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Source: The Auk, 134(3) : 628-643

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-16-192.1

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The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 134, 2017, pp. 628–643
DOI: 10.1642/AUK-16-192.1

RESEARCH ARTICLE

Environmental cues used by Greater Sage-Grouse to initiate altitudinal migration

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Submitted September 13, 2016; Accepted March 14, 2017; Published May 24, 2017

ABSTRACT

Migration is a behavioral strategy to access resources that change across a landscape. Animals must ultimately interpret cues to properly time movements that match changing resource quality. Many animals do this by responding primarily to indirect indicators of resource quality such as an internal biological clock or photoperiod. Others are heavily dependent on more direct indicators such as weather or plant phenology. Timing of movement also can be modified by factors specific to individuals. We used time-to-event models for Greater Sage-Grouse (*Centrocercus urophasianus*) to investigate whether an altitudinal avian migrant was influenced by direct indicators of resource quality when timing migration, and whether timing was influenced by individual characteristics, during the spring (winter to breeding range), summer (breeding to summer range), and fall (summer to winter range) transitional seasons. Greater Sage-Grouse interpreted direct indicators of resource quality, especially temperature, when timing movements between seasonal ranges. Timing was also dependent on individual characteristics including location, reproductive status, and habitat use. After we identified which migration cues were important, we evaluated if migratory and nonmigratory individuals were experiencing similar environmental conditions, which may partly explain why there are different behaviors in a partially migrant population. For the summer and fall transitions, migratory grouse experienced more stimulatory migration cues because of differences in elevation of seasonal ranges. Migratory birds were likely avoiding more rapid plant desiccation in warmer breeding ranges and avoiding higher snow accumulation in colder summer ranges with more precipitation. Altitudinal migrants are likely to use direct indicator cues because they have great utility when migration distances are relatively short. In addition, landscapes with altitudinal migrants have sharp environmental gradients creating conditions conducive for partially migratory behavior in a population.

Keywords: timing cues, direct resource indicators, partial migration, *Centrocercus urophasianus*

Señales ambientales usadas por *Centrocercus urophasianus* para dar inicio a la migración altitudinal

RESUMEN

La migración es una estrategia comportamental para acceder a recursos que cambian a través del paisaje. Los animales deben ser capaces de interpretar señales que les ayuden a sincronizar los movimientos que se ajustan a la calidad de los recursos cambiantes. Muchos animales lo hacen respondiendo principalmente a indicadores indirectos de la calidad de los recursos, como un reloj biológico interno o el fotoperiodo. Otros dependen fuertemente de indicadores más directos como el clima o la fenología de las plantas. La sincronización del movimiento también puede ser modificada por factores específicos de cada individuo. Usamos modelos de predicción del tiempo que falta para un evento en *Centrocercus urophasianus* para investigar si estas aves migrantes altitudinales son afectadas por indicadores directos de la calidad de los recursos al sincronizar su migración, y si la sincronización está relacionada con características individuales durante las temporadas transicionales de primavera (del área de invernada al área de reproducción), verano (del área de reproducción al área de verano) y otoño (del área de verano al área de invernada). Los individuos interpretaron indicadores directos de la calidad de los recursos al sincronizar sus movimientos entre áreas de uso estacional, especialmente la temperatura. La sincronización también dependió de las características individuales, incluyendo la ubicación, el estado reproductivo y el uso del hábitat. Después de que identificamos cuáles señales migratorias eran importantes, evaluamos si los individuos migrantes y los no migrantes experimentaron condiciones ambientales similares, lo cual podría explicar en parte por qué hay comportamientos diferentes en una población parcialmente migratoria. Las aves que migraron en las transiciones de verano y otoño experimentaron más señales estimulantes de la migración debido a las diferencias en elevación de sus distribuciones estacionales. Las aves migratorias probablemente estaban evadiendo la desecación rápida de las plantas en áreas de reproducción más cálidas, y también evitando mayor acumulación de nieve en las áreas de verano más frías y con mayor precipitación. Es probable que los migrantes altitudinales usen señales directas como indicadoras porque son más útiles cuando las distancias migratorias son relativamente cortas.

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Además, los paisajes con migrantes altitudinales tienen gradientes ambientales marcados que crean condiciones que llevan a un comportamiento migratorio parcial en una población.

Palabras clave: Centrocercus urophasianus, indicadores directos de recursos, migración parcial, señales de sincronización

INTRODUCTION

Migration is a behavioral adaptation used by many animals when faced with selecting heterogeneous resources (Dingle and Drake 2007). Resources need to be predictable both spatially and temporally to create a life history strategy of annual to-and-fro or round-trip migration (see Dingle and Drake 2007 for definitions of types of migration). Migrants leave their seasonal range where resource conditions are usually waning to seek new seasonal ranges where conditions are stable or improving. Migrating individuals must ultimately interpret internal or environmental cues to initiate movements that will properly time arrival on stopover sites or the next season's range. Mismatching arrival and optimal resource conditions could result in negative fitness consequences such as reduced survival or reproductive success (McNamara et al. 2011). Some species, such as many mid- to long-distance latitudinal migrants, use internal biological clocks (circannual rhythms) and/or photoperiod to initiate migratory movements (e.g., Gwinner 1996, Meunier et al. 2008). Both internal biological clocks and photoperiod should be relatively easy for an individual to interpret because of no yearly variation in the cue; however, they will not consistently be well correlated with changes in the timing of resource quality on the next season's range, which can have significant yearly variation (Bradshaw and Holzapfel 2007). Therefore, internal biological clocks and photoperiod are deemed indirect indicators of resource quality. Other species, such as mule deer (*Odocoileus hemionus*), an altitudinal migrant, also use more direct indicators of resource quality such as weather or plant phenology (Monteith et al. 2011). Direct indicators can be useful if they reflect changes in the environment of the current range that are consistent with changes occurring on the next season's range. However, direct indicators may be more difficult to interpret if they vary considerably from day to day. Thus, the utility of migration timing cues can depend on how interpretable they are and how well they track environmental changes of destinations. Though research has been done on latitudinal avian migrants and non-avian altitudinal migrants, little work has been conducted on altitudinal avian seasonal migrations (but see Hahn et al. 2004, Boyle et al. 2010, and Boyle 2011).

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") is a temperate species where many populations exhibit altitudinal movements between seasonal ranges (e.g., Dalke et al. 1963, Klebenow and Gray 1968, Fischer et al. 1997, Beck et al. 2006, Caudill et al. 2016) and at least one population exhibits relatively short-distance latitudinal migrations (Tack et al. 2012, Smith 2013). Sage-grouse access different habitats throughout the annual cycle resulting in distinct breeding, summer, and winter seasons (Connelly et al. 2011). Sage-grouse can be nonmigratory, have 2 unique seasonal ranges (to-and-fro migration), or have 3 unique seasonal ranges (round-trip migration; Connelly et al. 2000). Breeding habitat generally includes large areas of sagebrush-dominated (*Artemisia* spp.) plant communities in the vicinity of leks that also include an herbaceous layer (Holloran 1999, Connelly et al. 2000, Holloran and Anderson 2005, Hagen et al. 2007, Connelly et al. 2011). Summer habitat can include a wide variety of plant communities within sagebrush-dominated landscapes that have areas with a greater source of moisture that keeps plants from desiccating (e.g., riparian, montane sagebrush, wet meadows, and irrigated hayfields or pastures; Klebenow and Gray 1968, Wallestad 1971, Fischer et al. 1996, Connelly et al. 2011). Winter habitat occurs in sagebrush-dominated plant communities, where sagebrush plants provide food and cover, particularly in areas where tall sagebrush or topography permit sagebrush to extend above snow (Beck 1977, Remington and Braun 1985, Connelly et al. 2000, Connelly et al. 2011). Seasonal movements for sage-grouse are presumed to be tied to forage quality and availability. Sage-grouse appear to depart their breeding range because of decreased forage quality when plants desiccate, depart their summer range because of decreased forage quantity when snow limits availability, and depart their winter range to return to breeding range under favorable conditions (i.e. spring green-up; Dalke et al. 1963, Berry and Eng 1985, Dunn and Braun 1986, Connelly et al. 1988, Fischer et al. 1996).

