EFFECTS OF SCAVENGING ON ASSUMPTIONS OF MORTALITY ANALYSES OF RADIO-MARKED GAMEBIRDS

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ABSTRACT—Survival estimation is critical to studies of wildlife population biology, and recent model developments allow for temporal covariates on mortality risk. To test model assumptions that scavengers do not influence either perceived mortality cause or location, we randomly placed 24 radio-marked Chukar (*Alectoris chukar*) carcasses over gradients of grassland habitat conditions in eastern Montana in both April 2017 and July 2018, and monitored scavenging activity at intervals relevant to gamebird telemetry studies. High rates of scavenging (12.5–78%, depending on season and relocation interval) suggest that scavenging activity could confound determination of cause-specific mortality, but that its influence varies with season. Scavenging activity did not significantly influence perceived mortality locations regardless of season or local habitat conditions with a relocation interval of 3 d (8% of carcasses moved), but mortality locations may be biased over longer periods (50% of carcasses moved in 7-d period), particularly in warm seasons or regions.

Key words: *Alectoris chukar*, Andersen-Gill models, Chukar, habitat, Montana, mortality risk, survival

Survival is an important determinant of wildlife population biology. Over the past few decades, estimation of survival has improved in both insightfulness and rigor (Lebreton and others 1992; Murray 2006). In particular, the modeling of survival relative to intrinsic and environmental conditions has received significant attention (Murray and Patterson 2006). Recent development of time-dependent survival analyses has improved our ability to understand the demographic consequences of individual behaviors by establishing clear linkages between habitat use and survival (Johnson and others 2004; Halstead and others 2012). Use of models such as shared frailty models and the Andersen-Gill formulation of the Cox proportional hazards model has rapidly increased due to several advantages over other known-fate survival models, including the ability to incorporate spatial covariates on cause-specific mortality risk (Andersen and Gill 1982; Johnson and others 2004; Murray and Patterson 2006; Fleming and Harrington 2011; Halstead and others 2012; Coates and others 2017). These models have been used in studies of multiple taxa (Smith and others 2010; White and others 2010; Halstead and others 2012; Taylor and others 2016; Senner

and others 2017), including gamebirds (Åhlen and others 2013; Dinkins and others 2014; Winder and others 2014; Coates and others 2017).

Data for time-dependent survival models are structured so that a single animal has multiple observations, each of which represents a different interval of risk (Halstead and others 2012; Therneau and Grambsch 2013). For individuals that die, the final interval is represented by the mortality time and is compared to a series of intervals during which the live animal was tracked and which represent nonmortality locations. Mortality events are discovered or represented as a binomial status at the end of each interval, so the conditions influencing mortality risk are typically measured at that end location (Johnson and others 2004). Previous work found slight differences in coefficient estimates for habitat conditions affecting mortality risk depending on when the conditions for a given nonmortality interval were measured, but no systematic bias (Johnson and others 2004), suggesting that the habitat variables related to nonmortality locations adequately represent conditions influencing mortality risk. However, there have been no similar studies testing the

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assumption that habitat conditions at carcass locations represent the habitat conditions influencing mortality risk. If a carcass is moved after death, by either the original predator or a scavenger, then inferences based on the habitat conditions measured at the mortality location will be biased. Moreover, if scavenging activity confounds determination of cause-specific mortality, estimates of cause-specific mortality risks may result in incorrect inferences and inappropriate management recommendations.

We used radio-marked Chukar (*Alectoris chukar*) carcasses to test the common assumptions that scavenging activity does not confound field-based determination of cause-specific mortality, and mortality locations from telemetry studies of gamebirds accurately represent the habitat characteristics where individual animals die. Given relatively high but seasonally changing occurrence of both avian and mammalian scavengers at our study area (Vold 2018), we hypothesized that: (1) a non-zero proportion of carcasses would exhibit signs of scavenging within a week of being placed, thus resulting in incorrect classification of cause-specific mortality; (2) scavenged carcasses would be moved from their original locations; (3) the probability that a carcass is scavenged would be mediated by local habitat conditions; and (4) seasonality would influence scavenging activity and potential biases associated with survival estimation.

