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Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics

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Abstract. Phenological events of plants and animals are sensitive to climatic processes. Migration is a life-history event exhibited by most large herbivores living in seasonal environments, and is thought to occur in response to dynamics of forage and weather. Decisions regarding when to migrate, however, may be affected by differences in life-history characteristics of individuals. Long-term and intensive study of a population of mule deer (*Odocoileus hemionus*) in the Sierra Nevada, California, USA, allowed us to document patterns of migration during 11 years that encompassed a wide array of environmental conditions. We used two new techniques to properly account for interval-censored data and disentangle effects of broad-scale climate, local weather patterns, and plant phenology on seasonal patterns of migration, while incorporating effects of individual life-history characteristics. Timing of autumn migration varied substantially among individual deer, but was associated with the severity of winter weather, and in particular, snow depth and cold temperatures. Migratory responses to winter weather, however, were affected by age, nutritional condition, and summer residency of individual females. Old females and those in good nutritional condition risked encountering severe weather by delaying autumn migration, and were thus risk-prone with respect to the potential loss of foraging opportunities in deep snow compared with young females and those in poor nutritional condition. Females that summered on the west side of the crest of the Sierra Nevada delayed autumn migration relative to east-side females, which supports the influence of the local environment on timing of migration. In contrast, timing of spring migration was unrelated to individual life-history characteristics, was nearly twice as synchronous as autumn migration, differed among years, was related to the southern oscillation index, and was influenced by absolute snow depth and advancing phenology of plants. Plasticity in timing of migration in response to climatic conditions and plant phenology may be an adaptive behavioral strategy, which should reduce the detrimental effects of trophic mismatches between resources and other life-history events of large herbivores. Failure to consider effects of nutrition and other life-history traits may cloud interpretation of phenological patterns of mammals and conceal relationships associated with climate change.

Key words: climate change; life-history characteristics; mule deer; NDVI; nutritional condition; *Odocoileus hemionus*; plant phenology; risk averse; risk prone; Sierra Nevada; snow depth; trophic mismatch.

Received 17 September 2010; revised 25 October 2010; accepted 29 October 2010; final version received 6 April 2011; **published** 27 April 2011. Corresponding Editor: M. Festa-Bianchet.

Citation: Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. doi:10.1890/ES10-00096.1

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Introduction

Climate change is expected to alter ecosystem structure and function, including community composition and distributions of species (Walther et al. 2002). Overwhelming evidence from long-term research supports the influence of climate change on phenology (i.e., timing of seasonal activities) of plants and animals (Stenseth et al. 2002, Badeck et al. 2004, Gordo and Sanz 2005). Spring activities of numerous taxa have occurred progressively earlier and in the direction expected from climate change since the 1960s, including breeding by birds, arrival of migrant birds, appearance of butterflies, chorusing and spawning of amphibians, and flowering in plants (Walther et al. 2002, Parmesan and Yohe 2003 for reviews). Corresponding delays in the initiation of autumn events also have been reported, but those phenological shifts are less apparent (Walther et al. 2002, Carey 2009). For example, during a 42-year study of migration in eight species of birds, three species advanced, three delayed, and two did not change the timing of autumn migration (Adamik and Pietruszkova 2008). Indeed, the timing of seasonal activities may be one of the simplest processes to track changes in the ecology of a species responding to climatic change (Walther et al. 2002). Addressing questions related to climate change, however, requires long-term studies to disentangle influences of large-scale climate and individual life-history patterns on phenological events.

Migration is a well-recognized life-history strategy involving numerous taxa over the globe (Baker 1978, Swingland and Greenwood 1983, Fryxell et al. 1988, Alerstam et al. 2003); effective conservation actions are necessary to maintain intact patterns of migration (Berger 2004, Bolger et al. 2008). Nevertheless, our understanding of the biology of migration by large herbivores is fragmentary, and consequences of climate change on those phenological patterns remain largely unknown (Bolger et al. 2008, Wilcove 2008). In strongly seasonal environments, large herbivores typically migrate between discrete ranges, which is thought to have evolved in response to the dynamic patterns of forage quality and availability (Morgantini and Hudson 1989, Albon and Langvatn 1992, Hebblewhite et al. 2008), predation risk (Fryxell et al. 1988), and weather patterns (Nelson and Mech 1981, Loft et al. 1989, Kucera 1992, Grovenburg et al. 2009). Indeed, migrants often acquire a selective advantage through enhanced fitness (Dingle 1985, Fryxell et al. 1988), avoid resource bottlenecks by obtaining access to greater food supplies in larger and less densely inhabited ranges, and obtain forage in the most nutritious phenological stages (McCullough 1985, Fryxell and Sinclair 1988, Fryxell et al. 1988, Albon and Langvatn 1992, Holdo et al. 2009, Zeng et al. 2010).

At most mid- to high-latitude regions, frost-free periods have increased with a concomitant 10% decrease in snow cover since the late 1960s (Walther et al. 2002). Temporal and spatial advance in seasonal resource availability by a warming climate may reduce the reproductive success of animals that fail to adjust life-history events to correspond with temporal changes in peak forage availability, resulting in a trophic mismatch (Post and Forschhammer 2008, Post et al. 2008). Nevertheless, large herbivores may be capable of adjusting their timing of migration to enhance nutrient gain in an attempt to compensate for the trophic mismatch at a large spatial scale (Post and Forschhammer 2008), unless their migratory patterns are fixed by day length rather than other environmental cues (Garrott et al. 1987, Post and Forschhammer 2008). If large herbivores respond to milder winter conditions with flexibility in timing of migration, animals should depart winter range earlier in spring and remain on summer ranges for a longer duration in autumn to gain access to forage under circumstances of reduced intraspecific competition (Albon and Langvatn 1992), increased plant diversity (Mysterud et al. 2001), and at a more nutritious phenological stage (Klein 1965, Pettorelli et al. 2007, Hamel et al. 2009). Consequently, natural selection should favor those individuals that respond to climatic change by timing seasonal migration to correspond with phenological advances in plant growth, resulting in improved nutritional gains (White 1983, Mysterud et al. 2001, Voeten et al. 2009).

Although effects of climatic patterns and plant phenology on the timing of migratory events for large herbivores have been documented (Albon and Langvatn 1992, Kucera 1992, Nelson 1995, Sabine et al. 2002, Fieberg et al. 2008), the influence of intrinsic factors, such as age, location

of summer residency (which may differ for populations using the same winter range), and reproductive and nutritional state, rarely have been considered (White et al. 2010). Failure to recognize other important factors related to individual life-history characteristics may lead to spurious correlations between indices of climate and the timing of migration.

The behavioral responses of an individual may be affected by their current nutritional state. For instance, studies of avian ecology have suggested that the timing of long-distance migration in bird species may be under strong endogenous control (Mitrus 2007, Pulido 2007). Despite the well-recognized carry over of nutritional condition from the energetic costs and benefits from previous seasons (Parker et al. 2009), few studies have considered whether differences in nutritional condition among individuals affect the timing of migration by large herbivores (Bolger et al. 2008). Maternal females, or those in poor nutritional condition, may be less able to afford the presumed risk associated with altering timing of migration (Ruckstuhl and Festa-Bianchet 1998, Ciuti et al. 2006). Large herbivores are long-lived and those in adequate nutritional condition have the opportunity to reproduce annually; consequently, females should adopt a strategy to promote their survival and opportunity for future reproduction, while simultaneously protecting their current reproductive investment (Stearns 1992).

Most knowledge on timing and synchrony of migration in large herbivores has been derived from short-term studies, which limits the probability of observing variable weather conditions (Fieberg et al. 2008), and precludes the evaluation of effects of large-scale climate on migratory events (Forchhammer and Post 2004). Our objective was to assess a long-term dataset to evaluate effects of climatic conditions, plant phenology, and individual life-history characteristics of mule deer (*Odocoileus hemionus*) in the western Great Basin on timing and synchrony of seasonal migration. Our first objective was to evaluate the influence of extrinsic variables including, broad-scale climate, local weather, and plant phenology on timing of migration. Global climate change is expected to alter the phenological patterns of life-history events for numerous taxa, including seasonal migration by vertebrates (Walther et al. 2002, Forchhammer and Post 2004). Effects of winter weather and snow depth, as well as progression in plant phenology, on timing of seasonal movements by large herbivores have been well documented (Garrott et al. 1987, Kucera 1992, Albon and Langvatn 1992, Sabine et al. 2002, Fieberg et al. 2008, Zeng et al. 2010). Therefore, we expected current weather conditions, driven by broad-scale climate, to influence the timing of seasonal migrations among mule deer. Furthermore, progression in plant phenology, particularly in spring, should correspond to the timing of migratory events between seasonal ranges across years. Following the identification of extrinsic factors that affected seasonal migration of mule deer, we evaluated the influence of intrinsic factors among individual mule deer on timing of migration. We hypothesized that timing of migration would be influenced by individual life-history characteristics including nutritional condition, reproductive status, age, and location of summer residency. Migration by large herbivores is a spectacular phenomenon occurring across a wide array of landscapes, however, many of these migrations are imperiled by anthropogenic disturbances, which is likely indicative of major ecological changes (Berger 2004, Bolger et al. 2008, Wilcove 2008). Our approach will provide a better understanding of the mechanisms underpinning this biological process and should aid in the conservation of these large, vagile mammals and their unique behaviors.

Study Area

We monitored the timing of migration for a population of mule deer that wintered on the east side of the Sierra Nevada in Round Valley (37°24′ N, 118°34′ W), Inyo and Mono counties, California, USA (Fig. 1). Mule deer inhabited approximately 90 km^2 of Round Valley during November-April, but the size of this area was dependent on snow depth (Kucera 1988). Annual snow depth in a drainage adjacent to Round Valley (Station ID: RC2, California Department of Water Resources) was highly variable during our study; the coefficient of variation of snow depth in April was 57% and ranged from 25.4 to 139.7 cm. Precipitation in the study area is strongly seasonal, with 75% occurring between November