Timing of migration also has been shown to be influenced by individual characteristics such as reproductive status or distance of migration events (Yong et al. 1998, Mitrus 2007, Monteith et al. 2011, Lendrum et al. 2013). For example, an individual with dependent young offspring may delay migration (Schroeder and Braun 1993, Fischer et al. 1996), or those that travel farther may advance migration timing. Our first objective was to evaluate whether Greater Sage-Grouse were influenced by direct indicators of resource quality and whether they also were influenced by individual characteristics when timing migration during the spring (winter to breeding range), summer (breeding to summer range), and fall (summer to

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winter range) transitional seasons. We thus examined 3 hypotheses that represented (H_1) grouse only using indirect indicators of resource quality, (H_2) grouse using direct indicators of resource quality, and (H_3) grouse using direct indicators and influenced by individual characteristics. Altitudinal migrations are shorter than mid- to long-range latitudinal migrations and environmental changes at seasonal ranges closer together are more likely to be correlated (Tombre et al. 2008); therefore, we predicted sage-grouse would use direct indicators of resource quality. For sage-grouse, distances traveled are likely short enough that correlated environmental changes between seasonal ranges will provide added utility over the easily interpretable nature of indirect indicators of resource quality. This is consistent with research that determined summer and fall movements of sage-grouse were influenced by vegetal moisture and precipitation, respectively (Fischer et al. 1996, Caudill et al. 2016). We built on this research by completing a more precise and comprehensive analysis investigating all seasons with more variables and with daily observations.

Partial migration, where some individuals in a population are migratory, has been argued to be the most widespread form of migration found in all major taxa, including sage-grouse (Chapman et al. 2011, Fedy et al. 2012). A popular question is why only some of the individuals are migratory, which has been explained in 2 ways. First, migration may be condition-dependent, based on age, sex, physical condition, or dominance. Chapman et al. (2011) contend that the bulk of the documented evidence for partial migration is from species with condition-dependent migration. The second possibility is that there are differences in behavior among individuals that are determined through their genetic makeup or learned behaviors during ontogeny (Sweanor and Sandegren 1988, Pulido et al. 1996, Nelson 1998). The latter seems more likely with sage-grouse because of consistency in behavior for individuals from year to year (Berry and Eng 1985). What is not frequently addressed is the landscape context that these individuals are in; specifically, what environmental changes they are exposed to. This is not necessarily mutually exclusive of the 2 proposed answers but could add qualification to them. The variation in environmental conditions individuals are exposed to may influence whether they exhibit migratory behavior (Cagnacci et al. 2011). Thus, our second objective, after identifying which migration cues sage-grouse use, was to determine whether migratory and nonmigratory individuals experienced different environmental conditions that could explain variation in their behavior. Because migratory and nonmigratory individuals in our study population were intermixed spatially we predicted that they would experience the same environmental changes.

METHODS

Study Area

We obtained field data from 2 study areas located across sagebrush-steppe landscapes (Knight et al. 2014) of central Wyoming and the Bighorn Basin of north-central Wyoming and extreme south-central Montana (Figure 1). Both areas were composed of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations with mountain big sagebrush (*A. t. vaseyana*) occurring at higher elevations. Black sagebrush (*A. nova*) was abundant in localized areas.

Bighorn Basin. The 30-year (1981–2010) normal average annual precipitation and temperature were 31 cm and 7.0°C, respectively (PRISM Climate Group 2016). There was a strong gradient in temperature and precipitation with elevation (Figure 2). At low elevations the sagebrush-steppe transitioned to Gardner's saltbush (*Atriplex gardneri*) desert and at high elevations it transitioned to coniferous forest. The Bighorn Basin study area was further split into 3 research sites that represented relatively distinct populations (i.e. no documented mixing of radio-tagged grouse), topographies, and available summer habitat (Figure 1). The Carbon site (45.1°N, 108.7°W) ranged in elevation from ~1,210 m to ~2,660 m. Summer habitat included riparian areas and irrigated hayfields/pastures at lower elevations and high-elevation montane meadows. Elevation at the Shell site (44.7°N, 108.0°W) was ~1,220 m to ~1,940 m. Summer habitat included irrigated hayfields/pastures and relatively low-elevation montane sagebrush. Hyattville (44.2°N, 107.7°W) ranged in elevation from ~1,180 m to ~2,880 m and summer habitat included irrigated hayfields/pastures and mid- to high-elevation montane sagebrush.

Central Wyoming. The Central Wyoming study area (42.6°N, 107.9°W) varied less in elevation (~1,560 m to ~2,750 m) and vegetation diversity compared to the Bighorn Basin study area. Average annual 30-year normal precipitation and temperature were 26 cm and 6.1°C, respectively (Prism Climate Group 2016). Summer habitat included riparian areas and mid-elevation montane sagebrush.

Data Collection

Sage-grouse were captured by spotlighting and hoop netting (Giesen et al. 1982, Wakkinen et al. 1992) near leks during spring 2011–2014 in Shell and Hyattville, 2012–2014 in Central Wyoming, and 2013 and 2014 in Carbon. Additional grouse were located and captured during summer at night-roosting locations of previously tagged birds. Grouse were tagged with Global Positioning System (GPS) equipped Platform Transmitter Terminals (22-g Solar Argos/GPS PTT-100 [~ 32 g with harness; Microwave Telemetry, Columbia, Maryland, USA] or

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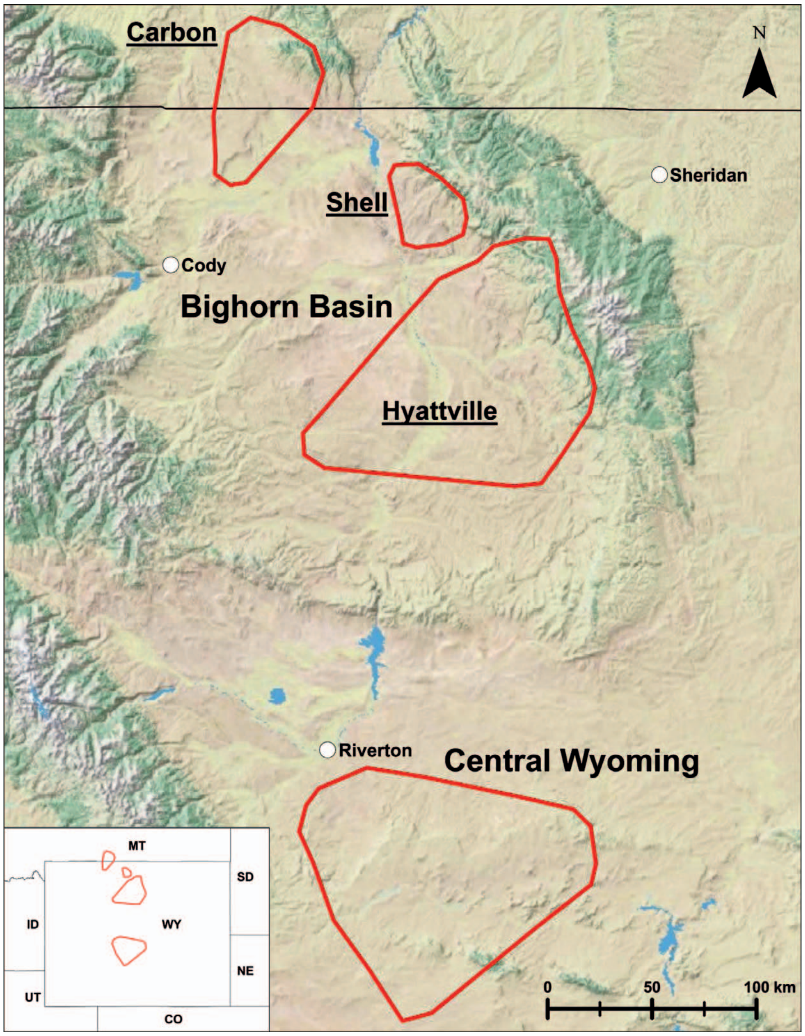

FIGURE 1. Maximum extent of locations of GPS-tagged Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015.

