Greater sage-grouse apparent nest productivity and chick survival in Carbon County, Wyoming

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Greater sage-grouse *Centrocercus urophasianus* populations across North America have been declining due to degradation and fragmentation of sagebrush habitat. As part of a study quantifying greater sage-grouse demographics prior to construction of a wind energy facility, we estimated apparent net nest productivity and survival rate of chicks associated with radio-equipped female sage-grouse in Carbon County, Wyoming, USA. We estimated apparent net nest productivity by using a weighted mean of the average brood size and used a modified logistic-exposure method to estimate daily chick survival over a 70-day time period. Apparent nest productivity was 2.79 chicks per female (95% CI: 1.46–4.12) in 2011, 2.00 chicks per female (95% CI: 1.00–3.00) in 2012, and 1.54 chick per female (95% CI: 0.62–2.46) in 2013. Chick survival to 70 days post-hatch was 19.10% (95% CI: 6.22–37.42%) in 2011, 4.20% (95% CI: 0.84–12.31%) in 2012, and 16.05% (95% CI: 7.67–27.22%) in 2013. These estimates were low, yet within the range of other published survival rates. Chick survival was primarily associated with year and chick age, with minor effects of average temperature between surveys and hatch date. The variability in chick survival rates across years of our study suggests annual weather patterns may have large impacts on chick survival. Thus, management actions that increase the availability of food and cover for chicks may be necessary, especially during years with drought and above-average spring temperatures.
regional and range-wide sage-grouse productivity. Our objectives were to estimate sage-grouse apparent nest productivity and chick survival rates, while evaluating hypotheses related to the influence of weather and demographic variables on sage-grouse chick survival. Our research was also part of a larger study collecting >3 years baseline data on sage-grouse prior to construction of a wind energy facility that will consist of 1000 turbines and produce 2000–3000 megawatts of energy (Power Company of Wyoming LLC 2009). Thus, our ultimate goal is for our baseline knowledge of chick survival and nest productivity to be used in a before–after, control–impact design that will evaluate whether energy development has any impacts on sage-grouse productivity.

Study area

Our study area encompasses the approximately 1295 km² Overland Trail Ranch (OTR) and surrounding areas in Carbon County, Wyoming, USA (Fig. 1). Elevations range from about 1890 m at the North Platte River to about 2590 m near the Continental Divide in the southwestern portion of the study area. Over the past 60 years, annual precipitation averaged 22.8 cm in Rawlins, WY which is 6 km from the northern boundary of the study area and 24.6 cm in Saratoga, WY which is 14 km from the eastern edge of the study area (Western Regional Climate Center 2013). The average monthly temperature range varies from

Figure 1. Map showing the surface ownership on and near the Overland Trail Ranch, Carbon County, WY, USA, where we studied greater sage-grouse apparent nest productivity and chick survival from 2011–2013.
0.7°C–12.7°C between November and April and 15.3°C–
28.5°C between May and October (Western Regional
Climate Center 2013).

The OTR consists of three ecoregions, including rolling
sagebrush steppe, salt desert shrub basins and foothill shrub-
blands (Chapman et al. 2004). Rolling sagebrush steppe cov-
ers the majority of the OTR and is characterized Wyoming
big sagebrush *Artemisia tridentata wyomingensis* at lower
elevations, mountain big sagebrush *A. t. vaseyana* at higher
elevations, silver sagebrush *A. cana* in mesic areas, and black
sagebrush *A. nova* on exposed, rocky soils (Chapman et al.
2004). Other common vegetation species in this ecoregion
include rabbitbrush *Chrysothamnus* spp. and *Ericameria
nauseosa*, cushion-like phlox *Phlox* spp., mock goldenweed
*Stenotus* spp., clover *Trifolium* spp., madwort *Alysum* spp.,
vetch *Astragalus* spp., western wheatgrass *Pascopyrum smithii*,
bluebunch wheatgrass *Pseudoroegneria spicata*, needle-and-
thread *Hesperostipa comata*, Idaho fescue *Festuca idahoensis*,
Sandberg bluegrass *Poa secunda* and prairie junegrass *Koeleria
macrantha*.

