

Survival of Greater Sage-Grouse Chicks and Broods in the Northern Great Basin

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ABSTRACT Reduced annual recruitment because of poor habitat quality has been implicated as one of the causative factors in the range-wide decline of sage-grouse (*Centrocercus urophasianus*) populations since the 1950s. Because chick and brood survival are directly linked to annual recruitment and may be the primary factors that limit sage-grouse population growth, we estimated 28-day survival rates of radiomarked chicks and broods from 2000 to 2003. We examined relationships between survival and several habitat variables measured at brood sites, including food availability (insects and forbs); horizontal cover of sagebrush, grasses, and forbs; and vertical cover of sagebrush and grass. We monitored 506 radiomarked chicks from 94 broods; chick survival was 0.392 (SE = 0.024). We found evidence that both food and cover variables were positively associated with chick survival, including Lepidoptera availability, slender phlox (*Phlox gracilis*) frequency, total forb cover, and grass cover. The effect of total grass cover on chick survival was dependent on the proportion of short grass. The hazard of an individual chick's death decreased 8.6% (95% CI = -1.0 to 18.3) for each percentage point increase in total grass cover when the proportion of short grass was >70%. Survival of 83 radiomarked broods was 0.673 (SE = 0.055). Lepidoptera availability and slender phlox frequency were the only habitat variables related to brood survival. Risk of total brood loss decreased by 11.8% (95% CI = 1.2–22.5) for each additional Lepidoptera individual and 2.7% (95% CI = -0.4 to 5.8) for each percentage point increase in the frequency of slender phlox found at brood sites. Model selection results revealed that temporal differences in brood survival were associated with variation in the availability of Lepidoptera and slender phlox. Years with high brood survival corresponded with years of high Lepidoptera availability and high slender phlox frequency. These foods likely provided high-quality nutrition for chicks during early growth and development and enhanced survival. Habitat management that promotes Lepidoptera and slender phlox abundance during May and June (i.e., early brood rearing) should have a positive effect on chick and brood survival in the short term and potentially increase annual recruitment. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):904–913; 2009)

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Greater sage-grouse (*Centrocercus urophasianus*) populations have declined range-wide since the 1950s (Connelly and Braun 1997, Connelly et al. 2004). Several factors have been implicated in population declines of sage-grouse including reduced annual recruitment because of poor-quality brood-rearing habitat (Crawford and Lutz 1985, Connelly and Braun 1997). Chick and brood survival are directly linked to annual recruitment and may be the factors most limiting sage-grouse population growth, yet they are poorly understood aspects of sage-grouse reproductive ecology (Aldridge and Brigham 2001, Connelly et al. 2004, Crawford et al. 2004). Considerable research has been conducted on use and selection of brood-rearing habitat through monitoring of radiomarked sage-grouse females with broods (Wallestad 1971, Drut et al. 1994a, Sveum et al. 1998, Aldridge and Brigham 2002). Habitat relationships identified from these studies have been used to develop guidelines and management recommendations targeted to improve recruitment of sage-grouse chicks (Connelly et al. 2000, Crawford et al. 2004). However, habitat selection by females with broods may not provide a direct link between habitat resources and chick and brood survival (Morrison 2001). An understanding of the mechanisms that directly influence daily survival

rates of chicks and broods is a prerequisite for development and implementation of habitat management strategies that affect annual recruitment and, ultimately, sage-grouse populations.

Several habitat factors could influence sage-grouse chick and brood survival, including food availability and habitat structure (e.g., cover and ht of vegetation) in brood-rearing habitat (Southwood and Cross 1969, Hill 1985, Park et al. 2001). Forb and insect abundance could affect survival because they are the primary foods of sage-grouse chicks and critical sources of nutrients necessary for maintenance, growth, and development (Klebenow and Gray 1968, Peterson 1970, Johnson and Boyce 1990, Pyle 1992, Drut et al. 1994b). Insect abundance may be particularly critical because research on captive sage-grouse chicks (Johnson and Boyce 1990) and red grouse (*Lagopus lagopus*) chicks (Park et al. 2001) revealed that they require insects for growth and survival. The insect taxa consumed by chicks may be equally important for chick growth and survival because of differences in nutritional quality among taxa (Borg and Toft 2000). Habitat structure may also be important for survival because chick mortality from predation and exposure may be related to the availability of vertical and horizontal cover provided by shrubs, grasses, and forbs (Wallestad 1971, Sveum et al. 1998, Aldridge 2005).

Only recently have researchers monitored the survival of individually marked sage-grouse chicks and investigated the direct relationships between vegetative cover at brood

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locations and chick survival (Burkepile et al. 2002, Aldridge 2005, Gregg et al. 2007). Linkages among insect availability and chick survival or effects of habitat resources on brood survival have not been investigated and remain unknown. The critical period for survival of sage-grouse chicks is the first 4 weeks after hatching (Gregg et al. 2007). Therefore, our objective was to determine the key habitat factors linked to chick and brood survival by investigating the relationships between measures of habitat resources and 28-day survival rates of radiomarked sage-grouse chicks and broods.

STUDY AREA

We conducted our study at 3 sites within northwestern Nevada, USA, and southeastern Oregon, USA. Sheldon National Wildlife Refuge (SNWR; 41°45'N, 119°15'W), Nevada, and Hart Mountain National Antelope Refuge (HMNAR; 42°30'N, 119°36'W), Oregon, were administered by the United States Fish and Wildlife Service (USFWS) and encompassed 232,294 ha and 114,375 ha, respectively. Beatys Butte (42°05'N, 119°20'W) in Oregon was administered by the Bureau of Land Management and encompassed 110,682 ha. We selected these study sites because they were >40 km apart and accessible during spring, represented typical habitat found in the northern Great Basin, and provided a previously compiled long-term data set on sage-grouse habitat use and productivity (Gregg 1991, Barnett 1992, Drut 1992, Coggins 1998, Davis 2002). Grazing by domestic livestock was eliminated from the SNWR during 1994 and from the HMNAR during 1991. Domestic livestock grazing on Beatys Butte averaged 26,121 animal unit months (AUMs) from 1983 to 1989 and 14,000 AUMs since 1989 (Bureau of Land Management 1994).

All 3 sites were characteristic of shrub-steppe and consisted of flat sagebrush (*Artemisia* spp.) plains interrupted by rolling hills, ridges, draws, and upland meadows. Elevation ranged from 1,200 m to 2,450 m across areas, and annual average precipitation and average minimum and maximum temperatures ranged from 29 cm to 33 cm and from 22°C to 38°C, respectively (Western Regional Climate Center 2005). During our study, annual precipitation ranged between a low of 17.9 cm in 2002 and a high of 33.3 cm in 2003 (M. Gregg, USFWS, unpublished data). Primary shrub species included Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*), mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*), little sagebrush (*Artemisia arbuscula*), antelope bitterbrush (*Purshia tridentata*), western snowberry (*Symphoricarpos occidentalis*), and green rabbitbrush (*Chrysothamnus viscidiflorus*). Grasses consisted largely of bluegrass (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), needlegrass (*Stipa* spp.), fescue (*Festuca* spp.), basin wildrye (*Leymus cinereus*), and bottlebrush squirreltail (*Elymus elymoides*). Cheatgrass (*Bromus tectorum*) was a minor component of all study areas but most prevalent on Beatys Butte. Common annual and perennial forbs included deserparsley (*Lomatium* spp.), mountain-dandelion (*Agoseris* spp.), milkvetch (*Astragalus* spp.), hawksbeard (*Crepis* spp.), pussytoes (*Antennaria* spp.),

aster (*Aster* spp.), buckwheat (*Eriogonum* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.).

