

# Merriam's Turkey Nest Survival and Factors Affecting Nest Predation by Mammals

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**ABSTRACT** Nest success is an important parameter affecting population fluctuations of wild turkeys (*Meleagris gallopavo*). Factors influencing mammalian predation on turkey nests are complicated and not well understood. Therefore, we assessed nest hazard risk by testing competing hypotheses of Merriam's turkey (*M. g. merriami*) nest survival in a ponderosa pine (*Pinus ponderosa*) ecosystem during 2001–2003. We collected nesting information on 83 female Merriam's turkeys; annual nest success averaged 50% for adult females (range = 45–59%) and 83% for yearling females (range = 75–100%). Proportional hazard modeling indicated that precipitation increased the hazard of nest mortality. However, estimated hazard of nest predation was lowered when incubating females had greater shrub cover and visual obstruction around nests. Coyotes (*Canis latrans*) were the primary predator on turkey nests. We hypothesize that precipitation is the best predictor of nest survival for first nests because coyotes use olfaction effectively to find nesting females during wet periods. Temporally, as the nesting season progressed, precipitation declined and vegetation cover increased and coyotes may have more difficulty detecting nests under these conditions later in the nesting period. The interaction of concealment cover with precipitation indicated that nest hazard risk from daily precipitation was reduced with greater shrub cover. Management activities that promote greater shrub cover may partially offset the negative effects of greater precipitation events. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1765–1774; 2008)

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Population modeling indicates that annual nesting rates and nest success are important parameters in population fluctuations of wild turkeys (*Meleagris gallopavo*; Wakeling 1991, Roberts et al. 1995, Roberts and Porter 1996). Most unsuccessful nest attempts by Merriam's turkeys (*M. g. merriami*) are caused by nest predation (Wakeling 1991, Rumble and Hodorff 1993, Flake and Day 1996). However, the underlying factors associated with nest predation and annual variability in nest success for ground-nesting gallinaceous birds are not well understood (Storaas 1988, Roberts and Porter 1998, Pleasant et al. 2003). Gaining an understanding of these processes involves modeling daily nest survival or nest failure events using a set of candidate models with measured covariates that were based on previous research (Dinsmore et al. 2002, Shaffer 2004, Heisey et al. 2008).

Nest-site selection by turkeys at scales encompassing larger areas than the immediate area surrounding the nest may affect hazard risk (Martin and Roper 1988, Thogmartin 1999). Larger patches of habitat were good predictors for nest location but poor predictors of nest survival for eastern turkeys (Thogmartin 1999). Investigation at the fine scale indicates that Merriam's turkeys select nest sites that are characterized by dense hiding cover provided by surrounding vegetation (Schemnitz et al. 1985, Lutz and Crawford 1987, Day et al. 1991, Wakeling 1991, Rumble and Hodorff 1993). Increased nest concealment by vegetation or other forms of visual obstruction have been hypothesized to

enhance nest survival (Badyaev and Faust 1996, Liebezeit and George 2002). Shrubs and woody debris can provide important nesting cover for Merriam's turkeys (Petersen and Richardson 1975, Ffolliot et al. 1977, Schemnitz et al. 1985, Lutz and Crawford 1987, Rumble and Hodorff 1993). Increased slope at nest sites may also be an important characteristic for nest success (Petersen and Richardson 1975, Schemnitz et al. 1985, Rumble and Hodorff 1993).

In Arizona, USA, successful nests were associated with larger-diameter ponderosa pine (*Pinus ponderosa*) trees, greater conifer density, and less understory deciduous vegetation (Wakeling et al. 1998). In the central Black Hills, South Dakota, USA, Merriam's turkeys selected nest sites with greater visual obstruction than random sites, but only aspect and overstory canopy cover differed between successful and unsuccessful nests (Rumble and Hodorff 1993).

Previous research suggested that mammalian predation of nests may be increased during or shortly after precipitation (Palmer et al. 1993, Roberts et al. 1995, Roberts and Porter 1998). Palmer et al. (1993), Roberts et al. (1995), and Roberts and Porter (1998) hypothesized that incubating females that are wet produce more scent from increased bacterial growth on skin and feathers (Syrotuck 1972), enabling mammalian predators to better locate nests by smell. These studies associating nest predation to precipitation occurred in fragmented ecosystems and in more mesic environments than the Black Hills. In semiarid environments, no link was found between precipitation and nest survival for scaled quail (*Callipepla squamata*; Pleasant et al. 2003).

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We found no published research evaluating wild turkey nest survival in relation to nest-site habitat covariates with simultaneously collected daily precipitation. We modeled nest mortality using a demographic response study design with proportional hazard functions (Allison 1995, Heisey et al. 2008) to identify factors associated with nest mortality for Merriam's turkeys in a semiarid contiguous ponderosa pine ecosystem. We evaluated competing hypotheses that may explain mechanisms underlying mammalian nest predation:  $H_1$ , moisture-facilitated nest predation hypothesis—precipitation increases the rate of nest predation;  $H_2$ , nest concealment hypothesis—increased visual obstruction prevents detection of nests by predators;  $H_3$ , moisture-facilitated and nest concealment nest predation hypothesis—the interaction of precipitation and visual obstruction affects the rate of nest predation; and  $H_4$ , scale hypothesis—certain nest-site metrics at the coarse-scale level may lead to greater risk of nest predation and within this level fine-scale attributes may further facilitate mammalian predation of nests.

