RESEARCH ARTICLE

Factors affecting seasonal movements of juvenile Greater Sage-Grouse: A reconceptualized nest survival model

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ABSTRACT

Estimating the climatic and habitat factors that affect animal movement patterns (e.g., migration, dispersal, site fidelity) is informative for management and conservation. Juvenile Greater Sage-Grouse (*Centrocercus urophasianus*) have been identified as having a significant influence on population growth, but relatively little is known about factors that influence survival, movement, and the potential interrelation between the two. Movement out of fall habitat has been suggested to influence the survival of juvenile Greater Sage-Grouse. We reconceptualized the nest survival model (equating movement out of a focal area with failure of a nest) to extend its use to movement data on juveniles in south-central Utah. We found that juveniles' seasonal movements were affected by a linear trend in time ($\beta = -0.655$, 95% confidence interval [CI]: -1.049 to -0.26) and by precipitation ($\beta = -3.718$, 95% CI: -6.687 to -0.749), with an interaction between the parameters ($\beta = 0.360$, 95% CI: 0.002–0.718). In the absence of precipitation, the probability of movement increased weekly through time (within a year). Weekly precipitation increased the probability of movement in earlier weeks, but the effect of precipitation attenuated in later weeks (i.e. interaction parameter). The precipitation was likely non-accumulating snowfall, given the observed below-freezing temperatures. Our results suggest that changes in precipitation (mainly snowfall) that result from climate change could influence the timing and duration of seasonal movements (i.e. population-level time to complete movement) in migratory populations of Greater Sage-Grouse. Furthermore, our results demonstrate the utility of the nest survival model for evaluating the factors that affect animal movements with "ragged" data.

Keywords: Centrocercus urophasianus, dispersal, Greater Sage-Grouse, juvenile, migration, nest survival model, Program MARK, seasonal movement

Factores que afectan los movimientos estacionales de las aves jóvenes en *Centrocercus urophasianus*: una aproximación a partir de modelos de supervivencia de los nidos

RESUMEN

Estimar los factores climáticos y del hábitat que afectan los patrones animales de movimiento (e.g. migración, dispersión, fidelidad al sitio) brinda información para el manejo y la conservación de especies. Se ha determinado que las aves jóvenes de *Centrocercus urophasianus* tienen una influencia significativa en el crecimiento poblacional, pero se sabe relativamente poco sobre los factores que afectan su supervivencia, movimientos e interacciones entre estas dos variables. Se ha sugerido que los movimientos fuera del hábitat de otoño afectan la supervivencia de las aves jóvenes de *C. urophasianus*. En este trabajo volvemos a conceptualizar el modelo de supervivencia de los nidos equiparando el movimiento hacia afuera de un área focal con el fracaso de los nidos para extender su uso a los datos de movimiento de aves jóvenes de *C. urophasianus* en el centro-sur de Utah. Encontramos que el movimiento estacional de los jóvenes en *C. urophasianus* fue afectado por una tendencia lineal en el tiempo ($\beta = -0.655$, 95% IC $= -1.049$ a -0.26) y la precipitación ($\beta = -3.718$, 95% IC $= -6.687$ a -0.749), y que existía una interacción entre los parámetros ($\beta = 0.360$, 95% IC $= 0.002–0.718$). En ausencia de precipitación, la probabilidad semanal de movimiento se incrementó con el tiempo (en un año). La precipitación semanal incrementó la probabilidad de movimiento en las primeras semanas, pero el efecto de la precipitación se atenuó semanas más tarde (i.e. parámetro de interacción). Probablemente la precipitación correspondía a nieve que no se acumulaba debido a las temperaturas bajo el punto de congelamiento. Nuestros resultados sugieren que los cambios en precipitación, principalmente de nieve, que resulten del cambio climático podrían afectar la sincronización y duración (i.e. el tiempo a nivel poblacional para completar el movimiento) de los movimientos estacionales de *C. urophasianus* en las poblaciones migratorias. Además demostramos la utilidad del modelo de supervivencia de los nidos para evaluar los factores que afectan los movimientos de animales con datos imperfectos.