Salt desert shrub ecoregions, characterized by less pre-
cipitation and alkaline soils, comprise approximately 19%
of the OTR and are dominated by Gardner’s saltbush
*Pandalion gardneri*, shadscale *Arillips confertifolium*, black grease-
wood *Sarcobatus vermiculatus*, mock goldenweed and
*Phlox* spp., with sporadic inclusions of Wyoming
big sagebrush and basin big sagebrush *A. t. tridentata* in soils
with sustained moisture. Foothill shrublands comprise
approximately 15% of the OTR and receive the most pre-
cipitation. Common vegetation species in this ecoregion
include mountain big sagebrush, snowberry
*cotoneaster*, mountain mahogany *Cercocarpus* spp., aspen
*Populus tremuloides*, limber pine *Pinus flexilis*, vetch, clover,
lupine *Lupinus* spp., prairie junegrass, bluebunch wheatgrass
and western wheatgrass (Chapman et al. 2004).

**Methods**

**Field methods**

**Capture**

During March and April of 2010–2013, we captured female
sage-grouse using spotlighting techniques (Giesen et al.
1982) across the study area and attached 30 g rump-mounted
(Rappole and Tipton 1991) solar Argos GPS PTTs. All trans-
mitters attached were <3% of the female body weight. We
classified birds as adult (>2 years old) or yearling (1–2 years
old) by examining primary feather characteristics on wings
(Eng 1955). Capture and handling protocols were approved
by the Univ. of Missouri Animal Care and Use Committee,
permit no. 6750 and Wyoming Game and Fish Department
Chapter 33 Permit, permit no. 752.

**Apparent nest productivity**

We scheduled GPS PTTs to collect eight locations per
day and transmit Ultra High Frequency (UHF) signals for
approximately 8 h per day to facilitate ground-tracking dur-
ing the nesting season. We downloaded GPS PTT location
data from Argos satellites every 3–5 days and verified nests
in the field when >3 consecutive GPS locations occurred
within a 50 m radius over a 48 h period. We used the UHF
signal to locate nesting females and observed the bird using
binooculars >10 m from the nest to limit disturbance.

When a nest was confirmed, we estimated the approxi-
mate hatch date using estimated initiation of incubation,
determined from GPS locations, and an incubation period
of 27 days (Schroeder 1997). Starting the day before the
approximate hatch date, we began daily visual observations
of the nesting female until incubation ceased. We used GPS
PTT data to inform us of the exact hatch date, evidenced by
>3 consecutive GPS locations >50 m from the nest. After
the female left the nest, we inspected the nest to estimate
the number of successfully hatched chicks by counting eggshells
with detached membranes (Girard 1939).

**Chick survival**

Dahlgren et al. (2010b) found that 100% of chicks were
detected using spotlighting techniques, while only 72%
detected using walking methods during the day. Thus,
we conducted repeated nocturnal spotlight surveys from May
to September 2011–2013 to count the number of chicks
associated with each radio-equipped brood-rearing female.
We did not consistently monitor broods in 2010, so we did
not include those data in the analysis. Chicks <42 days of
age usually roosted underneath the female, so we carefully
approached brood-rearing females on foot, facilitated with
a hand-held UHF antenna and receiver, and flushed the
female to count chicks using a handheld spotlight (Dahlgren
et al. 2010b). Chicks older than 42 days were usually roosted
next to the adult female, so they could be counted without
flushing. After counting the chicks, we immediately left
the site to minimize disturbance. We did not count chicks
during or immediately after rain events to lessen the risk of
exposure-related mortality. We initiated spotlight surveys as
early as the first night post-hatch and repeated surveys at
1–2 week intervals until all chicks were absent and assumed
to be dead or the brood reached 70 days of age, representing
chick independence (Beck et al. 2006). We assumed perfect
detection based on our field observations (Dahlgren et al.
2010b), but could not assess the possibility of chick adoption
or brood mixing (Dahlgren et al. 2010a) because we did
not mark chicks.

**Analytical methods**

**Apparent nest productivity**

We estimated average brood sizes for initial nests and renests
immediately after hatching using data collected from nest
monitoring and initial brood spotlighting. We estimated
apparent net nest productivity using a weighted mean of the
average brood size, which is the product of the average brood
size and the rate of nest success for initial nests and renests
(Skalski et al. 2005: 100).