METHODS

Data Collection

We captured female sage-grouse with spotlights and nets (Giesen et al. 1982) during March and April 2000–2003 and fitted each female with a 20-g necklace-mounted radio-transmitter (Advanced Telemetry Systems, Isanti, MN). We monitored radiomarked females during spring to locate nest sites (Gregg et al. 2006). We estimated hatch date and determined initial brood size (i.e., no. of chicks that departed nest) for females with successful nests (Gregg et al. 2007). After flushing radiomarked females with broods, we captured all chicks that we could visually locate (Gregg et al. 2007). We weighed chicks to the nearest 0.1 g, recorded age (i.e., days posthatch), and implanted radiotransmitters (model BD2-A, Holohil Systems Ltd., Carp, ON, Canada) subcutaneously with placement anterior to the scapulae (Gregg et al. 2007). We monitored radiomarked chicks daily for 28 days following capture to estimate survival and to determine causes of mortality (Gregg et al. 2007). We did not intentionally flush females and broods during monitoring, and we assumed that radiomarked chicks found within a 30-m radius of the female were alive. At the end of the monitoring period, we flushed radiomarked broods using bird dogs to determine brood status. We considered broods successful if ≥ 1 chick was present with the female. Grouse capture and transmitter attachment procedures were approved by the Oregon State University Institutional Animal Care and Use Committee (Animal Care and Use proposal no. 2656).

We estimated relative abundance of forbs, grasses, and shrubs along 2 perpendicular, 10-m transects, intersecting at the center of each daily brood location. We used the brood female's location as the plot center, which we identified by a Universal Transverse Mercator coordinate obtained during brood monitoring. We established transects with a random compass bearing and used the line-intercept method (Canfield 1941) to estimate canopy cover of sagebrush along each transect. We measured height of intercepted shrubs from the ground to the top of the shrub canopy (excluding flowering stalks) and classified them as short (<40 cm) or tall (≥ 40 cm). We visually estimated the percentage of total forb cover, short grass (<18 cm) cover, and total grass cover in 5 plots measuring 20 × 50 cm and spaced equidistantly along each transect (Daubenmire 1959). We recorded frequency of primary food forbs in 3 (10 × 25 cm, 20 × 25 cm, and 20 × 50 cm) nested frames at each of the 5 plots (Hironaka 1985). We added individual frequencies to obtain a summed frequency for each primary food forb (Smith et al. 1986). We classified short grass based on droop height and excluded flowering stalks. Grass cover and height measurements included residual and new growth. We quantified vertical cover of grass and sagebrush by calculating the proportion of horizontal grass and sagebrush cover that consisted of short grass and short sagebrush.

Table 1. Habitat variables collected at brood locations and used in models of greater sage-grouse chick and brood survival in southeastern Oregon, USA, and northwestern Nevada, USA, 2000–2003.

Type	Code	Variable	Description
Food ^a	COL	Coleoptera	No. of beetles collected in pitfall traps
	HYM	Hymenoptera	No. of ants (primarily Formicidae) collected in pitfall traps
	ORT	Orthoptera	No. of grasshoppers and crickets collected in pitfall traps
	LEP	Lepidoptera	No. moth and butterfly larva and adults collected in pitfall traps
	AGF	Mountain dandelion	Nested frequency
	CRF	Hawksbeard	Nested frequency
	PHF	Slender phlox	Nested frequency
	ASF	Milkvetch	Nested frequency
Cover	TFC	Total forb cover	Visually estimated % cover of all forbs
	TOG	Total grass cover	Visually estimated % cover of grasses
	PSG	Proportion of short grass	% of total grass cover <18 cm tall
	SCC	Sagebrush canopy cover	% canopy cover of sagebrush measured by line-intercept
	PSS	Proportion of short sagebrush	% of total sagebrush cover <40 cm tall

^a Insects and forbs consumed by juv sage-grouse were identified from previous (Klebenow and Gray 1968, Peterson 1970, Pyle 1992, Drut et al. 1994b) and concurrent (M. Gregg, U.S. Fish and Wildlife Service, unpublished data) diet studies.

We sampled ground-dwelling insects in 5 pitfall traps (e.g., 473-mL plastic cups) placed equidistantly along one of the transects (Morrill 1975). We buried traps flush to the ground, filled them with a nontoxic glycerin glycol solution, covered them to exclude rodents and other debris, and set them for 6 days. We identified and counted common insect taxa found in chick diets (i.e., Coleoptera, Hymenoptera, Lepidoptera, Orthoptera) to estimate relative abundance at each brood location. We identified forb and insect taxa consumed by sage-grouse chicks from previous (Klebenow and Gray 1968, Peterson 1970, Pyle 1992, Drut et al. 1994b) and concurrent (M. Gregg, unpublished data) research.

Data Analysis

Chick survival.—We estimated Kaplan–Meier (KM) survival rates (Kaplan and Meier 1958) and Cox regression models (Cox 1972) with PROC PHREG (version 8.02; SAS Institute, Cary, NC) to examine relationships between habitat variables and 28-day survival rates of individually radiomarked chicks. We considered time of chick death as the day we discovered a chick dead (Gregg et al. 2007). For the few cases ($n = 3$) in which the exact day of the chick death was unknown, we used the midpoint between the last known day the chick was alive and the day we discovered it dead. We right-censored chicks alive at the end of the 28-day monitoring period and chicks with unknown fate (e.g., radio failure, transmitter loss, and chick adoption) to the last date they were known to be present with the radiomarked female. We identified transmitter failure by changes in signal characteristics or irregular performance immediately preceding the disappearance of chicks and identified transmitter loss when we found undamaged radios near radiomarked broods and no additional evidence was present to confirm death. We also verified transmitter failure and loss from subsequent recaptures of previously radiomarked chicks. A sensitivity analysis indicated that censoring chicks with unknown status was random and independent of chick fate (Gregg 2006). We defined the day of marking as *time* =

0 for all chicks and included the age of chicks at capture in all regression analyses. We treated individually radiomarked chicks as independent sampling units but accounted for intrabrood correlations in our regression analyses using the COVSANDWICH option in SAS statistical software (P. Allison, University of Pennsylvania, personal communication). We used a bootstrap resampling method (Efron and Tibshirani 1993, Flint et al. 1995) with 500 replicates to adjust standard errors for 28-day KM chick survival estimates.