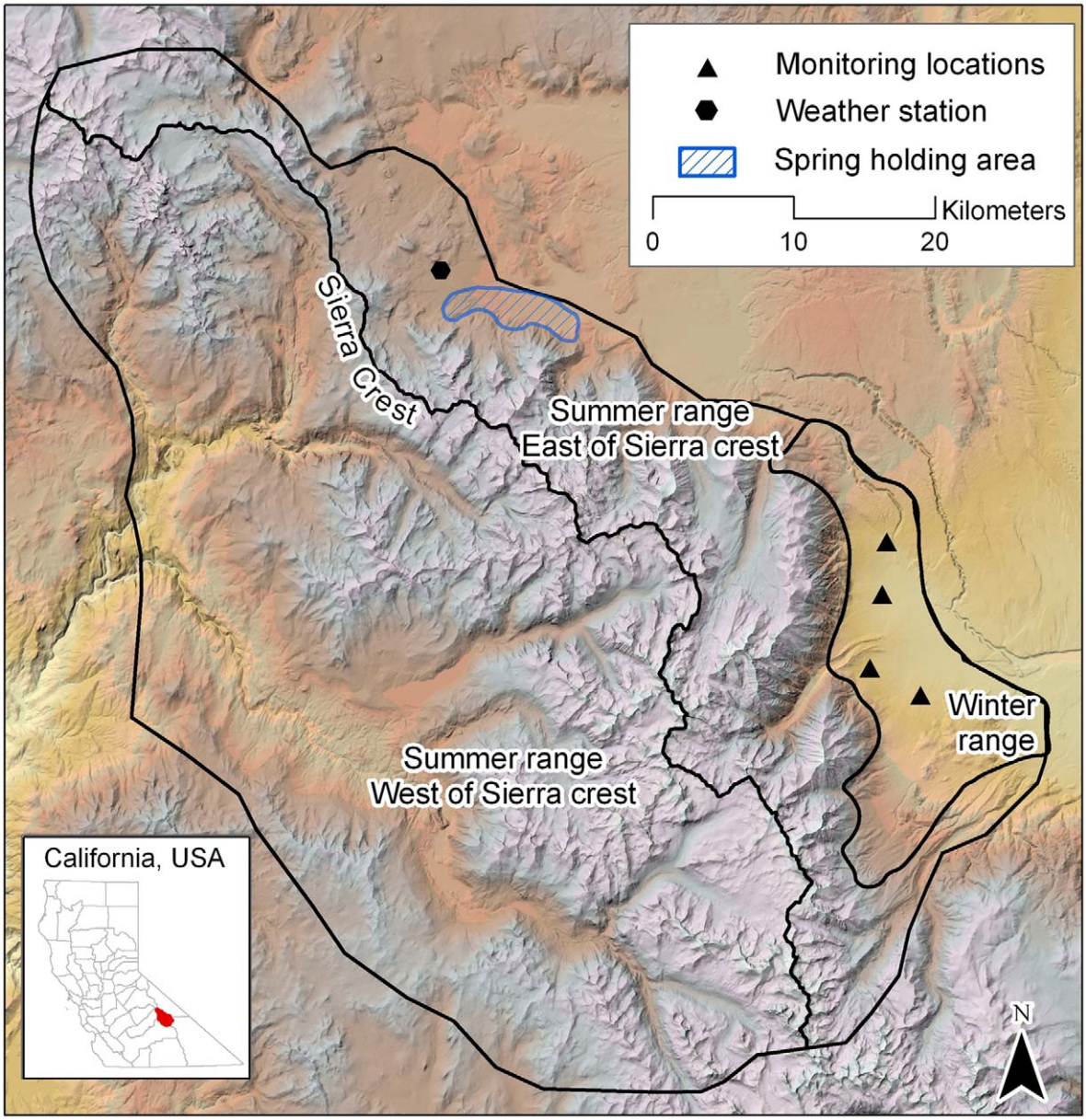

Fig. 1. Seasonal ranges occupied by female mule deer during winter, and the distinct ranges on both sides of the crest of the Sierra Nevada (Sierra crest), California, USA during summer. The four monitoring locations on winter range are indicated as well as the spring holding area for deer and location of the weather station near Mammoth Lakes, California.

and March (Kucera 1988). Daily temperatures near Mammoth Lakes, California, USA during 1999–2009 ranged from −27 to 33°C (Western Regional Climate Center). The region is typified by dry, hot summers (June–September), short, mild autumns with cooling temperature and increasing precipitation (October), and long, cold winters, with most annual precipitation accumulating as snow (November–April). Spring is short and characterized by decreasing precipitation and increasing temperatures (May; Fig. 2).

Round Valley is bounded to the west by the

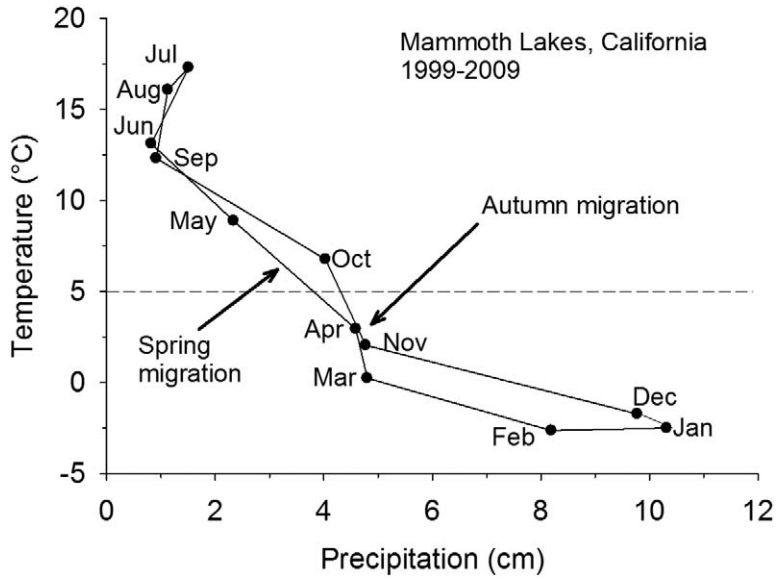

Fig. 2. Climograph of the mean monthly temperature and precipitation at Mammoth Lakes, California, USA, 1999–2009, which is located adjacent to summer range and the traditional migratory route for mule deer occupying winter range in Round Valley. Autumn and spring migration correspond to average timing of seasonal migration, 1999–2009, and dashed line represents an index to a temperature threshold (5°C) for growth of plants (Chapin 1983).

Sierra Nevada, to the south by large boulders and granite ridges of the Tungsten Hills and Buttermilk Country, and to the east by US Highway 395. The northern end of Round Valley gradually rises from the valley floor at 1,375 m to the top of the Sherwin Grade at 2,135 m. Open pastures comprised about 18.3 km^2 of the eastern portion of the valley; 3.2 km^2 was low-density residential housing (Pierce et al. 2004). Vegetation in Round Valley was characteristic of the western Great Basin and sagebrush-steppe ecosystem (Storer et al. 2004).

Summer range for mule deer that winter in Round Valley occurred on both sides of the crest of the Sierra Nevada (hereafter Sierra crest; Fig. 1) at elevations ranging from 2,200 to >3,600m (Kucera 1988). Winter storms from the Pacific Ocean deposit moisture as they move up the western slope with a substantial rain shadow, resulting in a more arid landscape on the eastern slope, where the Great Basin Desert begins (Storer et al. 2004, Bleich et al. 2006). The dense pine-fir (*Pinus-Abies*) stands and rivers on the west side of the Sierra crest contrast with the sparse forests transitioning to sagebrush scrub with only a few small streams on the east side. Indeed, the formidable Sierra crest sharply delineates the western slope from the eastern slope of the Sierra Nevada, and is traversable only by a series of passes that increase in elevation from north to south (Kucera 1988). Mule deer typically migrate northward and westward to high-elevation ranges in spring (Kucera 1992, Pierce et al. 1999); most migrate over the aforementioned passes to the west side of the Sierra Crest (Fig. 1), while some remain on the east side (Kucera 1992, Pierce et al. 2000). Prior to completion of migration to summer range, mule deer from Round Valley make extensive use of a spring holding area at higher elevation (>1,200 m) located on the east side of the Sierra Nevada, just southeast of Mammoth Lakes, California, USA (Kucera 1992; Fig. 1). Mule deer often remain on the spring holding area until snow on summer range has receded (Kucera 1992).

Methods

Animal capture

During March 1997–2009 and November 2002–2008, we captured adult female (>1 yr old) mule

deer on winter range in Round Valley using a hand-held net gun fired from a helicopter (Krausman et al. 1985). We hobbled and blindfolded each animal prior to moving it by helicopter to a central processing station with shelter for animals and handling crews. To allow age determination by cementum annuli (Matson's Laboratory, Milltown, Montana, USA), we removed one incisiform canine using techniques described by Swift et al. (2002); this procedure has no effect on body mass, percent body fat, pregnancy rate, or fetal rate of mule deer (Bleich et al. 2003). We fitted each animal with standard, VHF radiocollars (Telonics, Inc., Mesa, Arizona, USA; Advanced Telemetry Systems, Isanti, Minnesota, USA) equipped with a mortality sensor. We attempted to maintain radiocollars on >75 adult females by capturing new, unmarked animals to replace animals lost to mortality.

We conducted ultrasonography using an Aloka 210 portable ultrasound device (Aloka, Wallinford, CT), with a 5-MHz transducer, to measure maximum thickness of subcutaneous fat deposition at the thickest point cranial to the cranial process of the tuber ischium to the nearest 0.1 cm (Stephenson et al. 2002). We complemented ultrasonography with palpation to determine a body-condition score, validated for mule deer (Cook et al. 2007), to estimate nutritional condition of deer that have mobilized subcutaneous fat reserves (<5.6% ingesta-free body fat). We calculated rLIVINDEX as subcutaneous rump-fat thickness plus rump body-condition score (Cook et al. 2007). We then used rLIVINDEX to calculate ingesta-free body fat (IFBFat), where $\text{IFBFat} = 2.920 \times \text{rLIVINDEX} - 0.496$ (Cook et al. 2007). During deer captures in March, we used an ultrasound with a 3-MHz linear transducer to determine pregnancy and fetal rates (number of fetuses per female) of females during the second one-third of gestation (Stephenson et al. 1995).

During each autumn, we attempted to determine reproductive status of all marked females as they arrived on winter range in late-October through November. We located radiocollared females using ground-based telemetry and stalked to within visible range of deer (<200 m). We observed each female using binoculars or spotting scopes until we could confidently determine the number of young-at-heel. We identified the number of young-at-heel by observing nursing and other maternal behavior (Miller 1971), and determined recruitment status based on the presence or absence of young-at-heel identified each autumn. Animal capture and research methods were approved by an independent Institutional Animal Care and Use Committee at Idaho State University (protocol #: 650-0410), were in accordance with guidelines of research on large mammals by the American Society of Mammalogists (Ganon et al. 2007), and followed California Department of Fish and Game protocols for wildlife restraint.

Timing of migration

We determined the presence or absence of radiomarked mule deer on winter range with radio telemetry from four monitoring locations, which were strategically distributed across Round Valley during 1999–2009 (Fig. 1). Although we did not attempt to determine exact locations of animals by triangulation, the topography of the Sierra Nevada that bounded Round Valley on three sides conveniently blocked the signal of animals that were not present in the valley. We conducted telemetry from fixed-wing aircraft to locate animals that were not present in Round Valley. Aerial telemetry also was used to locate all females on their summer range during mid-summer and to categorize animals based on the side of the Sierra crest (east or west) that they occupied (Fig. 1).

We attempted to monitor animals from the ground a minimum of 3 days per week beginning on 1 October and continuing through 30 April each winter. Logistical constraints during some years, however, affected the frequency and duration of monitoring. We censored animals that died prior to migration in either autumn or spring because, in some instances, we were unable to determine exact date of death. We assumed that censoring of individuals was independent of the migratory strategy exhibited by deer.

Local weather and climate

We obtained data on daily weather from a station located near the town of Mammoth Lakes, California, USA (Western Regional Climate Center 1998–2009), which was near the summer range of deer, and was immediately

adjacent to the traditional migratory route and spring holding area for mule deer from Round Valley (Kucera 1992; Fig. 1). Daily data on weather were not available for winter range; therefore, we used weather data from the nearby station at Mammoth Lakes, California, for all analyses (Appendix). Because deer also likely respond to changing weather patterns rather than simply absolute daily measurements of weather (Sabine et al. 2002, Grovenburg et al. 2009), we calculated a metric of change in weather to represent a change in weather on a particular day relative to previously experienced weather patterns. This metric reflected the difference in the daily weather relative to the mean of that particular weather variable during the previous 2 weeks, which we arbitrarily chose to represent the relative magnitude of change in weather on a day.

Annual weather patterns in the western US have been correlated with the annual mean of the southern oscillation index (SOI; Trenberth and Hurrell 1994, Marshal et al. 2002, Stenseth et al. 2003). Accordingly, we used the standardized SOI (National Oceanic and Atmospheric Administration, Climate Prediction Center) as a measure of variation in large-scale climate (Stone et al. 1996). For autumn migration, we used the annual mean of the SOI during the previous October through September, and for spring we used the mean SOI during the previous April through March in migration models.

Plant phenology

Temperature is one of the most critical factors influencing phenology in plants (Rachlow and Bowyer 1991). Therefore, we calculated an index to growth and senescence of plants based on mean daily temperatures (Chapin 1983). For each spring, we calculated the number of growing-degree days per day (the number of degrees that the mean daily temperature was >5°C, summed across all previous days beginning on 1 January) as an index to growth of plants (Chapin 1983). For each autumn, we calculated a metric of senescence of plants by the opposite of growing-degree days, which we termed senescent-degree days (the number of degrees that the mean daily temperature was <5°C, summed across all previous days beginning on 15 September).