METHODS

This study was conducted in eastern Montana, 16 km south of Sidney, Montana (centered on UTM: Zone 13N, 0571465E, 5268907N), in April 2017 and July 2018, to assess scavenging activity in both cool (April, spring) and warm (July, summer) seasons. Our study area was located in the northern mixed-grass prairie, within an area typical for the region dominated by contiguous rangelands and managed for livestock grazing. The study area was primarily Great Plains mixed-grass prairie, interspersed with Great Plains badlands and wooded draws and ravines (LANDFIRE 2013). Average annual precipitation was 35.3 cm, and average high and low temperatures were 14.7 and –1.0°C in April and 29.4 and 12.7°C in July. Based on both point-count surveys and camera-trap data collected during 2016–2017, potential scavengers in our study area during the time of this experiment included Coyote (*Canis latrans*), Northern Raccoon (*Procyon lotor*), American Badger (*Taxidea taxus*), Striped Skunk (*Mephitis mephitis*), Short-tailed Weasel (*Mustela ermine*), Peregrine Falcon (*Falco peregrinus*), Prairie Falcon (*Falco mexicanus*), Northern Harrier (*Circus cyaneus*), Red-tailed Hawk (*Buteo jamaicensis*), Golden Eagle, (*Aquila chrisaetos*), Great Horned Owl (*Bubo virginianus*), American Crow (*Corvus brachynrhynchos*), Black-billed Magpie (*Pica hudsonia*), and Turkey Vulture (*Cathartes aura*) (Vold 2018). All of the mammalian species are residents and, of the avian species, the Prairie Falcon, Golden Eagle, Great Horned Owl, and Black-billed Magpie are resident, while the remaining avian species are migratory, passing through the study area beginning in April, with some individuals remaining to breed.

Twenty-four Chukar carcasses were obtained in both April 2017 and July 2018. Carcasses used in 2017 were obtained from a National Shoot to Retrieve Trial in Savage, Montana; all birds were killed by hunters using shotguns. Hunter-killed carcasses were not available in 2018, so we obtained frozen carcasses directly from a private game bird production facility. Carcasses were outfitted with 18-g VHF radio-transmitters with an elastic necklace harness (model A4050; Advanced Telemetry Systems, Isanti, MN), and placed at randomly selected locations with a minimum distance of 350 m between points to satisfy the assumption of site independence (Lesmeister and others 2015). Carcasses were then checked at 3 and 7 d post-placement, and any scavenging activity and movement of either the carcass or the transmitter were recorded. Intervals of 3 and 7 d were chosen to represent intervals between consecutive locations used in many studies that were unable to monitor study animals daily (Murray 2006; Dinkins and others 2014; Winder and others 2018) and so represent relative time periods during which scavengers would have an opportunity to scavenge carcasses. Scavenging activity was classified as either mammal, avian, or unknown scavenger (Elbroch 2003). Scavenging activity from invertebrates was not recorded as it is not relevant to studies of gamebird mortality. Scavenging was classified as mammalian if bite marks, chewed feathers, or mammalian tracks or scat were present (Elbroch 2003). Scavenging was classified as avian if the carcass had been decapitated or cleaned of the breast muscle with no bite marks, or if the

feathers had only been plucked (Elbroch 2003). Scavenging was classified as an unknown scavenger if the entire carcass was removed (only an unmarked transmitter remained). All Chukars used in this experiment were intact carcasses with no previous signs of damage other than gunshots, and all carcasses were handled similarly and placed in the field within 24 h of being obtained.

Habitat conditions were measured at both the initial locations where carcasses were placed and their locations at 3 d post-placement if the carcass had been moved >12 m. In our study, a distance of 12 m represents the minimum distance at which the subsequent local habitat conditions would differ from those measured at the initial carcass location (MC Milligan, unpubl. data). We recorded visual obstruction readings (VOR) at the carcass location and at 4 points 6 m from the carcass in each cardinal direction. At each point, VOR was measured in each cardinal direction from a distance of 2 m and a height of 0.5 m using a Robel pole (Robel and others 1970). We also estimated non-overlapping vegetation cover (percent new grass, residual grass, forbs, shrubs, bare ground, and litter) at 12 subsampling locations within 6 m of the carcass using a 20 × 50 cm sampling frame to characterize the vegetation composition (Daubenmire 1959). In addition to vegetation conditions, we measured habitat variables previously found to be important for prairie grouse (*Tympanuchus* spp.) survival, including distances to houses, oil pads, and roads, and 2 measures of habitat fragmentation: distance to grassland patch edge and density of edge habitat (Hovick and others 2014). Variables representing anthropogenic disturbances were based on road datasets from Montana and North Dakota (Montana State Library, North Dakota GIS Hub Data Portal) and landcover analyses utilized the 30 m resolution LANDFIRE data depicting vegetation type (LANDFIRE 2013).