## STUDY AREA

The study area (1,213 km<sup>2</sup>) was located in Custer and Fall River counties in southwestern South Dakota and consisted of interspersed public and private land in the Black Hills physiographic region (Johnson et al. 1995). Elevations ranged from 930 m to 1,627 m above mean sea level. The climate was semiarid, with mean annual precipitation of 44 cm and mean annual temperature of 8° C; approximately 60% of annual precipitation occurred during the nesting season (Apr–Jul; National Climatic Data Center 1973–2003). The study area was mostly ponderosa pine forest (48%) and meadows (23%). Wildfires burned 29% of the study area in 2000 and 2001. Rare stands of Rocky Mountain juniper (*Juniperus scopulorum*) and deciduous draws (<1%) occurred on the area. Western snowberry (*Symphoricarpos occidentalis*) and common juniper (*Juniperus communis*) were common shrubs in the understory, whereas serviceberry (*Amelanchier alnifolia*), bearberry (*Arctostaphylos uva-ursi*), and chokecherry (*Prunus virginiana*) occurred less frequently (Hoffman and Alexander 1987). Common native grasses included needle and thread (*Stipa comata*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), little bluestem (*Schizachyrium scoparium*), and prairie dropseed (*Sporobolus heterolepis*; Larson and Johnson 1999). In April 2000, a spring snowstorm caused limb and treetop breakage on ponderosa pine, creating pine slash on the forest floor throughout the study area; some pine slash was also created by logging.

## METHODS

We captured wild turkeys during winter (1 Dec–31 Mar) from 2001 to 2003 using cannon nets (Dill and Thornsberry 1950, Austin et al. 1972), rocket nets (Thompson and Delong 1967, Wunz 1984), and drop nets (Glazener et al. 1964). Following capture, we aged female turkeys as adult (>1 yr old) or yearling (<1 yr old) based on presence or

absence of barring on the 9th and 10th primary feathers (Williams 1961). We secured 98-g radiotransmitters using a shock cord harness and backpack-mount. Transmitters (Advanced Telemetry Systems, Isanti, MN) were equipped with an activity signal, short-term nonmoving signal, and mortality signal set to activate after 8 hours of inactivity. We used Model R2000 receivers to locate radiomarked wild turkeys (Advanced Telemetry Systems). Prior to nesting (15 Mar–10 Apr), we located birds 5–6 days each week; however, after turkeys initiated laying behavior we located birds daily by direct observation or triangulation aided with a handheld Yagi antenna. All wild turkey trapping and monitoring procedures were approved by the South Dakota State University Research Committee (Animal Use Approval 00-A039).

We monitored nesting activity of hens and nest predation events on nests from 10 April to 6 August, 2001–2003. We identified female turkeys as attempting a nest when they localized, or decreased distances between daily movements during laying but did not subsequently incubate nests (Little and Varland 1981, Lehman et al. 2005). When it became apparent a nest was initiated based on localized movements we attempted to locate the nest during the laying period by watching the bird from a nearby location aided with a handheld Yagi antenna. We determined dates of initiation of laying, initiation of incubation, and nest hatching. Our observations did not appear to disturb nesting females during the laying period; no females abandoned nests following visual observations. If we did not find the nest during the laying period, we located the nest early in the incubation period and marked the immediate nest area with flags in multiple directions. We recorded all nest locations with a Global Positioning System. On subsequent visits to the nest, investigators stayed >300 m away while monitoring to determine if it was successful or failed.

We estimated annual reproduction parameters with radiomarked birds as the experimental units. We defined nesting rate as the proportion of females alive on 1 April that attempted to nest, and nest success as the proportion of all known nests in which  $\geq 1$  egg hatched (Cowardin et al. 1985). Adjusted nest success, or an estimate of annual nest success included additional nests lost during the laying period that we did not observe directly in the field but were based on localized movements post hoc (Lehman et al. 2005). We defined female success as the proportion of females that successfully hatched  $\geq 1$  poult and reneest rate as the proportion of females unsuccessful on their first nesting attempt that attempted another nest (Cowardin et al. 1985). We calculated annual nest success estimates for both first nests and reneests. Herein, we refer to nest success as an annual estimate and nest survival as proportional hazard modeling of nest failure events.

We confirmed the predator of some nests using 2 infrared cameras placed while female turkeys were away from the nest and by identifying dorsal guard hairs collected at depredated nests. We moved cameras to different nests throughout each nesting season as nests hatched or were

predated. We searched shrubs, downed woody debris, and other vegetation at nest predation sites for dorsal guard hairs of predators, which we identified using a microscope (Moore et al. 1974). To increase certainty that predator hair found at predated nests were attributed to the predation event, we searched for hair on shrubs or pine woody debris at reference sites 20 m away (or closest proximity to 20 m) in each cardinal direction from nests that were predated. If we did not find hair 20 m from the nest, we inferred that hair at the nest represented that of the predator that destroyed the nest.

We measured precipitation daily during the nesting season. Precipitation can be variable at the local level in the Black Hills, so we examined soil and vegetation near nests to confirm precipitation. If both understory vegetation and surface soil were wet from precipitation, we determined the female was likely wet following the precipitation event and we used the precipitation data (cm) from the nearest weather station as the value for daily precipitation. We obtained precipitation data from 1 of 5 weather stations in the area. One rain gauge was located at our field station near Pringle, South Dakota, and we also used records from 4 National Oceanic and Atmospheric Administration weather stations (National Climatic Data Center 2001–2003). Measured precipitation values may only represent an approximate amount at each nest site because weather stations were usually several kilometers from nests. We monitored sites adjacent to nests twice daily, once in the morning and once in the afternoon, to determine if incubating female turkeys would have likely become wet from the previous evening or during the present day. We avoided disturbing incubating females when checking for precipitation on nests by staying at distances 300–500 m from the nest.

We entered nest locations into a Geographic Information System and overlaid with the Black Hills National Forest Service Resource Information System (RIS) coverage (Black Hills National Forest Vegetation Database, United States Forest Service, Custer, SD, 2000). Each land cover polygon (4–32 ha) in the RIS coverage is assigned a vegetation structural stage category (Buttery and Gillam 1983). We delineated polygons of vegetation on private land within the area and assigned land cover attributes by comparing these polygons with classified polygons from adjacent Forest Service land and 1:24,000 digital orthophotographs. We calculated land cover patch size for each polygon in which nests were located. Land cover categories included 1) meadows, 2) open-canopy pine with 1–40% canopy cover, 3) mid-canopy pine with 41–70% canopy cover, and 4) dense-canopy pine with >70% canopy cover. We calculated a ruggedness index for the area surrounding each nest site at 3 spatial scales. Using a 30-m-grid digital elevation model, we buffered nest sites at 60-m, 120-m, and 240-m levels. Then, using neighborhood analysis, we calculated the standard deviation of elevation change within each buffer using ArcGIS. Distance (m) to nearest edge, such as a road

or ecotone (i.e., meadow–pine interface), we paced and truncated at 100 m.

