inference. Although stocking rate influenced vegetation structure, the only nest failures related to stocking rate were from trampling. Trampling events were too infrequent to test for treatment effects (only 1 nest of each species), but occurred in the moderate and high stocking treatments. Additional variables were related to variation in nest failure from predation, but we found no support for the hypothesis that these causes of failure were affected by stocking rate. For savannah sparrows, daily probability of nest success (95% CI) = 0.97 (0.96–0.98); predation = 0.018 (0.008–0.028); and trampling = 0.001 (0.000–0.004). For horned larks, daily probability of nest success = 0.96 (0.95–0.98); predation = 0.029 (0.012–0.045); and trampling = 0.003 (0.000–0.007). Our results suggest grasslands managed for livestock may generally be compatible with grassland songbird conservation, at least for the species and stocking rates examined here. The most effective conservation strategies for improving nest success will involve decreasing risk of nest predation. However, we found no evidence that management of stocking rate is an effective method for doing so. © 2012 The Wildlife Society.

KEY WORDS avian demography, cause-specific nest failure, grazing intensity, horned lark, nest success, Pacific Northwest Bunchgrass Prairie, predation risk, rangeland management, savannah sparrow, stocking rate.

Grasslands are the most converted and least protected habitat in North America (Hoekstra et al. 2005); tallgrass, mixed-grass, and shortgrass prairies have declined in extent by

approximately 80% since the 1800s (White et al. 2000), and Pacific Northwest bunchgrass prairie in the United States has declined by 99% (Tisdale 1982, Noss et al. 1995). Not surprisingly, many species of wildlife associated with grasslands have experienced similar population-level declines. In particular, grassland-nesting songbirds have become a focal group of conservation concern because between 1966 and 2002, 17 species declined (Askins et al. 2007). One of the most influential factors correlated with these declines is loss of suitable grassland habitat (Askins et al. 2007).

Remaining grasslands support large numbers of herbivores, and are primarily used by humans for domestic livestock production (White et al. 2000). In the United States,

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livestock grazing occurs on >3 million km² annually (Lubowski et al. 2006). Thus, grazing practices in grasslands may have widespread implications for grassland-associated wildlife populations. Grassland birds, which are primarily ground-nesters, seem particularly responsive to livestock grazing (Milchunas et al. 1998), leading researchers to suggest grazing may be used as a tool to manage for grassland bird populations by creating specific habitat conditions through different management techniques (Holechek 1981, Derner et al. 2009). However, before grazing strategies intended to benefit grassland birds are implemented, understanding effects of different grazing management techniques on avian nest success is necessary. The presence of large herbivores during the nesting season, along with grazing-induced changes to vegetation physiognomy, could potentially have strong direct and indirect effects on grassland bird nest success. Livestock grazing is a complex disturbance in both time and space, and factors such as stocking rate, defined as the number of livestock on a given area for a specified time, could influence nest failure rates because it largely determines the amount and distribution of vegetation available for use by grassland birds (Fuhlendorf and Engle 2001), as well as the length of time nests are exposed to potential trampling by large herbivores.

Attributing risk of nest failure from specific causes (e.g., trampling, predation) to particular grazing management scenarios will provide management-specific demographic parameters critical to developing appropriate conservation strategies for grassland birds, assuming land managers can target sources of failure (e.g., predators or livestock numbers; Etterson et al. 2007a). Cause-specific nest failure is rarely estimated because few analytical methods are available that account for both discovery bias (the bias associated with discovering nests at different stages in the nesting cycle; Mayfield 1961) and irregular nest-monitoring schedules (Etterson et al. 2007a). Of the methods available, (e.g., Heisey and Fuller 1985) none incorporate model selection or allow the use of covariates. However, estimation of nest failure rates using a Markov transition matrix can incorporate multiple, competing causes of failure even when exact failure dates are unknown (Etterson et al. 2007a, b). Here, we use a combination of a replicated field experiment and the Etterson et al. (2007a, b) framework to evaluate hypotheses regarding risk of nest failure from specific causes associated with livestock grazing.

Our goal was to evaluate whether cattle stocking rates influenced the probability of nest failure from specific causes for grassland-nesting songbirds. We hypothesized that as stocking rate increased, risk of nest failure from trampling would increase (Paine et al. 1996, Nack and Ribic 2005). We also expected grazing by livestock to influence risk of nest predation if nest concealment is reduced, or if it creates patchier habitat structure with fewer potential nest sites predators must search before encountering a nest, and that these effects might be more severe with greater stocking rates (Martin and Roper 1988, Fuller and Gough 1999, Chalfoun and Martin 2009). Stocking rate may also influence predation risk by affecting predator abundance or activity through

creation of habitat characteristics preferred by predators (e.g., habitat edges; Uresk et al. 1982, Phillips et al. 2003, Sutter and Ritchison 2005).