We used an information-theoretic approach to determine support for models that represented alternative hypotheses of the influence of habitat resources on chick survival (Burnham and Anderson 2002). We used knowledge from previous (Johnson and Boyce 1990, Pyle 1992, Drut et al. 1996a, Sveum et al. 1998, Aldridge 2005) and concurrent (Gregg 2006; M. Gregg, unpublished data) research to develop a set of a priori candidate models using food and cover variables collected at brood locations. Food variables included insect and forb abundance, and cover variables included horizontal measures of sagebrush, grass, and forbs and vertical measures of sagebrush and grass (Table 1). We used Akaike's Information Criterion values adjusted for small sample size (AIC_c) to compare among our set of a priori models. We calculated the Akaike weight (w_i) for each model AIC_c to choose the best-approximating model for our data (Burnham and Anderson 2002). Our full model included all food, horizontal cover, and vertical cover variables and the interactions between horizontal and vertical cover. We investigated multicollinearity by examining a correlation matrix and tolerances of all our covariates (Allison 1999). All habitat variables were time dependent (i.e., cumulative means). We evaluated linear relationships for all variables, which assumed their effect on survival changed at a constant rate. We carried forward cumulative means of habitat variables for chicks with uneven intervals (i.e., missing data points) to fill data gaps (Allison 1995). In addition to habitat variables, we included chick weight (adjusted for age at capture) in all candidate models to

account for potential variation in viability among chicks (Gregg 2006). To adjust chick weights, we regressed weight against chick age and added the residuals to the mean weight of all chicks. We calculated model-averaged parameter estimates, robust standard errors (i.e., adjusted for lack of independence among chicks in the same brood), hazard ratios, and 95% hazard ratio confidence intervals to evaluate the effect of habitat variables on the daily hazard of an individual chick's death (Allison 1995, Burnham and Anderson 2002), and we calculated maximum, rescaled, generalized r^2 values to assess the variation in chick survival explained by our models (Allison 1999).

Brood survival.—We used data from radiomarked broods to estimate brood survival. We calculated KM survival rates (Kaplan and Meier 1958) with PROC PHREG. We used Cox regression models (Cox 1972) to examine relationships between important habitat variables identified from chick survival analyses and 28-day survival rates of radiomarked broods (P. Allison, personal communication). We defined day of marking as *time* = 0 for all broods and included brood age at capture in all regression models. We considered time of total brood loss as the day we discovered a female without chicks. We identified total brood loss when the female no longer displayed brooding behavior (e.g., located with other broodless F) on multiple (>2) monitoring occasions and when we confirmed all radiomarked chicks in a brood dead. We right-censored broods with ≥ 1 chick at the end of the 28-day monitoring period.

We developed a set of 8 candidate models using Lepidoptera, total forb cover, total grass cover, proportion of short grass, and the interaction between total grass cover and proportion of short grass. We also evaluated 3 models with year and study area effects to determine whether temporal and spatial variation in brood survival was associated with habitat variables in our candidate models. We included initial brood size, hatch date, and cumulative means of daily brood movements in all candidate models to account for the effect of these nonhabitat variables on brood survival (Gregg 2006). We determined daily brood movement by measuring the distance between daily, radiomarked brood locations. In addition, we created a variable that quantified the number of transmitter-caused deaths and chicks that died <1 day following capture in each brood and included this variable in all candidate models. We used AIC_c values and w_i to select the best-approximating model from our candidate set and calculated model-averaged parameter estimates, hazard ratios, and 95% hazard ratio confidence intervals to evaluate the effect of habitat variables on the daily hazard of total brood loss (Allison 1995, Burnham and Anderson 2002). We also calculated maximum, rescaled, generalized r^2 values to assess the variation in brood survival explained by our models (Allison 1999).

RESULTS

Chick Survival

We captured, radiomarked, and monitored 506 chicks from 94 broods for 6,480 chick exposure-days. Hatch dates

ranged from 10 May to 22 June for all years. Initial brood size averaged 7.1 ± 0.1 (SE) and 6.1 ± 0.4 (SE) chicks for first nests ($n = 77$) and renests ($n = 17$), respectively. Age of chicks at capture averaged 1.5 days and ranged from 1 day to 5 days. The 28-day survival rate for radiomarked chicks was 0.392 (SE = 0.024). At the end of the 28-day monitoring period, 70 chicks were alive, 308 were dead, and fate was unknown for 128 chicks. Of the 308 dead chicks, we right-censored from analysis 8 transmitter-caused deaths (i.e., chicks found dead with antennas tangled in vegetation) and 32 chicks that died <1 day following capture. We attributed remaining chick deaths to predation (81%, $n = 251$), unknown causes (4%, $n = 14$), and exposure (1%, $n = 3$). We classified chicks as unknown fate because of transmitter failure ($n = 88$), transmitter loss ($n = 31$), and adoption ($n = 9$).

We used 480 radiomarked chicks from 87 broods in regression analyses because we did not collect insect data for 7 broods ($n = 26$ chicks). We found no evidence of multicollinearity ($r > 0.85$ or *tolerance* < 0.40) among our habitat variables; correlation and tolerances ranged from 0.00 to 0.59 and 0.47 to 0.88, respectively. Of the 14 models we evaluated, 4 were strongly supported by our data, and all included food and cover variables (Table 2). All remaining models received little support and were >4.0 AIC_c units from the best model (Table 2). We found evidence that both food and cover variables were positively related to chick survival (Table 3). In many cases, uncertainty of the effect was high because hazard ratio confidence intervals encompassed 1.0. However, Lepidoptera abundance, slender phlox frequency, total forb cover, and interaction between total grass cover and proportion of short grass showed the least variability and the greatest effect on chick survival (Table 3). The interactive effect of grass cover on chick survival revealed that the hazard of an individual chick's death decreased 8.6% (95% CI = -1.04 to 18.3) with each percentage point increase in total grass cover when the proportion of short grass was >70% at brood sites (Fig. 1). Hens with broods did not use areas with tall, dense grass cover (Fig. 1). We found little evidence that canopy cover or height of sagebrush influenced chick survival (Table 4). Predictive power of our models was low, explaining only 15% of the variation in chick survival.