We estimated nest-site characteristics within 1–2 days after nest termination due to hatching or predation. We quantified nest-site metrics using transects centered at the nest bowl and we averaged data collected along transects for each variable of interest. We estimated overstory canopy cover from 50 point measurements at 1-m intervals along one transect using a Geographic Resource Solutions densitometer (Stumpf 1993). We oriented each transect in a random direction by turning the housing of a compass to obtain a bearing. We measured understory visual obstruction readings (VOR) of vegetation by placing a Robel pole with 2.54-cm increments (Robel et al. 1970, Benkobi et al. 2000) in the nest bowl and at 1 m from the nest in the 4 cardinal directions. We recorded the lowest visible increment on the pole from a distance of 4 m. We estimated VOR from the 4 cardinal directions at the nest bowl; however, at the peripheral 1-m measurements we estimated VOR from 3 cardinal directions minus the VOR measurement back across the nest bowl so as to not duplicate visual obstruction readings across the nest bowl. Estimation of understory visual obstruction was consistent because investigators kneeled to a height of 1 m while taking VOR. We measured height of any live vegetation with a ruler each time we recorded the VOR measurements. We estimated percent canopy cover (Daubenmire 1959) of total herbaceous cover, grass, forbs, shrubs, and plant species using a 0.1-m<sup>2</sup> quadrat at the nest bowl and at 2-m intervals in the cardinal directions along 4 transects ( $n = 30$ ).

We measured tree characteristics in 3 plots, with one centered at the nest bowl and 2 plots 30 m on either side of the nest along the contour. When nests were located on flat topography, we oriented transects randomly using the method described above. We recorded all trees  $\geq 15.24$  cm diameter at breast height in a variable-radius plot using a 10-factor prism (Sharpe et al. 1976). We also recorded data for trees <15.24 cm diameter at breast height in a 5.03-m fixed-radius plot. Using a compass, we recorded aspect as the prevailing downhill direction from the nest; we estimated slope along this same gradient with a clinometer. We interpolated downed woody debris (t/ha) for forest area surrounding the nest from a pictorial guide (Simmons 1982).

We defined shrub nests as those located primarily under a concealing canopy of shrubs using the method described above with a 0.1-m<sup>2</sup> quadrat (Daubenmire 1959). We defined woody debris nests as those located primarily under a canopy of pine slash or other woody debris combined with greater downed woody debris values (>25 t/ha). We categorized nests as other when concealed primarily by grass or when guard objects provided most of the concealment. In some instances, there was little if any vegetation cover over or around the nest and the primary screening cover was a guard object. Guard objects such as rocks, stumps, or bases of large trees were located immediately

**Table 1.** Number of females ( $n$ ), number of nests (nests, localized nests), nest rates, reneest rates, observed nest success, and adjusted nest success calculated annually for adult Merriam's turkeys in the southern Black Hills, South Dakota, 2001–2003.

Yr	$n^a$	Nests <sup>b</sup>	Localized nests <sup>c</sup>	Nest rate <sup>d</sup>		Renest rate <sup>e</sup>		Nest success <sup>f</sup>		Adjusted nest success <sup>g</sup>	
				%	SE	%	SE	%	SE	%	SE
2001	33	41	6	97	3.0	83	9.7	51	7.8	45	7.3
2002	36	39	7	97	2.8	71	13.1	69	7.4	59	7.3
2003	45	53	11	100	0.0	72	10.6	59	6.8	48	6.2
Pooled yr	114	133	24	98	1.3	75	6.3	59	4.3	50	4.0

<sup>a</sup> No. of radiomarked F alive 1 Apr monitored during the nesting season. No. of F in 2002 and 2003 includes radiomarked F from previous yr. Overall, we monitored 73 radiomarked F for 3 yr.

<sup>b</sup> No. of nests that we directly observed.

<sup>c</sup> No. of nests determined using localized movements (Lehman et al. 2005).

<sup>d</sup> Proportion of F alive on 1 Apr that attempted to nest (Cowardin et al. 1985).

<sup>e</sup> Proportion of F unsuccessful on their first nesting attempt that attempted to reneest (Cowardin et al. 1985).

<sup>f</sup> Proportion of all observed nests in which  $\geq 1$  egg hatched (Cowardin et al. 1985).

<sup>g</sup> Adjusted nest success (includes additional nests that we did not observe directly in the field but were based on localized movements post hoc; Lehman et al. 2005).

adjacent to nesting females and provided some lateral concealment.

We used maximum likelihood to evaluate log-linear models (PROC CATMOD; SAS Institute, Cary, NC) comparing annual nest success estimates between years and between first nests and reneests. We compared proportion of days with precipitation events between first nest and reneest incubation periods using likelihood ratio tests (PROC LOGISTIC; SAS Institute). We set the significance level at  $P = 0.10$  for these comparisons.

We modeled nest hazard functions with several covariates using proportional hazard models (Cox 1972; PROC PHREG, SAS Institute). We used proportional hazard modeling for nest mortality analyses (Heisey et al. 2008). We modeled nest age at which failure occurred using both fixed and time-dependent covariates expressed as

$$\log b_i(t) = \alpha(t) + \beta_1 x_{i1} + \beta_2 x_{i2}(t),$$

where  $b_i(t)$  was the hazard (or risk) that the  $i$ th nest would fail at time  $t$ ,  $x_{i1}$  was a fixed covariate, and  $x_{i2}(t)$  was a covariate that varied with time. We used the Efron approximation (Efron 1977) for ties and plotted deviance residuals to assess if data were adequately fitted by models (Allison 1995). We estimated hazard ratios and estimates of percent change in the hazard for unit increases in the covariate. We modeled first nests and reneests to account for temporal change in vegetation growth, precipitation patterns, and nest-site selection.