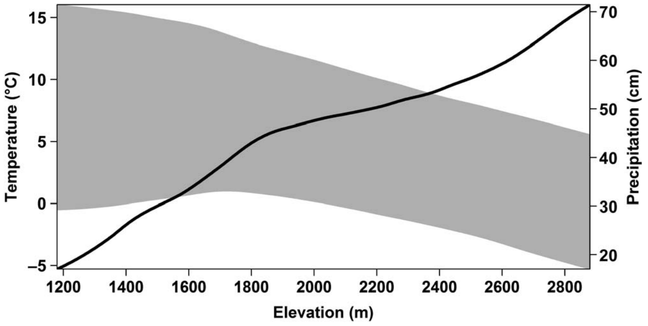

FIGURE 2. Mean 30-year normal (1981–2010; Prism Climate Group 2016) annual maximum and minimum temperatures (shaded region; °C) and precipitation (line; cm) relative to the range of elevations (m) represented by seasonal ranges of GPS-tagged Greater Sage-Grouse in the Bighorn Basin, USA, 2011–2015.

Model 22 GPS PTT [North Star Science and Technology, King George, Virginia, USA]). Transmitters were rump-mounted, solar-powered, and uploaded GPS locations (± ~20-m error) to satellites used by the Argos system (CLS America, Largo, Maryland, USA) every 3 days. They were programmed to acquire 3 locations per day from November 1 to March 14 (at 0900, 1200, and 1500 hours), 4 locations per day from March 15 to April 30 and August 25 to October 30 (at 0700, 1000, 1300, 1600 hours), and 5 locations per day from May 1 to August 24 (at 0600, 0900, 1200, 1500, 1800 hours). This schedule included locations on a 3-hour interval during daytime hours with first locations recorded at about 1–1.5 hours after sunrise to about 2 hours before sunset. Transmitters also were programmed to include a location at midnight (2400 hours).

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Migration Identification

We defined a grouse as migratory if it demonstrated use of seasonally dependent nonoverlapping ranges. We believe this definition encapsulates the 2 most important aspects of migration outlined in Dingle and Drake (2007), though we propose sage-grouse as an excellent example of how migratory and resident behavior fall along a continuous gradient (Cagnacci et al. 2011, Fedy et al. 2012). Nonoverlapping ranges represented infrequent movements on a greater spatial scale connecting distinct areas of frequent, smaller-scale movements termed "station-keeping" activities. In addition, the use of these ranges corresponded with the periodicity of seasonal habitat use on the annual cycle, which is one of the longest timescales experienced by an animal. We identified seasonal ranges using a combination of contour levels of a utilization distribution and by calculating displacement. We calculated a 95% utilization level to identify and delineate large concentrations of use, for the lifespan of each individual, from a dynamic Brownian bridge movement model with a moving window size of 9 locations and a margin of 3 locations (move R package, R version 3.2.4, R Core Team 2016; Kranstauber et al. 2012). We evaluated several different combinations of window sizes and margins and all produced similar results for the extent of the 95% contour level. This combination was reasonable given our location fix rate relative to the type of changes in movement we could detect. We evaluated different contour levels relative to their ability to distinguish seasonal ranges. Contour levels above 95% tended to include all grouse locations, even for those that were obviously migratory, while contour levels below 95% created too many polygons. In 24% of instances, we used a 90% contour level if the only grouse locations included within the 95% level and not the 90% level were initiations or completions of migration events. To guide determining whether nonoverlapping polygons delineated by the utilization distribution were seasonally dependent we visually inspected a plot of net-squared displacement (adehabitatLT R package; Bunnefeld et al. 2011) looking for characteristic "plateaus" (i.e. displacement was larger between seasonal ranges than within seasonal ranges). Breeding range, as defined for females, was focused around the concentration of locations from the pre–egg-laying, nesting, and early brood-rearing periods.

A migration initiation event was recorded on the day a grouse left the extent of its current seasonal range and met at least 1 of 2 criteria: (1) approached closer to the next seasonal range than its current seasonal range, or (2) moved in the direction of its next seasonal range (i.e. distance to next seasonal range was less than any portion of its current seasonal range) and did not return for >1 day. Under this definition an individual could have multiple events for each season-year. We included all departure events because we presumed that grouse were deciding when to leave based on conditions of the current range, but could ultimately decide to return after acquiring additional information of conditions along the migration route or at the next seasonal range. Once an individual was spending more time inside the next seasonal range than outside, it was considered no longer able to initiate migration even if it did happen to make a return trip into its first seasonal range. If there were continuous missed location fixes for >72 hours, then observations on that bird were censored after the last known day it remained completely in a seasonal range. The start and end of a transitional season was the earliest and latest ordinal date that migration events were observed, respectively. An individual was considered available for migration if the date was within the defined transitional season, the bird was present in seasonal range, and it was not incubating a nest. We visually inspected boxplots of migration event dates for each season to identify potential outliers. Leaving winter range was slightly skewed early and leaving summer range was slightly skewed late but no recorded events were considered significant outliers.

Data Analysis

We used mixed-effects Cox proportional hazards regression models (coxme R package; Cox 1972) to relate migration events for the 3 transitional periods per our 3 hypotheses represented by applicable daily-dependent predictor variables. We developed and compared the best models to represent each hypothesis using second-order Akaike's information criterion corrected for small sample sizes (AIC_c; AICcmodavg and MuMIn R packages; Burnham and Anderson 2002).

Modulating variables. We included variables that we considered to have a modulating effect on migration timing (Table 1). We expect these variables do not determine migration at the seasonal scale, but can modulate timing by a few days. These variables included wind speed, precipitation (sum of rain and snow), and change in atmospheric pressure. We hypothesized that migration would be avoided during days of high wind speed or precipitation even if other cues were encouraging migration. We predicted that migration may be encouraged or discouraged if grouse can forecast weather patterns by interpreting changes in atmospheric pressure. For example, a grouse may want to leave summer range in advance of stormy weather as indicated by dropping atmospheric pressure. Change in atmospheric pressure was the difference in daily average pressure (measured at nearest weather station; NCEI 2016) of the current day from the previous day. We also considered change in atmospheric pressure in its quadratic form to evaluate whether grouse were selecting for unchanging conditions. Modulating variables could compete in all 3 hypotheses. We utilized raster data for wind speed, precipitation (rain and snow), and snow depth (described as a Direct indicator

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TABLE 1. Predictor variables used to investigate timing of Greater Sage-Grouse migration during the spring, summer, and fall transitional seasons in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Variable	Description
Modulating variables	
prec	Daily total precipitation (rain + snow, water equivalent [cm])
wspd	Daily average wind speed ($m\ s^{-1}$)
atmp [a,b]	Atmospheric pressure trend (current day mean minus previous day mean [mmhg])
Direct indicators	
tmin [a]	Daily minimum temperature (°C)
tmea [a]	Daily average temperature (°C)
tmax [a]	Daily maximum temperature (°C)
rpre [a]	Daily total rain precipitation (cm)
rlag [a]	Rain precipitation with lag effect of 1–7 days (cm)
spre [a,c]	Daily total snow precipitation (water equivalent [cm])
slag [a,c]	Snow precipitation with lag effect of 1–7 days (water equivalent [cm])
snod [a,c]	Snow depth at beginning of day (cm)
savi [a]	Vegetation "greenness" index (0–1)
sslo [a]	Daily change in "greenness" index (slope)
Individual characteristics	
area	Location (Bighorn Basin,[d] Central Wyoming)
site	Location (Carbon, Shell, Hyattville,[d] Central Wyoming)
styp [e]	Summer range type (presence of artificial water) [d]
elev	Elevation of destination (m)
dist	Distance to destination (km)
nfat [f]	Days since nest fate
brod [f]	Brood rearing [d]

[a] Considered different levels of temporal-weighting (α).
[b] Considered quadratic form.
[c] Only relevant for spring and fall transition.
[d] Bighorn Basin, Hyattville, summer range without artificial water, and grouse without broods were the reference categories.
[e] Only relevant for summer and fall transition.
[f] Only relevant for summer transition.

below) with 750-m resolution. These data were obtained from a meteorological distribution model (MicroMet; Liston and Elder 2006b) and a snow-evolution model (SnowModel; Liston and Elder 2006a). These models have been implemented and validated in several landscapes in the western USA and other countries (e.g., Hiemstra et al. 2002, Liston and Hiemstra 2011).