**Chick survival**

We modified the logistic-exposure method typically used
for modeling nest survival to analyze chick survival because
it allows for unequal sampling intervals (Shaffer 2004,
Shaffer and Thompson 2007, Schôle et al. 2011). The logistic-
exposure method estimates survival as an exponential function
of the number of days in the interval between observations. We applied the method to brood observations which consisted of multiple binary trials representing the number of chicks alive at the start and end of the interval. Due to the lack of independence among chicks within the same brood, we fit repeated measures models using generalized estimating equations in PROC GENMOD (SAS 9.3) with the individual female as the repeated effect. Mixed models require identification of the appropriate covariance structure of the data to obtain unbiased parameter estimates (Littell et al. 2006). Consequently, we evaluated exchangeable, independent, and unstructured covariance structures using the Quasi-likelihood under the ‘independence model criterion’ (QIC) statistic (Pan 2001).

We evaluated survival of chicks using a multi-stage, information-theoretic modeling approach (Franklin et al. 2000, Burnham and Anderson 2002). First, we formulated a priori models based on hatch date, chick age, and available weather data, collected from Rawlins, WY airport, located ~6 km north of the study area. We hypothesized chick survival would vary by year (Bergerud 1988); decrease with advancing hatch date (Thompson 2012); increase with chick age (Bergerud 1988); increase with average daily temperature over the interval between observations (Thompson et al. 2006); and decrease with the sum of precipitation over the interval between observations (Bergerud 1988, Roberts and Porter 1998). We hypothesized chick survival rates would be higher with adult brood-rearing females (Curio 1983, Guttery et al. 2013), but we excluded this variable from survival models because only two yearling females had chicks. We also hypothesized chick survival would vary by region of our study area, but sample sizes were too low to test this hypothesis. Detailed reasoning behind variables used in a priori models can be found in Schreiber (2013).

We compared biologically-relevant, non-linear forms of continuous variables (Franklin et al. 2000) using Akaike’s information criterion adjusted for small sample size (AICc) values. We used the most supported form if it was > 2 AICc, units better than the linear form. We checked for multicollinearity between covariates by calculating Pearson’s correlation coefficient (r) using PROC CORR (SAS 9.3) and removed the least biologically meaningful covariates from models if r > 0.65. We ranked all models in our set based on AICc, and Akaike weights. If model uncertainty existed, we averaged models that added up to 90% of the Akaike weight and used model-averaged parameter estimates to calculate daily survival rates (Burnham and Anderson 2002). We graphically demonstrated the variation in chick survival by varying explanatory variables of interest while holding other variables in the models at their average values.

Results

We monitored 44 radio-marked female sage-grouse (n = 12 yearlings, n = 32 adults) in 2011, 52 female sage-grouse (n = 2 yearlings, n = 50 adults) in 2012, and 46 female sage-grouse (n = 1 yearling, n = 45 adults) in 2013. Average hatch dates were approximately three weeks earlier and renesting rates were ~50% lower in 2012, than in 2011 or 2013. Clutch size for successful nests was similar across years, but apparent net nest productivity decreased ~25% per year from 2011–2013 (Table 1).

We monitored chicks from 14 broods in 2011, 14 broods in 2012, and 9 broods in 2013 (n = 2 yearling maternal females, and n = 35 adult maternal females). The daily survival rate was lowest in 2012 (0.956; 95% CI: 0.934–0.971), while estimates in 2011 (0.977; 95% CI: 0.961–0.986) and 2013 (0.974; 95% CI: 0.964–0.982) were similar. These daily survival rates equate to 70-day survival probabilities of 19.10% (95% CI: 6.22–37.42%) in 2011, 4.20% (95% CI: 0.84–12.31%) in 2012, and 16.05% (95% CI: 7.67–27.22%) in 2013.

Of the nine models we evaluated, there was strong support (w = 0.810) for the model that included a quadratic form of chick age, year, and average daily temperature over the interval between observations (Table 2). There was modest support (w = 0.166) for the model containing the quadratic form of chick age, year and hatch date (Table 2). Daily survival rates of chicks increased with chick age until approximately 50 days post-hatch, then dropped slightly until 70 days (Fig. 2). Average temperature between successive surveys and hatch date did not have significant effects on chick survival rates (Table 3), but trends suggested increasing chick survival with warmer temperatures and later hatch dates (Fig. 2).

Discussion

Sage-grouse chick survival rates have been estimated with varying sampling techniques (e.g. transmitter attachment, brood spotlighting, etc.) over many time intervals across their range, which makes comparisons challenging (Connelly et al. 2011). Chick survival was 34% to 21 days in North Dakota (Herman-Brunson 2007), 39.2% to 28 days in the Great Basin (Gregg and Crawford 2009), 50% to 42 days in Utah (Dahlgren et al. 2010a), 14–23% to 50 days in Alberta (Aldridge and Brigham 2001), and 13.7–45.4% to 112 days in Colorado (Thompson 2012). We cannot make direct comparisons, but constraining our data to the time intervals used in previous studies indicates our highest estimates

Table 1. Average hatch date, number of verified initial nests and renests, number of successful nests, average clutch size, and average apparent net nest productivity (chicks per female) of female greater sage-grouse in Carbon County, WY, USA from 2011–2013.

