Journal of Wildlife Management 74(6):1286–1294; 2010; DOI: 10.2193/2009-093

Management and Conservation Article

Achieving Better Estimates of Greater Sage-Grouse Chick Survival in Utah

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ABSTRACT Declining sage-grouse (*Centrocercus urophasianus*) populations may be characterized by poor recruitment largely attributed to low chick survival. However, few published studies have explicitly examined factors that influence chick survival. We used a suture method to radiomark 1–2-day-old sage-grouse chicks ($n = 150$) in 2005–2006 on Parker Mountain in south-central Utah, USA, and monitored their survival to 42 days. We modeled effects of year, hatch date, chick age, brood-female age, brood-mixing, and arthropod abundance on chick survival. Our best model revealed an average survival estimate of 0.50 days to 42 days, which is the highest level ever documented for this long-lived species. Brood-mixing occurred in 21% (31/146) of chicks and 43% (18/42) of broods we studied. Moreover, yearling females had more chicks leave their broods than did adults. We found that survival may be higher among chicks that switch broods compared to those that stayed with their natal mother until fledging. Thus, brood-mixing may be an adaptive strategy leading to increased sage-grouse chick survival and higher productivity, especially among chicks born to yearling females. Our findings also indicate that arthropod abundance may be an important driver of chick survival, particularly during the early brood-rearing period and, therefore, sage-grouse populations may benefit from a management strategy that attempts to increase arthropod abundance via brood habitat management.

KEY WORDS brood-mixing, *Centrocercus urophasianus*, chick survival, greater sage-grouse, productivity, radiotelemetry, suture method, Utah.

Range-wide, greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) population declines have been attributed to environmental factors affecting production (Connelly and Braun 1997; J. W. Connelly, Western Association of Fish and Wildlife Agencies, unpublished report). Recruitment, a key and highly variable component of production in North American grouse species (Tetraoninae), largely depends on chick survival (Bergerud 1988, Gotelli 2001). The quality of brooding-rearing habitat is an important component of sage-grouse recruitment (Drut et al. 1994, Connelly et al. 2000, Aldridge and Boyce 2007, Gregg et al. 2007).

Arthropod abundance is also critical for survival of young chicks (<21 days old; Klebenow and Gray 1968, Peterson 1970, Johnson and Boyce 1990). Thompson et al. (2006) found sage-grouse productivity (measured by harvested wing samples and F with broods) was positively associated with arthropods (medium-sized Hymenoptera and Coleoptera) and herbaceous components of sagebrush habitats. Insect abundance may be related to plant diversity within sagebrush systems (especially intact sagebrush communities) but may be more highly associated with annual productivity (moisture dependent) within specific habitats (Wenninger and Inouye 2008). However, the direct relationship between insect availability and sage-grouse chick survival in a natural setting is poorly understood.

In addition to habitat quality and arthropod abundance, the age and experience of brood females may also influence chick survival and productivity (Newton 1998). Curio (1982) found that young birds (avian species in general) reproduce more poorly than older birds. In general, adult sage-grouse females have a higher probability of nesting and may have higher chick survival than yearling females (Connelly et al. 1993, Gregg 2006).

Chick survival in sage-grouse has been difficult to study. Estimates reported from field studies have been low, even among studies where chicks were individually radiomarked (12–22% for the first few weeks of survival; Aldridge and Boyce 2007, Gregg et al. 2007). Additionally, posthatch brood amalgamation (termed brood-mixing in precocial species), as a form of alloparental care, may confound survival estimates from studies that did not include both radiomarked brood females and chicks (Flint et al. 1995). Sage-grouse, compared to other gallinaceous species, are long-lived with lower reproductive output (Patterson 1952, Schroeder et al. 1999). Thus, sage-grouse share life strategy characteristics with other species that brood-mix. However, this phenomenon has rarely been discussed in the sage-grouse literature. Brood-mixing may afford adoptive parents several selective advantages, including increased survival of their progeny by earlier detection of predators and dilution of predation on natal offspring because of increased brood sizes (Riedman 1982). Concomitantly, younger, inexperienced mothers may improve their offspring's chances of survival by giving them up to older, more experienced mothers (Eadie and Lumsden 1985, Eadie et al. 1988).

We monitored radiomarked sage-grouse brood females and approximately 1-day-old sage-grouse chicks to evaluate temporal effects of hatch date, chick age, brood-female age, brood-mixing, year, and arthropod abundance on chick survival. We hypothesized that yearling females are more likely to lose offspring via brood-mixing events and that offspring that leave their natal broods experience higher survival. Additionally, we hypothesized that arthropod abundance is associated with higher chick survival during the early brood-rearing period (<21 days), when chicks are

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most susceptible to mortality due to lack of nutrition (Johnson and Boyce 1990).