The normalized difference vegetation index (NDVI) is derived from satellite imagery that measures the greenness of vegetation. NDVI is sensitive to environmental change (Pettorelli et al. 2005), is associated with fluctuations in dietary quality (Christianson and Creel 2009, Hamel et al. 2009), and thus, is related to numerous aspects of the ecology of large herbivores (Loe et al. 2005, Pettorelli et al. 2007). From the Earth Resources and Observation Science Center of the U.S. Geological Survey, we obtained a time series of 14-day composite NDVI with 1-km^2 spatial resolution recorded by the Advanced Very High Resolution Radiometer aboard the polar-orbiting weather satellites of the National Oceanic and Atmospheric Administration. Data were further processed to remove effects of atmospheric contamination with the method of Swets et al. (1999). We extracted mean NDVI values for each 2-week interval from 1999–2009 for pixels that occurred within the winter range and spring holding area for mule deer (Kucera 1988; Fig. 1). We extracted data for the spring holding area rather than the extensive summer range occupied by deer from Round Valley (Fig. 1), because habitat on the spring holding area was comparable with that occurring on winter range and deer made extensive use of holding areas in spring (Kucera 1992). We calculated a daily NDVI for both areas by interpolating between 14-day composites of NDVI, assuming a linear progression between change in NDVI composites and time increment for each period. We also expected deer to respond to progressive changes in NDVI; therefore, analogous to metrics of change for weather variables, we also calculated a metric of daily change in NDVI by the difference in daily NDVI relative to the mean NDVI during the previous 2 weeks. To describe annual deviations in patterns of green-up and senescence, we used program TIMESAT (Jönsson and Eklundh 2004) to calculate variables derived from NDVI data including: Julian date of onset of spring and onset of autumn, rate of increase in NDVI at the beginning of the season, rate of decrease in NDVI at the end of the season, and maximum and minimum NDVI for seasonal ranges (Reed et al. 1994, Pettorelli et al. 2005).

Statistical analyses

We evaluated relationships between the annual

mean (October–September) of the SOI and the corresponding annual sum in snowfall and precipitation, and the annual average of mean daily temperature using linear regression (Neter et al. 1996), with one-tailed tests, because the direction of the expected relationships have been established previously (Trenberth and Hurrell 1994, Marshal et al. 2002). We used two-tailed *t*-tests to evaluate differences in annual phenological metrics between winter range and the spring holding area (Zar 1999), to determine if patterns of plant phenology differed between seasonal ranges.

Daily weather.—We used principal component analysis (PCA) of local weather data, based on the variance–covariance matrix (McGarigal et al. 2000), to reduce the dimensionality of those variables and derive independent composite variables that described daily weather. In the PCA, we included 12 variables representing absolute daily weather and a metric of change in daily weather for: minimum, maximum, and average temperature (°C), snowfall (cm), snow depth (cm), and precipitation (cm). We selected 5 principal components because they each explained >1% of the variation in daily weather and were biologically relevant (Appendix). Principal component 1 explained 74.2% of the variation in daily weather and represented an absolute measure of daily depth of snow from lower (negative loadings) to higher snow depths (positive loadings). Principal component 2 explained 12.1% of the variation in daily weather and reflected daily changes in snow depth from decreasing snow depth (negative loadings) to increasing snow depth (positive loadings). Absolute daily temperatures from cold temperatures (negative loading) to warm temperatures (positive loading) were represented by principal component 3, which explained 8.1% of the variation in daily weather. Daily snowfall and precipitation from lower (negative loadings) to higher (positive loadings) was reflected by principal component 4, which explained 3.0% of the variation in daily weather. Finally, a metric of change in daily temperatures from cooling temperatures (negative loadings) to warming temperatures (positive loadings) was represented by principal component 5, which explained 1.7% of the variation in daily weather.

Migration timing.—We censored 1 deer that was resident all year on winter range in Round Valley, and 2 deer that failed to return to winter range in 2006 and 2007. We censored those individuals because we were not interested in testing hypotheses regarding mixed-migration strategies (Nicholson et al. 1997); ≥99% of deer in Round Valley were obligate migrators. We also chose to restrict analyses of timing of migration in autumn to the period between 15 September and 31 December, because events beyond that date in any particular year were sparse. Restriction of analyses for autumn migration resulted in the censoring of 14 migratory events that occurred after 31 December, during 1999–2009. We also censored 1 migratory event during spring migration when an individual deer migrated on 15 January, whereas all other migratory events occurred after 6 March.

Logistical constraints precluded continuous sampling to identify the exact day of departure and arrival on winter range in our study. Average monitoring interval per season ranged from 11.5 days for autumn 1999 to 1.3 days for spring 1999. Average censor interval for migratory events per season ranged from 20 days for autumn 2000 to 1 day for spring 2002. The timing of a migratory event could only be attributed to an interval of time. Data collected under this coarse sampling regime are known as interval-censored and require proper accounting for the uncertainty of the timing of events (Johnson et al. 2004, Fieberg and DelGiudice 2008).

To properly account for interval-censored data, we applied the method of Johnson et al. (2004) to calculate a robust measure of mean date of migration and a corrected measure of the SD of the distribution of migratory events to determine synchrony (Gochfeld 1980). This method is an extension of Sheppard's correction, which allows unequal sampling intervals (bin size; Johnson et al. 2004). We used the method of Johnson et al. (2004) and the associated 95% CI to evaluate differences in timing of migration among years, recruitment status of females in autumn (presence of young-at-heel), and summer residency (east versus west side of the Sierra crest). We used multiple-regression analysis (Neter et al. 1996) to evaluate the relationship between annual mean and synchrony (SD) of seasonal migration with annual metrics of large-scale climate and plant phenology including: annual

SOI; Julian date of onset of spring and onset of autumn; and rate of increase or decrease in NDVI between seasons, respectively. Before interpreting results of our multiple-regression analyses, we evaluated residual plots for compliance with assumption of normality and homogeneity of variance (Neter et al. 1996). We did not include annual averages of local weather variables in the multiple-regression analysis, because of collinearity with SOI and Julian date of onset of spring ($r > 0.50$). We examined fit of multiple regression models with R^2_{adj} and the contribution of each variable by reporting partial correlations ($r^2_{partial}$; Neter et al. 1996, Zar 1999). We determined whether mean date of seasonal migration of mule deer was advancing or receding during 1999–2009 using simple linear regression (Neter et al. 1996). We also used linear regression to determine if there were directional changes in annual precipitation, snowfall, mean temperature, SOI, Julian date of start of season, and Julian date of end of season relative to time (Neter et al. 1996).

Migration modeling.—We adopted methods of survival analysis that have been developed for interval-censored data, which are used to analyze data addressing the time of a specific event (Dinsmore et al. 2002); events in our study were the dates of arrival to and departure from winter range. We used interval-censored models to evaluate effects of extrinsic and intrinsic factors on the distribution of migratory events for seasonal migration in mule deer. We estimated daily probability of not migrating as a function of Julian date using the nest-survival option in Program MARK (White and Burnham 1999, Dinsmore et al. 2002) and subsequently, we calculated daily probability of migrating as one minus the daily probability of not migrating. These models were developed to analyze nest-survival data (Dinsmore et al. 2002), but provide a powerful tool to investigate other biological phenomena, including timing of migration in relation to time-specific and individual-based covariates (Fieberg and DelGiudice 2008). Nevertheless, nest-survival models do not account for repeated measurements between years (although it does account for them within years). We partitioned our dataset into individuals monitored during ≤ 3 years versus individuals monitored >3 years and calculated mean date of seasonal migration ($\pm 95\%$ CI) using Johnson et al. (2004) to evaluate whether repeated monitoring of some individuals had an effect on our analyses. There was no difference in timing of migration between individuals monitored for ≤ 3 years compared with >3 years, which indicated that repeated sampling of individuals likely did not have a strong influence on our analyses.

Input files for Program MARK included three variables required for each deer: the day since the beginning of the interval that the deer was available to migrate (i), the day the deer was monitored immediately prior to a migratory event (j), and the day the deer was monitored immediately after a migratory event (k; notation follows Dinsmore et al. 2002). We scaled the beginning of the monitoring interval for each season (i) so that the first day of the monitoring interval was the same Julian date across all years. For autumn, j_i represented the last observation when absent from winter range, and k_i represented the first observation on winter range. For spring, j_i represented the last day present on winter range, and k_i represented the subsequent observation when absent from winter range. Each autumn, a few individuals arrived on winter range prior to the initiation of monitoring of radio signals in Round Valley. In those instances, we assigned j_i as 15 September of the current autumn, which we assumed was prior to the earliest date expected for individuals to arrive on winter range. Each spring, a few individuals also remained on winter range when we ceased monitoring in Round Valley. For those individuals, we assigned k_i to 15 May of the current spring, which we assumed was the latest date any individual would be expected to depart winter range.

We employed an information-theoretic approach to identify extrinsic and intrinsic factors that influenced timing of migration in mule deer. In the first stage of the modeling, we examined all possible combinations of extrinsic predictor variables that might influence timing of migration in mule deer: annual SOI, daily weather variables and weather change metrics from the PCA, growing- or senescent-degree days, daily range-specific NDVI and change in NDVI, and a quadratic time-trend. We included year as a nuisance parameter to account for variation among years that was not specifically addressed by our other annual environmental variables. We

also fit a quadratic time-trend that allowed daily probability of migration to follow a curvilinear pattern, which we expected to occur because seasonal patterns of migration commonly occur in a pulse with tails on either side (Garrott et al. 1987, Kucera 1992, Brinkman et al. 2005, Grovenburg et al. 2009). We expected potential interactions between principal components for weather and NDVI, but did not include those interactions because of multicollinearity between the interaction terms and principal components representative of those weather variables ($r > 0.70$). For each model, we calculated Akaike's information criterion adjusted for small sample size (Akaike 1973; AIC_c), ΔAIC_c, and Akaike weight (w_i; Burnham and Anderson 2002). We then calculated model-averaged parameter estimates and unconditional standard errors (SE) for each predictor variable (Burnham and Anderson 2002). We determined if model-averaged parameter estimates differed from zero by examining whether their 95% CI, based on unconditional SEs, overlapped zero. We evaluated the relative importance of variables based on their importance weights, which we calculated as the sum of w_i across all models that contained a particular variable (Burnham and Anderson 2002).

After we identified the extrinsic variables that affected the timing of seasonal migration among mule deer, we added intrinsic covariates characterizing the life-history of groups (e.g., summer residency) and individuals (e.g., nutritional condition), to evaluate whether life-history traits among individuals affected their timing of migration. We partitioned the dataset to include only those individuals where data on life-history characteristics were available. We believe the sample of individual animals with data on life-history characteristics was representative of the population, because we attempted to determine reproductive status of all marked females on winter range during autumn, captured 50% of collared females in November, and attempted to capture every marked female each March.

We modeled all possible combinations of the extrinsic variables that were significant (based on 95% *CI*) in the first stage of the modeling approach, and individual life-history characteristics that we hypothesized would affect the timing of seasonal migration including: age (years); summer residency (east versus west side of the Sierra crest); nutritional condition (ingesta-free body fat; IFBFat); fetal rate (for spring migration only); and recruitment (presence or absence of young-at-heel for autumn migration only). We also evaluated interactions based on ΔAIC_c and confidence intervals of interaction terms for life-history characteristics (e.g., recruitment × IFBFat), and between life-history characteristics and daily weather (e.g., IFBFat × PC1). None of the interactions we investigated were significant, or resulted in a significant improvement of model fit. Interaction terms were removed from subsequent analyses. For both spring and autumn models, we also included age as a quadratic term (age^2) to allow timing of migration to be a curvilinear function of age. Finally, we again used model averaging, 95% CI, and importance weights to evaluate the effects of life-history characteristics on the timing of migration (Burnham and Anderson 2002). Following the identification of important life-history variables on the timing of migration by mule deer, we calculated the daily probability of migration for east- and west-side females (i.e., summer residency), for females in relatively poor nutritional condition (4% IFBFat), and good nutritional condition (18% IFBFat), and for old (12.4 years old) and young females (2.4 years old) to illustrate the effects of age, summer residency, and nutritional condition on the daily probability of seasonal migration of mule deer. All assigned values for each life-history characteristic were within the range we observed for deer in Round Valley and were in accordance with that reported for mule deer elsewhere (Gaillard et al. 2000, Cook et al. 2007).