Brood Survival

We used 83 radiomarked broods in our brood survival analysis. In addition to the 7 broods with missing insect data, we censored 4 broods for which the timing of the brood loss or the final status was unknown. Of the 83 broods, 29 (35%) suffered total brood loss. The 28-day survival rate for radiomarked broods was 0.673 (SE = 0.055). Brood survival differed among years (2000: $\hat{s}_{28} = 0.889$, SE = 0.105, $n = 9$; 2001: $\hat{s}_{28} = 0.522$, SE = 0.104, $n = 23$; 2002: $\hat{s}_{28} = 0.444$, SE = 0.096, $n = 27$; 2003: $\hat{s}_{28} = 0.917$, SE = 0.056, $n = 24$; $\chi^2 = 16.66$, df = 3, $P = 0.001$) but was similar across study areas (Hart: $\hat{s}_{28} = 0.593$, SE = 0.095, $n = 27$; Sheldon: $\hat{s}_{28} = 0.687$, SE = 0.082, $n = 32$;

Table 2. Akaike's Information Criterion (AIC) for candidate models used to examine the effect of habitat resources on survival of greater sage-grouse chicks ($n = 480$) in southeastern Oregon, USA, and northwestern Nevada, USA, 2000–2003. Akaike's Information Criterion adjusted for small sample size (AIC_c) represents the difference between the AIC value for a particular model and the best-fitting model with the lowest AIC value. Akaike weights (w_i) are the likelihood of a particular model i being the best model.

Hypothesis	Model ^{a,b}	K^c	AIC_c	w_i	r^2
Food and cover with interaction	col + hym + ort + lep + agf + crf + phf + asf + tfc + tog + scc + psg + pss + tog \times psg + scc \times pss	18	0.000	0.336	0.15
Food and understory cover	col + hym + ort + lep + agf + crf + phf + asf + tfc + tog + psg	14	0.657	0.242	0.13
Food and vertical cover	col + hym + ort + lep + agf + crf + phf + asf + psg + pss	13	1.322	0.173	0.13
Food and cover	col + hym + ort + lep + agf + crf + phf + asf + tfc + tog + scc + psg + pss	16	1.413	0.166	0.14
Food	col + hym + ort + lep + agf + crf + phf + asf	11	4.799	0.030	0.12
Food and horizontal cover	col + hym + ort + lep + agf + crf + phf + asf + tog + scc	14	5.223	0.025	0.13
Food and overstory cover	col + hym + ort + lep + agf + crf + phf + asf + scc + pss	13	5.405	0.023	0.12
Cover with interaction	tfc + tog + scc + psg + pss + tog \times psg + scc \times pss	10	9.379	0.003	0.10
Cover	tfc + tog + scc + psg + pss	8	13.587	0.000	0.09
Vertical cover	psg + pss	5	16.715	0.000	0.07
Understory cover	tfc + tog + psg	6	18.617	0.000	0.07
Overstory cover	scc + pss	5	23.012	0.000	0.06
Horizontal cover	tfc + tog + scc	6	26.768	0.000	0.05
No habitat effect	intercept	3	28.684	0.000	0.04

^a Variables included in models: Coleoptera (col), Hymenoptera (hym), Orthoptera (ort), Lepidoptera (lep), mountain dandelion frequency (agf), hawksbeard frequency (crf), slender phlox frequency (phf), milkvetch frequency (asf), total forb cover (tfc), total grass cover (tog), sagebrush canopy cover (scc), proportion of short grass (<18 cm) cover (psg), and proportion of short sagebrush (<40 cm) cover (pss).

^b All models included chick age at capture and age-adjusted chick wt.

^c No. of parameters in the model, including the intercept.

Beatys Butte: $\hat{s}_{28} = 0.667$, $SE = 0.096$, $n = 24$; $\chi^2 = 0.47$, $df = 2$, $P = 0.792$). In general, successful broods used areas with greater food availability compared with unsuccessful broods (Table 4). The best approximating model ($w_i = 0.585$) for brood survival was our food model (Table 5). Our second-best model ($w_i = 0.287$) contained only Lepidoptera. All remaining models received little support and were >4.0 AIC_c units from the top model (Table 5). Hazard ratios for model-averaged parameter estimates revealed a strong relationship between Lepidoptera and brood survival (Table 6). Risk of total brood loss decreased by 11.8% (95% CI = 1.2–22.5) for each additional Lepidoptera individual found at brood sites (Fig. 2a). We also found evidence of a positive relationship between slender phlox frequency and

brood survival (Table 6). Risk of total brood loss decreased by 2.7% (95% CI = –0.4 to 5.8) for each percentage point increase in frequency of slender phlox at brood sites (Fig. 2b).

Results of model selection revealed that year differences in brood survival were associated with food abundance. The models with year and study area as the only explanatory covariates were not competitive with any of the models that contained the Lepidoptera or slender phlox variables. Years with high and low Lepidoptera abundance and slender phlox frequency corresponded with years of high and low brood survival (Fig. 3). Predictive power of our models was low, explaining 23% of the variation in brood survival.

Table 3. Model-averaged parameter estimates, standard errors, hazard ratios, and 95% hazard ratio confidence intervals for habitat variables used to examine patterns in greater sage-grouse chick survival ($n = 480$) in southeastern Oregon, USA, and northwestern Nevada, USA, 2000–2003.

Habitat variable ^a	Estimate	SE	Hazard ratio ^b	95% CI
Food				
Coleoptera	–0.001	0.005	0.999	0.989–1.008
Hymenoptera	0.000	0.000	1.000	1.000–1.001
Orthoptera	–0.011	0.024	0.989	0.942–1.036
Lepidoptera	–0.027	0.013	0.975	0.949–1.001
Mountain dandelion.	–0.007	0.010	0.993	0.974–1.012
Hawksbeard	0.007	0.011	1.007	0.985–1.029
Slender phlox	–0.013	0.008	0.987	0.971–1.002
Milkvetch	0.002	0.018	0.998	0.962–1.033
Cover				
Total forb cover	–0.039	0.031	0.962	0.900–1.023
Total grass cover	0.012	0.043	1.012	0.928–1.095
Sagebrush canopy cover	0.002	0.037	1.002	0.929–1.075
Proportion short grass	–0.004	0.010	0.996	0.977–1.015
Proportion short sagebrush	0.006	0.008	1.006	0.989–1.022
Vertical and horizontal grass cover interaction	–0.090	0.049	0.914	0.817–1.010
Vertical and horizontal sagebrush cover interaction	0.007	0.072	1.007	0.866–1.147

^a Refer to Table 1 for variable descriptions.

^b Hazard ratios <1 indicate a positive effect and hazard ratios >1 indicate a negative effect on chick survival.

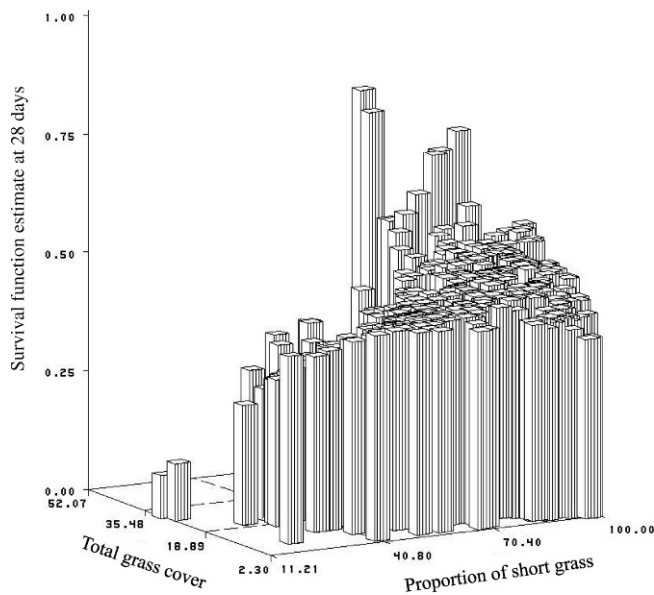


Figure 1. Estimated survivor function for 480 radiomarked greater sage-grouse chicks at 28 days posthatch for interactive effect between total grass cover and proportion of short grass at brood locations on 3 sites in Oregon and Nevada, USA, 2000–2003. We held other variables in the full model at their mean value.