STUDY AREA

We conducted our study at The Nature Conservancy's Zumwalt Prairie Preserve (ZPP) in northeastern Oregon, USA (Fig. 1). The ZPP is approximately 13,000 ha and part of the larger Zumwalt Prairie ecosystem (approx. 65,000 ha; Kennedy et al. 2009). The ZPP is dominated by Idaho fescue (*Festuca idahoensis* [Elmer]) and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) prairie on a high-elevation plateau (approx. 1,500 m), and is classified as part of the Pacific Northwest bunchgrass prairie (Tisdale 1982). Climate is semi-arid and during 2007–2008, average monthly temperatures and monthly total precipitation from May to July fell within 2 standard deviations of the 31-year average (Hansen et al. 2010, Western Regional Climate Center 2011). Growing season aboveground primary production at our study site was <225 g/m² on average (T. DelCurto, Oregon State University, and R. V. Taylor, The Nature Conservancy, unpublished data). The ZPP has been grazed by domestic livestock since the early 1700s, first by horses belonging to Native Americans and since the 1800s by cattle and sheep (Bartuszevige et al. 2012). Grassland birds breeding in this system were savannah sparrow (*Passerculus sandwichensis*), horned lark (*Eremophila alpestris*), western meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), vesper sparrow (*Pooecetes gramineus*), and less commonly, Brewer's sparrow (*Spizella breweri*). In this article, we focus on 2 species: savannah sparrows and horned larks. These species are the 2 most common at our study site, providing us with a large enough sample to estimate cause-specific nest failure for each species. Further, they represent contrasting preferences for vegetation cover at the nest from high (savannah sparrow) to low (horned lark), allowing us to evaluate differences in cause-specific nest failure rates for species nesting in different habitats within the same grazing treatment.

METHODS

Experimental Design

Our experiment was a randomized complete block design with 1 factor (livestock grazing) and 4 grazing treatment levels (stocking rate). Blocking allowed us to control for potential environmental heterogeneity created by variation in historical grazing management. We rested study paddocks from grazing for 3 years prior to the start of our experiment. In 2006, we erected fences around 4 blocks of land each 160-ha in size, and within each block, partitioned 4 40-ha paddocks (Fig. 1). Each of the 4 blocks contained 1 replicate paddock of each assigned stocking rate ($n = 4$ replicates of each stocking rate). We randomly assigned stocking rates to paddocks within each block. We determined a moderate stocking rate of 28.8 animal unit months (AUMs; the amount of forage a mature cow and her calf use in a month) based on average stocking rates for the entire Zumwalt