STUDY AREA

Parker Mountain is located in south-central Utah, USA, and is on the southern edge of the sage-grouse range. The area is a high-elevation (approx. 2,000–3,000 m) plateau that was largely dominated by black sagebrush (*Artemisia nova*); however, there were also landscapes of mountain big (*A. tridentata vaseyana*) and silver (*A. cana*) sagebrush at the highest elevations (S and W sagebrush boundaries). This area contained one of the largest contiguous sagebrush habitats and one of the few remaining stable populations of sage-grouse in Utah (Beck et al. 2003). Parker Mountain was largely composed of public land including Bureau of Land Management (BLM), United States Forest Service (USFS), and Utah State and Institutional Trust Lands Administration. Primary land use on the mountain was domestic livestock grazing. In general, the sage-grouse population used lower elevation sagebrush landscapes for wintering, prelaying, and lekking habitat, whereas females gradually moved up in elevation for nesting and brood-rearing activities, using the highest elevations and habitats along the southern and western boundaries of the plateau (Chi 2004, Dahlgren 2006). Thus, late brood-rearing activities were concentrated at these elevations in most years. For more detailed information concerning the study area please see Dahlgren et al. (2006).

METHODS

Field Methods

We captured and radiomarked female sage-grouse on or near leks during March and April of 2005 and 2006 (Giesen et al. 1982). We conducted research under protocols approved by the Utah State University International Animal Care and Use Committee permit number 945R. We fitted captured females with 19-g necklace-style radiotransmitters (Holohil Systems, Carp, ON, Canada). We aged females according to wing primary characteristics and weights (Beck et al. 1975). We relocated females on their nest using telemetry and visually observed them using binoculars from >10 m to avoid disturbing the female. We estimated approximate hatch date using an incubation period of 27 days (Schroeder 1997). Throughout the incubation period we monitored nest fate every other day using binoculars. As the approximate hatch date approached we began daily monitoring of the nest. When a female ceased incubation we inspected the nest bowl to determine nest fate. If ≥1 egg hatched we considered the nest successful.

Within 24–48 hours of hatch we flushed successful radiomarked brood females and captured all detected chicks by hand. We captured most broods just before or after sunrise or sunset. When chicks were being brooded by the female due to reduced temperatures, we believed all available chicks to have been captured. On the rare occasion when chicks were not being brooded, we usually captured ≥50% of the brood with thorough searches. We placed captured chicks in a brooding box with a heat source (a small lunch cooler with a hot water bottle) during handling. We weighed all chicks to the nearest gram and externally radiomarked a random subset with 1.5-g transmitters (Advanced Telemetry Systems, Isanti, MN [2005], Holohil Systems [2006]) using a suture technique (Burkepile et al. 2002). We radiomarked all chicks at the capture location and attempted to mark 3–8 chicks/brood.

We monitored radiomarked broods every 1–2 days until chicks were 42 days old; however, some monitoring periods were longer because of difficulty in locating the radiomarked brood. We monitored the brood and brood capture sites the day after capture to assess chick death due to capture and handling. We used ground-based telemetry throughout the 42-day monitoring period, and we assumed chicks in close proximity (approx. 50 m) to the radiomarked female to be alive. We subsequently searched for radiomarked chicks that we did not detect near the radiomarked female to attain a visual observation. If we found a radiomarked chick alive in another brood with an unmarked female, we classified the chick as a brood-mixed chick (i.e., posthatch brood amalgamation; Eadie et al. 1988). If we found a dead radiomarked chick, we searched the remains, radio, and immediate vicinity to determine cause of death.

We classified cause of death as predation, exposure, or unknown. We determined chicks that we found dead at the capture–marking site with intact bodies and no signs of predation to have died due to handling. If the brood moved away from the capture site, we then recorded exposure as the cause of death if we found an intact chick body with no indication of predation. We identified predation as cause of death when remains or radio indicated teeth or talon marks or if only the radio remained with some feathers and skin attached to sutures. It is possible that chicks may have died due to causes other than predation and were subsequently scavenged, though it was impossible to determine this outcome. We did not detect some chicks with the radiomarked female at some point during the monitoring period and did not find them in another brood. We rigorously searched for these chicks starting at the last known location and radiating out (approx. 3 km), for ≥2 consecutive days. Chick radios had a limited range (approx. 300–400 m straight line), and signals were difficult to detect once a chick left the radiomarked female. Additionally, we periodically scanned for missing chick frequencies throughout the remainder of the field season.

We conducted arthropod sampling only in 2006. Sampling occurred once per week for each brood; however, we used no random sites. We centered arthropod sampling sites on the brood female location. To capture arthropods, we used tin can (6.6-cm diam, 11-cm depth) traps filled to approximately 4 cm from the bottom with a 50% water and 50% ethylene glycol (antifreeze) solution. We set traps (n = 5/site) at the crossing and ends of 2 20-m transects (random directions) and left them open for approximately 48 hours. We buried traps flush to the ground surface. This method of sampling may be biased toward ground-dwelling insects important to sage-grouse (Coleoptera, Orthoptera, and Hymenoptera; Fischer et al. 1996) compared to vegetationdwelling insects (Poulin and Lefebvre 1997). We gathered arthropods and subsequently categorized them by order (Orthoptera, Coleoptera, Hymenoptera, Lepidoptera, and miscellaneous, e.g., spiders). We separated ants from the Hymenoptera order to analyze them separately because of their availability, abundance, and importance to sage-grouse chicks compared to the rest of the order (Klebenow and Gray 1968, Peterson 1970, Fischer et al. 1996, Nelle et al. 2000). We used volume (mL) displacement as the unit of measurement for arthropod abundance due to ease of calculating volume in our lab.