We developed nest hazard models using a combined approach. We developed an initial set of candidate models and covariates using the information-theoretic approach (Burnham and Anderson 1998, 2002). Because of the large set of possible covariates that could be associated with nest hazards we reduced the number of candidate models by conducting univariate logistic regression for continuous covariates (PROC LOGISTIC; SAS Institute) and chi-square contingency tables (PROC FREQ; SAS Institute) for categorical covariates at  $P \leq 0.10$  (Hosmer and Lemeshow 2000, Steidl 2006). We selected a more liberal  $\alpha$ -level because the 0.05 level can fail in identifying variables

known to be important (Hosmer and Lemeshow 2000). We evaluated covariates for correlations ( $r > 0.6$ ) and we included only one variable from a correlated set in the final set of candidate models. We ranked a final parsimonious set of models and compared them for both first nest hazards ( $n = 16$  models) and reneest hazards ( $n = 8$  models). We included the global model as a candidate in the final set of models because of the restrictive model screening process (Guthery et al. 2005). We compared hazard models using Akaike's Information Criterion (QAIC) for discrete data (Burnham and Anderson 2002). We computed QAIC using the log likelihood and number of parameters. We interpreted models  $\leq 2.0 \Delta QAIC$  for nest hazards.

## RESULTS

We captured and radiomarked 73 adult and 10 yearling females during winter 2001–2003. During the laying period, 62% of relocations were visual observations and 38% were triangulated (mean polygon error = 0.76 ha [SE = 0.17]; mean no. of bearings/relocation = 3.94 [SE = 0.06]). We estimated nesting parameters from 157 nests (111 first nests, 46 reneests; Table 1). We censored 2 nesting attempts because females abandoned nests during the incubation period because of investigator disturbance. Most females that failed on their first nest attempt only attempted one reneest ( $n = 35$  F). Only 2 females reneested multiple times; one adult female reneested twice in 2002 and another adult female reneested 3 times in 2003. One female reneested after loss of her 2-day-old brood in 2003.

Median date for onset of incubation was 10 May and median date of hatching was 6 June for first nests. Median date for onset of incubation for reneests was 15 June and median date of hatching was 12 July. For the entire study, 90% of radiomarked females were incubating first nests within the period from 3 May through 29 May; for reneests, the range of dates was 23 May through 11 July. Nesting rate for adults was 98% (SE = 1.3; Table 1). Nesting rate for yearling females was 50% (5 of 10 for pooled yr) and annual nest success for yearlings was 83% (5 of 6 were successful for pooled yr). Reneest rates for adults did not differ among

**Table 2.** Means (SE) and comparisons of covariates measured for first nest ( $n = 92$ ) and renest ( $n = 41$ ) sites for Merriam's turkeys in the southern Black Hills, South Dakota, USA, 2001–2003.

Covariate	First nests						Renests					
	Successful		Unsuccessful		Comparison <sup>a</sup>		Successful		Unsuccessful		Comparison <sup>a</sup>	
	$\bar{x}$	SE	$\bar{x}$	SE	$\chi^2$	$P$	$\bar{x}$	SE	$\bar{x}$	SE	$\chi^2$	$P$
Coarse-scale metrics												
Meadow habitat <sup>b</sup>	5.0		7.0				4.0		1.0			
Open-canopy pine (1–40% OCC) <sup>b</sup>	18.0		16.0				15.0		5.0			
Mid-canopy pine (41–70% OCC) <sup>b</sup>	21.0		13.0				8.0		5.0			
Dense-canopy pine (71–100% OCC) <sup>b</sup>	9.0		4.0				2.0		0.0			
Overall $\chi^2$ test for land cover					2.49	0.48					1.75	0.63
Ruggedness index (60-m buffer)	7.9	0.4	7.6	0.7	0.24	0.63	5.6	0.4	5.7	0.7	0.03	0.87
Ruggedness index (120-m buffer)	8.0	0.4	7.2	0.6	1.27	0.26	5.9	0.5	5.6	0.6	1.15	0.69
Ruggedness index (240-m buffer)	7.4	0.3	6.7	0.5	1.59	0.21	5.8	0.4	5.2	0.5	0.96	0.33
Land cover patch size (ha)	269.5	24.2	903.9	580.3	2.93	0.09	336.1	35.9	217.2	42.0	3.71	0.05
Distance to edge (m)	60.5	5.5	55.9	6.2	0.58	0.82	40.8	6.4	43.7	12.0	0.06	0.81
Fine-scale metrics												
North aspect (316–45°) <sup>b</sup>	17.0		10.0				11.0		2.0			
West aspect (226–315°) <sup>b</sup>	16.0		10.0				5.0		3.0			
South aspect (136–225°) <sup>b</sup>	6.0		6.0				6.0		0.0			
East aspect (46–135°) <sup>b</sup>	14.0		14.0				7.0		6.0			
Overall $\chi^2$ test for aspect					1.41	0.70					5.90	0.12
Overstory canopy cover	39.9	2.5	36.8	3.5	0.57	0.45	29.6	4.0	37.5	7.0	1.05	0.31
Basal area (m <sup>2</sup> /ha)	13.8	1.1	13.9	1.4	0.01	0.95	12.5	1.5	13.8	2.1	0.20	0.65
Large tree ( $\geq 15.23$ cm) dbh (cm)	29.2	0.8	27.7	1.2	1.22	0.27	26.6	1.8	28.3	1.6	0.38	0.54
Small tree ( $< 15.23$ cm) density (trees/ha)	334.9	47.6	467.1	122.3	1.24	0.27	209.4	66.1	243.2	53.4	0.09	0.76
Small tree dbh (cm)	8.2	0.5	7.7	0.7	0.36	0.55	7.0	0.9	8.4	1.0	0.81	0.37
Total herbaceous cover (%)	52.5	2.8	40.5	3.7	6.72	0.01	62.9	4.8	59.2	6.7	0.18	0.67
Grass cover (%)	12.1	1.9	15.8	3.6	0.93	0.33	22.9	3.7	25.5	7.7	0.11	0.74
Forb cover (%)	6.1	0.8	3.8	0.7	4.30	0.04	8.1	2.0	7.1	2.1	0.10	0.75
Shrub cover (%)	36.5	3.3	21.0	2.6	11.87	$< 0.01$	44.8	4.6	40.9	7.3	0.21	0.65
Vegetation ht (cm)	19.2	2.6	9.9	1.5	10.44	$< 0.01$	31.4	3.5	24.2	4.4	1.42	0.23
Visual obstruction (cm)	31.3	2.1	24.5	2.1	4.93	0.03	34.7	3.2	22.2	5.2	4.44	0.04
Woody debris (t/ha)	22.4	2.4	18.3	2.2	1.46	0.23	15.6	2.9	15.1	2.9	0.01	0.91
Slope (%)	28.0	2.2	19.9	1.9	7.49	0.01	16.4	2.6	19.2	4.9	0.29	0.59