Indirect indicator. If grouse solely use an indirect indicator of resource quality, such as an internal biological clock or photoperiod, then migration timing should not significantly vary from year to year. In addition, direct indicators, which do vary from year to year, should not explain any significant variation in the observations. Therefore, the indirect-indicator hypothesis was simply represented by a null model.

Direct indicators. The direct indicators of resource quality we considered included temperature, rain precipitation, snow precipitation, snow depth, and plant phenology (Table 1). Because organisms likely interpret environmental changes over a time period greater than one day we calculated all direct indicator variables (as well as change in atmospheric pressure) with a "linear predictor" that included α as a weighting factor of the current day's value relative to previous days' values (Gienapp et al. 2005). As α approached 1, the current day's value had increasing influence over previous days' values (see figure 1 in Gienapp et al. 2005). When $\alpha = 1$ it was equivalent to the current day's value. When α was small it acted like a smoothing parameter that represented a trend over the entire season. We considered values for α in increments of 0.01 from 0.01 to 0.1 and in increments of 0.05 from 0.1 to 1. We started calculations from 30 days prior to the first day of each season and the value on day 0 was the average of those first 30 days. This was to prevent extreme starting values having undue influence over the calculations when α was small.

We considered temperature (4-km resolution; PRISM Climate Group 2016) as a minimum, mean, or maximum daily measurement as grouse could interpret temperature in any of the 3 forms, but we only selected one because they were all highly correlated. Because we considered precipitation events, on the day of, as a modulating variable we considered rain and snow with lag effects and trends as direct indicators, which may have an opposite effect on migration initiation (Caudill et al. 2016). For example, increasing snowfall may encourage migrating from summer range but grouse may not leave on the day of precipitation. We only considered rain and snow accumulation variables with an α lower than that which was not correlated ($|r| < 0.6$) with precipitation of the current day. We considered lag effects for daily rain and snow amounts from 1 to 7 days. Snow depth was a variable that could increase probability of migration from summer range and decrease probability from winter range. Plant phenology was represented by the modified soil-adjusted vegetation index (SAVI; Qi et al. 1994), a vegetation greenness index, in 2 different forms based on MODIS MOD09Q1 surface reflectance data available at 8-day intervals (250-m resolution; LP DAAC 2016). The first plant phenology variable was the normalized SAVI values. Normalized SAVI was calculated in several steps: (1) obtaining data for one year centered on the season in question; (2) setting negative values (i.e. snow) to no data; (3) setting all values below the 0.025 quantile, and no data, as 0 (to represent no vegetation activity during winter); (4) applying a 3-observation moving median filter; (5) rescaling the values between 0 and 1; and (6) linearly interpolating values

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within the 8-day data acquisition window (Bischof et al. 2012). The second plant phenology variable was the change in SAVI measured by the slope between the previous and next observation for every normalized 8-day observation. The measured slopes were also linearly interpolated between observations to obtain daily values.

All variables, except atmospheric pressure, were calculated based on a weighted average of the utilization distribution for the departure seasonal range in question. For example, the value for snow depth for a given day–bird–year combination for the spring transition (leaving winter range) was the weighted average snow depth for that day based on the utilization distribution for that bird-year's winter range. The final utilization distribution for each bird–season–year was based on nonmigratory locations bookended by arrival and departure dates. We defined the seasonal arrival date as the day the bird started spending more time within the seasonal range than migrating from or in its previous season, and the seasonal departure date was the day the bird started spending more time outside the seasonal range than within.

Individual characteristics. The individual characteristics we considered included location, summer range type, elevation of next seasonal range, distance to next seasonal range, days since nest fate, and whether the bird was brood rearing (Table 1). These are individual-specific characteristics that could encourage a grouse to advance or delay departure compared to other individuals. We also considered interactions between the individual characteristic variables and the direct indicator variables. Location could be important because of behavioral differences among populations or different landscape contexts. Location was represented by study area (Bighorn Basin or Central Wyoming) or research site (Carbon, Shell, Hyattville, or Central Wyoming). Artificially maintained water sources in irrigated hayfields and pastures could influence migration timing to and from summer range so each grouse was assigned to a categorical summer range type of irrigated hayfield/pasture or a summer range absent of artificial water sources. A grouse's prior knowledge of the variation in timing of environmental changes based from elevational gradients could explain differences among individuals with destinations at different elevations. For example, a grouse whose breeding range was at a high elevation, with a persistent snowpack, may have left winter range later than another grouse whose breeding range occurred at lower elevation. We naturally expected that individuals who travel farther would leave sooner than those closer to the next seasonal range. Reproductive activity could place restraints on how an individual can respond to migration cues when leaving breeding range. Days since nest fate was the number of days since a grouse's nest was depredated or hatched. For males and females who did not incubate a nest, days since nest fate were set equal to the incubating female with the earliest nest fate that year. The brood female variable was categorically dependent on whether the bird was a female with a successful nest.

Variable screening and sequential modeling. First, we investigated whether to use sex and/or individual as random effects. A null model with individual and not sex was the top-performing model for all seasons so all models for remaining analysis steps included individual as a random effect. This accounted for non-independence of multiple events from an individual within and among years. We then compared single-variable models with AIC$_c$ to select the most supported α value for linear predictors or lag amounts. In addition, we assessed whether the linear or quadratic form of atmospheric pressure was most supported, assessed temperature variables (minimum, mean, or maximum), and determined if study area or site were more predictive. We carried forward the most predictive variable within each variable class. We assessed correlation of remaining variables and did not allow correlated ($|r| \geq 0.6$) variables to compete in the same models. Variables that failed to meet the proportional hazards assumption as demonstrated by a non-zero slope for the Schoenfeld residuals were excluded from analysis (Schoenfeld 1982). The variables considered within each hypothesis were as follows: (H_1) a null model with modulating variables for the indirect-indicator-only hypothesis; (H_2) modulating variables and direct indicators for the direct-indicators hypothesis; and (H_3) modulating variables, direct indicators, and individual characteristics for the direct-indicators-plus-individual-characteristics hypothesis. We compared all possible combinations of the appropriate variables to create the most parsimonious model to represent each hypothesis and then compared the 3 hypotheses using AIC$_c$. We only present individual variable results ($\beta \pm$ SE) from significant variables ($P < 0.1$) in the top Cox proportional hazards regression model.

Migratory vs. nonmigratory. Only data from migratory individuals were used to identify migration timing cues. After we identified which cues determined timing, we calculated the relevant environmental conditions experienced by migratory and nonmigratory grouse to investigate whether differences in environmental conditions could help explain partial-migratory behavior in sage-grouse. Seasonal bounding dates for nonmigratory grouse were the mid-points between seasonal departure and arrival dates calculated from migratory birds. Seasonal utilization distributions were then calculated based on locations within these bounding dates. We calculated the average environmental conditions over the total length of each transitional season for every individual's departing seasonal range. We then compared average conditions (mean ± SE) experienced between migratory and nonmigratory individuals with a 2-sample t-test (2-tailed).

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TABLE 2. Number of migration events observed during the spring, summer, and fall transitional seasons from GPS-tagged Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015.

	Bighorn Basin									
	Carbon		Shell		Hyattville		Central Wyoming		Total	
Season	events	grouse	events	grouse	events	grouse	events	grouse	events	grouse
Spring	5	3	1	1	41	25	20	14	67 [a]	43 [a]
Summer	14	9	17	11	54	43	16	10	101 [b,c]	73 [b]
Fall	11	6	16	6	61	45	36	27	124 [d,e]	84 [d]

[a] 1 event from a male grouse.
[b] 11 events from 9 male grouse.
[c] 35% brood rearing and 28% summer range with artificial water.
[d] 5 events from a male grouse.
[e] 23% summer range with artificial water.