INTRODUCTION

Animal movements are inherently linked to population dynamics (Kernohan et al. 2001), such that the energetic and survival costs associated with movement and acquisition of resources may affect individual fitness. Consequently, understanding the factors that affect the movement of individuals is useful when establishing management guidelines to conserve species. Environmental cues elicit responses by individuals or specific cohorts (e.g., Vuren and Armitage 1991, Both and Visser 2001, Marra et al. 2005), ostensibly to provide a survival or reproductive advantage. Oscillation in the timing of these environmental triggers, however, may influence survival and reproduction, particularly with respect to human-mediated regulation of a species (e.g., harvest). There is thus a need to elucidate behavioral responses to environmental conditions in order to inform management and conservation efforts.

Greater Sage-Grouse (*Centrocercus urophasianus*) populations have experienced long-term population declines and habitat degradation (Schroeder et al. 2004, Connelly et al. 2011, Garton et al. 2011), thereby becoming a species of conservation concern throughout western North America (Canadian Sage Grouse Recovery Team 2001, U.S. Fish and Wildlife Service 2010). Climate appears to significantly influence numerous aspects of the species' biology (Guttery et al. 2013a, Caudill et al. 2014a). Although juveniles may be critical to population dynamics (Johnson and Braun 1999, Taylor et al. 2012), the demographics (e.g., survival, predation, movement) of juveniles are poorly understood (Crawford et al. 2004, Taylor et al. 2012; e.g., Beck et al. 2006, Caudill et al. 2014b). Greater Sage-Grouse populations can be classified as either migratory or nonmigratory, and fall movement of migratory populations is similar for adults and juveniles (Connelly et al. 1988). In migratory populations, climatic variability may influence juvenile survival by affecting the timing of seasonal movements and spacing of individuals in fall (Caudill et al. 2014b). However, the factors that affect the timing and duration of seasonal movement are poorly documented. In juveniles, brood breakup occurs prior to fall movements to wintering areas (Klebenow and Gray 1968, Browers and Flake 1985; see Connelly et al. 2011). Studies have documented fall movements of Greater Sage-Grouse in relation to descriptive measures by relating climate to movement; Dunn and Braun (1986) concluded that movement was tied to snowfall, which influenced availability of sagebrush. However, in several grouse species, snowfall-stimulated fall movements occur before food availability becomes limited by snow depth (Bergerud and Gratson 1988). Furthermore, studies have reported conflicting results regarding the temporal nature of migratory movements from late-summer areas to wintering areas for Greater Sage-Grouse, where movements were rapid in some instances and prolonged in others (e.g., Wallestad 1971, Connelly and Markham 1983, Dunn and Braun 1986, Connelly et al. 1988). Knowledge of the timing and spatial arrangement of movement is requisite to optimizing many conservation actions. For example, management of seasonal-use areas requires accurate information on the explicit timing of movement and the variability in use both within and across seasons (e.g., function of climatic conditions).

Despite the development and use of numerous methods to evaluate animal movements (Horne et al. 2007, Terhune et al. 2010, McClintock et al. 2012; see Millspaugh et al. 2012), many methods are focused on intensively sampling a few individuals (e.g., "random walk" approaches), which may have pitfalls (see White and Garrott 1990, Kenward 1992, 2001, Otis and White 1999). In many instances, there is a trade-off between sample size and transmitter technology: Fewer global positioning system (GPS) units can be deployed, given their cost, compared with very-high-frequency (VHF) transmitters (Hebblewhite and Haydon 2010). A primary advantage of more advanced transmitter technology (e.g., GPS) is the ability to record more locations per individual on a predefined schedule; nevertheless, marked individuals are the sampling unit and, consequently, larger sample size—at the expense of sampling rate per individual—could be preferable (see Börger et al. 2006, Lindberg and Walker 2007). Conversely, VHF transmitters could facilitate larger sample sizes at the cost of number and schedule of relocations when logistical constraints (e.g., field conditions, number of personnel, competing project objectives) lead to more irregular data (or "ragged data"). Despite the inherent need, many approaches to analysis of movement data do not lend themselves to ragged data (i.e. unequal monitoring intervals among animals and time; see Rotella et al. 2004). The nest survival model (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999), however, has been extended to accept ragged radiotelemetry data for evaluation of survival; it allows the inclusion of group and individual covariates, as well as complex time structures and time-varying covariates (e.g., Hartke et al. 2006, Mong and Sandercock 2007, Collier et al. 2009, Amundson and Arnold 2011, Augustine and Sandercock 2011, Gue et al. 2013). Thus, we reconceptualized the widely used nest

survival model to evaluate the influence of various environmental factors on the timing of seasonal movements of juvenile Greater Sage-Grouse.