<sup>a</sup> We used single-variable logistic regression models for continuous covariates and we used contingency tables for categorical covariates.

<sup>b</sup> Total no. instead of means (SE) for successful and unsuccessful nests in each categorical variable. We categorized pine habitats by overstory canopy cover (OCC).

years ( $\chi^2 = 1.02$ ,  $df = 2$ ,  $P = 0.60$ ) and averaged 75% (SE = 6.3; Table 1). Adjusted annual nest success did not differ among years ( $\chi^2 = 1.99$ ,  $df = 2$ ,  $P = 0.37$ ) and averaged 50% (SE = 4.0; Table 1). Nest success of renests (62%, SE = 17.0) was higher ( $\chi^2 = 3.50$ ,  $df = 1$ ,  $P = 0.06$ ) than for first nests (45%, SE = 4.0).

We identified cause of failure for 49 of 53 failed nests by Merriam's turkeys in the southern Black Hills. We were not able to positively identify 4 (7%) nest failures because sign was not evident or we could not identify the hair in the lab. One female died from disease while incubating (2%, 1 of 53) and one nest failure was attributed to great horned owl (*Bubo virginianus*) predation of the marked female while incubating a nest (2%, 1 of 53). Presence of dorsal guard hairs (46 sites) and in some instances infrared cameras photos (6 sites) identified 47 (89%) nest failures as being attributed to mammals. Five sites had both hair and camera photos as evidence. Of sites with hair, 44 (96%) were identified as coyotes (*Canis latrans*) and 2 (4%) were bobcats (*Lynx rufus*). We placed infrared cameras at 15 nests and 9 nests hatched successfully while being monitored. Infrared camera photos provided photographic evidence at 4 sites where

coyotes were the predator and 2 sites where bobcats were the predator. Also, photographic evidence verified great horned owl predation of a nesting female. We did not find evidence of mammalian hair at adjacent 20-m reference sites.

Average distance of nests from nearest weather stations was 6.16 km (SE = 0.34). Proportion of daily precipitation events was greater ( $\chi^2 = 7.51$ ,  $df = 1$ ,  $P = 0.006$ ) during the first nest incubation period ( $\bar{x} = 0.46$ , SE = 0.05) than the renest incubation period ( $\bar{x} = 0.26$ , SE = 0.05).

We modeled nest hazard functions from 135 nests (93 first nests, 42 renests) initiated by 78 female Merriam's turkeys. Eighty-two nests were successful and 53 were unsuccessful; however, only 2 unsuccessful nests were confirmed not to be related to mammalian predation, so we modeled nest hazard functions for mammalian predation using 51 unsuccessful events.

Several metrics differed between successful and unsuccessful first nest sites (Table 2). Land cover patch size was a coarse-scale metric that was smaller for successful nests, and total herbaceous cover, forb cover, shrub cover, vegetation height, visual obstruction, and slope were fine-scale metrics that differed (Table 2). Total herbaceous cover, vegetation

**Table 3.** Proportional hazard models for first nest daily survival ( $n = 92$  first nests;  $n = 2,040$  daily observations) for Merriam's turkeys in the southern Black Hills, South Dakota, USA, 2001–2003. Log likelihood ( $-2\ln L$ ), number of parameters ( $K$ ), Akaike's Information Criterion (QAIC), Kullback–Leibler distances rescaled as simple differences ( $\Delta QAIC$ ), Akaike weights ( $w_i$ ), and evidence ratios (ER). We present only models with evidence ratios  $\leq 4$ .

Model	$-2\ln L$	$K$	QAIC	$\Delta QAIC$	$w_i$	ER
$h_1(t) = -0.03(\text{shrub}^a) - 0.02(\text{slope}^b) + 0.87(\text{precipitation}^c) + 0.02(\text{shrub} \times \text{precipitation})$	265.32	5	276.03	0.00	0.28	1.00
$h_2(t) = -0.04(\text{shrub}^a) + 0.86(\text{precipitation}^c) + 0.02(\text{shrub} \times \text{precipitation})$	267.83	4	276.30	0.27	0.24	1.14
$h_3(t) = -0.02(\text{shrub}^a) - 0.02(\text{slope}^b) + 0.86(\text{precipitation}^c) - 0.02(\text{VOR}^d) + 0.02(\text{VOR} \times \text{precipitation})$	265.09	6	278.09	2.06	0.10	2.78
$h_4(t) = -0.03(\text{shrub}^a) - 0.02(\text{slope}^b) + 0.87(\text{precipitation}^c)$	269.65	4	278.11	2.09	0.10	2.84
$h_5(t) = -0.02(\text{shrub}^a) - 0.02(\text{slope}^b) + 0.86(\text{precipitation}^c) - 0.02(\text{VOR}^d) + 0.02(\text{shrub} \times \text{precipitation})$	265.12	6	278.12	2.09	0.10	2.85

<sup>a</sup> Shrub cover (%) around nest sites.