DISCUSSION

Availability of Lepidoptera and slender phlox was directly linked to sage-grouse chick survival and related to the temporal variation in brood survival. No other research on free-ranging sage-grouse populations has, to our knowledge, identified direct linkages between food resources at brood sites and survival of individual chicks and broods. Drut et al. (1994a, b) reported that long-term differences in sage-grouse productivity between 2 areas in Oregon were concordant with forb and insect availability and amount of forbs and insects in the diet of chicks. Similarly, chick survival and productivity of free-ranging red grouse (*Lagopus lagopus scoticus*; Park et al. 2001) and the grey and red-legged

partridge (*Perdix perdix* and *Alectoris rufa*; Southwood and Cross 1969, Green 1984, Rands 1985) populations in Europe were correlated with insect availability and the amount of insects consumed by chicks. Authors of these studies suggested relationships between availability and consumption of food and chick survival, but survival of individually marked chicks was not monitored. Our results, based on survival of individual chicks, confirmed the critical role of food availability for chick survival and particularly the role of insects on development of sage-grouse chicks identified in captive studies (Johnson and Boyce 1990, Park et al. 2001).

Lepidoptera larvae are an important component of chick diets for several grouse species (Baines 1996, Norton et al. 2001, Wegge et al. 2005). Consumption of Lepidoptera by sage-grouse chicks has not been well documented in the literature. However, data collected concurrent with our study revealed that 24% of sage-grouse chick crops analyzed ($n = 111$) contained Lepidoptera (M. Gregg, unpublished data). Similarly, Hill (1985) reported that Lepidoptera larvae were a preferred food of ring-necked pheasant (*Phasianus colchicus*) chicks in Great Britain. Lepidoptera larvae provide high levels of energy and protein for growing chicks, and greater intake of nutrients by sage-grouse chicks during years with abundant Lepidoptera species likely increases growth rates and survival (Landry et al. 1986, Johnson and Boyce 1990). Lepidoptera larvae may also provide a higher quality food source compared with other insects. Growth rates of spruce grouse (*Falcipennis canadensis*) chicks were 30% greater when diets included Lepidoptera larvae as opposed to diets that consisted of only ants and spiders (Norton et al. 2001). Hence, insect taxa may not be interchangeable nutritionally, and insect abundance and quality may be equally important (Borg and Toft 2000).

Several researchers have reported that sage-grouse broods are typically found at sites with the greatest forb availability, relative to the surrounding area (Wallestad 1971, Drut et al.

Table 4. Mean values for habitat variables collected at greater sage-grouse brood locations ($n = 83$ broods, 1,887 locations) in southeastern Oregon, USA, and northwestern Nevada, USA, 2000–2003.

Habitat variable ^a	Successful brood		Unsuccessful brood		All broods	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Food						
Coleoptera	23.7	0.8	21.0	1.2	23.2	0.7
Hymenoptera	338.5	19.7	267.8	28.9	325.4	16.9
Orthoptera	5.3	0.1	6.1	0.4	5.5	0.1
Lepidoptera	8.7	0.4	4.3	0.4	7.9	0.3
Mountain dandelion	12.3	0.4	9.4	0.8	11.8	0.4
Hawksbeard	10.8	0.4	11.5	0.9	10.9	0.4
Slender phlox	23.7	0.7	15.7	1.1	22.2	0.6
Milk-vetch	5.6	0.3	6.0	0.6	5.7	0.2
Cover						
Total forb cover	7.6	0.1	7.7	0.3	7.6	0.1
Total grass cover	14.9	0.3	14.8	0.6	14.9	0.3
Sagebrush canopy cover	17.9	0.003	15.6	0.005	17.4	0.003
Proportion short grass	74.7	0.01	75.6	0.01	74.8	0.01
Proportion short sagebrush	59.3	0.01	61.7	0.02	59.8	0.01

^a Refer to Table 1 for variable descriptions.

Table 5. Model selection criteria for candidate models used to examine the effect of habitat resources on survival of greater sage-grouse broods ($n = 83$) in southeastern Oregon, USA, and northwestern Nevada, USA, 2000–2003. Akaike's Information Criterion adjusted for small sample size (AIC_c) represents the difference between the AIC value for a particular model and the best-fitting model with the lowest AIC value. Akaike weights (w_i) are the likelihood of a particular model i being the best model.

Hypothesis ^a	Model ^{b,c}	K^d	AIC_c	w_i	r^2
Food	lep + phf	8	0.000	0.585	0.23
Insect food	lep	7	1.424	0.287	0.20
Insect food and grass cover	lep + tog + psg + tog \times psg	10	4.836	0.052	0.23
Food and grass cover (full model)	lep + phf + tfc + tog + psg + tog \times psg	12	5.826	0.032	0.25
Herbaceous food	phf	7	5.861	0.031	0.15
Herbaceous food and grass cover	phf + psg + tog \times psg	10	8.879	0.007	0.18
No habitat effect ^e —temporal variation	yr	7	10.688	0.003	0.10
No habitat effect—spatial variation	study area	7	12.606	0.001	0.08
No habitat effect—temporal and spatial variation	yr + study area	8	12.635	0.001	0.10
Understory cover	tfc + tog + psg + tog \times psg	9	13.140	0.001	0.12
Grass cover	tog + psg + tog \times psg	10	15.038	0.000	0.12

^a Habitat variables used in candidate models were identified from survival analyses of individually marked sage-grouse chicks.

^b Variables included in models: Lepidoptera (lep), slender phlox frequency (phf), total forb cover (tfc), total grass cover (tog), and proportion of short grass (<18 cm) cover (psg).

^c All models included brood age at capture, initial brood size, hatch date, and cumulative means of daily brood movements.

^d No. of parameters in the model including the intercept.

^e The no-habitat-effect models included yr and study area to examine relationships between habitat variables and temporal and spatial variation in brood survival.

1994b, Sveum et al. 1998, Holloran 1999). Chicks select for certain forbs in their diet and slender phlox, an annual, was one of the top-selected food forbs by sage-grouse chicks in Oregon (Pyle 1993, Drut et al. 1994b). Forbs not only provide important food for chicks but also forb abundance is positively associated with invertebrate biomass (Southwood and Cross 1969, Hill 1985, Jamison et al. 2002), and individual forb species function as host plants for insects, particularly Lepidoptera.