Statistical Analysis

We first examined the influence of female age on probability of chicks leaving their broods in a brood-mixing event using logistic regression (Hosmer and Lemeshow 2000). We then estimated chick survival. We assigned the following survival histories to chicks classified as missing: 1) we right-censored missing chicks from the data set; 2) we treated missing chicks as mortalities in a separate analysis (Appendix, available at <http://dx.doi.org/10.2193/2009-093.s1>); and 3) we treated missing chicks as though they survived within their original broods in a separate analysis (Appendix). Missing chicks may have resulted from radio failure (though never documented directly), death due to predation or exposure with subsequent scavenging that precluded our detection ability (e.g., burial by scavenger or predator or carried off by an avian predator), or an undetected (due to the weak signal from the small chick radio) brood-mixing event. Right-censoring a missing chick (analysis action 1) yields the least biased estimate of chick survival if missing occurred at random. However, analysis actions 2 and 3 provide a lower and upper limit to possible nonrandom fates of missing chicks as well as estimates of chick survival (Appendix).

We right-censored from their original broods radiomarked chicks we classified as brood-mixed, and we assigned them to a new brood. If a chick went missing after it brood-mixed, we always right-censored it from the data set. We based this decision on our inability to detect weaker chick signals in broods where the female was not radiomarked relative to the stronger signal from a natal radiomarked female.

We then estimated chick survival using a maximum likelihood extension to the Mayfield estimator (Manly and Schmutz 2001). To accommodate potential lack of independence among brood mates, the Manly and Schmutz (2001) model estimates the dependence in fates among brood members (denoted as D) using a quasi-likelihood model with a normal approximation to binomial variance multiplied by D, a constant dispersion factor (Flint et al. 1995, Schmutz et al. 2001, Fondell et al. 2008). Estimating D takes into account all forms of unobserved heterogeneity (but does not distinguish among them) influencing chick survival, including factors such as single predation events killing multiple chicks (i.e., fate dependence) and the influence of a brood female on such events over the entire survival period. As the estimate of D nears the average brood size, the greater the dependence of fate among brood members, whereas the closer D is to 1, the more independent each brood member's fate is from the others. Moreover, effects of chick age (measured categorically) and covariates (continuous or categorical) on chick survival can be estimated using a log-link function (McCullogh and Nelder 1989, Manly and Schmutz 2001).

Using this flexible modeling approach, we evaluated the impact of various combinations of a chick's age (7-day age classes up to one 42-day age class), temporal variables (yr: 2005 or 2006; hatch date denoted in Julian days), and individual characteristics of brood females (F age: yearling or ad; and brood type: mixed or not) on chick survival. When evaluating female age we used a restricted data set that did not include the variable mixed broods because we did not collect information about these variables for unmarked females of broods into which marked chicks mixed. To compare models we used a quasi-likelihood version of Akaike's Information Criterion explicitly calculated with the estimated D of each model, adjusted for sample size ($QAIC_c$; Akaike 1973, Burnham and Anderson 2002). Unlike the ad hoc approach of calculating a $\hat{c}$ value to correct AIC for overdispersion in the data, D is uniquely estimated for each model. As such, if estimates of D between 2 competing models are different, their $QAIC_c$ values can be drastically different, even among the top few models (Manly and Schmutz 2001, Fondell et al. 2008). We further assessed statistical precision of β'_is in our best models based on the extent to which 95% confidence intervals overlapped zero (Graybill and Iyer 1994).

We then evaluated the best parameterization of age-structured chick survival to 21 days, and further assessed the influence of arthropods on chick survival during this early brood-rearing period (days 1–21). Because sage-grouse chicks depend most on an arthropod diet during the early brood-rearing period (Johnson and Boyce 1990, Fischer et al. 1996), we modeled the effect of arthropod availability (based on vol displacement measures of abundance; continuous variables) on chick survival during this period alone. Measures of arthropod abundance included that for ants, bees, Hymenoptera (all families), Coleoptera, Orthoptera, Lepidoptera, miscellaneous (e.g., spiders), and total arthropods. For this analysis we used a restricted data set (only 2006 data were available) in which we used only observations of survival following arthropod sampling for each brood. We performed model selection according to methods described above. For all covariate analyses described above we included a null model in our a priori candidate set of models, designated as that with the best parameterization of age-structured chick survival but no covariates (see Table 1). We performed all survival analyses using recently updated statistical software developed by Manly and Schmutz (2001). Vegetation sampling and evaluation also occurred during our study, but our findings indicated no direct relationship between vegetation and chick survival (see Dahlgren 2009).