Results

We monitored spring and autumn migration of radiocollared mule deer each year during 1999–2009. We documented 850 and 882 migratory events by mule deer in the autumn and spring, respectively, by monitoring 297 individual deer for 1 to 22 seasonal migrations. During 1999–2009, female mule deer resided on summer range ($\bar{X} = 191$, $SD = 12.6$ days) 10% longer than on winter range ($\bar{X} = 174$, $SD = 8.9$ days). The southern oscillation index (SOI) was negatively related to total snowfall ($\beta = -129.6$, $r^2 = 0.26$, $P = 0.053$), and approached a significant positive

relationship with mean annual temperature ($\beta = 0.54$, $r^2 = 0.17$, $P = 0.13$), but exhibited little correlation with total precipitation ($\beta = -7.32$, $r^2 = 0.06$, $P = 0.36$; Appendix). In addition, there was no directional change during 1999–2009 in annual precipitation ($\beta = -2.06$, $r^2 = 0.02$, $P = 0.67$), snowfall ($\beta = -10.61$, $r^2 = 0.02$, $P = 0.65$), average temperature ($\beta = 0.06$, $r^2 = 0.10$, $P = 0.34$), SOI ($\beta = 0.04$, $r^2 = 0.01$, $P = 0.80$), Julian date of start of season ($\beta = -0.40$, $r^2 = 0.01$, $P = 0.85$), or Julian date of end of season ($\beta = -2.54$, $r^2 = 0.15$, $P = 0.24$).

Julian date of onset of spring (as derived from NDVI) was similar between seasonal ranges, but rate of green-up differed and occurred at more than twice the rate on the spring holding area compared with winter range (Table 1). Likewise, date of the onset of senescence was similar between ranges, whereas the rate of senescence was significantly faster on the spring holding area (Table 1). Maximum greenness of vegetation, as indicated by peak values in NDVI, was significantly greater on the spring holding area compared with winter range (Table 1). Moreover, during 1999–2009, daily mean NDVI remained significantly greater (based on 95% CI) on the spring range compared with winter range in Round Valley from 2 April until the end December (Fig. 3). Annual minimum values of NDVI during winter did not differ between seasonal ranges (Table 1), which would be expected when snow covered those ranges. Nevertheless, snow cover was sparse during some winters in Round Valley.

Autumn migration

Snowfall during October ranged from 0 to 110 cm (CV = 196%), whereas mean daily temperature ranged from 4.2 to 10.2°C (CV = 28%), during 1999–2009. Despite such variation in winter weather during October, mean date of autumn migration (28 October) for mule deer only ranged from 18 October to 8 November, and generally was not different among years (Fig. 4). In addition, mean date of autumn migration coincided with the onset of winter as temperatures declined below 5°C, and winter precipitation began to increase (Fig. 2). Mean date of annual migration did not exhibit directional change during 11 years ($\beta = -0.21$, $r^2 = 0.01$, $P = 0.74$). Multiple-regression analysis revealed little relation between annual metrics of large-scale climate and plant phenology, and the annual mean and synchrony of autumn migration ($R^2_{adj} = 0.35$, $P = 0.12$, $R^2_{adj} = 0.23$, $P = 0.20$, respectively). Synchrony (SD) within years was highly variable ranging from 17.1 to 62.1 days (mean SD = 39.0 days).

Migration models that included year received nearly 100% of the Akaike weight. Indeed, model-averaged daily probability of migration varied considerably in shape and magnitude among years, and the annual cumulative proportion of mule deer migrating increased at different rates among years (Fig. 5). Although mean date of autumn migration did not differ statistically during 1999–2009, based on predictive models, the date at which 90% of adult female mule deer had completed autumn migration ranged from 29 October in 2004 when early snowfall and cold temperatures occurred, to 2 December in 1999, which was characterized by a mild autumn (Fig. 5).

Extrinsic factors affecting the daily probability of autumn migration among years included daily snow depth (PC1), daily temperature (PC3), daily snowfall (PC4), and daily change in temperature (PC5; Table 2). Daily probability of migration increased as daily snowfall and snow depth increased, and as daily temperature and rate of change in temperature decreased. Based on Akaike importance weights, those four weather variables all had comparable roles in determining the daily probability of autumn migration in female mule deer (Table 2). For example, early snowfall in the absence of cold temperatures caused only modest increases in the daily probability of migration (Fig. 6a, b), whereas snowfall events coincident with cold and declining temperatures resulted in dramatic increases in the expected proportion of individual deer migrating that day (Fig. 6b, c).

Metrics of plant senescence, including daily senescent degree-days, daily NDVI, daily change in NDVI, end of season date, and rate of decrease in NDVI at end of season, received minimal support (importance weights <0.51) and their model-averaged parameter estimates did not differ from zero (Table 2). Indeed, mean date of autumn migration occurred prior to senescence of plants on summer range (Fig. 3), which supports the association between patterns of

Table 1. Mean, SE, and statistical results from *t*-tests to evaluate differences in annual phenology metrics between winter range and the spring holding area (Fig. 1) for mule deer in the Sierra Nevada, California, USA, 1999–2009. Phenology metrics were calculated following Reed et al. (1994).

	Seasonal range						
	Winter		Spring		*t*-test		
Phenology metric	Mean	SE	Mean	SE	*t*	*df*	*P*
Date of onset of spring†	92.50	4.30	94.60	4.70	0.33	20	0.750
Rate of increase in NDVI	0.03	2×10^{-3}	0.07	4×10^{-3}	7.10	20	<0.001
Date of end of season†	364.60	5.00	366.20	6.50	0.19	20	0.850
Rate of decrease in NDVI	0.03	3×10^{-3}	0.07	7×10^{-3}	5.30	20	<0.001
Maximum NDVI	0.34	0.01	0.60	7×10^{-3}	19.30	20	<0.001
Minimum NDVI	0.11	0.01	0.15	0.02	1.80	20	0.083

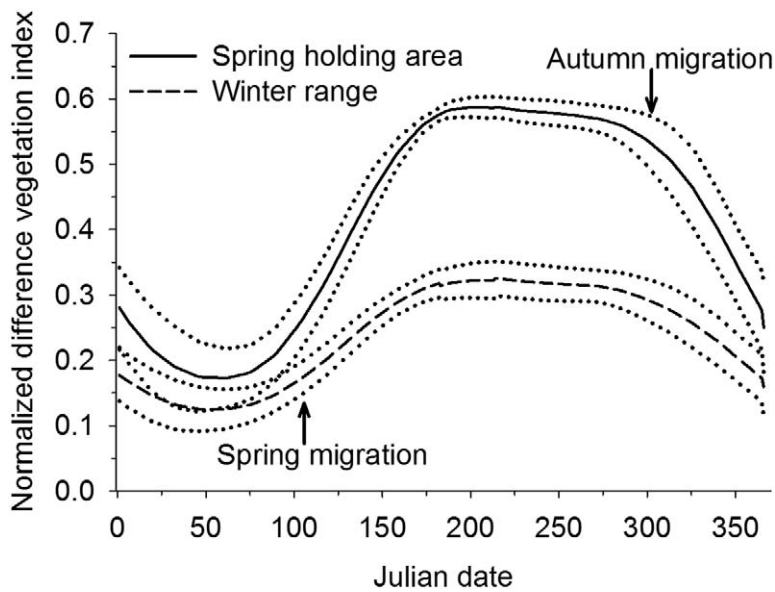

Fig. 3. Normalize difference vegetation index (NDVI) for winter range in Round Valley and the spring holding area (Fig. 1) for mule deer in the Sierra Nevada, California, USA, 1999–2009. Data are mean ±95% CI (dotted lines), and were scaled between 0 and 200. Arrows for autumn and spring migration correspond to average timing of seasonal migration.

winter weather and autumn migration.

Spring migration

During 1999–2009, mean snow depth adjacent to the spring holding area (Fig. 1) during April varied considerably from 0.13 to 87.7 cm (CV = 179%), while mean daily temperatures for April ranged from 0.54 to 5.4°C (CV = 60%). Mean date of departure from winter range for mule deer in Round Valley during 1999–2009 was 18 April, which was coincident with the onset of spring as precipitation declined and temperatures increased above 5°C (Fig. 2). Mean date of spring migration differed among years (Fig. 4), with early departure dates in 2002 and 2007, and delayed departure in 2005 and 2006. Mean date of spring migration did not exhibit a directional change during 1999–2009 ($\beta = -0.02$, $r^2 < 0.001$, $P = 0.98$). Spring migration (SD = 17.3 days) within years was significantly more synchronous than autumn migration (SD = 39.0 days; $t = 4.15$, $df = 20$, $P = 0.001$). Although there was no relation between annual metrics of climate and plant phenology, and synchrony of spring migration

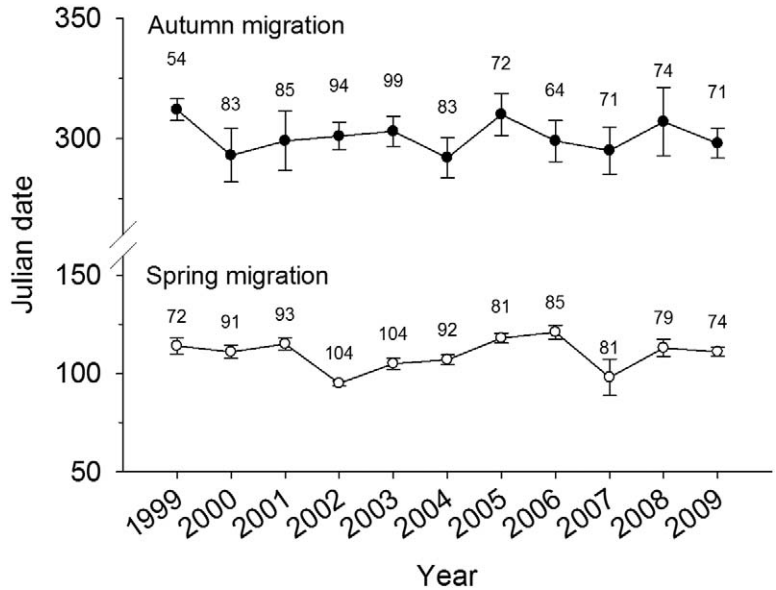

Fig. 4. Mean Julian date (±95% CI) of spring and autumn migration for female mule deer occupying winter range in Round Valley in the eastern Sierra Nevada, California, USA, 1999–2009. Values above means are number of deer monitored during each season.

($R^2_{adj} < 0.001$, $P = 0.77$), a strong relationship existed between those metrics and annual mean date of migration ($R^2_{adj} = 0.71$, $P = 0.014$). Both SOI and Julian date of onset of spring were positively related to the mean date of spring migration, but SOI ($\beta = 5.90$, $r^2_{partial} = 0.20$) accounted for slightly more variation in date of spring migration than the Julian date of onset of spring ($\beta = 0.33$, $r^2_{partial} = 0.15$).

Interval-censored models for spring migration supported an effect of year, with models that contained year having nearly 100% of the Akaike weight (Table 2). The shape and magnitude of the daily probability of spring migration varied markedly among years, as did the date of initiation and trajectory of the cumulative proportion of deer departing winter range (Fig. 7). Of the variables we hypothesized to influence the timing of spring migration, only daily snow depth (PC1), daily NDVI, and daily ΔNDVI had high importance weights and model-averaged parameter estimates that differed from zero (Table 2). As absolute daily snow depth decreased with a concomitant increase in daily NDVI and a positive ΔNDVI, daily probability of departure from winter range increased. Indeed, years of low snow depth with early increases in NDVI resulted in earlier initiation and mean dates of spring migration (Fig. 8b), whereas late snowfall events delayed spring migration (Fig. 8a). Moreover, years with substantial snowfall and later green-up resulted in substantial delays in departure from winter range by mule deer (Fig. 8c). Based on model-averaged estimates of the cumulative proportion migrated in spring, the date at which 90% of adult females had completed spring migration ranged from 13 April in 2002, which was characterized by low snow depth with early advances in plant phenology (Fig. 7, 8b), to 3 May in 2006, when heavy snow pack delayed advances in plant phenology (Fig. 7, 8c).