METHODS

We studied a migratory population (*sensu* Connelly et al. 1988) of Greater Sage-Grouse on Parker Mountain in south-central Utah, at the southern extent of the species' range (Schroeder et al. 2004). Winter habitats of juveniles on Parker Mountain are geographically distinct (Caudill 2011). The mountain ranges in elevation from 2,200 to 3,000 m; it receives 65–80 frost-free days and 40–50 cm of precipitation annually, most of which occurs during winter as snow (60%; Jaynes 1982). The vegetation was primarily black sagebrush (*Artemisia nova*) on ridges and mountain big sagebrush (*A. tridentata vaseyana*) in the swales. Quaking aspen (*Populus tremuloides*), pinyon pine (*Pinus edulis*), and juniper (*Juniperus* spp.) occurred on the study area. Parker Mountain is predominantly publicly owned (98.6%; 947 km^2).

We captured juveniles using night spotlighting (Giesen et al. 1982) from August 1 to September 30 annually (2008–2009). We defined juveniles as young-of-the-year that were >80 days old. Accordingly, individuals were captured after brood breakup (Klebenow and Gray 1968, Browers and Flake 1985) and can be considered independent. We used characteristics of the first secondary flight feather to distinguish adults from juveniles and ascertained sex on the basis of primary length and molt patterns (Beck et al. 1975 [adapted from Eng 1955]). We later confirmed sex through DNA analysis (Guttery et al. 2013b), and field classification was 100% accurate (see Caudill et al. 2014b). In cases where molt had not progressed enough to implement the methods outlined by Beck et al. (1975), we relied on DNA analysis for sex classification ($n = 32$). We recorded the molt progression of primary feathers for all captured individuals to index juvenile age. Age was standardized by dividing molt progression by ordinal date of capture. Juveniles were fitted with suture-on backpack or necklace-style VHF transmitters (American Wildlife Enterprises, Monticello, Florida, USA). Each transmitter weighed 15 g and did not exceed 3% of the individual's body mass (Thirgood et al. 1995). Transmitters were battery powered and equipped with mortality switches (activated after 12 hr of inactivity). Survival status was confirmed remotely using the pulse signal emitted by the transmitters. Radio frequencies were monitored from the ground daily from August 15 to December 15, but signals were not always detected. Because survival was the primary objective of field methods, locations were acquired 1–4 times mo^{-1}, a location interval similar to those used in previous studies in this species (e.g., Connelly et al. 1988). Transmitter type appeared to affect the survival of

juveniles (Caudill et al. 2014b) but not movement (Caudill et al. 2013), so we included both types in our analysis. The study protocols were approved by the Utah State University Institutional Animal Use and Care Committee (IACUCC no. 942R).

Both temperature and precipitation have been hypothesized to affect Greater Sage-Grouse biology (e.g., Caudill et al. 2013, Guttery et al. 2013a, Caudill et al. 2014a, b), and fall movements appear to be influenced by snowfall, which presumably limits the availability of sagebrush (Dunn and Braun 1986). However, for many grouse species, including Greater Sage-Grouse, movement occurs before snow depth limits food availability (Bergerud and Gratson 1988). Clearly, temperature and precipitation work in tandem to influence snow conditions, and accordingly we compiled climatic variables averaged by calendar week for snow depth, minimum temperature mean (MTmean), and precipitation (snow and rain). In addition, we included weekly minimum temperature (MTM) and weekly total snow accumulation. Climatic data were downloaded from the U.S. Department of Agriculture, Natural Resources Conservation Service SNOTEL website (http://www.wcc.nrcs.usda.gov/snow/). All SNOTEL covariate data were averaged across the 2 stations in proximity that were representative of our study site, Black Flat–U.M. Creek (site no. 348; 2,884 m elevation) and Donkey Reservoir (site no. 452; 2,986 m elevation); these two SNOTEL sites are 23.66 and 9.41 km from our study area, respectively. We developed an a priori candidate model set by combining year, linear trend in time (by week within a year, T), and climatic variables in additive and interactive forms (total number of candidate models = 29). Climatic variables that were correlated with time (e.g., MTM, MTmean, snow depth) were not included in models with a linear trend in time effect. Correlation between parameters, Pearson's coefficient, was assessed using the "cor" function in R version 3.0.0 (R Development Core Team 2013). We tested for the effect of juvenile age and sex in a post hoc analysis, treating both parameters as potential nuisance parameters. Sex and age were added to the best-performing (AIC$_c$) climatic model as additive terms, and a likelihood ratio test (LRT) was performed to test parameter effects.