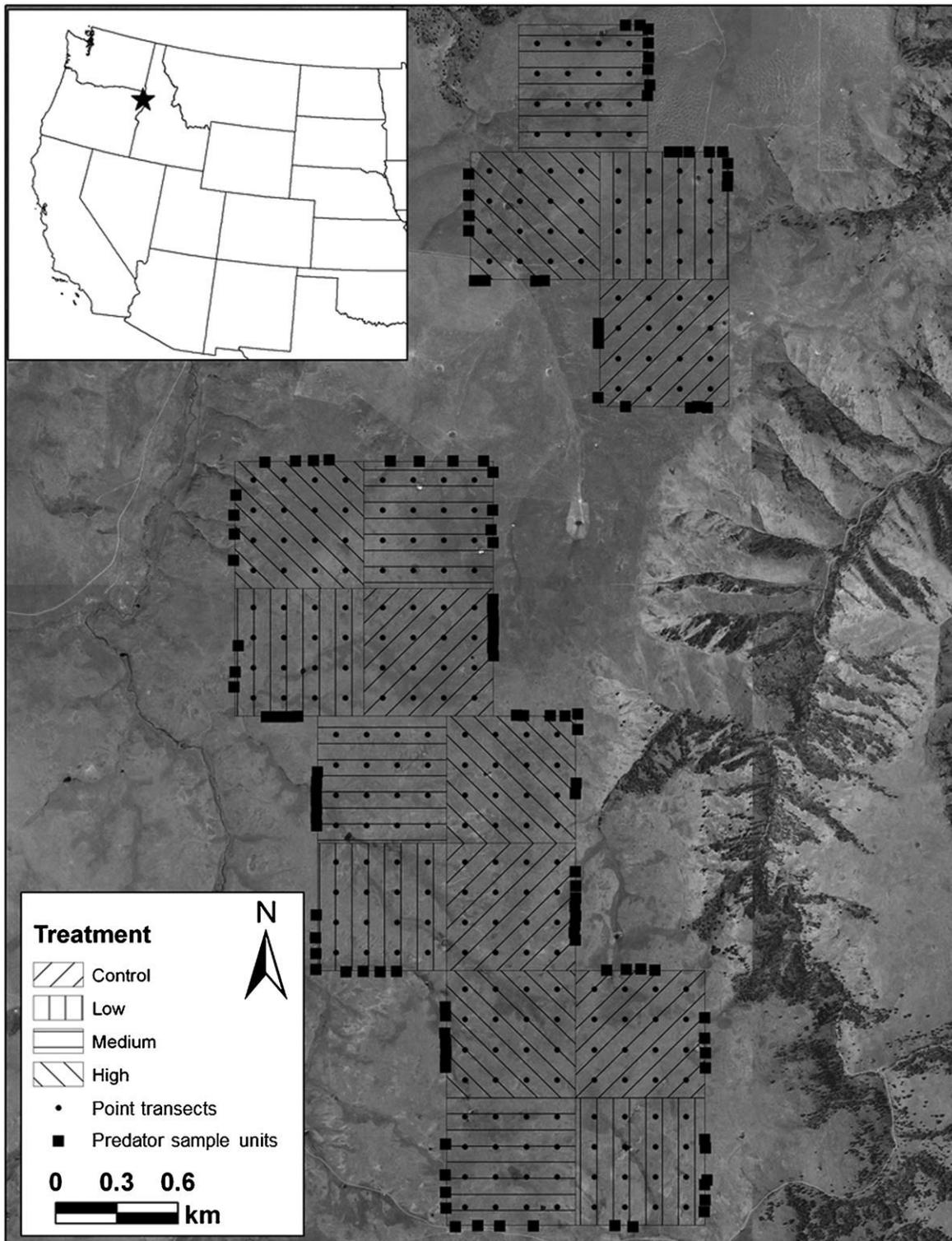


Figure 1. Experimental paddocks, predator sample units, and point transects used to evaluate effects of stocking rate on nest success and failure of grassland passerines in 2007 and 2008 at the Zumwalt Prairie Preserve, northeastern Oregon, USA.

Prairie, and from pilot data on vegetation utilization by cattle collected at the ZPP (T. DeCurto and J. Williams, Oregon State University, unpublished data). We expected 40% of available vegetation to be used in moderately stocked paddocks. We expected 3 other stocking rates (control: 0 AUMs, low: 14.4 AUMs, and high: 43.2 AUMs) to represent 0%, 20%, or 60% utilization of vegetation by livestock, respec-

tively. In 2007 and 2008, we stratified 192 Oregon State University cow-calf pairs and 48 yearling heifers by age and body condition and randomly assigned them to a stocking rate treatment (Wyffels 2009) in cattle-grazed paddocks from 21 May to 3 July in 2007 and 29 May to 9 July in 2008. We measured amount of aboveground biomass removed within each paddock after 6 weeks of grazing

Table 1. Utilization of grassland forage corresponding to 4 cattle stocking rates at the Zumwalt Prairie Preserve in northeastern Oregon, USA during 2007 and 2008.

Treatment	Year	Mean % forage utilization (95% confidence limits)
Control ^a	2007	7.1 (6.6, 7.6)
	2008	11.9 (9.6, 14.3)
Low	2007	20.2 (14.7, 25.6)
	2008	20.2 (17.4, 23.0)
Moderate	2007	28.3 (23.9, 32.7)
	2008	35.0 (29.9, 40.0)
High	2007	38.0 (28.5, 47.5)
	2008	54.2 (47.3, 61.1)

^a No use by domestic livestock.

(Wyffels 2009). Although utilization tended to be greater in 2008, more biomass was removed with greater stocking rates in both years based on comparisons of 95% confidence intervals (Table 1). Utilization on control paddocks represented the percentage of forage removed by native herbivores including ungulates, ground squirrels, and invertebrates.