<table>
<thead>
<tr>
<th>Year</th>
<th>Average hatch date (SE)</th>
<th>No. initial nests (no. successful)</th>
<th>No. renests (no. successful)</th>
<th>Average clutch sizeb (SE)</th>
<th>Average apparent net nest productivity (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>13 June (12.2 days)</td>
<td>38 (16)</td>
<td>10 (4)</td>
<td>6.05 (1.32)</td>
<td>2.79 (0.68)</td>
</tr>
<tr>
<td>2012</td>
<td>22 May (8.6 days)</td>
<td>37 (14)</td>
<td>4 (2)</td>
<td>6.43 (1.09)</td>
<td>2.00 (0.51)</td>
</tr>
<tr>
<td>2013</td>
<td>10 June (13.0 days)</td>
<td>37 (11)</td>
<td>8 (1)</td>
<td>5.89 (1.17)</td>
<td>1.54 (0.47)</td>
</tr>
</tbody>
</table>

*a standard error.

bClutch size values represent only successful nests because it was often difficult to determine clutch sizes of depredated nests. Therefore, average clutch sizes also represent average brood sizes.
Table 2. Model structure, number of parameters (K), log likelihoods (LL), Akaike’s information criterion for small samples sizes (AICc), difference in AICc values from the most-supported model (ΔAICc), and Akaike weights (wi) of logistic exposure models explaining greater sage-grouse chick survival for 37 broods in Carbon County, WY, USA from 2011–2013.

<table>
<thead>
<tr>
<th>Model structure</th>
<th>K</th>
<th>LL</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chick age + chick age2 + average temperature + year</td>
<td>6</td>
<td>−247.435</td>
<td>510.870</td>
<td>0.000</td>
<td>0.810</td>
</tr>
<tr>
<td>Chick age + chick age2 + hatch day + year</td>
<td>6</td>
<td>−249.020</td>
<td>514.039</td>
<td>3.169</td>
<td>0.166</td>
</tr>
<tr>
<td>Chick age + chick age2 + hatch day + average temperature + precipitation + year</td>
<td>8</td>
<td>−247.315</td>
<td>518.209</td>
<td>7.338</td>
<td>0.021</td>
</tr>
<tr>
<td>Chick age + chick age2 + average temperature + precipitation</td>
<td>5</td>
<td>−254.976</td>
<td>522.678</td>
<td>11.808</td>
<td>0.002</td>
</tr>
<tr>
<td>Chick age + chick age2</td>
<td>3</td>
<td>−258.997</td>
<td>524.994</td>
<td>14.124</td>
<td>0.001</td>
</tr>
<tr>
<td>Average temperature + precipitation</td>
<td>3</td>
<td>−265.176</td>
<td>537.352</td>
<td>26.482</td>
<td>0.000</td>
</tr>
<tr>
<td>Year</td>
<td>3</td>
<td>−276.761</td>
<td>560.522</td>
<td>49.652</td>
<td>0.000</td>
</tr>
<tr>
<td>Hatch day + year</td>
<td>4</td>
<td>−276.344</td>
<td>562.427</td>
<td>51.556</td>
<td>0.000</td>
</tr>
<tr>
<td>Null</td>
<td>1</td>
<td>−295.162</td>
<td>592.477</td>
<td>81.607</td>
<td>0.000</td>
</tr>
</tbody>
</table>

*no. of days post-hatch.*

*aaverage daily temperature (°C) over the interval between observations.*

*bsum of daily amounts of precipitation (cm) between successive surveys.*

Figure 2. Daily survival rate of greater sage-grouse chicks from 37 broods as a function of chick age (a), average daily temperature over the interval between observations (b), and hatch date (c) in Carbon County, WY, USA during 2011 (red circles), 2012 (white triangles), and 2013 (blue squares). Lines representing 95% confidence intervals were omitted for clarity.