We defined late summer–early fall habitats (i.e. pre-movement habitats) by elevation. We reclassified a digital elevation model (DEM, 10 m resolution; obtained from the Natural Resources Conservation Service geospatial data gateway) to 12 jenks (Jenks and Caspall 1971 [see also "natural breaks"]). Twelve jenks represented 50 m resolution if dispersed evenly, which we consider a biologically meaningful scale for assessing movements of juvenile Greater Sage-Grouse. Visual inspection of data yielded all definitive premovement locations (August) occurring in the 3 highest-elevation jenks (i.e. +2,747 m elevation).

TABLE 1. Example encounter histories and interpretations of a reconceptualization of the nest survival model (Dinsmore et al. 2002) to evaluate single-direction movements.

Nest survival format [a]	Survival probability statement [b]	Reconceptualized movement probability statement [c]	Reconceptualized movement interpretation [d]
1 4 4 0	$S_1S_2S_3$	$F_1F_2F_3$	Entered during interval 1 in focal area; encountered alive and within focal area (i.e. fidelity) during intervals 2–4; and either died (apparent mortality) or contact was lost (and never regained) after interval 4.
2 7 7 0	$S_2S_3S_4S_5S_6$	$F_2F_3F_4F_5F_6$	Entered during interval 2 in focal area; encountered alive and within focal area during intervals 3–7 (i.e. survived entire period and never moved from focal area).
4 4 6 1	$1 - S_4S_5$	$1 - F_4F_5$	Entered during interval 4 in focal area; not relocated until interval 6, when it was alive and outside the focal area.
4 5 7 1	$S_4(1 - S_5S_6)$	$F_4(1 - F_5F_6)$	Entered during interval 4 in focal area; encountered alive and within the focal area during interval 5; not relocated until interval 7, when it was alive and outside the focal area.

[a] Format: First checked, last seen alive, last checked, fate.
[b] S_t = Survival during interval t.
[c] F_t = Fidelity (i.e. not moved from focal area) during interval t.
[d] Focal area = geographic area of interest (e.g., natal site, premigration fall habitat) or individual is still within a defined distance of interest (e.g., within a specified distance of the previous location or capture location).

We used the nest survival model in Program MARK to estimate seasonal movements out of the late summer–early fall habitats (i.e. 3 highest-elevation jenks). The nest survival model was reconceptualized such that survival equaled not moving out of fall seasonal habitat (i.e. exhibiting site fidelity; see Table 1), so we estimated one-way movements (i.e. out of focal area). Individuals that died prior to moving were right censored at the last known live (apparent survival) date. Individuals were considered "moved" (i.e. "dead" in the modeling framework) when they were located outside the late summer–early fall habitats (Table 1). Because we considered movement equal to "death" in our framework, individuals could not move out of and then back into the premovement habitat. However, we documented only 1 occurrence of this behavior, where the individual was considered to have broken site fidelity and thus was considered "moved" when it first left the focal area. However, the individual moved back into the focal area for only 1 wk.

The nest survival model was initialized for our analysis such that intervals in the modeling framework equaled calendar weeks. A priori candidate models were ranked using Akaike's Information Criterion adjusted for sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered equally supported by the data (Burnham and Anderson 1998). We used the delta method (Seber 1982:7–9) to derive standard error estimates when weekly movement rates were combined into longer intervals. To calculate confidence intervals for estimates derived using the delta method, estimates were transformed to the logit scale then back-transformed to the probability scale to ensure that estimates were appropriately bounded at 0 and 1.