RESULTS

We observed 67 migration initiation events (mean = March 17, range: January 20–May 3) from 43 GPS-tagged sage-grouse during 2011–2015 for the spring transition season (winter to breeding range; Table 2). We censored one event due to poor fix rate and 2 events because of unknown location of breeding range. The model representing direct indicator cues with individual characteristics (H_3) had overwhelming model support (model weight of evidence, $w_i = 0.99$) and significant variables included one modulating variable (prec), 2 direct indicators (tmin, savi), and 2 individual characteristics (area, elev; Table 3). There was convincing evidence that grouse were not initiating migration on days with precipitation ($\beta = -12.6 \pm 4.7$, $P = 0.007$). There also was evidence that grouse in Central Wyoming were migrating earlier ($\beta = 1.58 \pm 0.62$, $P = 0.01$) and grouse whose breeding ranges were at higher elevations were migrating later ($\beta = -1.44 \times 10^{-3} \pm 0.83 \times 10^{-3}$, $P = 0.08$). Timing of migration away from winter range was determined by increasing recent ($\alpha = 0.95$) minimum temperature and a moderate accumulation ($\alpha = 0.25$) of increasing SAVI (Table 4 and Figure 3A). In our study areas, 55% ($n = 77$) of the monitored population was migratory between winter and breeding range. Migratory and nonmigratory grouse experienced the same temperatures and SAVI levels during the spring transition (Table 4 and Figure 3A).

We observed 101 migration initiation events (mean = June 16, range: May 13–August 3) from 73 GPS-tagged grouse for the summer transition season (breeding to summer range; Table 2). We censored one event due to poor fix rate, 4 events because of unknown location of summer range, and 2 events from a female that was an inconsistent incubator during hot and dry conditions. Like the spring transition, the model representing direct indicator cues with individual characteristics (H_3) for the summer transition had overwhelming model support ($w_i = 1.00$; Table 3). Significant variables in this model included no modulating variables, one direct indicator cue (tmax), 4 individual characteristics (brod, styp, area, dist), and one interaction (savi × area). Brood-rearing grouse ($\beta = -0.994 \pm 0.266$, $P < 0.001$), grouse whose summer range included artificial water sources ($\beta = -0.969 \pm 0.321$, $P = 0.003$), and grouse that traveled farther ($\beta = -3.79 \times 10^{-2} \pm 2.15 \times 10^{-2}$, $P = 0.08$) all initiated migration at a slower rate relative to when they could migrate (i.e. no longer

TABLE 3. Top models representing the 3 migration-cues hypotheses for the 3 transitional seasons for Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015. Model selection statistics include number of model parameters (*K*), difference in AIC_c between model and top model (ΔAIC_c), and model weight of evidence (w_i).

Season	Model statistics		
Hypothesis (variables)	*K*	ΔAIC_c	w_i
Spring transition			
H_3: Dir ind + ind cha (prec + tmin + savi + rlag + area + elev + tmin × area)	8	0.00 [a]	0.99
H_2: Dir ind (prec + tmin + savi + rlag + snod)	6	8.59	0.01
H_1: Ind ind (prec + wspd)	3	24.86	0.00
Summer transition			
H_3: Dir ind + ind cha (tmax + savi + brod + styp + area + dist + savi × area)	8	0.00 [b]	1.00
H_2: Dir ind (atmp + tmax + savi)	4	16.72	0.00
H_1: Ind ind (atmp + $atmp^2$)	3	59.72	0.00
Fall transition			
H_3: Dir ind + ind cha (tmax + spre + rlag + rpre + styp + area + tmax × area + spre × area)	9	0.00 [c]	1.00
H_2: Dir ind (tmax + spre + rlag + rpre)	5	11.85	0.00
H_1: Ind ind (prec + atmp + $atmp^2$)	4	75.05	0.00

[a] $AIC_c = 293.30$
[b] $AIC_c = 527.00$
[c] $AIC_c = 674.25$

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TABLE 4. Variable coefficients (β) and the comparisons between migratory and nonmigratory Greater Sage-Grouse for significant direct indicator cues in top models for each of the 3 transitional seasons in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Season	Variable coefficient			Migratory			Nonmigratory			*t*-test		
Variable	β	SE	*P*	Mean	SE	*n*	Mean	SE	*n*	*t*	df	*P*
Spring												
tmin	0.222	0.060	<0.001	−5.53	0.26	42	−5.66	0.26	35	0.3	74	0.74
savi	1.81	0.95	0.06	0.506	0.025	42	0.495	0.024	35	0.3	75	0.76
Summer												
tmax	0.483	0.079	<0.001	18.5	0.3	67	17.4	0.4	25	2.3	49	0.03
Fall												
tmax	−0.155	0.027	<0.001	10.6	0.3	69	12.2	0.3	23	−3.9	71	<0.001
spre	3.20	0.82	<0.001	2.95 [a]	0.24 [a]	69	1.94 [a]	0.30 [a]	23	2.6	53	0.01
rlag	1.24	0.42	0.003	5.58 [a]	0.34 [a]	69	5.14 [a]	0.55 [a]	23	0.7	40	0.49
rpre	2.94	1.27	0.02	6.01 [a]	0.35 [a]	69	5.56 [a]	0.59 [a]	23	0.7	38	0.51

[a] $\times 10^{-2}$

incubating a nest). There also was evidence that Central Wyoming grouse initiated migration quicker relative to when they could migrate (β = 10.1 ± 4.7, $P = 0.03$) and they were more influenced by decreasing SAVI (β = −12.4 ± 5.6, $P = 0.03$) than Bighorn Basin grouse. Timing of migration away from breeding range was determined by the trend (α = 0.02) of increasing maximum temperatures (Table 4 and Figure 3B). In our study areas, 73% ($n = 92$) of the monitored population was migratory between breeding and summer range. Migratory individuals experienced 6% warmer temperatures than nonmigratory individuals (Table 4). Specifically, breeding seasonal ranges of migratory birds had the same trend, but warmer accumulated maximum temperature than nonmigrant breeding ranges during the summer transition (Figure 3B).

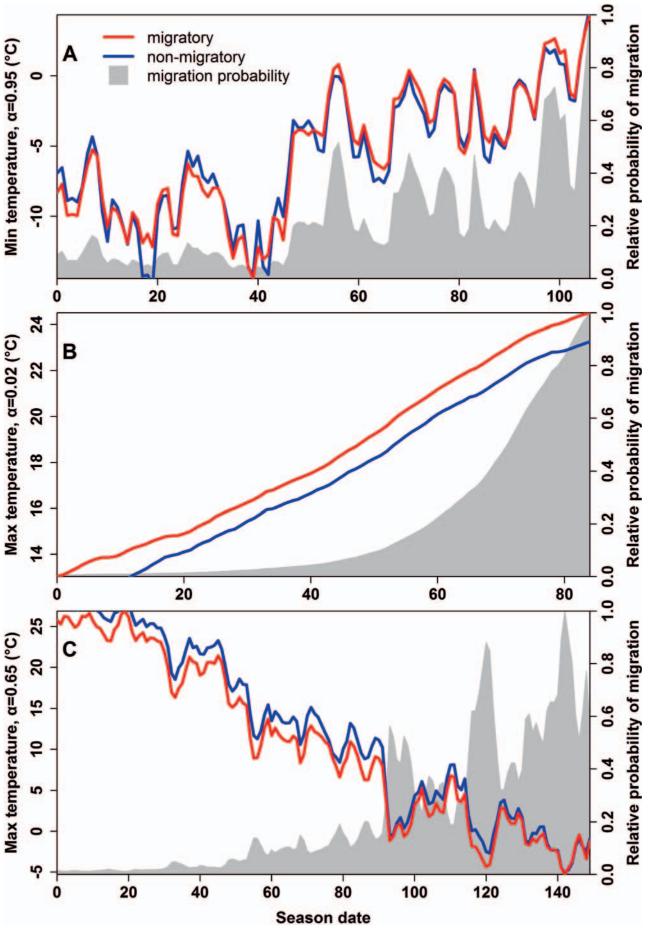

FIGURE 3. Temperature trend between seasonal ranges of migratory and nonmigratory Greater Sage-Grouse and effect on migration probability for the spring (**A**), summer (**B**), and fall (**C**) transitional seasons in Bighorn Basin and Central Wyoming, USA, 2011–2015.