<sup>b</sup> Slope (%) metric at nest sites.

<sup>c</sup> Time-dependent covariate precipitation (cm) that occurred daily during the incubation period.

<sup>d</sup> Visual obstruction readings (VOR; cm) around nest sites.

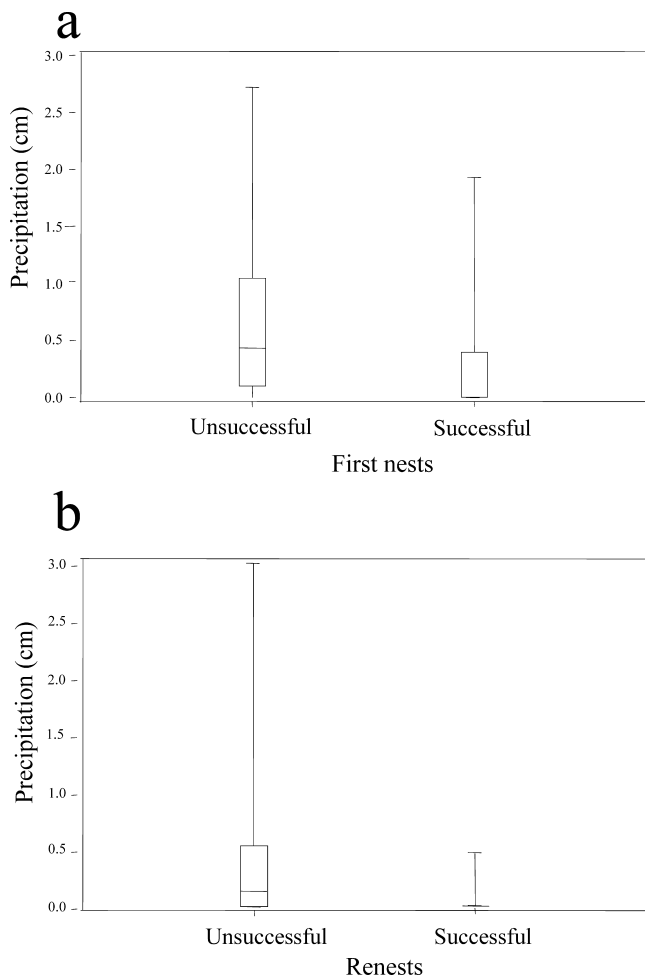
height, and shrub cover were correlated ( $r > 0.6$ ) and therefore we used only shrub cover in modeling nest hazard.

All nests that we found during the laying period survived to incubation so we modeled hazard functions for the incubation period. Two models had  $\Delta QAIC$  values

$\leq 2.0$  (Table 3). The best first nest model indicated nest hazard decreased with less daily precipitation, greater shrub cover, a shrub cover  $\times$  precipitation interaction, and steep slopes. The second best model was associated with less daily precipitation, greater shrub cover, and a shrub cover  $\times$  precipitation interaction (Table 3). Less precipitation occurred at successful first nests compared to unsuccessful first nests (Fig. 1). Deviance residuals for both models indicated the data were clustered into 2 groups of observations; however, there were no residuals  $\geq 3$  or  $\leq -3$ .

Hazard ratios indicated 3 covariates were associated with nest hazard (Table 4). Greater shrub cover and less precipitation were associated with lower hazard functions (Figs. 1, 2). The interaction of precipitation and shrub cover indicated that precipitation was less of a hazard when offset by increased shrub cover (Fig. 2). Females nesting in 20% shrub cover would be at risk with less daily precipitation ( $>0.50$  cm), whereas females nesting in 50% shrub cover could withstand more precipitation ( $>0.90$  cm) before being at risk of predation (Fig. 2). Nest mortality hazard decreased by 30% for every 10% increase in shrub cover at nest sites (Table 4). For every 1-cm increase in daily precipitation, hazard of nest mortality increased by 139% (Table 4); a 0.25-cm increase in daily precipitation would increase hazard by 24%, and a 0.50-cm increase would increase hazard by 55%. Primary screening cover for first nests was shrubs (51%), followed by woody debris or pine slash (32%), and other (17%). The other category for first nests had screening cover primarily comprised of tree and rock guard objects. Primary shrubs selected for first nests included common juniper (9.0%), western snowberry (6.4%), and chokecherry (4.9%).

Two metrics differed between successful and unsuccessful renests. Patch size (coarse-scale metric) and visual obstruction (fine-scale metric) were greater for successful nests (Table 2). Again, all renests located during the laying period were successful so we modeled hazard functions for the incubation period. Four models had  $\Delta QAIC$  values  $\leq 2.0$  (Table 5). The top 3 models carried the most weight (QAIC  $\geq 0.20$ ) and nest hazard risk decreased with greater visual obstruction, less precipitation, and a visual obstruction  $\times$



**Figure 1.** Successful and unsuccessful Merriam's turkey nests in relation to precipitation  $\leq 24$  hours before success or failure in the southern Black Hills, South Dakota, USA, 2001–2003. Precipitation was a time-dependent covariate in modeling nest hazard functions. Box-and-whisker plots for (a) first nests and (b) renests. Midpoint line = mean; box = standard deviation; whisker = range.

**Table 4.** Hazard ratios, percent (%) change, and chi-square statistics of covariates associated with daily nest survival for first nests and renests for Merriam's turkeys in the southern Black Hills, South Dakota, USA, 2001–2003. Only covariates from models  $\leq 2.0 \Delta Q A I C$  are presented and unless otherwise noted hazard ratio statistics were taken from the best top-ranking models.