We 1st evaluated models examining the effect of season (April = cool-spring; July = warm-summer) on the probability that a carcass was scavenged during the 3-d interval. We assumed that the importance of season relative to scavenging activity could vary depending on the length of the relocation interval. We then separately evaluated competing models examining the effects of small-scale vegetation and habitat risk factors on the probability that a
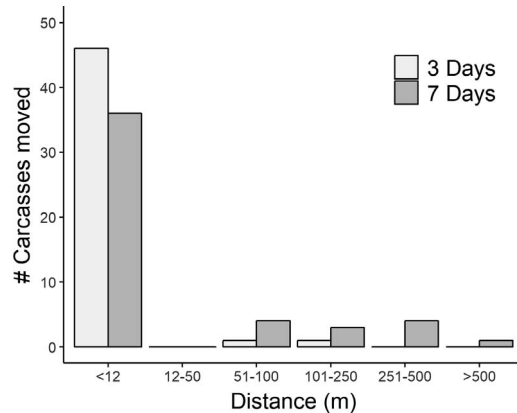

FIGURE 1. Number of carcasses scavenged and moved different distances during the 3- and 7-d intervals post-placement.

carcass was scavenged or moved during the 7-d interval. We also tested for additive effects with habitat risk factors and season. We assumed that habitat factors affecting the probability of scavenging would not differ between the 3-d and 7-d intervals. We used logistic regression to evaluate both the probability of scavenging and the probability that a carcass was moved ≥12 m. Models were compared using Akaike's Information Criterion adjusted for small sample sizes (AIC_c), and models with both large model weights ($w_i \geq 0.1$) and AIC_c values ≤2 from the best-fit model were considered equally parsimonious (Burnham and others 2011). Effects of variables were considered important if 85% confidence intervals of model-averaged slope coefficients did not overlap zero (Arnold 2010).

RESULTS

During the first 3-d post-placement, 7 of 24 carcasses (29%) were scavenged in April (6 by birds and 1 by a mammal), and 3 of 24 carcasses (12.5%) were scavenged in July (1 by birds and 2 by mammals). At 7-d post-placement, 12 of 24 carcasses (50%) were scavenged in April (10 by birds and 2 by mammals), and 19 of 24 carcasses (79.2%) were scavenged in July (2 by birds, 10 by mammals, and 7 by unknown scavengers). Only 2 carcasses (8%) were moved ≥12 m during the initial 3-d post-placement, with both being moved in July (Fig. 1). Two carcasses (8%) and 12 carcasses (50%) were moved ≥12 m during

TABLE 1. Support for candidate models predicting the probability of scavenging of Chukar carcasses experimentally placed in eastern Montana in April 2017 and July 2018 during the 7-d interval post-placement. Results for analyses examining effects of small-scale vegetation and habitat risk factors are included. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported.