Table 3. Model-averaged parameter estimates, standard errors (SE) and 95% confidence limits (L95% and U95%) explaining greater sage-grouse chick survival for 37 broods in Carbon County, WY, USA from 2011–2013.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>L95%</th>
<th>U95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.9725</td>
<td>1.0524</td>
<td>−1.1322</td>
<td>3.0772</td>
</tr>
<tr>
<td>Chick agec</td>
<td>0.0691</td>
<td>0.0199</td>
<td>0.0293</td>
<td>0.1088</td>
</tr>
<tr>
<td>Chick age2</td>
<td>−0.0007</td>
<td>0.0002</td>
<td>−0.0012</td>
<td>−0.0003</td>
</tr>
<tr>
<td>Average temperaturec</td>
<td>0.0625</td>
<td>0.0552</td>
<td>−0.0480</td>
<td>0.1730</td>
</tr>
<tr>
<td>Hatch date</td>
<td>0.0020</td>
<td>0.0043</td>
<td>−0.0066</td>
<td>0.0105</td>
</tr>
<tr>
<td>Year</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>0.1012</td>
<td>0.2963</td>
<td>−0.4914</td>
<td>0.6937</td>
</tr>
<tr>
<td>2012</td>
<td>−0.5595</td>
<td>0.2279</td>
<td>−1.0133</td>
<td>−0.1037</td>
</tr>
</tbody>
</table>

*no. of days post-hatch.*

*aaverage daily temperature (°C) over the interval between observations.*

*the estimate for 2013 is taken up by the intercept.*

were low, yet within the range of other published survival rates. We are uncertain why chick survival rates were low on our study area, given there were relatively few anthropogenic disturbances, limited cattle grazing, and vegetation cover appears to meet the requirements for brood-rearing habitat (Connelly et al. 2000). Dahlgren et al. (2010a) found that “brood mixing” or adoption occurred in 43% of broods they studied and might have been an adaptive strategy that improved survival. We did not account for brood mixing or adoption because we could not uniquely identify chicks. If chicks were assumed dead, but were actually adopted by another female, survival estimates could have been biased low. Survival estimates could also be biased low if imperfect detection is not modeled appropriately (Lukacs et al. 2004). However, we assumed imperfect detection was not a significant issue in our study because we used spotlighting methods to count chicks, which have reported 100% detection rates (Dahlgren et al. 2010b). There could be factors affecting sage-grouse vital rates that vary over decades that we could not examine. Sage-grouse populations exhibit a 6–10-year cyclic trend in abundance (Rich 1985, Fedy and Doherty 2011, Fedy and Aldridge 2011), and we started our study during a low point in the cycle according to historical lek count data. As such, our chick survival rates may not represent the long-term average for this population.

Annual differences in survival rates could be due to variability in weather or other environmental factors (Blomberg et al. 2012, Taylor et al. 2012). Our chick survival estimates in 2012 were 5 times lower than 2011, which may relate to below-average precipitation and drought conditions in 2012 (National Oceanic and Atmospheric Administration 2012).
Arthropods and forbs are critical food sources for sage-grouse chicks (Klebenow and Gray 1968, Johnson and Boyce 1990, Drut et al. 1994), and the protective cover that vegetation provides may be crucial to prevent predation and exposure-related chick mortality (Wallestad 1971, Klott and Lindzey 1990, Sveum et al. 1998). Low winter and spring precipitation inhibits herbaceous production (Bates et al. 2006, Cagney et al. 2010) and elevated temperatures may lower the palatability of some plants (Bidart-Bouzat and Imeh-Nathaniel 2008, Forbey et al. 2013), thereby reducing the food and cover resources available to sage-grouse chicks (Connelly et al. 2000). The lack of food and cover resources due to drought conditions reportedly leads to low chick survival (June 1963, Connelly et al. 2000, Aldridge 2005, Guttery et al. 2013), and high frequency of droughts over time can reduce the probability of sage-grouse persistence (Aldridge et al. 2008). Interestingly, we found no evidence that precipitation between surveys directly affected chick survival. This does not discount the influence of drought effects on chick survival, rather reinforces the concept that accumulated precipitation through winter and spring, and its subsequent effects on herbaceous vegetation growth, is more impactful on chick survival than direct, immediate effects of precipitation.