Effects of life-history characteristics

Following the identification of the extrinsic variables that influenced patterns of seasonal migration of mule deer, we subset our data to include only those individuals for which we had complete data on life-history characteristics in each season. For autumn migration, we obtained data on location of summer residency (side of the Sierra crest), age (years), recruitment (presence of young-at-heel), and nutritional condition (ingesta-free body fat; IFBFat) in November for 312

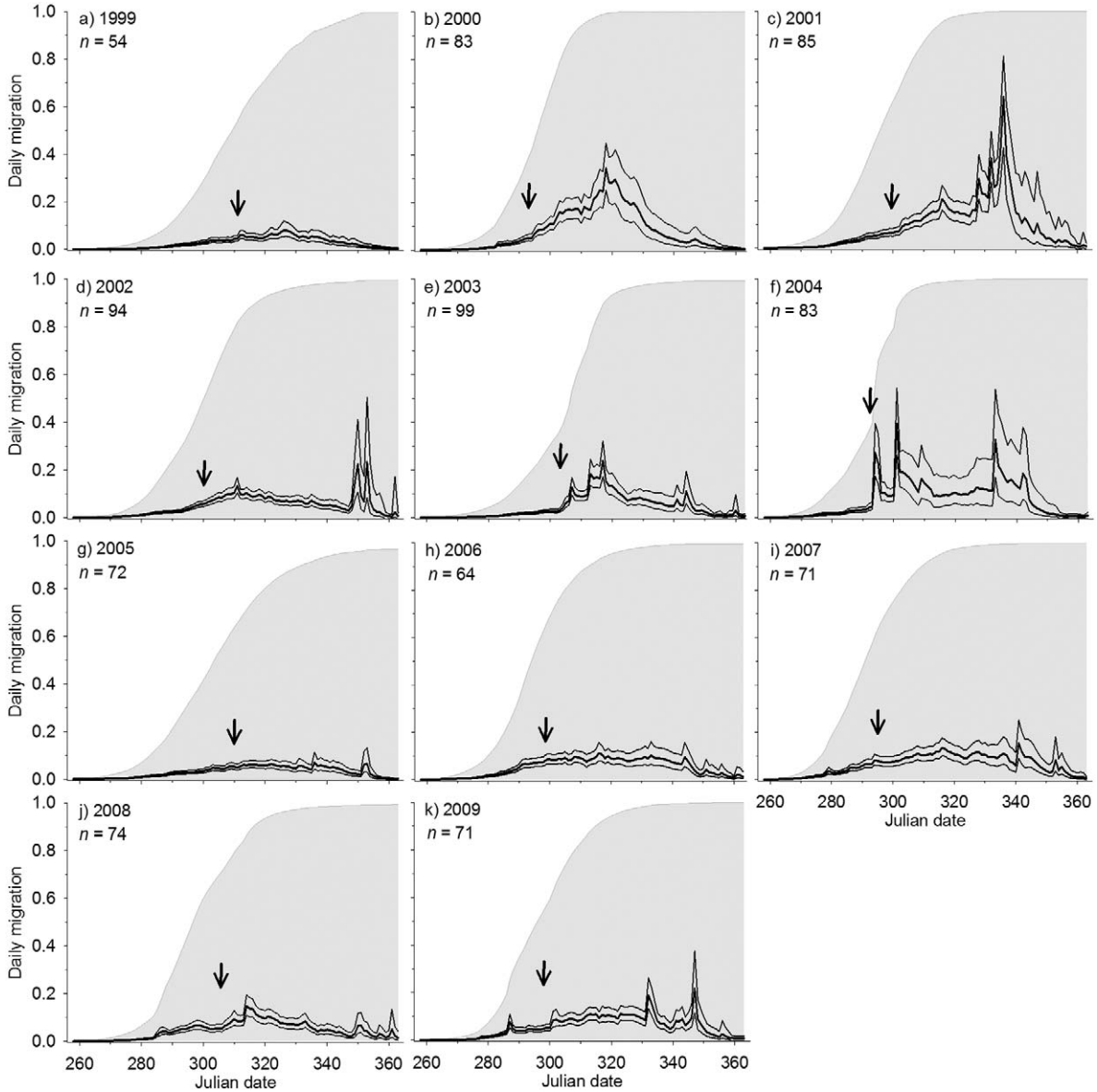

Fig. 5. Model-averaged estimates of the daily probability of migration (heavy line ±95% CI) and cumulative proportion migrated (shaded region) during autumn for adult (>1 year old) female mule deer relative to Julian date, Sierra Nevada, California, USA, 1999–2009. Black arrows indicate mean date of migration.

adult females during 7 years, 2002–2008. Of those females, 153 summered on the east side of the Sierra crest, and 159 on the west side. Age of females monitored in autumn ranged from 1.4 years to 15.4 years ($\bar{X} = 7.4$ years, SD = 2.8), and IFBFat ranged from 0.5% to 23.4% ($\bar{X} = 8.7\%$, SD = 5.3).

For spring migration, we obtained data on summer residency, age, fetal rate and IFBFat in March for 720 females during 11 years, 1999–2009. Of those females, 316 summered on the east-side of the Sierra crest and 404 summered on the west-side. Age of females monitored during spring ranged from 1.8 to 15.8 years ($\bar{X} = 6.8$ years, SD = 2.7), and fetal rate (number of fetuses per female) ranged from 0 to 3 ($\bar{X} = 1.6$, SD = 0.6). Ingesta-free body fat in March ranged from 0.5% to 15.5% ($\bar{X} = 5.1\%$, SD = 2.5), and was

Table 2. Model-averaged parameter estimates, 95% confidence intervals (95% CI), and Akaike importance weights for interval-censored models describing the relationship between the daily probability of autumn and spring migration of mule deer and 13 extrinsic variables, Sierra Nevada, California, USA, 1999–2009. Asterisks adjacent to parameter estimates indicate 95% CI do not overlap zero.

	Autumn				Spring			
		95% CI				95% CI		
Parameter	Estimate	Lower	Upper	Importance weight	Estimate	Lower	Upper	Importance weight
PC1	0.75*	0.12	1.37	0.85	−0.99*	−1.36	−0.62	1.00
PC2	0.22	−0.11	0.55	0.58	0.09	−0.03	0.20	0.59
PC3	−0.69*	−0.96	−0.41	1.00	0.13	−0.02	0.28	0.68
PC4	0.13*	0.01	0.24	0.84	1×10^{-3}	−0.04	0.04	0.26
PC5	−0.58*	−0.82	−0.35	1.00	0.06	−0.04	0.16	0.50
Degree-days	-2×10^{-3}	-6×10^{-3}	1×10^{-3}	0.51	-5×10^{-4}	-2×10^{-3}	9×10^{-4}	0.10
NDVI	0.72	−1.52	2.94	0.37	53.42*	46.02	60.78	1.00
ΔNDVI	3.20	−3.26	9.60	0.33	93.98*	28.42	159.32	0.99
Seasondate	-2×10^{-5}	-8×10^{-5}	2×10^{-5}	1×10^{-3}	-1×10^{-3}	-9×10^{-3}	6×10^{-3}	4×10^{-3}
ΔSeason	1×10^{-5}	-4×10^{-5}	7×10^{-5}	6×10^{-4}	n/a	n/a	n/a	n/a
SOI	8×10^{-4}	-8×10^{-4}	2×10^{-3}	1×10^{-3}	n/a	n/a	n/a	n/a
T	0.16*	0.13	0.18	1.00	0.11*	0.07	0.15	1.00
TT	-1×10^{-3}*	-1×10^{-3}	-1×10^{-3}	1.00	-1×10^{-3}*	-2×10^{-3}	-1×10^{-3}	1.00
Year	n/a	n/a	n/a	1.00	n/a	n/a	n/a	1.00

Notes: Factors in interval-censored models for seasonal migration included: daily snow depth (PC1), daily metric of change in snow depth (PC2), daily temperature (PC3), daily snowfall and precipitation (PC4), daily metric of change in temperature (PC5), cumulative degree days above or below 5°C for spring and autumn, respectively (degree-days), daily normalized difference vegetation index (NDVI), daily change in NDVI relative to previous 14 days (ΔNDVI), Julian date of start and end of season for spring and autumn respectively (Seasondate), rate of increase and decrease in NDVI at changing seasons for spring and autumn respectively (ΔSeason), mean of the southern oscillation index during 1 year previous to season (SOI), quadratic time trend (T and TT), and year (Year). Year was included as a nuisance parameter in models, however, the parameter estimates for each year are not biologically meaningful and were thus, not included.

significantly lower than IFBFat in November ($t = 14.4$, $df = 1{,}030$, $P < 0.001$).

Autumn migration.—Daily snow depth (PC1), absolute daily temperature (PC3), change in daily temperature (PC5), and the quadratic time trend all maintained their importance and significance for explaining the phenology of autumn migration in mule deer when life-history characteristics were included (Table 3). Daily snowfall (PC4) maintained a high importance weight, but the model-averaged parameter estimate was no longer significant. In addition, the effect of year as a nuisance parameter declined substantially in importance, compared with the first stage of the analysis that included only extrinsic variables (Table 3). Partitioning our dataset from 11 to 7 years may have affected that result; nevertheless, 2002–2008 included years with both extremes in weather patterns and expected probability of migration (Fig. 5).

Mean date of autumn migration was nearly identical between females with young-at-heel and those without young (Fig. 9a). Indeed, the model-averaged parameter estimate for recruitment status was not significant (Table 3). Three other life-history characteristics of individual mule deer, however, were highly important and significant for explaining timing of autumn migration: summer residency, age, and nutritional condition. Mean date of autumn migration between females that summered on either side of the Sierra crest approached a significant difference during most years, with east-side females generally exhibiting earlier dates of migration (Fig. 9b). Accordingly, interval-censored models of migration indicated that summer residency affected the daily probability of migration with east-side females arriving to Round Valley earlier than west-side females (Table 3). Older females had a lower daily probability of migration and, thus, tended to migrate to winter range later than younger females (Table 3). Lastly, ingesta-free body fat of individual females was negatively related to the daily probability of migration. Therefore, females in poor nutritional condition arrived to winter range earlier than females in good nutritional condition.