Table 1. Models of weekly greater sage-grouse chick survival for both non- and brood-mixed brood, and covariate comparison of brood type (regular or mixed), hatch date (Julian days), and year (2005 or 2006), Parker Mountain, Utah, USA, 2005–2006.

Model	K[a]	QAIC$_c$[b]	Δ_i[c]	w_i[d]
Null model determination				
age = week1 + week2 + week3 + week4 + weeks5–6	6	93.96	0.00	0.99999
age = week1 + week2 + week3 + weeks4–6	5	121.01	27.04	0.00000
age = weeks1–2 + weeks3–4 + weeks5–6	4	124.33	30.36	0.00000
age = weeks1–2 + weeks3–6	3	134.22	40.25	0.00000
age = week1 + week2 + weeks3–6	4	135.83	41.86	0.00000
age = week1 + weeks2–6	3	156.17	62.20	0.00000
age = weeks1–3 + weeks4–6	3	164.64	70.67	0.00000
age = weeks 1–6	2	168.88	74.91	0.00000
Covariate model comparison				
age + brood type[e]	7	39.21	0.00	0.99999
age (null model)[e]	6	93.96	54.76	0.00000
age + hatch date[e]	7	111.96	72.75	0.00000
age + yr[e]	7	126.37	87.16	0.00000

[a] K: no. of parameters in each model.

[b] QAIC$_c$: quasi-likelihood version of Akaike's Information Criterion.

[c] Δ_i: QAIC$_c$ difference between a model (i.e., model i) and the best performing model.

[d] w_i: Akaike model wt. By uniquely estimating D (heterogeneity factor for brood mates) each model's QAIC$_c$ values can be drastically different, even among the top few models. Thus, model wt can be highly skewed toward the top model.

[e] The best model of age = week1 + week2 + week3 + week4 + weeks5–6, which is shown in the null model determination. We then used the null model once determined to test for the importance of covariate structure in the modeling process.

RESULTS

In 2005 our sample included 21 radiomarked brood females ($n = 2$ unknown age, $n = 11$ yearlings, and $n = 8$ ad); whereas in 2006 we had 21 radiomarked brood females ($n = 21$ ad), 7 of which had broods in 2005. We captured and radiomarked 89 chicks in 21 broods and 61 chicks in 21 broods in 2005 and 2006 ($n = 150$), respectively. We classified only 2.6% of chicks ($n = 3$ in 2005, and $n = 1$ in 2006) as deaths due to handling or radiomarking and we excluded all from survival analyses. Therefore, we used 146 individual chick survival histories to estimate survival to 42 days. During this study we recovered 2 radios with no feathers or skin attached to the sutures, which could have possibly torn out of the skin or radio casing (sloughed off). These 2 chicks, along with 24 others ($n = 26$) had unknown fates (missing from the original radiomarked F broods), and we right-censored them from the data set. All other recovered radios ($n = 44$) had direct indications of predation or scavenging. Captured chicks per brood ranged from 1 to 8. Mean mass of chicks was 29.5 g (SE = 0.16) and, thus, radiotransmitters averaged 5.1% (SE < 0.001) of chick body mass at capture time. All marked females returned to their brood by the following day and most within a few minutes of brood release.

Brood-mixing occurred with 21% (31/146) of radiomarked chicks and within 43% (18/42) of monitored broods. We documented 2 radiomarked brood female mortalities during the brood monitoring period. In each case all radiomarked chicks were assimilated into unmarked broods within 48 hours of the documented female mortality. In 45% (9/20) of brood-mixing events, multiple radiomarked chicks (2 or 3) left their original broods and joined new broods (unmarked F) at the same time; one multiple-mixing event was due to brood female mortality. Probability of brood-mixing differed by female age ($\beta_{\text{hen age}} = 1.57$, SE = 0.75) and was notably higher in broods with yearling females ($P_{\text{yearling}} = 0.63$) relative to adult females ($P_{\text{adult}} = 0.27$). In 2005 all but one (a F of unknown age) of brood-mixing events occurred with yearling females, though we were unable to test for year effects because in 2006 all radiomarked brood females were adults. Disregarding mixing events due to brood female mortality, multiple chick mixing occurred in 71% (5/7) of yearling female broods and in only 20% (2/10) of adult female broods.

Brood-mixing occurred during weeks 1–6 of chick development, with 70% (14/20) of brood-mixing events taking place within weeks 2 and 3. Additionally, we found chicks from unmarked broods mixing into marked broods. We documented chicks that exceeded the range of chick weights (24–36 g) for 1- or 2-day-old chicks when capturing broods within 24–48 hours of hatch and presumably mixed into radiomarked broods during this time. Moreover, observations recorded when we inadvertently flushed chicks later in the monitoring period suggested a marked increase in number and size (relative to known age) of flushed chicks within a given brood. We assumed this a consequence of brood-mixing into the marked brood.