Nest attempt	Hazard ratio	% change <sup>a</sup>	$\chi^2$	P
First nests				
Precipitation (cm) <sup>b</sup>	2.39	139.0	21.79	<0.01
Shrub cover (%)	0.97	–30.0	8.94	<0.01
Slope (%)	0.98	–20.0	2.28	0.13
Shrub cover $\times$ precipitation	1.02	20.0	5.08	0.02
Renests				
Precipitation (cm) <sup>b</sup>	1.43	43.0	1.52	0.22
Visual obstruction (cm)	0.96	–40.0	3.97	0.05
Visual obstruction $\times$ precipitation	1.04	40.0	3.61	0.06
Land cover patch size (ha) <sup>c</sup>	1.00	0.0	0.36	0.55

<sup>a</sup> Estimated % change in the hazard for each 1-unit increase for the time-dependent precipitation (cm) covariate and 10-unit increase for the nest-site covariates. We estimated % change as  $100 \times (\text{hazard ratio} - 1)$ . The interaction terms used a 10-unit increase.

<sup>b</sup> Time-dependent covariate precipitation (cm) that occurred daily during the incubation period.

<sup>c</sup> Hazard ratio statistics taken from the fourth best renest survival model  $h_i(t) = -0.04$  (visual obstruction readings)  $- 0.002$  (land cover patch size).

precipitation interaction ( $\Delta Q A I C \leq 0.31$ ; Table 5). Deviance residuals indicated the data were adequately fitted by the best renest model with residuals between 2 and  $-2$ .

Hazard ratios indicated 2 covariates were associated with renest hazard (Table 4). Greater visual obstruction lowered hazard functions, and the visual obstruction  $\times$  precipitation interaction indicated an offsetting effect on hazard functions. Hazard of nest mortality decreased by 40% for every 10-cm increase in visual obstruction at renests (Table 4).

For renests, females primarily selected shrubs as screening cover (66%), and a smaller percentage selected woody debris (22%) and other (12%) for renests. Primary screening cover for the other category for renests was grass cover. For renests, primary shrubs selected included western snowberry (19.9%), chokecherry (4.6%), and poison ivy (*Toxicodendron rydbergii*; 3.6%).

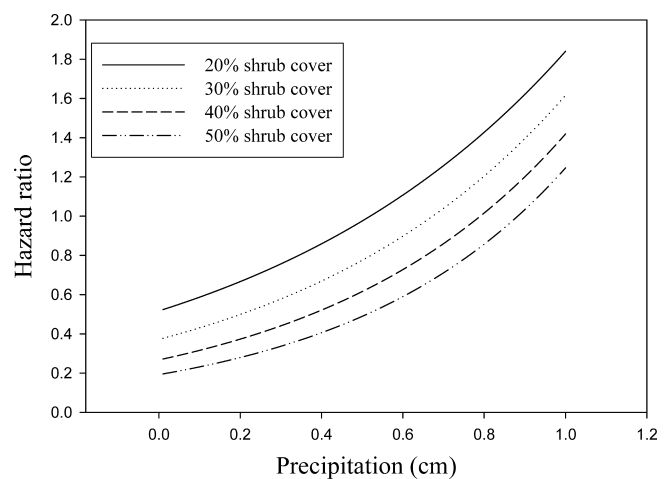
## DISCUSSION

Hazard modeling provided support for both the moisture-facilitated nest predation hypothesis and the nest concealment hypothesis in a semiarid contiguous ecosystem. Precipitation varied throughout the incubation period but generally declined by the renesting period, whereas visual obstruction from vegetation development gradually increased through the nesting season. The interaction of precipitation and concealment cover appears to influence mammalian nest predation in the southern Black Hills, and greater visual obstruction from shrub cover partially offsets the negative effects of precipitation during incubation. Shrub cover can be limited early during the first nest period because leaves of deciduous shrubs are not developed. Common juniper, an evergreen shrub, was the most selected shrub during the first nest period as screening cover for first nests. Deciduous vegetation was not an important covariate for nest survival in Arizona (Wakeling et al. 1998). Woody debris, or pine slash, was also selected as screening cover during the first nest period, but it was not a covariate that lowered hazard risk. Steeper slopes were included in the best first nest survival model and several successful nests were located on extremely steep slopes such as cliff ledges or

steep, rocky slopes of ravines. Also, many of these steep, rocky areas had high shrub densities. Nesting Merriam's females in Arizona also selected for shrubs along steep slopes (Wakeling and Shaw 1994).

Laying-period nest survival was 1.0 based on nests we found during this study; however, there was some nest predation occurring during the laying period based on movements examined post hoc (Lehman et al. 2005). We estimated that 15% of nests were lost during the laying period. Our observations indicated females spent little time at the nest during the laying period compared to the longer incubation period, which may explain why the laying-period nest survival rate was high. Because all nests found during laying survived to incubation, we assume that our presence did not alter female behavior during that period.

Merriam's turkeys in the southern Black Hills exhibited a better nesting effort and success than Merriam's populations found elsewhere in the current range of the subspecies. Nest



**Figure 2.** Hazard ratios in association with the interaction of shrub cover and precipitation for Merriam's turkeys in the southern Black Hills, South Dakota, USA, 2001–2003. Nest hazard functions were lower when shrub cover was greater in magnitude. Graph includes 20%, 30%, 40%, and 50% levels of understory shrub cover and its effects on nest hazard under varying levels of daily precipitation.

**Table 5.** Proportional hazard models for renest daily survival ( $n = 41$  reneests;  $n = 999$  daily observations) for Merriam's turkeys in the southern Black Hills, South Dakota, USA, 2001–2003. Log likelihood ( $-2\ln L$ ), number of parameters ( $K$ ), Akaike's Information Criterion (QAIC), Kullback–Leibler distances rescaled as simple differences ( $\Delta QAIC$ ), Akaike weights ( $w_i$ ), and evidence ratios (ER). We present only models with evidence ratios  $\leq 4$ .