For example, on Julian date 300 during 2005, predictive models indicated that only 11% of young females in poor nutritional condition

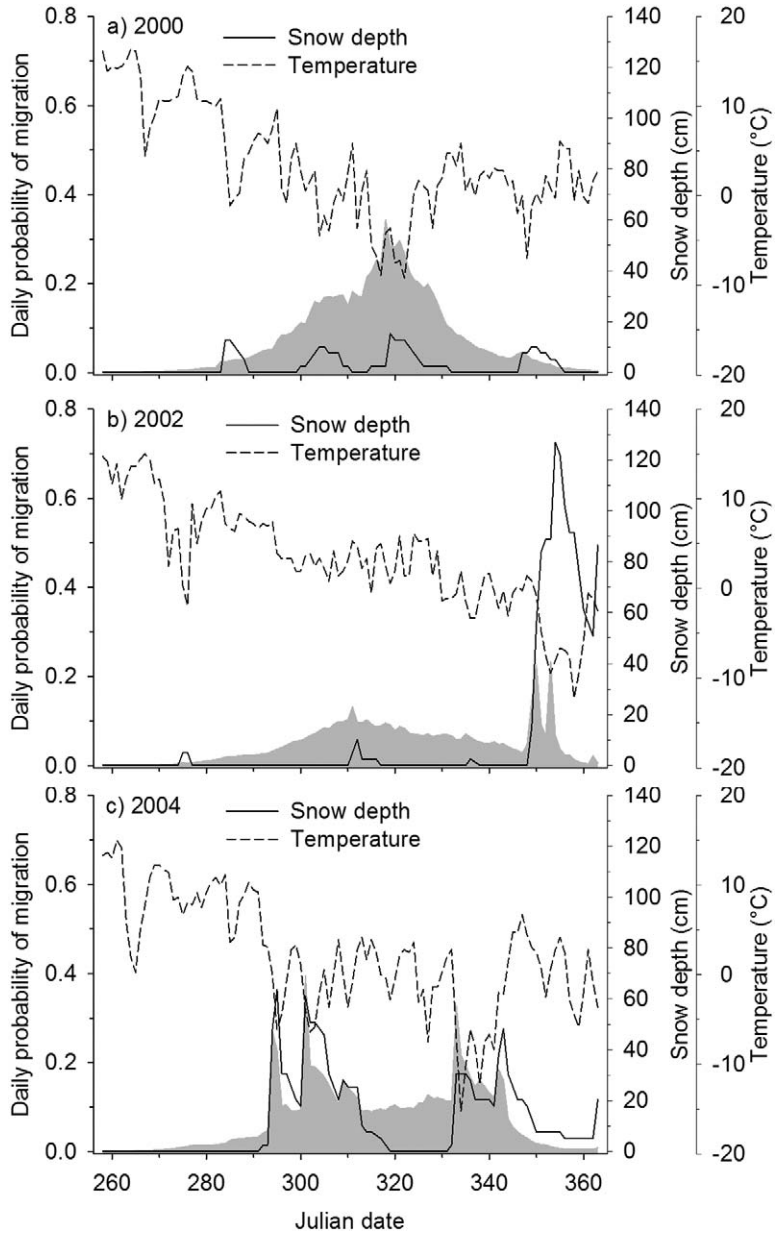

Fig. 6. Model-averaged estimates of the daily probability (shaded region) of autumn migration for adult (>1 year old) female mule deer, daily snow depth (cm), and average daily temperature relative to Julian date, Sierra Nevada, California, USA, during 3 years exhibiting differences in severity of autumn weather: 2000 (a), 2002 (b), and 2004 (c).

remained on summer range compared with 51% of old females in good nutritional condition (Fig. 10a). Furthermore, daily probability of migration for east-side females was higher than west-side females, with further effects of nutritional condition (Fig. 10d). On Julian date 300 during 2007, 92% of east-side females in poor nutritional condition had migrated to winter range, whereas 74% of west-side females in similar nutritional condition had migrated (Fig. 10c).

Spring migration.—In the second stage of the analysis that included life-history characteristics,

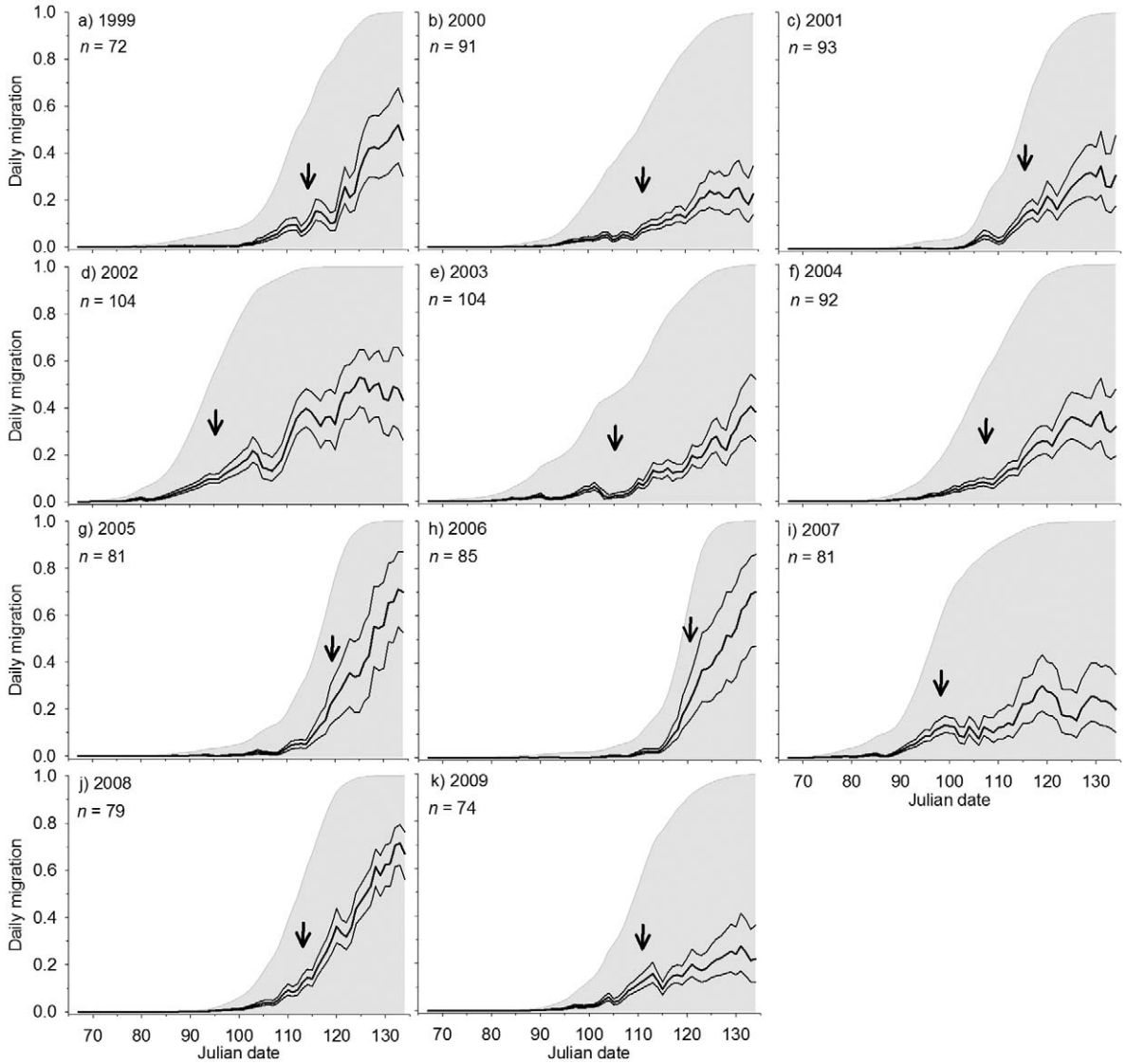

Fig. 7. Model-averaged estimates of the daily probability of migration (heavy line ±95% CI) and cumulative proportion migrated (shaded region) during spring for adult (>1 year old) female mule deer relative to Julian date, Sierra Nevada, California, USA, 1999–2009. Black arrows indicate mean date of migration.

departure from winter range by mule deer in spring was coincident with decreased snow depth (PC1) and increasing plant growth (NDVI and ΔNDVI), which was identical to the first stage of modeling that included only extrinsic factors. We did not detect significant effects of individual life-history characteristics on the daily probability of migration in spring (Table 4). Based on importance weights, summer residency, nutritional condition, and fetal rate were of negligible value in explaining patterns of spring migration. Likewise, mean date of departure from winter range was nearly identical for east-side and west-side females (Fig. 9a). Although the importance weight for age was >0.7, the model-average parameter estimate overlapped zero (Table 4).

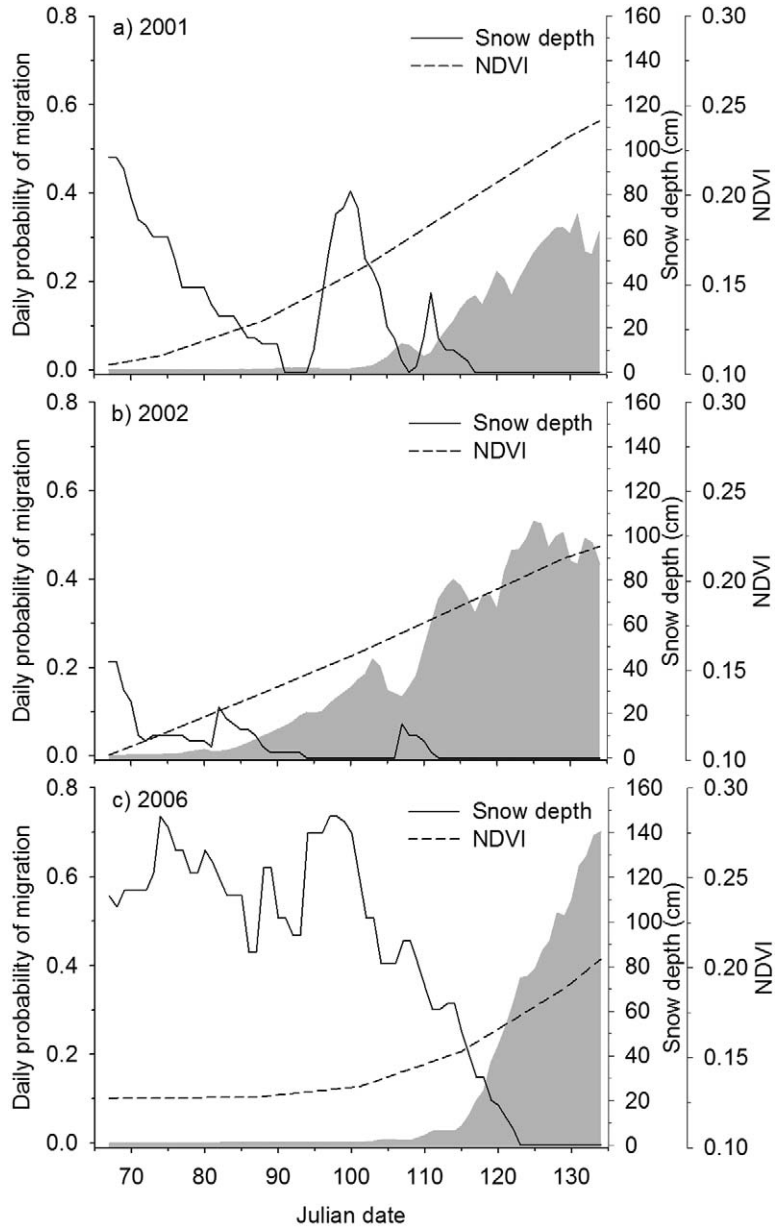

Fig. 8. Model-averaged estimates of the daily probability (shaded region) of spring migration for adult (>1 year old) female mule deer, daily snow depth (cm), and daily normalized difference vegetation index (NDVI) relative to Julian date, Sierra Nevada, California, USA, during 3 years exhibiting different patterns of snow melt and plant phenology: 2000 (a), 2002 (b), and 2006 (c).

Discussion

Long-term studies across a range of environmental conditions may be the key to understanding large-scale effects of climate on the phenological events of animals (Fieberg et al. 2008), a daunting task, especially for large, vagile mammals (McCullough 1979, Pierce et al. 2000, Stewart et al. 2005). Long-term and intensive study of a population of mule deer in the Sierra Nevada, California, USA, allowed us to monitor patterns of migration during years that encom-

Table 3. Model-averaged parameter estimates, 95% confidence intervals (95% CI), and Akaike importance weights for interval-censored models describing the relationship of the daily probability of autumn migration of mule deer with six extrinsic variables (variables that differed from zero in first stage of modeling), and four individual-based covariates with a quadratic term for age, Sierra Nevada, California, USA, 2002–2008. Asterisks adjacent to parameter estimates indicate 95% CI do not overlap zero.