Nest Searches and Fate Determination

We conducted systematic searches for grassland bird nests between 1 May and 25 July 3 times in 2007 and twice in 2008. We searched each paddock in its entirety using the rope-dragging method to flush incubating birds (Winter et al. 2003). We also found nests opportunistically during nest monitoring visits and vegetation surveys. Once we discovered a nest, we marked its location with a Global Positioning System (GPS), and placed survey flags and spray paint (because cows sometimes removed survey flags) 10 m and 30 m from the nest in a random direction to reduce the chances that nest predators learned our marking system. When a nest contained eggs, we determined nest age by flotation (Westerkov 1950); when nestlings were present, we determined age using detailed descriptions based on voucher photographs from previous research at our study site (P. L. Kennedy et al., Oregon State University, unpublished data). Using these 2 approaches, we accurately determined nest age to within 2 days for most nests. We attempted to visit nests every 1–4 days until the nesting attempt was complete. Observers used care to minimize the potential influence nest monitoring might have on the risk of nest failure. We conducted brief surveys (during which we detected no nest predators) preceding all nest visits; we treated all equipment and observers' boots with human scent killer; we kept

time spent at each nest to a minimum; we replaced disturbed vegetation as closely as possible to its prior state; we processed nest contents at least 10 m from a nest; and whenever possible, we approached nests from different directions or conducted nest checks from a distance with binoculars. All animal handling procedures were reviewed and approved by the Institutional Animal Care and Use Committee at Oregon State University (Animal Care and Use Proposal 3543).

We determined nest fates based on available evidence at the nest following procedures similar to those described by Manolis et al. (2000; Table 2). To minimize potential for misclassification error, for all nests that were sufficiently developed to have fledged during the final nest check interval, we assumed the nest was successful and discarded information collected after the last visit on which the nest was observed with contents (Stanley 2004). Causes of failure in our system included predation, trampling by ungulates, weather, abandonment, egg failure, and failures due to unknown causes. We combined nests that failed because of abandonment, egg failure, weather, and unknown causes into a single category called other, resulting in 3 cause-specific nest failure categories (predation, trampled, and other) included in the analysis.

Cause-Specific Nest Failure

Once we identified primary causes of nest failure and potential covariates, we generated a priori models specific to each failure category to create candidate models. Our set of 12 candidate models (see Appendices 1.1 and 1.2, available online at www.onlinelibrary.wiley.com) included covariates related to grazing treatment and the predator community (see the Measuring Covariates Section) that best describe our aforementioned predictions. We also included covariates that were independent of grazing treatment and predator abundance that we expected could influence variation in nest failure rates, such as nest age (Ricklefs 1969), date (Benson et al. 2010), and year (Greenwood et al. 1995). Because temporal factors (date and year) and those intrinsic to the bird's biology (nest age) likely influence the effect of habitat-related variables, after testing for block effects, we used an iterative modeling process in which we first identified covariates independent of habitat that explained patterns of nest failure. We subsequently retained those covariates with support and included additional covariates related to grazing treatment, vegetation structure, and the predator community to address our hypotheses (Benson et al.

Table 2. Evidence (modified from Manolis et al. 2000) used to categorize causes of nest failure for grassland-breeding songbirds at the Zumwalt Prairie Preserve in northeastern Oregon, USA during 2007 and 2008.

Cause of failure	Evidence
Predation	All eggs or young absent from a nest prematurely, or egg or nestling remains present and showing evidence of predation, or nest cup ripped apart or removed from the ground but no evidence of contents, or predation event observed
Trampled	Eggs or nestlings present in or near nest but were crushed, or nest was no longer intact and contents were spilled
Other (abandoned, weather, egg failure, unknown)	Adult not observed for more than 2 consecutive visits to a nest and nest contents were obviously not attended (e.g., cold or wet eggs, dead or dying nestlings, ants present in nest), or evidence of hail damage to eggs, or incubation extending beyond average length of incubation with no evidence of egg development (per flotation), or failure, but cause unclear

2010). Following well-established patterns observed for nesting birds, we expected age of nest to influence predation rates, with predation risk increasing from incubation to the nestling stage because activity levels at the nest should be higher when adult birds deliver food items and nestlings actively beg, thus increasing the risk of detection by predators (Martin et al. 2000). We also anticipated date-specific variation in failure rates, but made no assumption about the nature of the relationship between date and nest failure (Natarajan and McCullough 1999, Grant et al. 2005). We assumed a constant rate of failure for nests characterized in the other category in all analyses and do not make inferences regarding these causes of failure. We evaluated covariates for collinearity before estimating nest-failure probabilities; we identified no strong relationships (all $r < |0.70|$).