Model	K	AIC_c	ΔAIC_c	$AIC_c\ w_i$	Cum. W_i	LL
LOCAL VEGETATION						
Null	1	63.60	0.00	0.22	0.22	−30.76
% Residual	2	63.71	0.11	0.21	0.43	−29.72
% Litter	2	64.54	0.94	0.14	0.57	−30.13
% Shrub	2	65.23	1.63	0.10	0.66	−30.48
% New grass	2	65.35	1.75	0.09	0.76	−30.54
VOR	2	65.39	1.79	0.09	0.85	−30.56
% Forb	2	65.64	2.04	0.08	0.93	−30.68
% Bare	2	65.78	2.17	0.07	1.00	−30.75
HABITAT RISK FACTORS						
Season + Distance to oil pad	3	61.96	0.00	0.19	0.19	−27.71
Season + Distance to house	3	62.09	0.13	0.18	0.38	−27.77
Season	2	62.10	0.14	0.18	0.56	−28.92
Season + Edge density	3	63.64	1.68	0.08	0.64	−28.55
Season + Distance to grassland edge	3	63.99	2.03	0.07	0.71	−28.72
Season + Distance to road	3	64.31	2.35	0.06	0.77	−28.88
Dist. To oil pad	2	64.48	2.52	0.06	0.83	−30.11
Null	1	64.49	2.53	0.05	0.88	−31.20
Distance to house	2	64.60	2.64	0.05	0.93	−30.17
Edge density	2	66.00	4.03	0.03	0.96	−30.86
Distance to grassland edge	2	66.31	4.35	0.02	0.98	−31.02
Distance to road	2	66.60	4.64	0.02	1.00	−31.17

the 7-d post-placement in April and July, respectively. Both carcasses that were moved by 7-d post-placement in April were scavenged by birds and were moved 97 and 150 m, respectively. Half (50%) of the carcasses moved during the 7-d post-placement in July were scavenged by mammals, with the remainder scavenged by unknown scavengers. The carcasses placed in July were moved between 61 and 923 m, with a mean distance of 306 m (Fig.1). There was no significant difference in the probability of scavenging during the 3-d interval between April and July (null model: $\Delta AIC_c = 0$, $w_i = 0.51$), but during the 7-d interval, the probability that a carcass was scavenged was higher during July than April (Table 1).

Carcasses were initially placed across a range of habitat conditions (Fig. 2), but local vegetation conditions did not influence the probability that a carcass was scavenged (Table 1). Rather, the probability that a carcass was scavenged during the 7-d interval was best predicted by season (cool-spring or warm-summer), which, in combination with other variables, accounted for 76% of model weight (Table 1; Fig. 3). The probability of scavenging was higher during July than April ($\beta = 1.37 \pm 0.66$). There was also

evidence for an effect of anthropogenic structures on the probability that a carcass was scavenged (Table 1), with carcasses located closer to oil pads ($\beta = 0.03 \pm 0.02$; Fig. 3) and further from houses ($\beta = 0.06 \pm 0.04$) more likely to be scavenged. The odds of scavenging decreased 2.8% for every 100 m from an oil pad, and increased 6.6% with every 100 m from a house. The 85% confidence intervals on effects of all other variables overlapped zero and so were not considered important (Appendix Table S1). Four models describing the probability that a carcass was moved were supported by the data based on model weights >0.1 and AIC_c values ≤2 from the best-fit model (Table 2), but only the effects of distance to road, distance to oil pad, and distance to house were considered significant, with 85% confidence intervals that did not overlap zero (Appendix Table S2). The probability that a carcass was moved within 7 d was positively related to distance to the nearest road ($\beta = 0.08 \pm 0.04$) and distance to house ($\beta = 0.09 \pm 0.05$), and negatively related to distance to the nearest oil pad ($\beta = -0.04 \pm 0.02$). The odds of scavenging decreased 3.5% for every 100 m increase in distance from oil pads and increased 8.4% and 9.2% for every 100 m
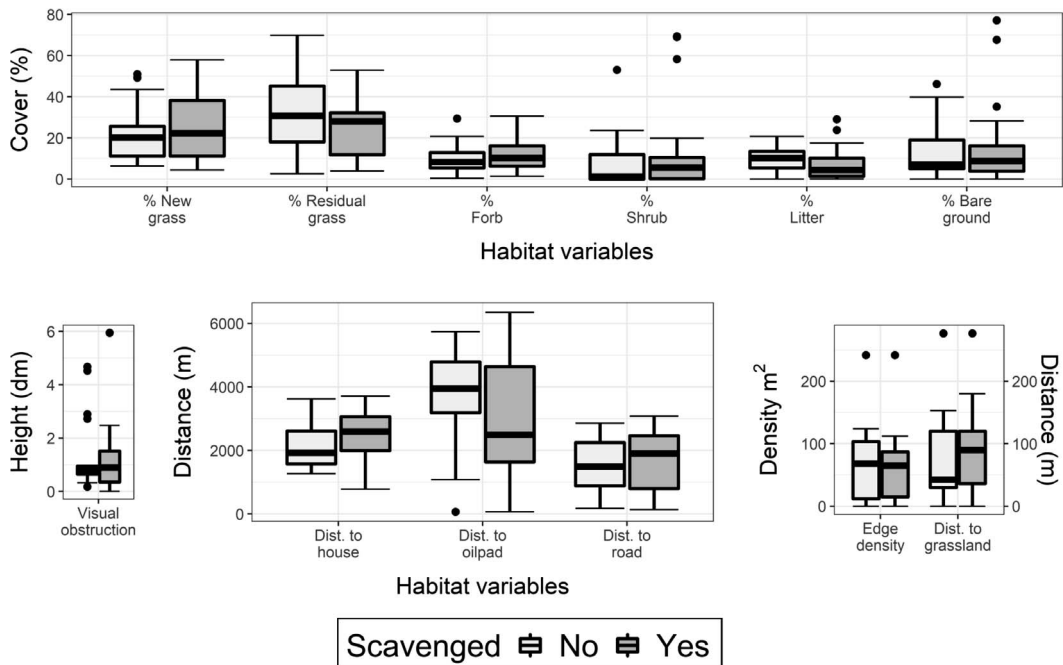
FIGURE 2. Habitat measurements at the locations where Chukar carcasses were experimentally placed in eastern Montana in April 2017 and July 2018. Measurements are separated by whether or not a carcass was scavenged during the 7-d period post-placement.