Lepidoptera and annual forb abundance are sensitive to climatic conditions (i.e., temp and precipitation), and annual populations fluctuate dramatically, with occasional boom years of extremely high abundance (Pollard 1988, Miller and Eddleman 2000, Roy et al. 2001). Sage-grouse populations often exhibit low annual reproductive success but occasionally have years of high productivity (Crawford et al. 2004).

Table 6. Model-averaged parameter estimates, standard errors, hazard ratios, and 95% hazard ratio confidence intervals for habitat variables used to examine patterns in greater sage-grouse brood survival ($n = 83$) in southeastern Oregon, USA, and northwestern Nevada, USA, 2000–2003.

Habitat variable ^a	Estimate	SE	Hazard ratio ^b	95% CI
Food				
Lepidoptera	−0.126	0.054	0.882	0.775–0.988
Slender phlox	−0.027	0.016	0.973	0.942–1.004
Cover				
Total forb cover	0.018	0.055	1.018	0.910–1.125
Total grass cover	0.057	0.078	1.059	0.906–1.212
Proportion short grass	0.005	0.021	1.005	0.963–1.046
Vertical and horizontal grass cover interaction	−0.113	0.110	0.893	0.678–1.109

^a Refer to Table 1 for variable descriptions.

^b Hazard ratios <1 indicate positive effect and hazard ratios >1 indicate negative effect on chick survival.

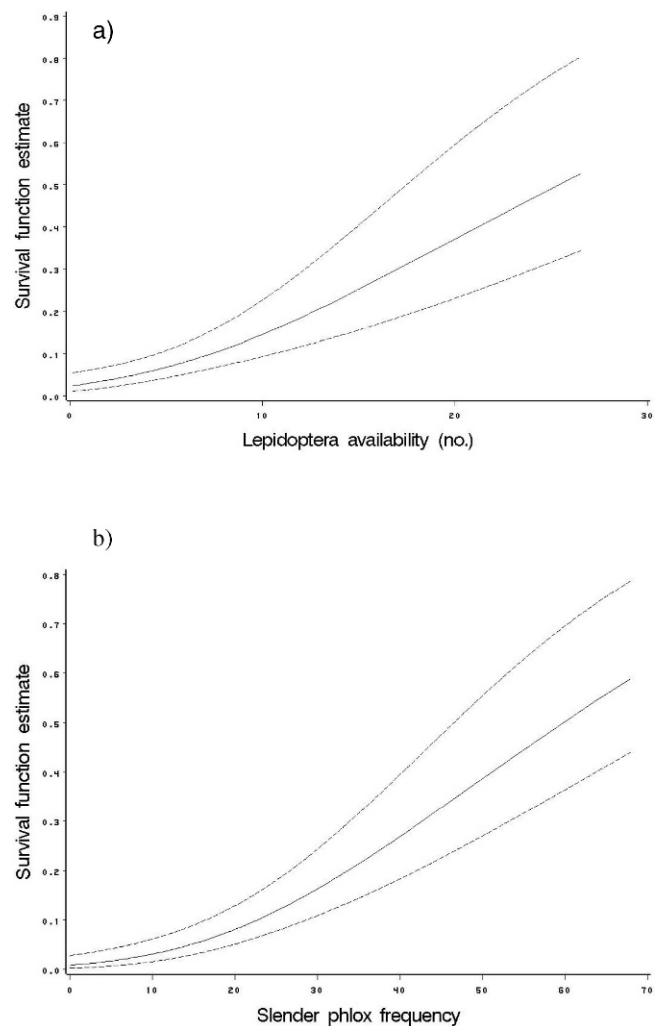


Figure 2. Estimated survivor function for 83 radiomarked greater sage-grouse broods at 28-days posthatch for the effect of (a) Lepidoptera availability and (b) slender phlox frequency at brood locations on 3 sites in Oregon and Nevada, USA, 2000–2003. We held other variables in the full model at their mean value. Dashed lines represent 95% confidence intervals for survival estimates.