Drought conditions continued into 2013, with below-average winter and spring precipitation, but, surprisingly, chick survival rates increased. In 2012, snowpack at the SNOTEL station on our study area (station number 1015) melted by 10 April, approximately one month earlier than average (Natural Resources Conservation Service 2014). In contrast, snowpack melted by May 11 in 2013. Inouye (2008) found a strong correlation between early snow melt and fewer flowering plants in Colorado, because vegetation that begins blooming early in the spring is more susceptible to freezing temperatures that kill plant buds. Blomberg et al. (2012) found a strong correlation between monthly snow depth and sage-grouse recruitment, but they did not specifically evaluate the effect of snowpack persistence on chick survival. The reduction in herbaceous food resources available to sage-grouse chicks due to early snowpack melt (Inouye 2008), combined with drought conditions could contribute to the difference in survival rates we observed between 2012 and 2013.

There is a strong association between chick age and survival (Gregg et al. 2007, Gregg and Crawford 2009, Dahlgren et al. 2010a, Thompson 2012, Guttery et al. 2013). Most chick mortality occurs within the first 21 days of hatch (Gregg et al. 2007); however, chick mortality might increase late in the brood-rearing period (Thompson 2012, Guttery et al. 2013). There is often a reduction in the amount of food and cover available to chicks in late summer due to desiccation of herbaceous vegetation (Verhulst and Nilsson 2008, Thompson 2012). Also, chicks become more independent, possibly rendering them more susceptible to mortality (Thompson 2012). These factors could explain the quadratic relationship we observed between chick age and survival.

There is likely an association between environmental conditions (e.g. precipitation), sage-grouse hatch date, and chick survival that varies temporally and spatially (Guttery et al. 2013). Thompson (2012) found a negative relationship between hatch date and chick survival, because warmer temperatures could lead to quicker vegetation desiccation, especially in drier climates (Verhulst and Nilsson 2008). Others found a positive association, because chicks that hatch later, during warmer temperatures, experience less extreme weather conditions (Goddard and Dawson 2009, Gregg and Crawford 2009). Drought conditions and early snowpack melt in 2012 may have caused hens on our study area to initiate nests earlier, resulting in hatch dates 2–3 weeks earlier than other years. Chicks that hatched this early may have been exposed to unfavorable environmental conditions, further reducing survival rates. In years with average temperatures and precipitation, snow often covered the ground over parts of our study area late into spring, so significant new grass and forb growth did not occur until late May or early June. Thus, sage-grouse chicks that hatched later typically experienced warmer weather with increased vegetative and food resources. Given the temporal and spatial variability of hatch dates, the effects of hatch date on chick survival may not be ubiquitous and should be estimated regionally.

Apparent net nest productivity decreased from 2011 to 2013, suggesting that the mechanisms affecting chick survival and apparent nest productivity differ. Increasing grass cover and height often lead to improved nest success due to added concealment from predators (Gregg et al. 1994, Holloran et al. 2005, Moynahan et al. 2007, Rebholz 2007, Herman-Brunson et al. 2009, Doherty et al. 2014). Nest success may be related to residual grass cover, because nests are initiated in spring, before new herbaceous growth (Connelly et al. 2000, Holloran 2005). This hypothesis was supported by studies in Oregon, Montana and Wyoming, where sage-grouse nests were more likely to succeed if they were protected by tall residual grass cover (Gregg et al. 1994, Holloran et al. 2005, Doherty et al. 2014). Favorable growing conditions during 2010 and 2011 might have led to adequate amounts of residual vegetation for nesting in 2011 and 2012, while nests in 2013 were subject to less residual herbaceous cover because of the poor growing season in 2012. We did not thoroughly test this hypothesis and there might be other factors influencing apparent nest productivity (e.g. extreme weather events or nest predator dynamics; Aldridge 2003, Coates et al. 2008). Thus, a more in-depth evaluation of nest success and productivity is warranted.

Our results demonstrate the variable nature of sage-grouse chick survival rates and apparent net nest productivity. Chick survival may be especially low during years with drought and unseasonably warm springs, and nest productivity may be low one year after such environmental conditions. Thus, we recommend managers take actions to improve brood-rearing and nesting habitat, which could include maintaining tall grasses (> 18 cm) within sagebrush stands (15–25% canopy cover) for nesting (Gregg et al. 1994, Connelly et al. 2000, Holloran et al. 2005, Doherty et al. 2014) and increasing the availability of forbs, arthropods and vegetative cover for chicks (Johnson and Boyce 1990, Hagen et al. 2007, Schreiber et al. 2015). We also encourage researchers and managers to use our knowledge of baseline chick survival rates and apparent nest productivity when evaluating the potential effects of wind energy development on sage-grouse productivity after the wind energy facility is constructed.
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