We estimated daily rates of nest survival and cause-specific failure and tested hypotheses about causes of variation in daily failure rates using a formulation of discrete competing risks based on Markov transition matrices (see Etmerson et al. 2007a, b for formulae). We implemented algorithms of Etmerson et al. (2007a, b) in a stand-alone graphical user interface written in MATLAB (Version 7.9, MathWorks, Natick, MA) and directly estimated nest failure partitioned into separate probabilities for each failure category. Finally, we estimated overall probabilities of nest success and failure for each category by taking the product of the daily transition matrices for nest survival and failure over all days in the nesting cycle for each species.

To determine how well a model fit our set of observations we used goodness-of-fit tests. Given the difficulty of testing goodness-of-fit for sparse multinomial models, we tested fit of competing models only using multiple statistics and methods, as recommended by Pigeon and Heyse (1999). These included a Hosmer–Lemeshow (Hosmer and Lemeshow 2000) test adapted for multinomial data (Bull 1994), the Pigeon–Heyse test (Pigeon and Heyse 1999), Pearson's χ^2 statistic, and by comparing the deviance of the fitted model to that of the saturated model (a model with as many parameters as the total number of observations on all nests). We assessed significance of the Hosmer–Lemeshow and Pigeon–Heyse statistics against a χ^2 distribution with appropriate degrees of freedom. We assessed significance of the Pearson χ^2 statistic and deviance by parametric bootstrap simulation (White et al. 2001) as the relative proportion of 500 simulated deviances or χ^2 statistics that were greater than or equal to the observed statistic. We also used these simulations to estimate overdispersion (\hat{c}) and to verify standard error estimates for estimated parameters.

We used information theoretic approaches outlined by Burnham and Anderson (2002) to select the best model. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike weights to rank models (Burnham and Anderson 2002), and also used 95% confidence intervals for slope coefficients (betas) to evaluate the strength of evidence for the importance of variables in competing models ($\Delta\text{AIC}_c \leq 2$). If we found >1 competing model, we present model-averaged parameter estimates

following equations presented in Burnham and Anderson (2002).

Measuring Covariates

Vegetation structure.—To test the hypothesis that stocking rate influenced nest predation through changes in vegetative cover at the paddock scale, in each paddock we described vegetation structure using visual obstruction (VO), which is a measure of the height and vertical density of vegetation and is correlated with standing aboveground biomass in grasslands (Robel et al. 1970). We measured paddock-level VO after 6 weeks of grazing (<24 hr after we removed cattle). We used a Robel pole held perpendicular to the ground, where an observer recorded the height of the lowest visible decimeter from 4 m away and 1 m above ground level (Robel et al. 1970). We measured VO at 10-m intervals along 8 100-m transects within each paddock, where we stratified VO transect locations randomly by physiography to account for variation in vegetation structure (e.g., by hilltop, swale, rocky outcroppings, and slopes). Because each paddock had slightly different distributions of physiographic features, the number of transects in each category of physiographic feature differed slightly among paddocks. We present the coefficient of variation of paddock-level VO as an index of structural heterogeneity in each paddock to address the hypothesis that nest predation risk is affected by the patchiness of vegetation structure.

To address the hypothesis that stocking rate influenced risk of nest failure from predation through changes in vegetation structure at the nest, we measured nest-level VO at the completion of each nesting attempt. Observers placed a Robel pole directly into the nest cup, and recorded VO from each cardinal direction. We used the average of these 4 VO measurements as a score for each nest.

Nest predators.—The pool of potential nest predators in this system included a wide variety of birds, mammals, and reptiles, including American kestrel (*Falco sparverius*), black-billed magpie (*Pica hudsonia*), common raven (*Corvus corax*), ferruginous hawk (*Buteo regalis*), golden eagle (*Aquila chrysaetos*), merlin (*Falco columbarius*), northern harrier (*Circus cyaneus*), prairie falcon (*Falco mexicanus*), red-tailed hawk (*Buteo jamaicensis*), short-eared owl (*Asio flammeus*), Swainson's hawk (*Buteo swainsoni*), badger (*Taxidea taxus*), Belding's ground squirrel (*Spermophilus beldingi*), coyote (*Canis latrans*), Ord's kangaroo rat (*Dipodomys ordii*), porcupine (*Erethizon dorsatum*), striped skunk (*Mephitis mephitis*), weasel (*Mustela* spp.), western harvest mouse (*Reithrodontomys megalotis*), yellow-bellied marmot (*Marmota flaviventris*), common garter snake (*Thamnophis sirtalis*), yellow-bellied racer (*Coluber constrictor*), northern pacific rattlesnake (*Crotalus viridis oregonus*), and rubber boa (*Charina bottae*).