	Autumn			
		95% CI		
Parameter	Estimate	Lower	Upper	Importance weight
PC1	0.87*	0.40	1.35	0.97
PC3	−0.99*	−1.39	−0.59	1.00
PC4	0.10	−0.24	0.04	0.64
PC5	−0.75*	−1.03	−0.47	1.00
T	0.20*	0.13	0.26	1.00
TT	-1×10^{-3}*	2×10^{-3}	-8×10^{-4}	1.00
Year	n/a	n/a	n/a	0.35
Age	−0.07*	−0.13	−0.01	0.98
Age^2	1×10^{-4}	-2×10^{-3}	2×10^{-3}	0.22
Summer Residency	0.66*	0.36	0.95	1.00
IFBFat	−0.04*	−0.06	−0.01	0.94
Recruitment	3×10^{-3}	-5×10^{-3}	0.01	0.03

Notes: Extrinsic factors in interval-censored models for autumn migration with individual covariates included: daily snow depth (PC1), daily temperature (PC3), daily snowfall and precipitation (PC4), daily metric of change in temperature (PC5), quadratic time trend (T and TT), and year (Year). Year was included as a nuisance parameter in models, however the parameter estimates for each year are not biologically meaningful and were thus, not included. Individual covariates included: age in years (Age), side of Sierra crest occupied during summer (summer residency), nutritional condition in November measured as ingesta-free body fat (IFBFat), and the presence or absence of young-at-heel in autumn (Recruitment).

passed a wide array of severity in patterns of weather, and consequently, plant phenology. This dataset allowed us to disentangle the influence of a suite of climatic and life-history variables thought to be responsible for migratory behavior (Table 5). These hypotheses included effects of broad-scale climate, weather patterns, plant phenology, and the effects of life-history characteristics on migration of individual deer (Table 5).

In support of our hypotheses, patterns of local weather and plant phenology were related to the timing of seasonal migration in mule deer, with some detectable effects of large-scale climate (Table 5). Although annual mean date of autumn migration was not statistically different among years, the phenological patterns of autumn migration among individuals varied markedly and were driven by the severity of arriving winter weather. In contrast, mean date of spring migration differed among years and was related to the southern oscillation index (SOI), and onset of spring green-up. Within years, phenological patterns of spring migration were more synchronous than autumn migration, and were clearly associated with snow melt and plant phenology. We also hypothesized, however, that life-history characteristics of individual females would influence their patterns of seasonal migration (Table 5). In accordance with that hypothesis, patterns of autumn migration were affected by location of summer residency, age, and nutritional condition of individual females. Females that summered on the east side of the Sierra crest tended to arrive at Round Valley earlier than females that summered on the west side (Table 5). In addition, older females and those in good nutritional condition remained on summer ranges longer in autumn compared with young females and those in poor nutritional condition (Table 5). During spring migration, however, life-history characteristics of individual females had little influence on timing of migration, which was closely linked to snow depth and plant phenology (Table 5).

The acquisition of continuous data on timing of migration or other life-history events under field conditions is challenging and sometimes impossible to achieve (Garrott et al. 1987, Johnson et al. 2004, Pulido 2007, Fieberg et al. 2008, Meunier et al. 2008), unless animal location data are obtained from collars with global positioning system technology (White et al. 2010). Because of logistical constraints, we were unable to monitor presence or absence of mule

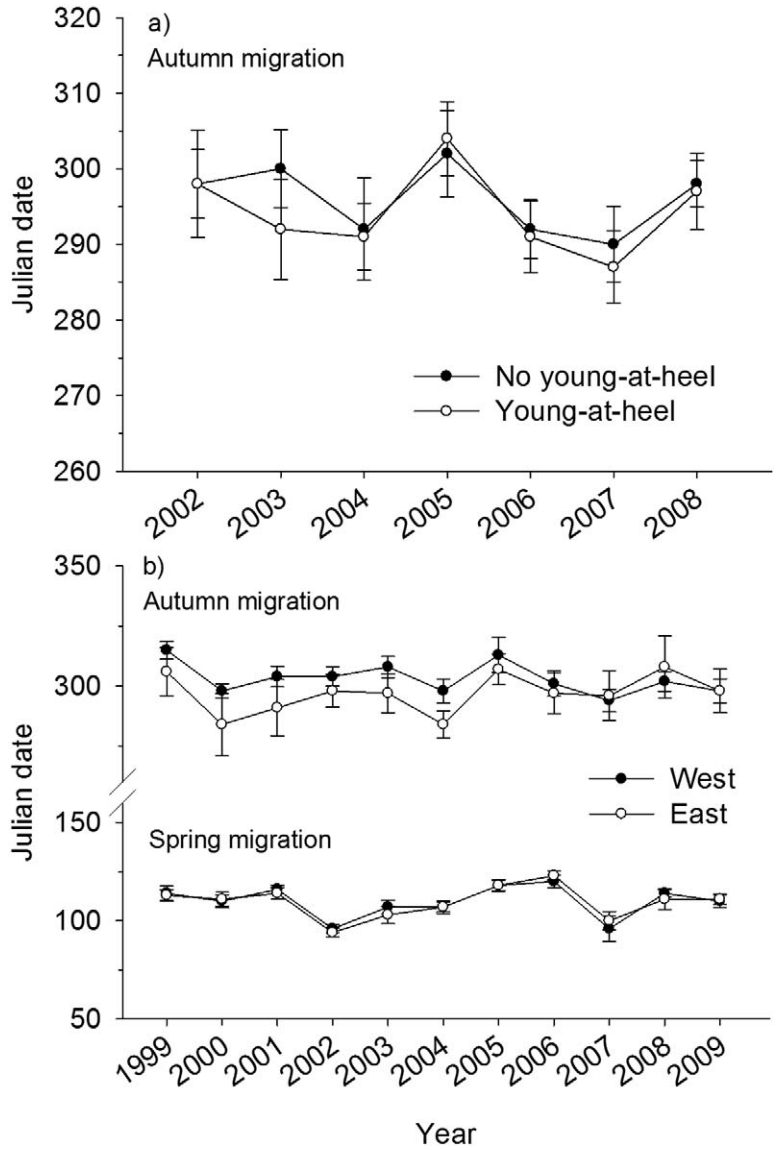

Fig. 9. Mean Julian date (±95% CI) of autumn migration of mule deer (a) relative to reproductive status, 2002–2008; and (b) mean Julian date (±95% CI) of spring and autumn migration relative to the location of summer residency (east or west of the crest of the Sierra Nevada), 1999–2009 for mule deer occupying winter range in Round Valley in the eastern Sierra Nevada, California, USA.

deer on winter range on a daily basis or at regularly spaced intervals (bins). The usual technique for coping with the absence of known dates of life-history events has been to assign the event date to the median date within the interval the event was known to occur (Nelson 1995, Sabine et al. 2002, Meunier et al. 2008). That procedure, however, often underestimates variance, may affect the estimates of regression parameters, and thus, bias their interpretation (Johnson et al. 2004, Fieberg and DelGiudice 2008). We used a procedure for estimating the timing of life-history events developed by Johnson et al. (2004), which is unbiased and allows for unequal time intervals (bins) in sampling, thereby providing a valid comparison of the mean dates and synchrony among years or groups of animals.

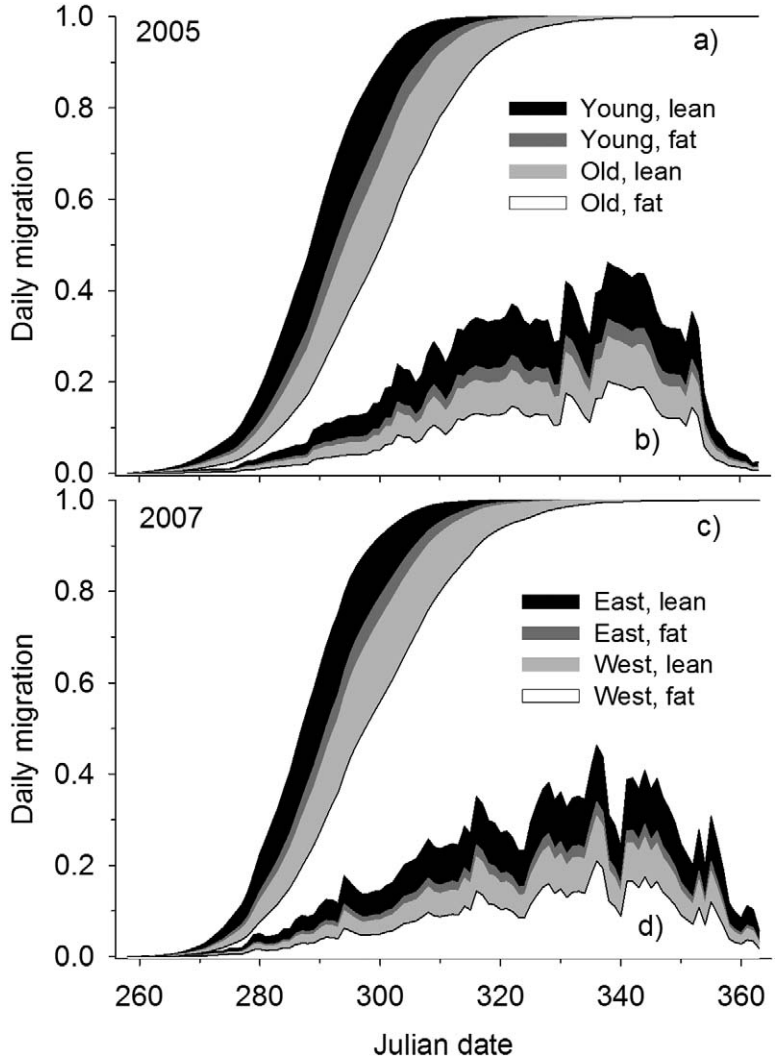

Fig. 10. Model-averaged estimates of the cumulative proportion migrated (a,c) and daily probability of migration (b,d) during autumn for adult (>1 year old) female mule deer illustrating the effects of age (young = 2.4 years old, old = 12.4 years old) and nutritional condition (lean = 4% IFBFat, fat = 18% IFBFat) during 2005 (a, b), as well as the effects of summer residency (east or west of the crest of the Sierra Nevada) and nutritional condition during 2007 (c, d), Sierra Nevada, California, USA.

Despite the marked variability in the timing of migration among individuals within a single population (Brinkman et al. 2005, Fieberg et al. 2008, Grovenburg et al. 2009), seasonal migration often is interpreted at the population level by using point estimates or thresholds in relation to summarized weather patterns. Consequently, the distribution of migratory events among individuals within a season has received little attention until recently (e.g., Meunier et al. 2008, Fieberg et al. 2008). Failure to incorporate the broad range of heterogeneity in timing of migration among individuals likely has hampered our understanding of the factors that affect the phenological patterns of migration of large herbivores. Indeed, analyses at the level of the population fail to ascertain the various migratory strategies among individuals or to identify the selective pressures operating on individuals (Williams 1966, Dingle 2006). To overcome the limitations of analyses at

Table 4. Model-averaged parameter estimates, 95% confidence intervals (95% CI), and Akaike importance weights for interval-censored models describing the relationship of the daily probability of spring migration of mule deer with five extrinsic variables (variables that differed from zero in first stage of modeling), and four individual-based covariates with a quadratic term for age, Sierra Nevada, California, USA, 1999–2009. Asterisks adjacent to parameter estimates indicate 95% CI do not overlap zero.

	Spring			
		95% CI		
Parameter	Estimate	Lower	Upper	Importance weight
PC1	−0.97*	−1.29	−0.64	1.00
NDVI	61.37*	61.23	61.50	1.00
ΔNDVI	99.57*	28.18	170.97	0.95
T	0.11*	0.06	0.16	1.00
TT	-1×10^{-3}*	-2×10^{-3}	-1×10^{-3}	1.00
Year	n/a	n/a	n/a	1.00
Age	−0.02	−0.07	0.03	0.76
Age^2	-4×10^{-4}	-2×10^{-3}	1×10^{-3}	0.15
Summer residency	0.01	−0.02	0.03	0.08
IFBFat	2×10^{-3}	−0.01	0.02	0.34
Fetalrate	-2×10^{-3}	−0.04	0.04	0.23

Notes: Extrinsic factors in interval-censored models for spring migration with individual covariates included: daily snow depth (PC1), daily normalized difference vegetation index (NDVI), daily change in NDVI relative to previous 14 days (ΔNDVI), quadratic time trend (T and TT), and year (Year). Year was included as a grouping variable in models, however the parameter estimates for each year are not biologically meaningful and were thus, not included. Individual covariates included: age in years (Age), side of Sierra crest occupied during summer (summer residency), nutritional condition in March measured as ingesta-free body fat (IFBFat), and fetal rate in March (Fetalrate).