increase in distance from roads and houses, respectively. Although low sample sizes precluded statistical analyses, habitat conditions were similar between the original locations and the locations where transmitters were recovered (Fig. 4).
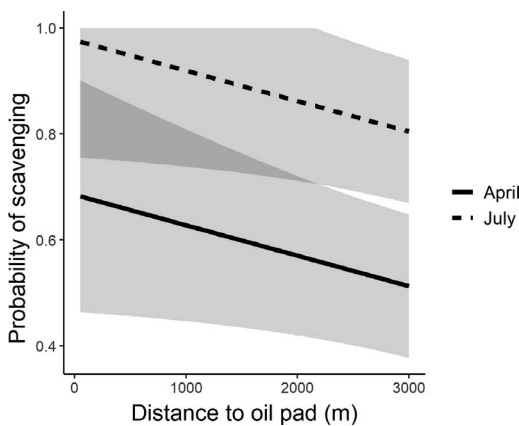

FIGURE 3. Predicted probability that experimentally placed Chukar carcasses in eastern Montana were scavenged during 2 seasons (April and July) in relation to oil pad locations.

DISCUSSION

Incorrect predator classification can introduce bias into telemetry studies when scavengers obscure evidence from the original predator, and inflate estimates of mortality due to predation if animals that die due to factors other than predation, such as disease, are misclassified as a result of scavenging activity (Larsen and others 2008). Similar to previous studies, we observed high levels of scavenging activity on gamebird carcasses in eastern Montana that would result in incorrect classification of cause-specific mortality (Dumke and Pils 1973; Bumann and Stauffer 2002; Larsen and others 2008), with rates of scavenging that were significantly greater in summer than spring.

Scavenging activity did not significantly influence perceived mortality locations regardless of season or local habitat conditions with a relocation interval of 3 d, but mortality locations may be biased over longer periods, particularly in warm seasons or regions. Previous studies found that radio-tagged carcasses were moved minimal distances, even over longer time intervals (Bumann and Stauffer 2002; Larsen and