Because the suite of potential nest predators was diverse, we used 3 different methods to quantify the predator community including a modified track survey technique for mesopredators and coyotes (after Kuehl and Clark 2002), opportunistic encounters of snake and avian predators, and point transect surveys for Belding's ground squirrels (see Appendix 2 for

details on survey methodologies, available online at www.onlinelibrary.wiley.com). Belding's ground squirrels (the only species of ground squirrel present) are extremely abundant at our study site, and ground squirrels have been reported as frequent songbird nest predators in other systems (Cottrell 1981, Morton et al. 1993, Renfrew and Ribic 2003). Although we did not directly observe ground squirrels depredating nests, we suspected they could be a significant source of nest failure in our study because of their high density. Thus, we concentrated exclusively on estimating ground squirrel density in experimental paddocks rather than surveying the entire rodent community. We calculated predator abundance and activity indices for each paddock (see Appendix 3, available online at www.onlinelibrary.wiley.com), and used each value as a paddock-level covariate assigned to each nest in our analysis.

RESULTS

We located and monitored 136 nests in 2007–2008. We excluded 3 nests because of insufficient data, and 2 nests failed because of observer-related causes. Thus, we included 131 nests in our nest failure analysis (see Appendix 4, available online at www.onlinelibrary.wiley.com). The mean length between nest visits was 2.3 days, and all intervals between nest visits were <7 days long. Nest predation accounted for most of the failed nests in our sample (78% of failed nests), with trampling and other causes accounting for a much smaller proportion of nest failures (see Appendix 4, available online at www.onlinelibrary.wiley.com). The low number of trampled nests ($n = 1$ for each species) precluded testing of any covariate effects for trampled nests; thus, we assumed constant rates of trampling. However, failures from trampling occurred in the moderate and high stocking rate treatments.

For savannah sparrows, 2 similar models competed for best fit (ΔAIC values <2; see Appendix 1.1, available online at www.onlinelibrary.wiley.com). We found consistencies between the 2 models, and the 95% confidence limits on beta estimates of covariates for these 2 models suggested weak effects of date and moderate effects of encounter rates of avian predators on the daily probability of predation. The top model suggested daily probability of predation increased over the course of the nesting season ($\beta = 0.011$), but 95% confidence limits included zero (-0.021 – 0.42); probability of predation increased with encounter rates of avian predators ($\beta = 3.366$) and 95% confidence limits did not include zero (0.271 – 6.462). The second model also suggested the daily probability of predation increased over the nesting season ($\beta = 0.028$), but the lower bounds of 95% confidence limits were very close to zero (0.001 – 0.054). The daily probability of predation was not affected by stocking rate, nor was the encounter rate of avian predators (T. Johnson, Oregon State University, unpublished data).

Daily probability of success (95% CI with lower bounds truncated at zero) for savannah sparrows at the mean value of each covariate was 0.97 (0.96–0.98). Daily probabilities of failure at the mean value for all covariates were as follows: predation = 0.018 (0.008–0.028) and trampled = 0.001

(0.000–0.004). The overall probability of nest success for savannah sparrows for a 24-day nesting cycle ranged from 0.63 (0.45–0.81) for early-season nests (initiated 7 May) in paddocks with low encounter rates of avian predators (0.05 per paddock) to 0.08 (0.00–0.29) for late-season nests (initiated 18 Jul) in paddocks with high encounter rates of avian predators (0.65 per paddock). Overall, probability of predation ranged from 0.15 (0.00–0.31) for early-season nests in paddocks with low encounter rates of avian predators to 0.82 (0.69–0.95) for late-season nests in paddocks with high encounter rates of avian predators. Overall, probability of trampling was 0.02 (0.00–0.05).

For horned larks, 4 models were competing (see Appendix 1.2, available online at www.onlinelibrary.wiley.com). The top model suggested a constant rate of failure for all causes. Other competing models suggested the probability of predation increased with date, year, and nest age, but support for these models was weak because 95% confidence limits included zero (date: $\beta = 0.114$; 95% CI = -0.015 – 0.043 ; year: $\beta = 0.409$; 95% CI = -0.760 – 1.578 ; age: $\beta = 0.0467$; 95% CI = -0.095 – 0.188). We found no evidence for an effect of grazing treatment on the daily probability of predation for horned larks. Daily probability of success (95% CI) at the mean value of each covariate was 0.96 (0.95–0.98). Daily probabilities of failure at the mean value for all covariates were as follows: predation = 0.029 (0.012–0.045) and trampled = 0.003 (0.000–0.007). Overall, probability of nest success for horned larks for a 20-day nesting cycle was 0.46 (0.29–0.63), whereas overall probability of failure due to predation was 0.42 (0.24–0.60) and due to trampling was 0.04 (0.00–0.11).