We observed 124 migration initiation events (mean = October 12, range: August 12–January 8) from 84 GPS-equipped grouse for the fall transition season (summer to winter range; Table 2). We censored one event due to poor fix rate and 11 events because of unknown location of winter range. Consistent with previous seasons, the direct indicators with individual characteristics (H_3) was the best supported ($w_i = 1.00$; Table 3) hypothesis. Significant variables included no modulating variables, 4 direct indicator cues (tmax, spre, rlag, rpre), one individual characteristic (styp), and one interaction (spre × area). Grouse whose summer range had an artificial water source were leaving sooner (β = 1.36 ± 0.39, $P < 0.001$). Timing of migration away from summer range was determined by decreasing recent (α = 0.65) maximum temperature, moderate accumulation (α = 0.3) of increasing snow, and increasing rain with a lag effect (α = 1, lag = 3 days) and rain trend (α = 0.06; Table 4 and Figure 3C). There also was suggestive evidence that Central Wyoming grouse were reacting differently to snow than were Bighorn Basin grouse (β = −13.0 ± 6.6, $P = 0.05$) in that they were initiating migration during relatively snow-free periods. In

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our study areas, 75% ($n = 92$) of the monitored population migrated between summer and winter range. Migratory and nonmigratory grouse experienced the same average rain amounts measured by daily values with lag effect and as a trend (Table 4). However, summer seasonal ranges of migratory grouse had 13% colder temperatures and 52% more snow during the fall transitional season (Table 4 and Figure 3C).

DISCUSSION

We found strong evidence that Greater Sage-Grouse use direct indicators of resource quality when deciding when to initiate migration, and are also influenced by individual characteristics, regardless of season. The timing of sage-grouse spring migrations were determined by increasing temperatures and advancing spring green-up, were modulated by not departing on days with precipitation, and also were dependent on location and breeding range elevation. Summer migrations were determined by increasing temperatures and were dependent on location, reproductive status, summer range type, and migration distance. Timing for fall migrations were determined by decreasing temperatures, increasing rain trends, increasing snow trends, and were dependent on location and summer range type. The closer an individual's seasonal range is to the next season's range the more correlated the environmental changes will be and the greater utility a direct indicator of resource quality should have (Tombre et al. 2008). Because altitudinal migrants are relatively short-distance migrants, they are likely to use direct indicators of resource quality. This has been demonstrated by research on a temperate ungulate migrant (Monteith et al. 2011) and by preliminary research on Greater Sage-Grouse, a temperate avian migrant (Fischer et al. 1996, Caudill et al. 2016). We were able to further elucidate the relationship between sage-grouse migration timing and direct indicator cues, beyond this preliminary research, because of our more precise (daily observations) and comprehensive (all seasons and additional variables) analysis. This use of direct indicators is also consistent with anecdotal evidence found in tropical avian migrants (Boyle et al. 2010, Boyle 2011). Pink-footed Geese (*Anser brachyrhynchus*) have been described using both direct (temperature) and indirect (photoperiod) indicators depending on where they were along their migration routes and how correlated their location was with the next stopover (Bauer et al. 2008, Duriez et al. 2009).

Temperature was consistently the most significant variable but whether it was maximum or minimum and whether it was accumulated over short or longer time periods depended on the season. Temperature has been documented to be a significant cue for migration in a variety of taxa (e.g., Bauer et al. 2008, Keefer et al. 2009, Monteith et al. 2011), as well as a cue for other avian activities (e.g., Gienapp et al. 2005, Visser et al. 2009). We expected a greater influence from those variables (savi, sslo) directly representing plant phenology as sage-grouse are presumed to change seasonal ranges because of growth and senescence of plants, at least for the spring and summer transitions (Fischer et al. 1996). Plant phenology has been proposed as the driving force for other altitudinal migrants (Bischof et al. 2012, Merkle et al. 2016). Migration timing did correlate well with expected grouse responses to plant phenology. Spring migration occurred during peak green-up, summer migration occurred when plants started desiccating, and fall migration occurred shortly before the onset of winter (Figure 4). SAVI did contribute to timing during the spring transition and the change in SAVI was correlated (but less predictive) with temperature during the summer transition. Plant phenology not playing a significant role during the fall transition is consistent with senescence of plants not being the reason grouse leave summer range, but the presence of snow limiting forage availability (Dunn and Braun 1986). Dingle and Drake (2007) stated that preemption, or when habitats are abandoned before quality has appreciably declined, is a key component of migration and that preemption cannot rely on proximate cues but on surrogates that forecast habitat deterioration. This is consistent with the apparent secondary role of plant phenology in promoting grouse to leave breeding range. Temperature could be the surrogate forecasting a state where plant desiccation becomes too extreme. Temperature, rain, and snow precipitation could also be playing this role forecasting conditions of decreased forage availability at the end of the summer season. Caudill et al. (2016) also documented precipitation as a significant driver of juvenile sage-grouse leaving summer range in Utah, USA. Red deer (*Cervus elaphus*) were described as exhibiting risk-averse behavior by leaving summer range before the onset of winter (Rivrud et al. 2016). For the spring transition, preemptive departure decisions are attempting to predict improving conditions on breeding range, not escaping deteriorating conditions, unless migratory birds are avoiding increased breeding competition on winter range (Kokko and Lundberg 2001, Gillis et al. 2008).

Even though we found evidence that sage-grouse were heavily influenced by direct indicator cues there could still have been an internal clock or photoperiod foundation that limited the extents of migratory seasons (Bradshaw and Holzapfel 2007). However, there is no question that direct indicators were used by sage-grouse to appropriately time movement within a transitional season according to environmental gradients in time and space. The advantage of internal biological clocks or photoperiod is that they do not vary from day to day or year to year so they should be easier to interpret than direct indicator cues, which can

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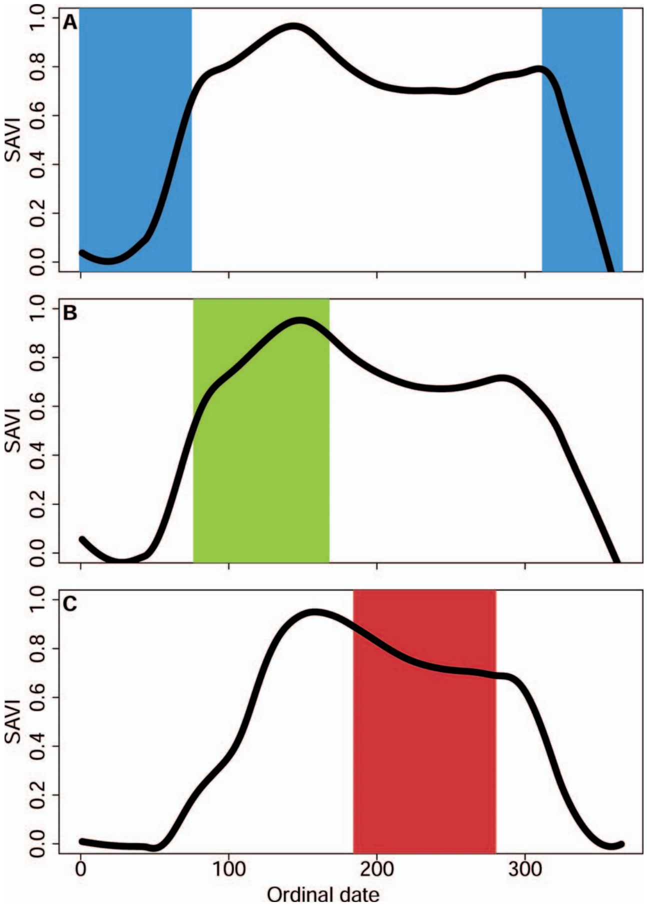

FIGURE 4. Timing of Greater Sage-Grouse presence (shaded regions; based on median departure and arrival dates) on winter (**A**), breeding (**B**), and summer (**C**) seasonal ranges relative to plant phenology as demonstrated by a smoothed soil-adjusted vegetation index (SAVI) curve (bold black line) in Bighorn Basin and Central Wyoming, USA, 2011–2015.

vary considerably (Bradshaw and Holzapfel 2007). Therefore, it would make sense that animals using direct indicator cues would interpret them accumulated over a longer period (i.e. low α). Bauer et al. (2008) determined the most predictive α level for temperature along 3 stages of geese migration was $\leq$0.03. We found grouse interpreting cues over a range of time periods ($\alpha = 0.02$–0.95). Interpreting temperature over a short time frame for the spring and fall transitions may reflect a greater chance for an individual to initiate movement prematurely than during the summer transition when temperature was interpreted over a longer time frame. However, this is contradicted by the consistency in the proportion of grouse with multiple events in a year for spring (18%, $n = 65$), summer (19%, $n = 97$), and fall (21%, $n = 113$). These cues accumulated over a shorter time frame appear to be as dependable, as evidenced by the consistency in premature migrations, which is not consistent with simulations described in Duriez et al. (2009) with Pink-footed Geese. This study argues that if geese initiate spring migrations based on recent temperatures there would be too many premature departures. However, a possible explanation is that these cues become dependable by moderation from additional cues including plant greenness and rain/snow precipitation for spring and fall, respectively (Duriez et al. 2009, McNamara et al. 2011).