TABLE 2.   Support for candidate models predicting the probability that Chukar carcasses experimentally placed in eastern Montana in April 2017 and July 2018 were moved by scavengers. Results for analyses examining effects of small-scale vegetation and habitat risk factors are included. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. W_i	LL
LOCAL VEGETATION						
Null	1	60.95	0.00	0.22	0.22	−29.43
VOR	2	61.10	0.15	0.20	0.42	−28.41
% Litter	2	61.33	0.38	0.18	0.60	−28.53
% Bare	2	62.82	1.87	0.09	0.69	−29.28
% Forb	2	62.87	1.92	0.08	0.77	−29.30
% New grass	2	62.98	2.02	0.08	0.85	−29.35
% Shrub	2	63.01	2.06	0.08	0.93	−29.37
% Residual	2	63.14	2.18	0.07	1.00	−29.43
HABITAT RISK FACTORS						
Dist. To road	2	58.79	0.00	0.27	0.27	−27.26
Dist. To house	2	59.81	1.02	0.16	0.43	−27.77
Season + Dist. To road	3	60.09	1.30	0.14	0.57	−26.77
Dist. To oil pad	2	60.34	1.55	0.12	0.69	−28.04
Season + Dist. To house	3	61.13	2.34	0.08	0.77	−27.29
Season + Dist. To oil pad	3	61.67	2.88	0.06	0.83	−27.56
Null	1	61.71	2.92	0.06	0.90	−29.81
Season	2	63.01	4.22	0.03	0.93	−29.37
Dist. To grassland edge	2	63.39	4.60	0.03	0.95	−29.56
Edge density	2	63.85	5.06	0.02	0.98	−29.79
Season + Dist. To grassland edge	3	64.78	5.99	0.01	0.99	−29.12
Season + Edge density	3	65.26	6.46	0.01	1.00	−29.35

others 2008). Furthermore, although sample sizes precluded analysis, habitat conditions were similar between the original locations and locations where transmitters were recovered. Therefore, for gamebird telemetry studies with a maximum relocation interval of 3 d, perceived habitat conditions at mortality locations should accurately represent those influencing mortality risk in the northern mixed-grass prairie, but caution should be exercised in studies with relocations intervals >3 d.

In our study, local vegetation conditions did not influence whether a carcass was scavenged. Previous work has found that factors including habitat, carcass size, temperature, and changes in the vertebrate scavenger community can all influence scavenging activity, although the importance of each factor varies by study (Selva and others 2005; Olson and others 2012; Moleón and others 2015; Turner and others 2017). While some studies have found specific habitat types to be important predictors of scavenging activity (Selva and others 2005; Turner and others 2017), other studies have found no influence of factors such as habitat structure, landscape connectivity or distance to edge habitat (Bumann and Stauffer 2002; Olson and others 2016), or have shown that other factors such as carcass type, temperature, or the local predator community were more important predictors (Olson and others 2012; Moleón and others 2015; Olson and others 2016). The habitat variables measured in our study were not categorical habitat types (for example see Selva and others 2005), but rather fine-scale continuous measures of vegetation structure, and differences in habitat measures could explain why our results differed from those of previous research.

In contrast, proximity to anthropogenic structures influenced both the probability of a carcass being scavenged and the probability that a carcass was moved. Carcasses located in closer proximity to oil pads were more likely to be scavenged and moved, while carcasses located close to roads and houses were less likely to be scavenged or moved. Anthropogenic structures related to energy development, including oil pads, have been associated with lower survival of grouse (Holloran 2005; Hovick and others 2014). Raptors are visual predators and utilize anthropogenic infrastructure as perch sites, which can facilitate the detection of both live prey and carcasses to scavenge (Prather and Messmer 2010; Slater and Smith 2010). More-
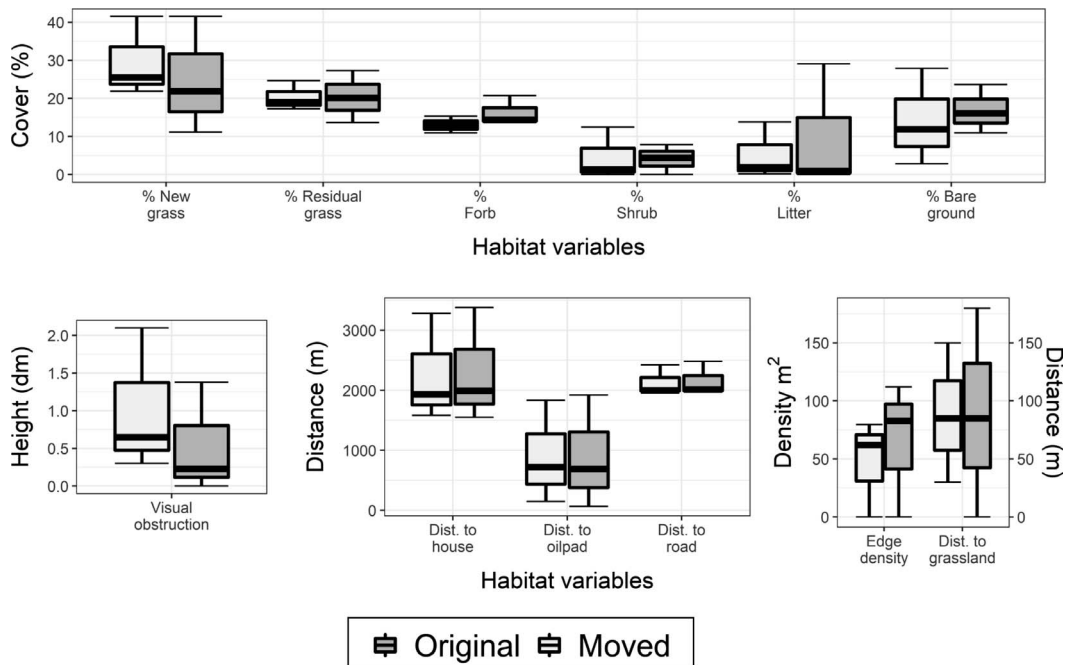
FIGURE 4. Habitat measurements at the locations where Chukar carcasses were experimentally placed in eastern Montana and the locations where transmitters were recovered.