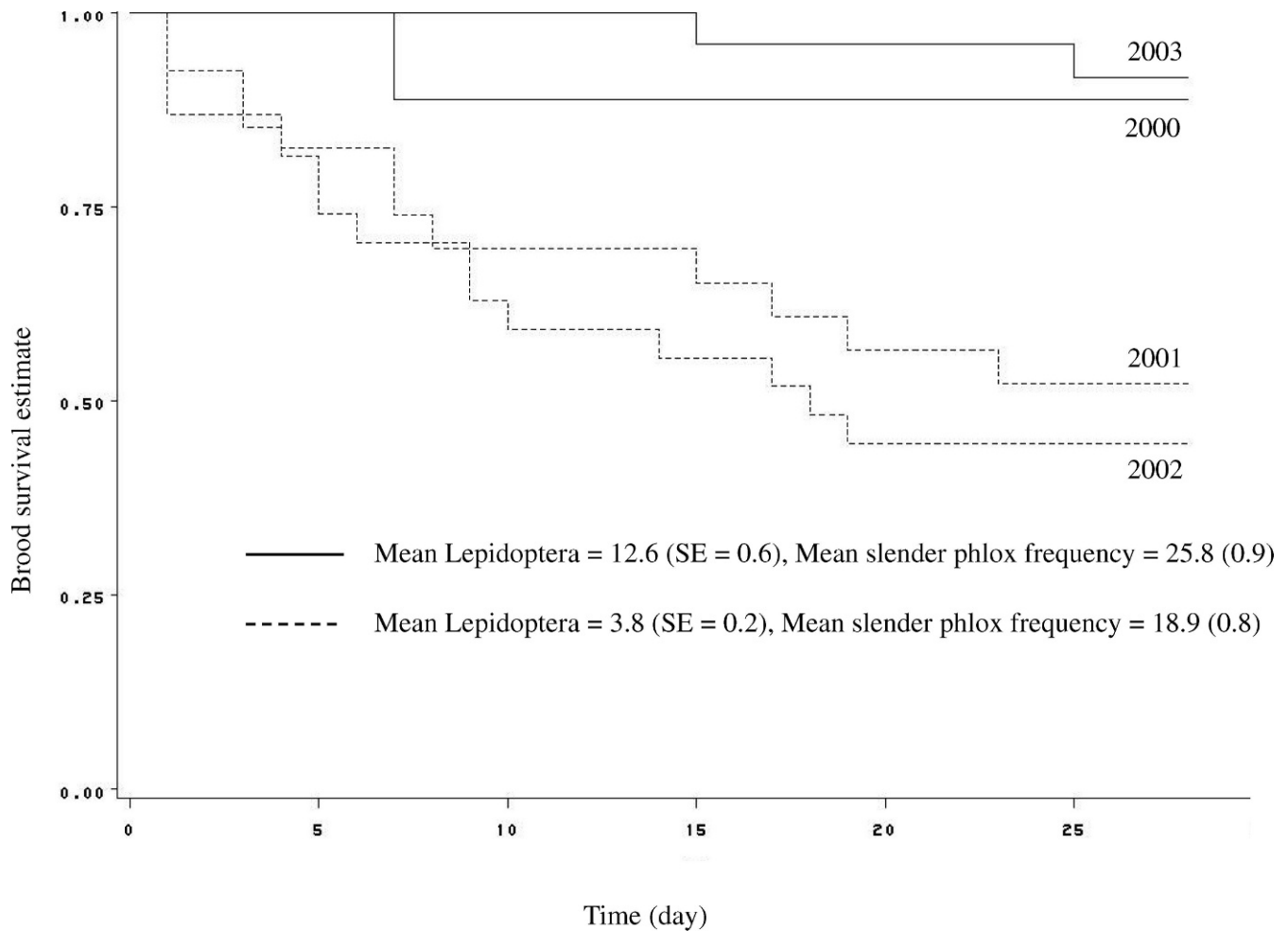


Figure 3. Observed Kaplan-Meier survival rates for 83 radiomarked greater sage-grouse broods at 3 sites in Oregon and Nevada, USA, 2000–2003, in relation to annual variation in Lepidoptera abundance and slender phlox frequency.

We suggest that years with high Lepidoptera and slender phlox abundance may be linked to years of high sage-grouse productivity. Baines (1996) reported a positive relationship between Lepidoptera availability and breeding success of black grouse (*Tetrao tetrix*) in Scotland. Greater availability of Lepidoptera and slender phlox may enhance productivity directly by providing a nutritious food source for growing chicks, or these variables may be an indicator of overall good breeding habitat conditions for sage-grouse. Many species of Lepidoptera depend on similar vegetative characteristics (i.e., herbaceous vegetation) as sage-grouse depend on for reproduction and survival, and herbaceous vegetation is influenced by amount and timing of precipitation. Hence, years of high Lepidoptera and slender phlox abundance may simply correspond with high sage-grouse productivity. Nevertheless, our results clearly indicated a relationship between Lepidoptera and slender phlox abundance and sage-grouse chick and brood survival.

The predictive power of our models was low in contrast with Hill (1985), who reported that insect abundance (Lepidoptera larvae, carabid beetles, chrysomelid beetles, and sawfly larvae) explained 67% of the between-year variation in survival of ring-necked pheasant chicks in Great Britain. The discrepancy in results between Hill (1985) and

our study may be related to the intensive predator control that is often conducted in association with upland game-bird management in Europe (Schroeder and Baydack 2001). Predation was the predominant cause of chick deaths during our study. Other researchers who have monitored individually marked sage-grouse chicks (Aldridge 2005) and chicks of other Galliformes (Riley et al. 1998, Hubbard et al. 1999, Larson et al. 2001) also identified predation as the primary source of mortality. No predator control was conducted during our study, and we did not measure predator abundance, which could potentially affect chick survival. In addition, other factors, including weather (i.e., temp and precipitation), female age, and maternal nutrition, likely influence chick survival (Beckerton and Middleton 1982, Barnett and Crawford 1994, Dunbar et al. 2005, Gregg 2006). Hence, the low predictive power of our models was not surprising given that our analysis did not include these other important variables.

Some variables associated with chick survival were of little or no importance to brood survival, which was not unexpected given that a variable must have a large effect on individual chick survival to produce a detectable effect on total brood loss. We did find a relationship between chick survival and grass cover. Chick survival increased as the

cover of short grasses (<18 cm) increased. Two of our study areas were not grazed by domestic livestock, and short grass was not the result of herbivory of tall grasses. Instead, the short grass component was provided by short-stature grass species (i.e., *Poa* spp.) and reflected the use of little sagebrush habitats for brood rearing. Sage-grouse chicks typically forage in open areas between sagebrush plants, and young chicks (<4 weeks old) remain motionless when disturbed and use their cryptic coloration to evade predators. Short-grass species likely provided adequate escape cover for chicks to avoid predation. Sage-grouse broods avoided areas with dense, tall grass cover. Similarly, Aldridge (2005) suggested that areas with tall, dense grass cover were avoided by hens with broods and speculated that tall grass may inhibit the ability of females to detect predators and alert chicks.

MANAGEMENT IMPLICATIONS

Our results revealed that chick and brood survival were directly linked to availability of food and cover. In areas of degraded habitat, active restoration may be necessary to increase availability of herbaceous vegetation and insects. However, management recommendations specific to Lepidoptera in brood-rearing habitat are not available because there is little information on the species of Lepidoptera consumed by chicks and the life histories of Lepidoptera in sagebrush habitats. The greatest diversity of Lepidoptera species are typically found in areas with the greatest diversity of vegetative structure and composition (Gardner et al. 1995). In sagebrush habitats, forbs and grasses are important host plants for Lepidoptera, but shrubs (e.g., rabbitbrush) are also used by some species (J. C. Miller, Oregon State University, personal communication). Hence, management practices in sage-grouse brood-rearing habitat that foster diversity, particularly native plants, in sagebrush stands should provide the necessary attributes for adequate chick survival. We recommend protection of sage-grouse brood-rearing habitat that is at the ecological site potential or that meets management guidelines provided in Connelly et al. (2000).

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LITERATURE CITED

Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation, University of Alberta, Edmonton, Canada.

- Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. *Condor* 103:537–543.
- Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Alberta. *Journal of Wildlife Management* 66:433–444.
- Allison, P. D. 1995. Survival analysis using the SAS system: a practical guide. SAS Institute, Cary, North Carolina, USA.
- Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.
- Baines, D. 1996. The implications of grazing and predator management on habitats and breeding success of black grouse *Tetrao tetrix*. *Journal of Applied Ecology* 33:54–62.
- Barnett, J. K. 1992. Diet and nutrition of female sage grouse during the pre-laying period. Thesis, Oregon State University, Corvallis, USA.
- Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. *Journal of Range Management* 47:114–118.
- Beckerton, P. R., and A. L. A. Middleton. 1982. Effects of dietary protein levels on ruffed grouse reproduction. *Journal of Wildlife Management* 46:569–579.
- Borg, C., and S. Toft. 2000. Importance of insect prey quality for grey partridge chicks *Perdix perdix*: a self-selection experiment. *Journal of Applied Ecology* 37:557–563.
- Bureau of Land Management. 1994. Beatys Butte allotment evaluation report. United States Department of the Interior, Lakeview, Oregon, USA.
- Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. *Wildlife Society Bulletin* 30:93–96.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Canfield, R. H. 1941. Application of the line interception method in sampling of range vegetation. *Journal of Forestry* 39:386–394.
- Coggins, K. A. 1998. Relationship between habitat changes and productivity of sage grouse at Hart Mountain National Antelope Refuge, Oregon. Thesis, Oregon State University, Corvallis, USA.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229–234.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies unpublished report, Cheyenne, Wyoming, USA.
- Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines for management of sage grouse populations and habitat. *Wildlife Society Bulletin* 28:967–985.
- Cox, D. R. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society Series B* 34:187–220.
- Crawford J. A., and R. S. Lutz. 1985. Sage grouse population trends in Oregon, 1941–1983. *Murrelet* 66:69–74.
- Crawford J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2–19.
- Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33:224–227.
- Davis, D. M. 2002. Breeding season habitat use and response to management activities by greater sage-grouse on Sheldon National Wildlife Refuge, Nevada. Thesis, Oregon State University, Corvallis, USA.
- Drut, M. S. 1992. Habitat use and selection by sage grouse brood in southeastern Oregon. Thesis, Oregon State University, Corvallis, USA.
- Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994a. Brood habitat use by sage grouse in Oregon. *Great Basin Naturalist* 54:170–176.
- Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994b. Diets and food selection of sage grouse chicks in Oregon. *Journal of Range Management* 47:90–93.
- Dunbar, M. R., M. A. Gregg, M. R. Giordano, D. M. Davis, M. W. Byrne, J. A. Crawford, and S. J. Tornquist. 2005. Normal hematologic and biochemical values for pre-laying greater sage-grouse (*Centrocercus urophasianus*) and their influence on chick survival. *Journal of Zoo and Wildlife Medicine* 36:422–429.