Not surprisingly, individual characteristics influenced migration timing in all 3 seasons (Schroeder and Braun 1993, Fischer et al. 1996). We found variations in sage-grouse behavior between Bighorn Basin and Central Wyoming suggesting effects from differences in topographies, underlying gene pool, or other population-specific factors. Identifying the timing of migratory movements has much conservation value for a species of concern such as sage-grouse whose range and abundance has declined drastically (Schroeder et al. 2004, WAFWA 2015) and whose conservation is dependent on regulatory mechanisms (USFWS 2015). Land-surface disturbance is temporally regulated via timing stipulations in Wyoming (State of Wyoming 2015) and Montana (State of Montana 2015) to minimize negative impacts on sage-grouse. However, our observations demonstrate that seasonal timing is location specific and local information is usually lacking (Appendix Figures 6 and 7). Migratory behavior also was influenced by presence of offspring, summer habitat use, and spatial and topographic characteristics of the destination seasonal range. Research on mule deer demonstrated that they are also influenced by individual characteristics such as age, body condition, migration distance, location, and anthropogenic disturbance (Monteith et al. 2011, Lendrum et al. 2013). Although body condition has been documented as influential on migratory behavior in birds (e.g., Yong et al. 1998, Mitrus 2007) we were not able to investigate this factor for sage-grouse.

We found mixed results as to whether migratory individuals were experiencing more stimulatory cues compared to nonmigratory individuals. There were no differences in environmental conditions for the spring transition. However, temperatures were warmer for migratory grouse during the summer transition and there were colder temperatures with more snow during the fall transition. The trends in these cues were the same between ranges of migratory and nonmigratory grouse, but the average levels were different. The differences in the average environmental conditions suggest that these migrations were facultative (Fischer et al. 1996, Dingle and Drake 2007). That is, if migratory grouse were moved to a different location where environmental conditions are different, or if there was an abnormal year where environmental conditions did not worsen to the normal extent, they may no longer exhibit migratory behavior (Skov et al. 2010). Changes in temperature and precipita-

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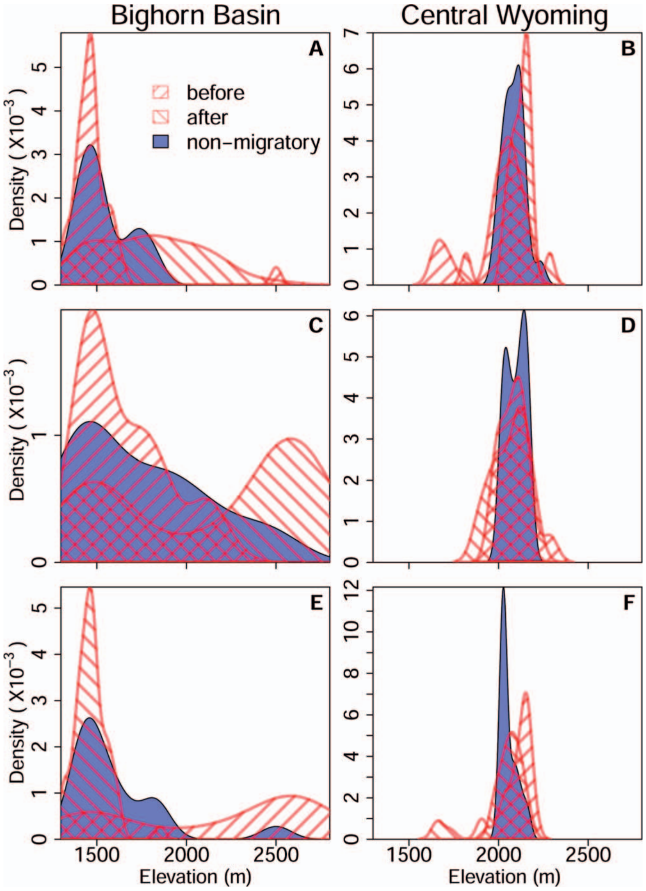

FIGURE 5. Elevations of seasonal ranges before and after spring (**A**, **B**), summer (**C**, **D**), and fall (**E**, **F**) migration and for nonmigratory Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015.

tion along an elevation gradient appeared to be the major drivers of what environmental conditions grouse experienced, especially in the Bighorn Basin (Figures 2 and 5). The pattern was similar in Central Wyoming, but on a much narrower scale because the range of elevations in Central Wyoming was much smaller. For the summer transition, migratory grouse breeding ranges were, on average, at lower elevations which were warmer and would have plants that desiccated faster than higher elevations. During fall, migratory grouse summer ranges were, on average, at higher elevations, which were colder with more snow. However, for the spring transition, the effects from elevational differences between migratory and nonmigratory grouse were not significant. Most winter ranges were at lower elevations and were used by both migratory and nonmigratory individuals. Many of these winter ranges were also used for breeding ranges so we suspect that migratory individuals were dispersing themselves among more abundant breeding habitat. These results are consistent with the presumed notion that migrant sage-grouse avoid higher plant desiccation during summer and higher snow accumulation during winter, but are just returning to their respective breeding ranges during spring (Dalke et al. 1963, Berry and Eng 1985, Dunn and Braun 1986, Connelly et al. 1988, Fischer et al. 1996).

Differences in environmental conditions between migratory and nonmigratory sage-grouse seasonal ranges demonstrate that there is a landscape context to migratory behavior. Some individuals migrate because they are experiencing different environmental conditions. There has been documentation of changes in the level of partial migration when the environment changes temporally (e.g., Fieberg et al. 2008), but less so if the change is spatial. One notable exception is Cagnacci et al. (2011) who showed that an interaction between snow and topography explained variation in levels of partial migration for roe deer (*Capreolus capreolus*) at a continental scale. Our research suggests that environmental gradients can explain partial migration at a population scale. This effect is more likely where the environmental gradient is sharp and the scale of migration is small compared to the geographic range of the population, which typifies sage-grouse range in the western USA. Partially migratory populations are increasingly recognized as more common than originally thought (Chapman et al. 2011). The landscape context of individuals may have significant influence on their behavior and could be a major contributing cause of why partially migratory species are so prevalent.

ACKNOWLEDGMENTS

We thank American Colloid Company for study initiation and funding support, numerous technicians who assisted with grouse capture and monitoring, private landowners who granted access to their property, and Glen Liston (Cooperative Institute for Research in the Atmosphere) for providing meteorological and snow depth data.

Funding statement: The Bighorn Basin study was predominately funded by the American Colloid Company with additional funding from Wyo-Ben and the Billings Field Office, Bureau of Land Management. The Central Wyoming study was predominately funded by the Wyoming Sage-grouse Conservation Fund and the Wind River/Sweetwater River Local Sage-Grouse Working Group with additional funding from the Bates Hole, Big Horn Basin, Southwest, and South Central Local Sage-Grouse Working Groups. No funders had input into the content of this manuscript and did not require approval before publication.

Ethics statement: Grouse capture and monitoring were approved by University of Wyoming Institutional Animal Care and Use Committee (protocols 03142011, 03132011, 20140228JB00065, and 20140128JB0059) and completed under permits from Wyoming Game and Fish Department (Chapter 33 Permits 800 and 801) and Montana Fish, Wildlife and Parks (Scientific Collector's Permits 2013-072, 2014-037, and 2015-76).

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Author contributions: ACP formulated the research questions, designed study, collected and analyzed data, and wrote the paper. KTS designed study, collected data, assisted in data analysis, and edited the paper. JLB designed study, provided resources, supervised research, and edited the paper.