over, energy development increases habitat fragmentation (Hovick and others 2014), and mesocarnivores often exhibit positive responses to habitat fragmentation (Andrén 1995; Winter and others 2000). Carcasses were also less likely to be moved when in close proximity to roads and houses, potentially reflecting avoidance of human presence, a trend found in previous studies (Burr and others 2017; Vold 2018). In our study area, oil pads were not being actively drilled and so human presence was minimal.

Similar to other studies, (Bumann and Stauffer 2002; Olson and others 2016; Turner and others 2017), estimates of scavenging activity during the 7-d interval differed between seasons, with greater scavenging activity during the warmer summer season. This suggests that temperature could be a significant factor influencing whether a carcass was discovered and may reflect differences in the scavenger community between seasons. Both the abundance and composition of the local scavenger community can have an important influence on scavenging activity (Turner and others 2017), and the community of scavengers appeared to shift between the seasons, although sample sizes precluded statis-

tical analyses. Seasonal changes in predator and scavenger communities have important implications for the determination of cause-specific mortality. In our study area, the majority of carcasses were scavenged by birds in April, while scavenging by mammals was more prevalent in July, which could be related to the difference in carcass movement between the 2 seasons. Avian scavengers in our study area, such as the Northern Harrier, typically pluck and consume prey on the ground, whereas it could be easier for larger-bodied mammals to move or cache a carcass (Harrington 1982; Thogmartin and Schaeffer 2000; Smith and others 2011). Misclassification of cause-specific mortality may be higher in areas where mammals are the primary scavengers (Bumann and Stauffer 2002). Therefore, both the scavenger assemblage and the timing of the study should be considered when applying our results to other locations. The biases associated with scavenging can vary throughout the year, with higher avian scavenging during migration and with greater scavenging by olfactory mammals during warmer seasons.

Our experiment only evaluates the effects of scavenging on the perceived mortality locations of gamebirds and does not include any movement of the carcass post-kill by the initial predator. The importance of this initial movement could vary depending on the predator assemblage in the area and, based on the scavenging activity in our study, could potentially be less pronounced in areas or for species where the dominant predators are avian. However, in areas with a higher proportion of mammalian scavengers, including well-known caching species such as Mountain Lions (*Puma concolor*) or woodrats (*Neotoma* spp.), this movement could be more significant (Bauer and others 2005; Larsen and others 2008).

Our study provides provisional evidence that scavenging can significantly confound field-based determination of cause-specific mortality, but, depending on the season and relocation interval of the study, may not have a significant influence on mortality locations of gamebirds in the northern mixed-grass prairie. However, both season and local vertebrate assemblages should be considered when determining the optimal tracking interval for telemetry studies if modeling the effect of habitat conditions on survival is an important priority. Biologists should be cautious when making inferences about cause-specific mortality when scavengers occupy their study areas.

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