- Efron, B., and J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.
- Flint, P. L., K. H. Pollock, D. Thomas, and J. S. Sedinger. 1995. Estimating prefledging survival: allowing for brood mixing and dependence of brood mates. *Journal of Wildlife Management* 59:448–455.
- Gardner, S. M., M. R. Cabido, G. R. Valladares, and S. Diaz. 1995. The influence of habitat structure on arthropod diversity in Argentine semi-arid Chaco forest. *Journal of Vegetation Science* 6:349–356.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224–231.
- Green, R. E. 1984. The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. *Journal of Applied Ecology* 21:817–830.
- Gregg, M. A. 1991. Use and selection of nesting habitat by sage grouse in Oregon. Thesis, Oregon State University, Corvallis, USA.
- Gregg, M. A. 2006. Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival. Dissertation, Oregon State University, Corvallis, USA.
- Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted radiotransmitters to estimate survival of greater sage-grouse chicks. *Journal of Wildlife Management* 71:646–651.
- Gregg, M. A., M. R. Dunbar, J. A. Crawford, and M. D. Pope. 2006. Total plasma protein and reneesting by greater sage-grouse. *Journal of Wildlife Management* 70:472–478.
- Hill, D. A. 1985. The feeding ecology and survival of pheasant chicks on arable farmland. *Journal of Applied Ecology* 22:645–654.
- Hironaka, H. 1985. Frequency approaches to monitor rangeland vegetation. Pages 84–86 in *Selected papers presented at the 38th Annual Meeting of the Society for Range Management*, 11–15 February 1985, Salt Lake City, Utah, USA. Society for Range Management, Wheat Ridge, Colorado, USA.
- Holloran, M. J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, Brigham Young University, Provo, Utah, USA.
- Hubbard, M. W., D. L. Garner, and E. E. Klaas. 1999. Wild turkey poult survival in southern Iowa. *Journal of Wildlife Management* 63:199–203.
- Jamison, B. E., R. J. Robel, J. S. Pontius, and R. D. Applegate. 2002. Invertebrate biomass: associations with lesser prairie-chicken habitat use and sand sagebrush density in southwestern Kansas. *Wildlife Society Bulletin* 30:517–526.
- Johnson, G. D., and M. S. Boyce. 1990. Feeding trials with insects in the diet of sage grouse chicks. *Journal of Wildlife Management* 54:89–91.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457–481.
- Klebenow, D. A., and G. M. Gray. 1968. The food habits of juvenile sage grouse. *Journal of Range Management* 21:80–83.
- Landry, S. V., G. E. Defoliart, and M. L. Sunde. 1986. Larval protein quality of six species of Lepidoptera (Saturniidae, Sphingidae, Noctuidae). *Journal of Economic Entomology* 35:107–108.
- Larson, M. A., M. E. Clark, and S. R. Winterstein. 2001. Survival of ruffed grouse chicks in northern Michigan. *Journal of Wildlife Management* 65:880–886.
- Miller, R. F., and L. L. Eddleman. 2000. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Oregon State University Agricultural Experiment Station Technical Bulletin 151, Corvallis, USA.
- Morrill, W. C. 1975. Plastic pitfall trap. *Environmental Entomology* 4:596.
- Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management* 65:613–623.
- Norton, M. L., J. F. Bendell, L. I. Bendell-Young, and C. W. Blanc. 2001. Secondary effects of the pesticide *Bacillus thuringiensis kurstaki* on chicks of spruce grouse (*Dendragapus canadensis*). *Archives of Environmental Contamination and Toxicology* 41:369–373.
- Park, K. J., P. A. Robertson, S. T. Campbell, R. Foster, Z. M. Russell, D. Newborn, and P. J. Hudson. 2001. The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks. *Journal Zoology London* 254:137–145.
- Peterson, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. *Journal of Wildlife Management* 34:147–155.
- Pollard, E. 1988. Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology* 25:819–828.
- Pyle, W. H. 1992. Response of brood-rearing habitat of sage grouse to prescribed burning in Oregon. Thesis, Oregon State University, Corvallis, USA.
- Rands, M. R. W. 1985. Pesticide use on cereals and the survival of grey partridge chicks: a field experiment. *Journal of Applied Ecology* 22:49–54.
- Riley, T. Z., W. R. Clark, D. E. Ewing, and P. A. Vohs. 1998. Survival of ring-necked pheasant chicks during brood rearing. *Journal of Wildlife Management* 62:36–44.
- Roy, D. B., P. Rothery, D. Moss, E. Pollard, and J. A. Thomas. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology* 70:201–217.
- Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. *Wildlife Society Bulletin* 29:24–32.
- Smith, S. D., S. C. Bunting, and M. Hironaka. 1986. Sensitivity of frequency plots for detecting vegetation change. *Northwest Science* 60:279–286.
- Southwood, T. R. E., and D. J. Cross. 1969. The ecology of the partridge: breeding success and the abundance of insects in natural habitats. *The Journal of Animal Ecology* 38:497–509.
- Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998. Use and selection of brood-rearing habitat by sage grouse in south-central Washington. *Great Basin Naturalist* 58:344–351.
- Wallestad, R. O. 1971. Summer movements and habitat use by sage grouse broods in central Montana. *Journal of Wildlife Management* 35:129–136.
- Wegge, P., T. Olstad, H. Gregerson, O. Hjeljord, and A. V. Sivkov. 2005. Capercaillie broods in pristine boreal forest in northwestern Russia: the importance of insects and cover in habitat selection. *Canadian Journal of Zoology* 83:1547–1555.
- Western Regional Climate Center. 2005. Historical climate information: western U.S. historical summaries (individual stations), Hart Mountain Refuge, Oregon; Sheldon, Nevada; Kings River Valley, Nevada, home page. <<http://www.wrcc.dri.edu>>. Accessed 17 Apr 2005.

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