Predation accounted for 32% (38/120) of known chick fates. Of documented chick predations, we attributed predation to avian ($n = 8$), mammalian ($n = 8$), and unknown ($n = 22$) causes. For the mammalian depredated chicks, we found 50% ($n = 4$) underground in long-tailed weasel (*Mustela frenata*) dens. We attributed 6 deaths to exposure.

The top-ranked model for age-specific chick survival indicated differences in survival among weeks 1, 2, 3, 4, and 5–6 (Table 1), and a 0.60 (95% CI = 0.51–0.72) probability of sage-grouse chicks surviving to 42 days. Age-specific mortality hazards were as follows: week 1 ($\hat{\beta} = 0.019$, SE = 0.006), week 2 ($\hat{\beta} = 0.018$, SE = 0.006), week 3 ($\hat{\beta} =$

Table 2. Estimates of greater sage-grouse chick daily survival rates for non- and mixed broods based on our best model (brood-type), Parker Mountain, Utah, USA, 2005–2006.

			Non brood-mixed		Brood-mixed	
Age[a]	β'_is	SE	DSR[b]	SE	DSR[b]	SE
Week 1	0.023	0.007	0.977	0.007	0.984	0.010
Week 2	0.026	0.008	0.975	0.009	0.982	0.011
Week 3	0.007	0.003	0.993	0.003	1.000	0.008
Week 4	0.023	0.007	0.977	0.008	0.984	0.010
Week 5–6	0.013	0.004	0.987	0.004	0.994	0.008

[a] We determined the null model age structure (in weeks) by QAIC$_c$ values in Table 1.

[b] DSR: daily survival rate for each week.

0.006, SE = 0.004), week 4 ($\hat{\beta}$ = 0.017, SE = 0.007), and weeks 5–6 ($\hat{\beta}$ = 0.007, SE = 0.003). Estimated heterogeneity of chick survival (D) in our top-ranked model for age-specific chick survival was 1.31 (95% CI = 0.97–1.65), indicating low dependence in fates among brood mates. When we added additional covariates to this model, we found little support for year or hatch-date effects on chick survival (based on QAIC$_c$ and 95% CIs for β'_is that overlapped zero; Table 1).

We did, however, find that brood type (mixed or not) affected chick survival (top model based on QAIC$_c$; Tables 1, 2). Based on the age and brood-type model, the effect of brood-type on chick survival was likely of biological importance but imprecisely estimated (95% CI overlapped zero; $\hat{\beta}_{\text{mixed}}$ = 0.007, 95% CI = −0.01–0.02). Averaged together, chicks in both brood types had a survival rate of 0.50–42 days (95% CI = 0.41–0.61), and separately chicks in non–brood-mixed broods had a survival rate of 0.48 (95% CI = 0.37–0.58) to 42 days, whereas chicks in brood-mixed broods had a survival rate of 0.65 (95% CI = 0.42–0.88) to 42 days. Accordingly, brood-mixed chicks had consistently higher estimates of daily survival rates to 42 days (Fig. 1; Table 2). According to our best models for analysis actions 2 (low estimate of survival) and 3 (high estimate of survival) chick survival estimates were 0.41 (SE = 0.05) and 0.61 (SE = 0.10), respectively (Appendix). Estimated heterogeneity of chick survival (D) in our brood-type (best) model was 1.01 (95% CI = 0.49–1.54), indicating even lower dependence in fates among brood mates when we add the brood-type covariate to the age-effects model. When we assessed brood female characteristics (restricted data set) our best model included an effect of female age ($\hat{\beta}$ = −0.01, 95% CI = −0.022 to −0.002) indicating higher chick survival for yearling females (Table 3).

During the early brood-rearing period (days 1–21), arthropod abundance, specifically Orthoptera, Lepidoptera, Coleoptera, and ants, appeared to influence chick survival (based on QAIC$_c$ criteria that beat the null model; Table 4). However, all β'_is in top models were imprecisely estimated (95% CIs overlapped zero), which may have occurred because of our restricted sample size (n = 59 survival periods) and, thus, we were not able to attain precise estimates of these biologically important relationships. Percent abundance of each order (based on vol displacement) was 12%, 12%, 19%, 17%, 7%, and 33% for ants (Hymenoptera), bees and wasps (Hymenoptera), Coleoptera, Lepidoptera, Orthoptera, and a miscellaneous group, respectively.