Goodness of fit tests for all competing models indicated that increases in deviance relative to a saturated model were no larger than would be expected by chance, except for the second best-fit model for savannah sparrows and only for the Pearson's χ^2 test (Table 3), suggesting a general pattern of good model fit. We found no indication of overdispersion of data for either species (\hat{c} range = 1.03–1.05).

DISCUSSION

Grassland-nesting birds typically experience relatively high levels of nest failure, and the rates we observed are comparable to those reported in other studies of grassland songbirds (Martin 1995, Winter 1999, Davis 2003). We were able to estimate failure rates for 2 potential causes of nest failure that have been associated with livestock grazing: predation and trampling by cattle. Several authors have hypothesized that livestock grazing may influence rates of nest predation through changes in vegetative cover or the predator community (Ammon and Stacey 1997, Fuller and Gough 1999, Klug et al. 2010). Further, trampling rates of artificial nests have been associated with increased cattle density (Jensen et al. 1990, Paine et al. 1996), but few tests of this hypothesis have occurred in natural systems (Nack and Ribic 2005).

Our experiment explicitly tested these hypotheses, and although we previously found greater stocking rates to be strongly related to decreases in vegetation structure and increases in patchiness of vegetation at the paddock-scale

Table 3. Goodness-of-fit (GoF) results for competing models of daily nest failure rates for savannah sparrows and horned larks breeding at the Zumwalt Prairie Preserve in northeastern Oregon, USA.

Species	Model ^a	GoF test ^b	Statistic	df	P	
Savannah sparrow	Predation (date + AVIAN), trampled (.)	Deviance	180.60	NA	0.41	
		Pearson χ^2	1046.30	NA	0.07	
		Hosmer–Lemeshow	29.96	28	0.37	
	Predation (date), trampled (.)	Pigeon–Heyse	29.99	27	0.32	
		Deviance	209.20	NA	0.42	
		Pearson χ^2	955.10	NA	0.03	
Horned lark	Predation (.), trampled (.)	Hosmer–Lemeshow	30.81	28	0.33	
		Pigeon–Heyse	30.84	27	0.28	
		Deviance	96.50	NA	0.47	
	Predation (date), trampled (.)	Pearson χ^2	377.60	NA	0.26	
		Hosmer–Lemeshow	30.74	28	0.33	
		Pigeon–Heyse	30.75	27	0.28	
	Predation (year), trampled (.)	Deviance	123.40	NA	0.44	
		Pearson χ^2	402.50	NA	0.28	
		Hosmer–Lemeshow	25.01	28	0.63	
	Predation (age), trampled (.)	Pigeon–Heyse	25.03	27	0.57	
		Deviance	124.50	NA	0.43	
		Pearson χ^2	505.00	NA	0.29	
		Predation (age), trampled (.)	Hosmer–Lemeshow	25.87	28	0.58
			Pigeon–Heyse	25.87	27	0.53
			Deviance	77.50	NA	0.48
			Pearson χ^2	255.60	NA	0.30
			Hosmer–Lemeshow	22.86	28	0.74
			Pigeon–Heyse	22.87	27	0.69

^a Model notation is as follows: date = day of breeding season, AVIAN = encounter rate for avian predators, year = 2007 or 2008, age = age of nest, . = constant.

^b The Pearson χ^2 statistic and deviance tests were assessed by parametric bootstrap simulation as the relative proportion of 500 simulated deviances or χ^2 statistics that were greater than or equal to the observed statistic.

(Johnson et al. 2011), we found no evidence supporting an increased risk of nest predation in association with greater stocking rates. We also found no evidence that stocking rate influenced nest predation risk through effects on predator abundance or activity as we measured it. Encounter rates of avian predators were associated with nest predation rates for savannah sparrows but surprisingly, we found no evidence that vegetation structure at the nest influenced risk of nest predation for either species. Our results support an alternative hypothesis we did not consider a priori: no relationship exists between vegetation structure and the probability of nest predation. Because the effect of nest concealment on nest predation can vary with composition of the predator community (Clark and Nudds 1991), this may suggest species in this system responsible for the majority of nest predation events are not avian, but instead are a species that does not rely solely on visual cues to locate prey (e.g., snakes). Predation through non-visual cues may not be affected by vegetative cover near the nest. Also, with the exception of density estimates of Belding's ground squirrels, our measurements of the predator community were activity indices, which may not be positively correlated with predator abundance. Finally, interactions between adult anti-predator behavior and food availability are known to influence risk of nest predation (Dewey and Kennedy 2001, Rastogi et al. 2006). Songbird food availability could be affected by grazing-induced changes in vegetation (Vickery et al. 2001, DeBano 2006), but we were unable to address this hypothesis with these data.