Model	$-2\ln L$	$K$	QAIC	$\Delta QAIC$	$w_i$	ER
$h_i(t) = -0.05(\text{VOR}^a)$	73.85	2	78.17	0.00	0.24	1.00
$h_i(t) = -0.05(\text{VOR}^a) + 0.36(\text{precipitation}^b) + 0.04(\text{VOR} \times \text{precipitation})$	69.29	4	78.40	0.24	0.21	1.12
$h_i(t) = -0.05(\text{VOR}^a) + 0.44(\text{precipitation}^b)$	71.83	3	78.48	0.31	0.20	1.17
$h_i(t) = -0.04(\text{VOR}^a) - 0.002(\text{LCPS}^c)$	72.61	3	79.26	1.09	0.14	1.73
$h_i(t) = -0.04(\text{VOR}^a) + 0.36(\text{precipitation}^b) + 0.03(\text{VOR} \times \text{precipitation}) - 0.001(\text{LCPS}^c)$	68.91	5	80.62	2.46	0.07	3.42
$h_i(t) = -0.003(\text{LCPS}^c)$	76.57	2	80.89	2.72	0.06	3.90

<sup>a</sup> Visual obstruction readings (VOR; cm) around nest sites.

<sup>b</sup> Time-dependent covariate precipitation (cm) that occurred daily during the incubation period.

<sup>c</sup> Land cover patch size (LCPS; ha).

success and renesting rates were similar to adult females from Colorado, USA (Hoffman et al. 1996), but higher than reported for Merriam's turkey populations in other ponderosa pine forests (Hengel 1990, Wakeling 1991, Rumble and Hodorff 1993, Thompson 1993). Renest success was higher than first nest success as has been observed in other studies, probably because of better nest concealment (Lockwood and Sutcliffe 1985, Rumble and Hodorff 1993). Hazard modeling indicated survival of reneests was most influenced by greater visual obstruction surrounding nests. For reneests in the central Black Hills, visual obstruction was greater than for first nests, and in the 1-m to 2-m area surrounding the nest bowl visual obstruction averaged 23 cm tall (Rumble and Hodorff 1993). Successful nest sites in Arizona also had greater visual obstruction (Wakeling and Shaw 1994, Wakeling et al. 1998). Percent shrub cover was not a covariate of influence for survival of reneests, probably because it was used by most females as the primary screening cover. Western snowberry was the most common shrub used as nest cover for reneests. By mid-May, snowberry had its leaves fully developed to provide greater concealment. Schmutz and Braun (1989) thought that spring vegetation growth, or some correlate thereof, controlled the onset of nesting of turkeys in Colorado. Spring precipitation, or some correlate thereof, may possibly act as a proximate cue for renesting by females in the central Black Hills (Rumble and Hodorff 1993). A counteracting effect may occur where greater precipitation leads to more nest predation early but later provides more cover for renesting females, which may offset some losses of production during the first nest period. Beasom and Pattee (1980) found lack of precipitation reduced recruitment of poults in Texas, USA, and a threshold of precipitation was needed to maintain productivity.

It has been hypothesized that precipitation increases nest predation rates on turkeys during nesting (Roberts et al. 1995, Roberts and Porter 1998). Mammalian predators use olfactory cues to locate nests (Storaas 1988), and evidence suggests that incubating female turkeys are more easily located by predators such as coyotes, red fox (*Vulpes vulpes*), and raccoons (*Procyon lotor*) during wet periods (Roberts and

Porter 1998). Our data indicated that coyotes were the primary mammalian predator of Merriam's turkey nests. Numerous other studies also report mammalian predators as the primary predators depredating wild turkey nests (Schemnitz et al. 1985, Kurzejeski et al. 1987, Wertz and Flake 1988, Palmer et al. 1993). Lack of predation on turkey nests by American crows (*Corvus brachyrhynchos*) was noteworthy given their importance as predators in the central Black Hills (Rumble and Hodorff 1993).

Only one previous study tested the moisture-facilitated nest predation hypothesis in a semiarid environment and results indicated little or no association of nest predation with precipitation; however, this study used a different modeling design and precipitation was not a time-dependent covariate over the entire nesting period for scaled quail (Pleasant et al. 2003). Although the southern Black Hills is also semiarid, most (60%) of the annual precipitation occurs during the nesting season for turkeys (National Climatic Data Center 1973–2003).

Precipitation appeared to influence hazard of predation of first nests more than reneests. However, precipitation generally declines later in the nesting period and vegetation development provides better concealment of nests during the renest incubation period. Our study provides support for the theory that water activates bacteria on the surface of the female turkey's skin (Syrotuck 1972, Roberts and Porter 1998) and more easily allows mammalian predators with an excellent sense of smell, such as coyotes, to locate incubating female nest sites. We theorize that coyotes are primarily using olfaction to detect nests, not visual cues. When females get wet they can be detected at greater distances from the nest; thus, the hazard probability increases during and immediately following precipitation events. Visual obstruction from vegetation cover was the most important covariate for renesting females, but the renesting period also received fewer precipitation events and coyotes may have had more difficulty detecting nests under these drier conditions. Temporally, as the nesting season progressed, drier conditions and greater vegetation cover resulted in improved nest survival. Future investigations should consider quantifying the relationship of precipitation, nest concealment, and mammalian nest predation in other

portions of the Merriam's turkey range with different precipitation and vegetation characteristics.

## MANAGEMENT IMPLICATIONS

Female turkeys that selected shrubs for nest cover had greater nest survival. The hazard of nest failure associated with increased daily precipitation can be partially compensated for by suitable nest areas with greater shrub cover. Predicted nest failure decreased by 30% for every 10% increase in shrub cover around first nests and 40% for every 10-cm increase in visual obstruction at re-nests. Common juniper occurred primarily beneath the forest canopy, and western snowberry and chokecherry were deciduous shrubs found in more open forests. Maintaining patches of moderate to dense forest canopy on some north- and west-facing aspects of the Black Hills will promote common juniper. Patches of open forest through timber harvest will promote conditions suitable for western snowberry and chokecherry. These deciduous shrubs, particularly chokecherry, can be reduced by excessive browsing by domestic and wild ungulates.

Although there is nothing managers can do about precipitation, they can expect reduced nesting success in years with increased occurrence of daily precipitation  $\geq 0.50$  cm during the primary incubation period. Tracking these daily precipitation events may provide managers an approximation of annual nest success. Implementation of management activities that promote greater shrub cover may partially offset the negative effects of greater precipitation events.

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