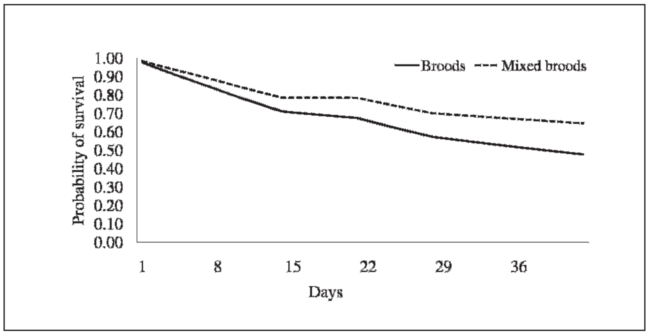

Figure 1. Survivorship curve for greater sage-grouse chicks, Parker Mountain, Utah, USA, 2005–2006.

DISCUSSION

Our best estimates of sage-grouse chick survival to 42 days exceeded previously published reports. Gregg et al. (2007) reported a considerably lower survival rate of 0.22 to only 28 days for chicks marked with subcutaneous implanted radios. Furthermore, Aldridge and Boyce (2007) used radiomarked chicks (same methods as we used) and reported a survival probability of 0.12–56 days. Our chick survival was also higher than estimates reported in studies that assessed survival (0.33) of unmarked sage-grouse chicks during the same approximate period (Schroeder 1997). Our high chick survival estimates could affect population modeling (e.g., population viability analysis) exercises and reflect recruitment estimates of a stable to increasing population (Dahlgren 2009).

Brood-mixing was a common occurrence among our radiomarked chicks and broods and was our most important covariate influencing chick survival. Though brood-mixing has been shown to occur in other galliformes (Keppie 1977, Maxson 1978, Lott and Mastrup 1999, Faircloth et al. 2005, Wong et al. 2009), to our knowledge brood-mixing has never been documented for sage-grouse prior to our work. Eadie et al. (1988) hypothesize that density of broods may influence brood-mixing. Our findings may support this hypothesis because sage-grouse broods generally concentrate in high-elevation late brood-rearing habitat at southern and western edges of Parker Mountain. Further research testing of this hypothesis is warranted.

Estimated effects of brood-mixing on chick survival differed by our analysis actions concerning missing chicks. When we right-censored missing chicks, higher survival rates in brood-mixed chicks were associated with some uncertainty (95% CI overlapped zero). However, when we classified missing chicks as dead, we could be more certain that brood-mixed chicks had a higher survival than their counterparts that did not mix (95% CI did not overlap zero; Appendix). Lastly, when we classified missing chicks as surviving within their original broods, the brood type model did not rank higher than the null model and beta estimates

Table 3. Models assessing the impact of greater sage-grouse brood female age (restricted data set without mixed broods because we did not determine female age for broods into which radiomarked chicks mixed) on chick survival, Parker Mountain, Utah, USA, 2005–2006.

Model	K^a	$QAIC_c{}^b$	$\Delta_i{}^c$	$w_i{}^d$
Null model determination				
age = week1 + week2 + week3 + week4 + weeks5–6	6	152.86	0.00	0.99999
age = week1 + week2 + week3 + weeks4–6	5	171.62	132.41	0.00000
age = weeks1–2 + weeks3–4 + weeks5–6	4	176.90	137.69	0.00000
age = week1 + week2 + weeks3–6	4	181.85	142.64	0.00000
age = weeks1–2 + weeks3–6	3	182.88	143.68	0.00000
age = week1 + weeks2–6	3	185.11	145.91	0.00000
age = weeks1–6	2	198.15	158.95	0.00000
age = weeks1–3 + weeks4–6	3	198.83	159.63	0.00000
Covariate model comparison				
age + hen age (yearling or ad)[e]	7	41.31	0.00	0.99999
age (null model)[e]	6	152.86	111.60	0.00000

[a] K: no. of parameters used in each model.

[b] $QAIC_c$: quasi-likelihood version of Akaike's Information Criterion.

[c] Δ_i: $QAIC_c$ difference between a model (i.e., model i) and the best performing model (i.e., model with the lowest $QAIC_c$ among the set of models examined).

[d] w_i: Akaike model wt. By uniquely estimating D (heterogeneity factor for brood mates) each model's $QAIC_c$ values can be drastically different, even among the top few models. Thus, model wt can be highly skewed toward the top model.

[e] The best model of age = week1 + week2 + week3 + week4 + weeks5–6, which is shown in the null model determination. We then used the null model once determined to test for the importance of covariate structure in the modeling process.

were not significant (Appendix). However, in all cases marked chicks that brood-mixed had higher daily survival estimates (Fig. 1; Table 2; Appendix), suggesting that brood-mixing may be advantageous for chick survival (Eadie et al. 1988, Nastase and Sherry 1997). Nastase and Sherry (1997) indicated that brood-mixing for Canada geese (*Branta canadensis*) aided survivorship of native brood members. However, our results suggested that brood-mixing may increase survival of chicks that are adopted into unmarked broods. We could not determine whether brood-mixing actions were initiated by chicks to improve their fitness or by adoptive mothers attempting to improve their fitness by increasing the chances of survival in their natal offspring. An alternate hypothesis is that brood-mixing occurred due to accidental separation from natal broods, especially in areas of high brood density.