RESULTS

We captured 91 juvenile Greater Sage-Grouse and collected 267 live locations from August 15 to December 3 of both years. Forty-four individuals were known to have moved (average number of locations per individual = 4.5) prior to actual death (i.e. apparent mortality) and were observed in wintering areas. Forty-seven individuals died (apparent mortality) prior to movement and were consequently right censored when last observed alive (i.e. apparent survival). Right censoring at apparent mortality date allowed us to glean inference and sample size from individuals that died prior to movement. Mortality locations were removed from analysis because predators may have moved carcasses, which could lead to misclassification of location within the context of seasonal movement.

There was a single most-supported model, seasonal movement ~ precipitation*time; no other models were considered competitive ($\Delta AIC_c < 2$; Table 2). The top model contained a linear trend though time (T) with a negative slope (Table 3 and Figure 1). The top model also contained an additive effect of precipitation and an interaction between precipitation and time, which had negative and positive slopes, respectively (Table 3 and Figure 1). Probability of not moving decreased through

TABLE 2. Models evaluated in Program MARK to estimate fall seasonal movement of juvenile Greater Sage-Grouse on Parker Mountain, Utah, USA, 2008–2009. Models are listed with their differences in AIC$_c$ (ΔAIC$_c$), AIC$_c$ weight (w_i), model likelihood ($w_i/w_{\text{best model}}$), number of parameters (k), and deviance.

Model [a,b]	ΔAIC$_c$ [c]	w_i	Model likelihood	k	Deviance
Precipitation*T	0.00	0.51	1.00	4	79.48
Precipitation + T	3.02	0.11	0.22	3	84.57
Snow accumulation + T	3.21	0.10	0.20	3	84.77
T	3.30	0.10	0.19	2	86.91
Year + snow accumulation + T	4.63	0.05	0.10	4	84.11
Precipitation + T + year	5.07	0.04	0.08	4	84.55
Year + T	5.28	0.04	0.07	3	86.84
Year*T	6.99	0.02	0.03	4	86.48

[a] Precipitation = weekly average of daily precipitation; T = linear trend in time; snow accumulation = total weekly snow accumulation; year = year effect; MTM = weekly minimum daily temperature minimum; MTmean = weekly average daily minimum temperature; snow depth = weekly average snow depth; constant = constant trend in time.
[b] Models with ΔAIC$_c$ $\geq$ 7 are not shown: precipitation + MTM; precipitation + MTmean; Precipitation + MTM + year; precipitation + MTmean + year; MTmean; MTmean + snow accumulation; year + MTmean; MTM; year + MTmean + snow accumulation; snow depth; precipitation + snow depth; year + snow depth; snow accumulation; year + snow accumulation; year + precipitation; precipitation + snow depth + year; precipitation; constant; constant + year.
[c] Lowest AIC$_c$ = 87.66.

TABLE 3. Beta estimates (logit scale) for the best-supported model (seasonal movement $\sim$ precipitation $\times$ linear trend in time) of fall movements of juvenile Greater Sage-Grouse on Parker Mountain, Utah, USA, 2008–2009.

Parameter [a]	Estimate	SE	95% confidence interval
Intercept	7.515	1.923	3.747 to 11.284
T	−0.655	0.201	−1.049 to −0.260
Precip	−3.718	1.515	−6.687 to −0.749
T*Precip	0.360	0.183	0.002 to 0.718

[a] T = linear trend in time; precip = weekly average of daily precipitation.

time in the absence of precipitation, and precipitation increased the probability of movement early in the season (Figure 1). However, given the interaction between time and precipitation, the effect of precipitation changed over time (Figure 1). As a result of the interaction, late precipitation could negatively affect the probability of movement (Figure 1). However, very few individuals remained in premovement areas late in time (Figure 2), so the effect of late precipitation could be an artifact of the interaction. Combined period-specific probabilities of movement demonstrate that fall movement occurred over the course of several weeks (Figure 2). Our post hoc LRT analysis revealed that neither sex (χ^2 = 1.04, df = 1, P = 0.31) nor juvenile age (χ^2 = 0.682, df = 1, P = 0.41) appeared to affect movement.