We were unable to test our hypothesis that risk of trampling was positively related to stocking rate because of the low number of nests in our sample that failed because of trampling. However, nests that were trampled were located in moderate and high stocking rates. The low incidence of trampling for savannah sparrows and horned larks, combined with our previous observation that VO at the nest of both species was not affected by stocking rate (Johnson et al. 2011) suggests that cattle may spend less time near nests of these species relative to nests of other species. Spatial variation in vegetation utilization by cattle can be affected by dietary preferences, topography, distance to water, and other factors (Cook 1966, Senft et al. 1985). Dissimilarity between areas preferred as nesting sites by birds and areas preferred as foraging or loafing sites by cattle could result in low trampling rates. Because native ungulates are present at our study site (mule deer [*Odocoileus hemionus*] and elk [*Cervus canadensis*]), all trampled nests may not have been a result of domestic livestock activity. However, native ungulates observed in our study paddocks spent much less time there and occurred in lesser densities than cattle (T. N. Johnson, personal observation).

Although a relatively small proportion of nest failure was caused by trampling in this study, greater stocking rates could lead to greater trampling rates. The greatest stocking rate in our study was 1.1 animal units/ha; however, in more mesic, productive grasslands (e.g., tallgrass prairie) stocking densities can be at least as high as 2.1 animal units/ha in early, intensive stocking grazing systems (Owensby et al. 1988).

Further, grassland bird densities vary regionally, and can be much greater in the Great Plains region of the United States than at our study site (Sauer et al. 2011). In systems with greater stocking rates or nest densities, trampling could potentially be a significant source of nest failure for grassland birds (Jensen et al. 1990).

Interpretation of evidence of nest fates has implications for estimating cause-specific failure probabilities, because the potential to misclassify nests exists. For example, we classified nests that failed >2 days before fledging as depredated when we found no evidence to indicate otherwise, which results in no classification error for depredated nests that were actually depredated. However, a nest may have initially failed because of abandonment but was scavenged before the next visit, resulting in misclassification as a depredated nest. Thus, predation probability estimates may be positively biased and remaining failure probabilities may be negatively biased, because nests with fates other than predation may have been included in the predation category (Etterson et al. 2007a). We treated all evidence of nest fates equally regardless of grazing treatment and assumed interpretation bias did not differ among stocking rates, and thus, would not influence our interpretation of stocking rate effects. Future studies of cause-specific nest failure would benefit from the use of cameras to identify exact causes of nest failure, especially if the aim is to estimate rates of depredation from different species or suites of predators (Thompson et al. 1999).

Our methods show how to make formal inference about cause-specific failure rates that take into account sample size and covariates to separate causes of failure. The framework we used produces probability estimates for cause-specific failure and incorporates model selection, allowing the identification of variables that explain variation associated with specific causes of failure. The ability to directly estimate the probability of failure from specific causes provides researchers with improved ways of directly testing hypotheses regarding nest failure. For instance, we were able to address the hypothesis that high stocking rates can decrease vegetation structure near the nest and influence risk of nest predation. Further, information on risk of failure from particular causes allows conservation efforts to be focused on the most significant causes of reproductive failure (here, nest predation), or alternatively, to be focused on causes of nest failure more easily affected by changes in management (trampling). Evaluating relationships among environmental variables, management strategies, and variation in nest failure from specific causes will be valuable in developing more effective conservation strategies. We suggest the framework presented here be used in future studies of nest failure, especially in systems where nests can fail from several different causes.

MANAGEMENT IMPLICATIONS

Our results have implications for livestock grazing management. Although we did observe negative effects of the high stocking rate treatment on abundance and nest density of some species (Johnson et al. 2011), we did not observe strong effects of our grazing treatments on the daily risk of nest failure for savannah sparrows or horned larks, the 2 most

abundant grassland songbirds breeding at our study site. These results suggest that grasslands managed for livestock grazing may be compatible with grassland songbird conservation, at least within the context of the stocking rates and songbird species examined here. In semi-arid, bunchgrass prairie, low to moderate stocking rates grazed for ≤ 6 weeks may have negligible effects on the risk of nest failure. Assuming conservation efforts for grassland songbirds are focused on increasing nest survival, our results suggest the most effective strategies will likely involve reducing risk of nest predation. However, we found no evidence that management of stocking rate is an effective method for doing so.

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