Eadie et al. (1988) hypothesized that parental age or experience may influence brood-mixing behavior. Although we could not address yearly effects of female age (no yearling brood F in 2006), in 2005 brood-mixing and more multiple-chick mixing occurred in broods reared by yearling females, which suggests that brood female age may be an important

Table 4. Models for greater sage-grouse chick survival during the early brood-rearing period (days 1–21) based on arthropod sampling at brood sites (data set restricted to arthropod sampling periods, which did not change based on differing assumptions), Parker Mountain, Utah, USA, 2005–2006.

Model	K^a	$QAIC_c{}^b$	$\Delta_i{}^c$	$w_i{}^d$
Null model determination				
age = weeks1–2 + week3	3	30.41	0.00	0.565476
age = week1 + week2 + week3	4	32.11	1.70	0.241165
age = weeks1–3	2	33.13	2.73	0.144562
age = week1 + week2–3	3	35.31	4.90	0.048797
Covariate model comparison				
age + Orthoptera[e]	5	15.60	0.00	0.473688
age + each arthropod type separately[e]	9	15.99	0.39	0.389495
age + Lepidoptera[e]	5	18.11	2.51	0.135037
age + Coleoptera[e]	5	28.62	13.02	0.000705
age + ants[e]	5	29.24	13.64	0.000517
age (null model)[e]	3	30.41	14.80	0.000289
age + bees[e]	5	31.24	15.64	0.000190
age + total arthropods[e]	5	33.65	18.05	0.000000
age + Hymenoptera[e]	5	35.60	20.00	0.000000
age + Miscellaneous[e]	5	45.26	29.66	0.000000

[a] K: no. of parameters in each model.

[b] $QAIC_c$: quasi-likelihood version of Akaike's Information Criterion.

[c] Δ_i: $QAIC_c$ difference between a model (i.e., model i) and the best performing model.

[d] w_i: Akaike model wt. By uniquely estimating D (heterogeneity factor for brood mates) each model's $QAIC_c$ values can be drastically different, even among the top few models. Thus, model wt can be highly skewed toward the top model.

[e] The best model of age = (weeks1–2) + (week3), which is shown in the null model determination. We then used the null model once determined to test for the importance of covariate structure in the modeling process.

factor concerning brood-mixing in sage-grouse. Our results lend support for the hypothesis that chicks born to a young female are more likely to join the brood of an experienced female, such that the young female may increase her own fitness by abandoning her young rather than bearing the cost of raising them herself (Eadie et al. 1988).

On our study area brood-mixing appeared to abate the potentially deleterious impact of brood female mortality when orphaned chicks were quickly assimilated into surrogate females broods. Brood-mixing of young in the event of parental mortality has not been discussed in previous works as an adaptive survival strategy, nor in relation to avian alloparental care (Riedman 1982, Eadie et al. 1988). The frequency and biological importance of this novel finding warrants further study.

We acknowledge that our monitoring may have increased the amount of brood-mixing by potentially simulating a predatory event. We found that brood females would often spread their chicks out and attempt to decoy us away from their broods. If other brood females were in the area following our departure, distressed chicks could have easily been adopted (mixed) by other, unmarked brood females. The monitoring–observer effect on probability of brood-mixing needs further investigation and could potentially be examined by using observer-effect nest survival (also a probability of occurrence) models (Rotella et al. 2000). Based on anecdotal information (commonly flushed non-marked broods while following marked broods, detecting broods while driving roads, historic radiomarked brood movements, and running pointing dogs for other research objectives) our marked broods were generally located in high-brood-density areas, though we did not attempt to estimate brood density.

Schroeder (1997) reported that female age did not appear to affect chick survival, but Gregg (2006) reported the opposite. We found a possible inverse effect of female age on chick survival with analysis actions 1 (we right-censored missing chicks) and 3 (we classified missing chicks as surviving in their original broods; but not with analysis action 2 [we classified missing chicks as mortalities]), indicating that yearling females had higher chick survival than adult females, which was unexpected given the importance of adult females in long-lived, low-reproductive species, such as sage-grouse, and our finding that yearling females had a higher probability of losing chicks to brood-mixing (Johnson and Braun 1999, Connelly et al. 2000). Higher chick survival for yearling females may have been the consequence of only the best yearling females making it to the brooding stage and rearing their own chicks. Yearling females were often eliminated from the brood female sample due to lower nest initiation rates (nest initiation averaged 0.85 and 0.56 for ad and yearlings, respectively) and lower nesting survival (nest survival averaged 0.67 and 0.38 for ad and yearlings, respectively; Dahlgren 2009). Moreover, chicks of yearling females were more apt to mix into other broods with unmarked females. In these events, we right-censored chicks from yearling female broods due to brood-mixing and did not include them in the female age analysis, which further decreased the sample size of chicks within yearling female broods. Thus, for several reasons, within-generation selection may have resulted in only the best yearling females being included in most of our sample (Vaupel and Yashin 1985). An alternate explanation of higher chick survival for yearling females could have been simply an artifact of confounding between higher survival of chicks that left their natal brood and higher rates of brood-mixing for yearling females. Yearling females occurred in our sample in 2005 but not 2006 and, thus, we were not able to assess temporal changes in the effect of female age on chick survival. Though it is possible that yearling females could experience higher average chick survival than adult females, we strongly suggest caution concerning interpretation of our results.