DISCUSSION

Dunn and Braun (1986) reported that movements of juvenile Greater Sage-Grouse were associated with snowfall where snow limited the availability of sagebrush. We found little evidence that either snow depth or snow accumulation influenced the probability of seasonal movement on Parker Mountain, though snow accumula-

tion provided limited explanatory value in multimodel inference (Table 2). Our results indicate that precipitation was the main climatic driver of seasonal movements among juveniles during fall; but, given the observed temperatures, many of the precipitation events were likely snow that was not accumulating. Consequently, our results appear to support the notion that snowfall cues fall movements, but not necessarily because food has become limited (sensu Bergerud and Gratson 1988). Similar to the findings of Connelly et al. (1988), movements from late summer–early fall habitats occurred over a period of several weeks (Figure 2), which is further evidenced by the overwhelming support for the linear time trend (Table 2). Early-season precipitation increased the probability of movement, whereas the interaction between precipitation and time suggested attenuation of the effect of precipitation through time (Figure 1). Greater Sage-Grouse harvest paradigms are linked to movements from fall to winter habitats, and our results provide insight where little information previously existed (e.g., Connelly and Markham 1983, Dunn and Braun 1986, Connelly et al. 1988). Variation in altitudinal migration or seasonal movements likely affect harvest rates in blue grouse (Dendragapus spp.; Mussehl 1960) and Greater Sage-Grouse (Caudill et al. 2014b), where hunters and predators may be keying on flocks of successful hen and juvenile Blue Grouse (Bendell and Elliott 1967, Redfield 1975) and Greater Sage-Grouse (Connelly et al. 2000, Wik 2002) in late fall. Our results demonstrate that movements from late fall habitat can be variable and, consequently, that the effect of harvest may vary with the timing of harvest in relation to seasonal movements. Moreover, our results and statistical approach could be used to build predictive fall movement models that allow managers to time the harvest in relation to fall movements and better regulate harvest composition (sensu Mussehl 1960, Bendell and Elliott 1967, Redfield 1975, Connelly et al. 2000, Caudill et al. 2014a).

Caudill et al. (2014b) suggested that the survival of juvenile Greater Sage-Grouse was tied to the timing and magnitude of climatic events through fall movements and
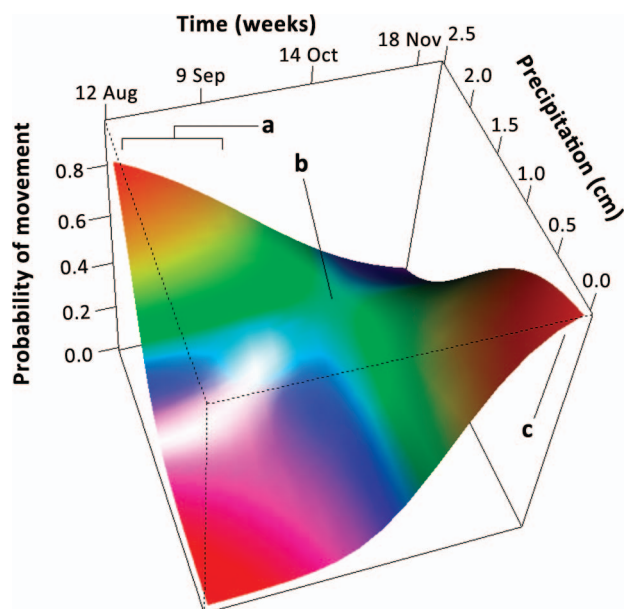
FIGURE 1. Predicted probability of seasonal movement in juvenile Greater Sage-Grouse on Parker Mountain, Utah, USA, 2008–2009, based on the best-supported model (movement ~ precipitation × linear trend in time). Early in the season, precipitation drives movement (a); the influence of precipitation on movement dissipates through time (b); and movement likelihood increases with time (c).

wintering areas is delayed. Our results corroborate previous findings that climate change may negatively affect Greater Sage-Grouse (Guttery et al. 2013a, Caudill et al. 2014a) and grouse in general (Forbey et al. 2013), underscoring the importance of evaluating spatial and temporal factors that influence seasonal movements.