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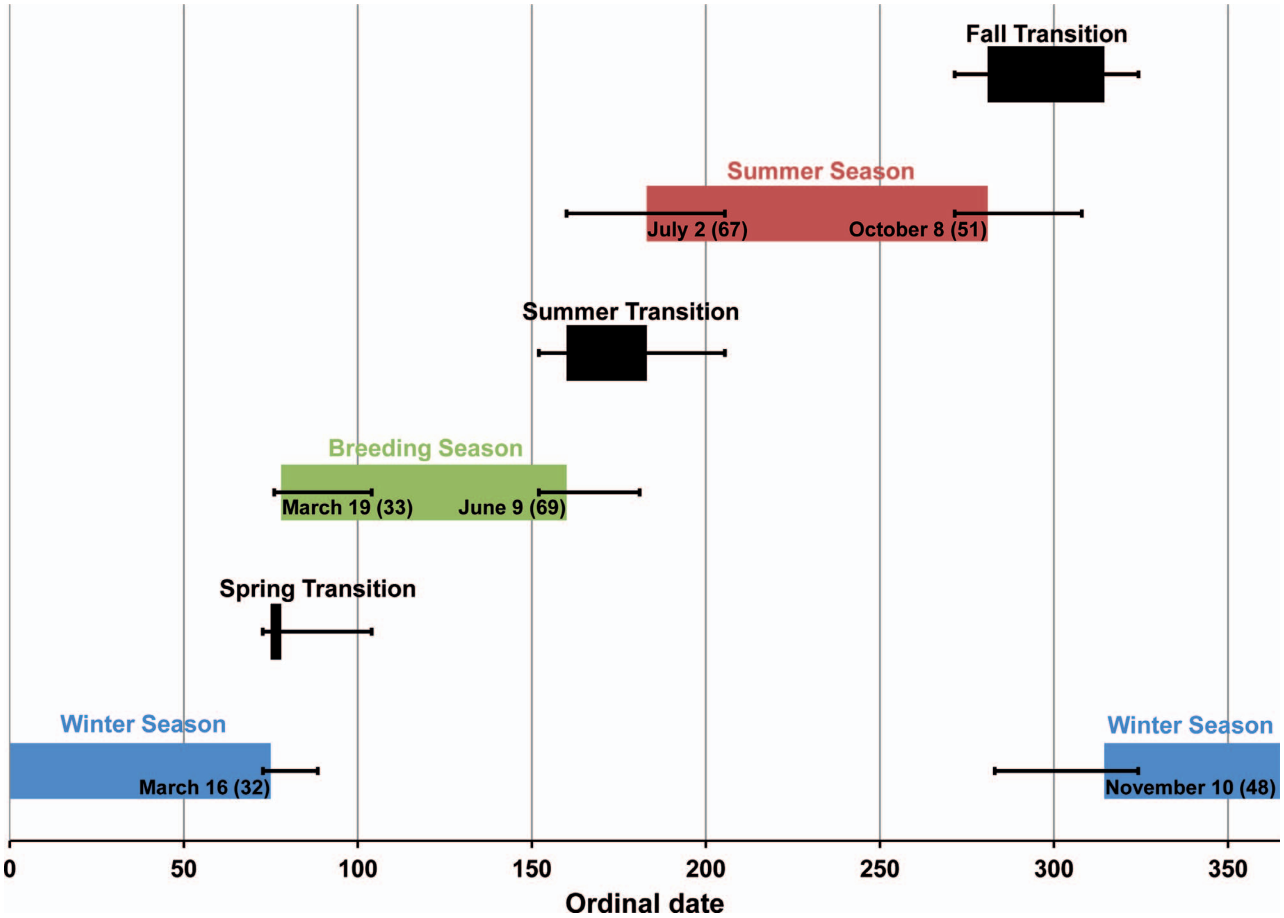
APPENDIX



APPENDIX FIGURE 6. Timing of presence within seasonal range and transitional movements for 68 GPS-tagged Greater Sage-Grouse in Bighorn Basin, USA, 2011–2015. Median dates (sample size in parentheses; error bars depict the 25th and 75th quartiles) are stated for arrival to and departure from seasonal range. Arrival and departure dates were defined as the threshold between spending more time inside a seasonal range than outside. Solid black rectangles depict when >50% of migratory grouse were in a state of seasonal transition (error bars depict >25%).

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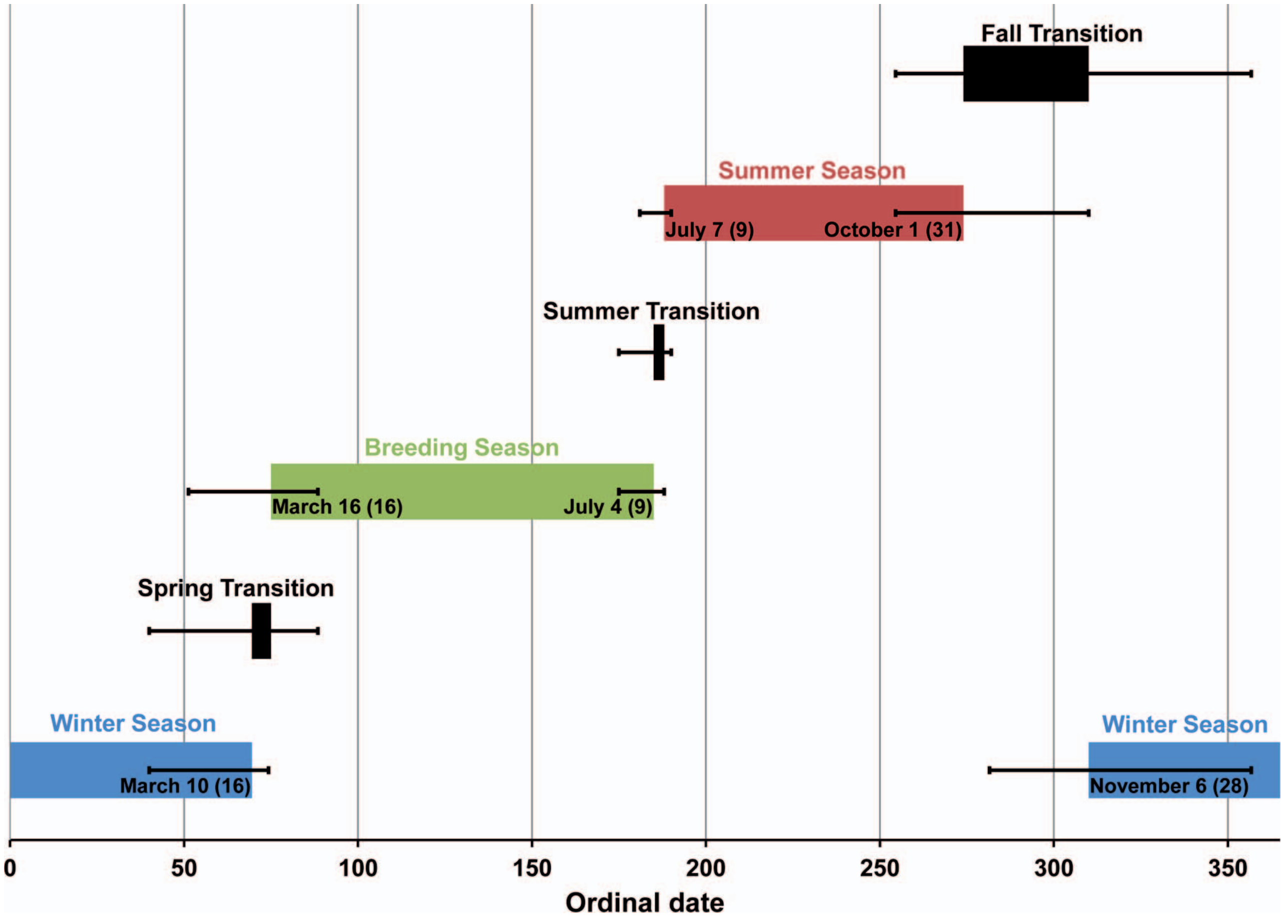

APPENDIX FIGURE 7. Timing of presence within seasonal range and transitional movements for 25 GPS-tagged Greater Sage-Grouse in Central Wyoming, USA, 2012–2015. Median dates (sample size in parentheses; error bars depict the 25th and 75th quartiles) are stated for arrival to and departure from seasonal range. Arrival and departure dates were defined as the threshold between spending more time inside a seasonal range than outside. Solid black rectangles depict when >50% of migratory grouse were in a state of seasonal transition (error bars depict >25%).

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