We did not find any indication of life-fate dependence among brood mates within our analyses. By explicitly estimating D, the Manly and Schmutz (2001) method automatically accounts for the amount of heterogeneity-dependence in survival among brood mates. Our estimate of D for our survival model with the best parameterization of chick age (Table 1) did not differ from 1.00 (nor with analysis actions 2 [we classified missing chicks as mortalities] and 3 [we classified missing chicks as surviving in their original brood]; Appendix). Moreover, our model that best captured variation in chick survival (chick age plus brood-type model) yielded an estimate that also did not differ from 1.00 (based on 95% CI). We improved our estimate of brood-mate dependence in survival by including brood-type (i.e., more covariate structure) in our model, but our estimate still indicated no dependence in fates among brood mates. Thus, sage-grouse chick mortality may be independent of other brood members. Possible explanations for independence among brood members may be a combination of the following: 1) brood behavior in response to predatory pressure resulted in randomly dispersed individual chicks across the landscape to avoid detection (commonly observed behavior during our study for radiomarked chicks as observers approached); 2) sage-grouse chicks are precocial and extract resources from the landscape individually; and 3) an onsite predator community that tends to consume prey singly.

Aldridge (2005) found that herbaceous and shrub cover had important impacts on sage-grouse chick survival at various landscape scales. Additionally, Gregg (2006) reported that vegetation at brood sites influenced chick survival. Vegetation parameters we measured at small scales (40-m transect/brood location site) around the brood sites could not predict chick survival (Dahlgren 2009). Furthermore, predation was our most common cause of mortality, and relationships among habitat, predation, and early life-cycle survival likely occur at much larger scales than we measured (Stephens et al. 2005). For instance, Dahlgren et al. (2006) found that sage-grouse broods on the same study area differentially selected habitat during the late brood-rearing period based on 40.5-ha plots.

Although we found no relationship between arthropods and vegetation measurements (Dahlgren 2009), our results suggest that arthropod abundance in the immediate vicinity of broods may have influenced chick survival during the early brood-rearing period, consistent with findings for captive reared sage-grouse chicks (Johnson and Boyce 1990). Fischer et al. (1996) found that sage-grouse broods selected specific habitat with higher abundance of Hymenoptera than random sites. All arthropods were important for our analysis, but specifically Orthoptera, Lepidoptera, Coleoptera, and ants (within Hymenoptera) accounted for more variation in chick survival than other orders. Connelly and Braun (1997) suggested that low-quality early brood-rearing habitat was related to declines in sage-grouse population recruitment. More research and evaluation with larger sample sizes may be needed to better estimate relationships between arthropod abundance and sage-grouse chick survival, particularly for the early brood-rearing period.

MANAGEMENT IMPLICATIONS

The Parker Mountain sage-grouse population we studied exhibited higher chick survival rates and occurrences of brood-mixing than previously reported in published literature. The increased incidences of brood-mixing, which may be a reflection of availability of brood-rearing habitat and thus brood density, afforded the Parker Mountain sage-grouse population a novel adaptive survival strategy. Because of the role of long-lived adult females in brood-mixing, and ultimately production, it is important to conserve this segment of the population. Our study also confirmed that in areas where brood-mixing may occur, chick survival rates obtained without radiomarking individuals, and other nonradiomarking methods (e.g., pit tags, leg bands) will underestimate survival.

In a captive setting, sage-grouse chick survival during the first few weeks of life depended on arthropod availability (Johnson and Boyce 1990). Our field research confirmed that arthropod availability was related to sage-grouse chick survival. However, we could not detect any relationship between vegetation parameters we measured and arthropod abundance. More information is needed regarding factors that influence arthropod abundance (e.g., precipitation, habitat management) as it relates to annual sage-grouse production and population dynamics.

ACKNOWLEDGMENTS

We thank the Parker Mountain Adaptive Resource Management Sage-Grouse local working group for support. We thank A. Taft and G. Hallows specifically for their support. We thank J. Lamb, Utah Division of Wildlife Resources (UDWR), for all his cooperative work. V. Bagley, Utah State University Extension, was invaluable in initiating this work within the local community. We thank N. Burkepile and J. Connelly for help concerning our chick marking methods and research advice. Our study was funded by grants provided by the UDWR, BLM, USFS, and Jack H. Berryman Institute, Utah State University. We thank D. Mitchell, UDWR; L. Greenwood and L. Armstrong, BLM; and J. Stenton, USFS for their efforts to secure funding.

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Associate Editor: Burger.