Estimating individual behavior (e.g., migration, dispersal, site fidelity) in relation to extrinsic factors (e.g., climate, habitat fragmentation) is useful for understanding the impacts of, and biological response to, changing habitat conditions and therefore aids in optimizing conservation actions. However, in some instances, evaluating the factors that affect movement will likely necessitate the use of data from studies in which movement was of interest in the initial design but was not the primary objective of the field methods. Moreover, estimating long-term trends in the effects of extrinsic factors (e.g., climatic variation, habitat fragmentation) on movement will likely require concatenation of several datasets with varying primary objectives, data discrepancies, and technologies employed (e.g., VHF vs. GPS transmitters). For instance, there is a trade-off between sample size and transmitter technology in many studies (Hebblewhite and Haydon 2010), and although technological costs will undoubtedly decrease (i.e. Cagnacci et al. 2010) and lessen the trade-off, long-term movement analysis will require flexible approaches accommodating multiple data types where sampling discrepancies arise as a result of the technology employed. In these instances, having model flexibility to incorporate ragged data while retaining a robust statistical framework will be necessary to attain valid biological inference. The flexibility of the nest survival model allowed us to evaluate seasonal movements of Greater Sage-Grouse out of a focal area (site fidelity) and incorporate critical parameters of interest (e.g., time varying covariates) while accounting for ragged telemetry data. Accordingly, we were able to elucidate seasonal movements of Greater Sage-Grouse to
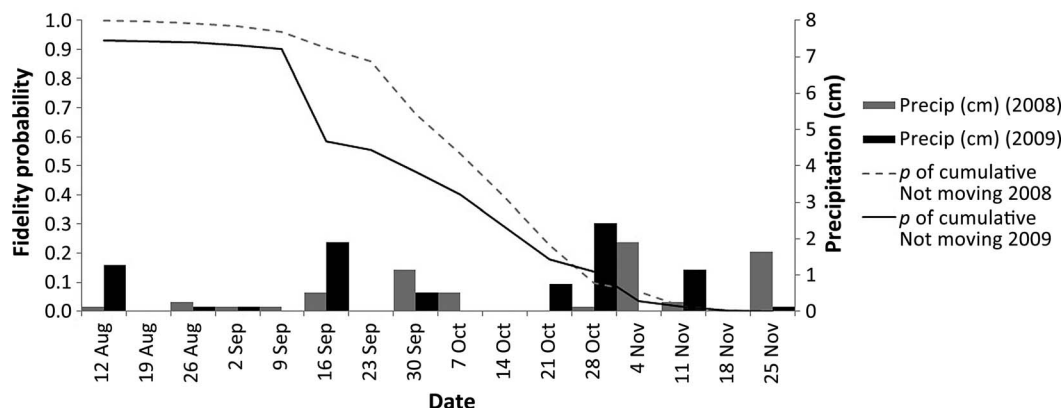
hypothesized that the effect could be a result of transition from fall (high mortality) to winter (high survival) strategies. Our results corroborate this notion, in that our derived cumulative estimate of movement (Figure 2) accelerates within days (3 in 2008; 2 in 2009) of the lowest juvenile survival rates of Greater Sage-Grouse reported in a concurrent study (Caudill et al. 2014b). Delayed onset of winter environmental conditions associated with climate change (e.g., snowfall; Knowles et al. 2006) may pose a threat to Greater Sage-Grouse conservation if seasonal movement patterns are altered such that movement to

FIGURE 2. Derived cumulative probability (p) of site fidelity in relation to precipitation for juvenile Greater Sage-Grouse during the population's fall seasonal movements on Parker Mountain, Utah, USA, 2008–2009.

better understand how climatic conditions influence demographics in, and management for, a species of conservation concern. Although we used geographic states to assess movement, one could incorporate distance (e.g., from last location, capture location) into this approach to parameterize fidelity (Table 1). Moreover, our approach could be extended to include other movement parameters, including onset and duration of migration, seasonal site fidelity of individuals to natal sites or groups, and onset and duration of breeding behaviors. We assumed that sampled individuals were independent, and thus a core assumption would be violated in cases with dependence among samples. However, our approach could be modified to include random effects (see Rotella et al. 2004) to account for intra-group correlation. Finally, while we assumed that movements of interest were in a single direction, another method should be considered when multidirectional movements are of interest (e.g., multistate models; *sensu* Terhune et al. 2010).

ACKNOWLEDGMENTS

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