Table 5. Hypotheses and general predictions tested regarding timing of migration for mule deer in the Sierra Nevada, California, USA, during autumn and spring, and the relative support (Yes or No) and direction of the relationship (+ or −) where relevant, 1999–2009.

Hypotheses	Predictions	Autumn	Spring
Broad-scale climate	SOI	No	Yes (+)
Weather patterns	Snow depth	Yes (+)	Yes (−)
	Snowfall	Yes (+)	No
	Temperature	Yes (−)	No
Plant phenology	Degree days	No	No
	NDVI	No	Yes (+)
	Onset of season	No	No
Life-history characteristics	Age	Yes (−)	No
	Nutritional condition	Yes (−)	No
	Summer residency	Yes	No
	Recruitment - Fetalrate	No	No

Notes: Abbreviations are: southern oscillation index (SOI), and normalized difference vegetation index (NDVI). Degree days represent the cumulative degree days above or below 5°C for spring (growing-degree days) and autumn (senescent-degree days), respectively.

the population level, we employed interval-censored, time-to-event models in program MARK, which incorporated the distribution of migratory events to assess their relationship to annual metrics of climate and plant phenology, time-specific covariates of local weather patterns and plant phenology, and allowed the integration of covariates specific to each individual monitored (sensu Dinsmore et al. 2002). Although there are potential weaknesses in using interval-censored models in program MARK, which include the absence of goodness-of-fit testing and the inability to account for repeated sampling of individuals between years, the congruence between migration models and direct hypothesis testing (Johnson et al. 2004) support the legitimacy of this approach.

Autumn migration

The initiation and daily probability of migra-

tion for mule deer during autumn was affected by changes in the severity of winter weather, namely increasing snow depth with coincident cooling temperatures (Fig. 6). Increased snow depth with concurrent reduction in ambient temperature results in a concomitant increase in the energetic costs associated with thermoregulation and locomotion in cervids (Telfer and Kelsall 1979, Parker et al. 1984). Furthermore, depth of snow experienced by large herbivores has direct effects on availability of forage (Fancy and White 1985), thereby affecting nutritional condition and probability of winter survival (Garroway and Broders 2005). During most years, however, a large proportion ($\geq$43%) of our marked animals already had migrated to winter range prior to the onset of severe winter weather (i.e., occurrence of snow with average temperatures below freezing) when daily probability of migration was highest (Fig. 5). Likewise, white-tailed deer commonly migrate in response to, and prior to, the accumulation of substantial snow (Nelson 1995, Sabine et al. 2002, Brinkman et al. 2005, Grovenburg et al. 2009).

By delaying autumn migration, deer risk being "trapped" on summer range by sudden winter storms that would increase nutritional, thermoregulatory, and locomotive costs (Parker et al. 1984), and may increase susceptibility to predation or other sources of mortality (Berger 1986, Patterson and Messier 2000, Bleich and Pierce 2001). Nevertheless, individuals that delay autumn migration, but successfully arrive on winter range, may benefit from a greater abundance, diversity, and higher-quality forage on summer range (Albon and Langvatn 1992, Mysterud et al. 2001). Forage quality in our study, as indicated by NDVI, remained significantly higher on summer range throughout autumn (Fig. 3), which supports the energetic advantage of mule deer remaining on summer ranges as long as possible. Even slight changes in diet quality through time can have multiplicative effects on the net energy available for somatic investment, growth, and reproduction (White 1983, Parker et al. 2009).

Spring migration

Mean date of departure from winter range by mule deer in the eastern Sierra Nevada differed over 11 years in response to the duration of snow cover and the timing of plant green-up. We documented strong association between daily snow depth and the probability of spring migration by mule deer. The parameter estimate for the relationship between change in snow depth (PC2) and daily migration for mule deer, however, was not significant, which indicated that the absolute depth of snow was more important in affecting long-distance movement by mule deer than was the rate of snow accumulation or disappearance (Table 2). Likewise, delayed spring migration following winters with heavy snow pack, and early migration in years with low snow pack and early vegetation green-up is common among large herbivores (Garrott et al. 1987, Nelson 1995, Brinkman et al. 2005, Grovenburg et al. 2009, White et al. 2010). The effect of snow pack on large herbivores can severely restrict mobility and exhaust energy reserves (Parker et al. 1984). During all years except 2003, when a late snowstorm occurred in mid-April, mean date of spring migration occurred when snow depth on the spring holding area was $\leq$12 cm. That snow depth is well below the point at which energy costs of locomotion for mule deer increase significantly (25 cm), regardless of the density of snow (Parker et al. 1984).

Migration to higher elevation during spring may allow the selection of the same plant at an earlier phenological stage (Klein 1965, Morgantini and Hudson 1989), when protein and digestibility are highest (Van Soest 1994, Barboza et al. 2009, Parker et al. 2009). Timing of altitudinal migration of red deer and North American elk (*Cervus elaphus*) coincided with the phenological delay in emergent vegetation at higher elevation (Morgantini and Hudson 1989, Boyce 1991, Albon and Langvatn 1992). Multiple altitudinal movements by golden takin (*Budorcas taxicolor*) in China were determined by the corresponding fluctuations in plant phenology and solar radiation (Zeng et al. 2010). Likewise, female mule deer departed winter range as NDVI began to increase and, thereafter, the daily probability of migration increased in response to both the absolute and daily change in NDVI (Table 2; Fig. 8).

Spring migration for female mule deer was nearly twice as synchronous as autumn migration (Fig. 4). Nutritional demands of pregnant females increase throughout gestation, with most

fetal growth (>90%) occurring during the last one-third of gestation (Moen 1978, Robbins and Robbins 1979, Pekins et al. 1998). Inadequate nutrition during gestation may result in fetal loss (Verme 1965), low birth weight and reduced probability of survival of young (Keech et al. 2000, Lomas and Bender 2007), and life-long consequences on the physical characteristics and quality of the individual (Hamel et al. 2009, Monteith et al. 2009). Extended duration of confinement on a traditional winter range can lead to depletion of available browse resulting in increased competition for limited forage (Nicholson et al. 2006). Mule deer wintering in Round Valley exhibited progressive shifts in diet from their main winter forage (*Purshia tridentata*) to forage of low nutritional value (*Artemesia tridentata*) as winter progressed and as population density increased (Kucera 1997, Pierce et al. 2004). Therefore, departure from winter range as soon as snow cover and foraging conditions allow was probably advantageous for mule deer in Round Valley.

Effects of life-history characteristics

The general stimulus for autumn migration is thought to be severe winter weather (Kucera 1992, Sabine et al. 2002, Brinkman et al. 2005, Grovenburg et al. 2009). The great variation among individuals within a single population, however, cannot be explained by this factor alone, especially because weather patterns generally are consistent across local areas. We tested the hypothesis that life-history characteristics of individuals would affect the timing of seasonal migration by incorporating individual-based covariates into interval-censored models. Although individual life-history characteristics were not related to timing of spring migration, location of summer residency, age, and nutritional condition were strongly related to the timing of autumn migration by female mule deer (Table 3).

Females that summered on the east-side of the Sierra crest generally arrived on winter range earlier than west-side females (Fig. 10b). Females inhabiting the west side occupied vast expanses of the Sierra Nevada, and migrated farther than females that occupied the more arid landscape on the east side of the Sierra crest (Kucera 1992). We do not believe greater distances migrated by females from the west side of the Sierra crest were responsible for their delayed arrival on winter range. Although autumn migration is typically rapid with little delay following severe weather (Kucera 1992), females summering on the west side of the Sierra crest may take advantage of comparatively milder conditions after crossing the crest for foraging and resting before proceeding to winter range (Sawyer et al. 2009). Likewise, Mysterud (1999) and White et al. (2010) reported little correlation between the timing of autumn migration and distance migrated in roe deer (*Capreolus capreolus*) and North American elk, respectively. The absence of a relationship between location of summer residency and the phenology of spring migration (Table 4) implies that individuals respond to their local environment. The population of mule deer occupied similar habitat within 90 km^2 in Round Valley during winter, whereas habitats and environmental conditions on summer range, which encompassed >2,800 km^2, differed markedly on either side of the Sierra crest (Bleich et al. 2006). We postulate that behavioral responses of individuals are implemented at fine-scales in the local environment they occupy; this pattern, in conjunction with individual life-history characteristics, holds the greatest potential to influence the timing of seasonal migration.

Understanding age-specific patterns in life-history traits remains a central issue in the ecology of iteroparous organisms (Stearns 1992, Nussey et al. 2008). The terminal-investment hypothesis predicts that mothers should exhibit increased investment in reproduction as they age in relation to their residual reproductive value (Clutton-Brock 1984, Bercovitch et al. 2009). Old female (sensu Gaillard et al. 2000) mule deer in the Sierra Nevada risked encountering severe weather by delaying autumn migration (Fig. 10), and were thus risk-prone (Stephens and Krebs 1986) with respect to the potential loss of foraging opportunities as a result of deep snow. Consequently, old females occupied summer range longer, which provided increased diversity and higher quality forage (Fig. 3), along with less intraspecific competition, when compared with the limited forage and high-density of animals on winter range (Morgantini and Hudson 1989, Albon and Langvatn 1992, Kucera 1992, Pierce et al. 2004). Conversely, young females were risk-

averse (sensu Stephens and Krebs 1986) and tended to arrive on winter range earlier in autumn (Fig. 10), ostensibly trading off risk of early winter storms on summer range against obtaining lower-quality, but predictable forage on winter range. Indeed, those age-specific patterns of migration support the terminal-investment hypothesis (Clutton-Brock 1984, Stearns 1992), where old females attempt to maximize nutritional gain in support of reproduction, in spite of increased risk of mortality.

The linear relationship between age and timing of autumn migration (Table 3), however, also supports an experiential explanation. Increased experience with age often is associated with enhanced reproductive performance in large herbivores (Cameron et al. 2000, Gaillard et al. 2000, Weladji et al. 2006; 2010), as well as the potential for improved knowledge of spatial and temporal patterns in the distribution and availability of forage (Mirza and Provenza 1992, Ortegareyes and Provenza 1993). Additional experience with weather patterns in autumn and distribution of forage may have allowed older females to enhance nutritional gain by delaying autumn migration (White 1983) without a detriment to survival, because older females may have better knowledge of the true risk associated with delayed migration. Although we failed to document mortality that was related to delaying autumn migration over 11 years (based on monitoring of collared individuals), late autumn migration can have fatal consequences (Berger 1986, Bleich and Pierce 2001). Despite the impending risk of mortality, older females delayed autumn migration, which could be explained by a combination of a more comprehensive knowledge of true risk, and differential strategies relative to residual reproductive value.

Body fat is the primary energy reserve of the body and is related to multiple demographic factors of large herbivores including timing of breeding (Cook et al. 2004), pregnancy and twinning rate (Keech et al. 2000, Stewart et al. 2005), gestation length (Garcia et al. 2006), birth mass (Keech et al. 2000, Lomas and Bender 2007), and survival (Cook et al. 2004, Bender et al. 2007). Although demographic factors may be directly affected by animal nutrition, we documented that behavioral decisions regarding when to migrate during autumn also had nutritional underpinnings for mule deer. Female mule deer that were nutritionally stressed (sensu Cook et al. 2007) exhibited risk-averse behavior by migrating to winter range early (Fig. 10), where forage resources were likely less palatable and diverse, but more predictable. In contrast, migratory patterns for birds reveal delayed migration for individuals in poor physical condition (Mitrus 2007, Pulido 2007). Energy expenditure and catabolism of somatic reserves associated with thermoregulation and locomotion in large herbivores, however, increases with reduced temperature, rising snow depth, and with the decline in availability and quality of forage (Mautz 1978). In response to those conditions, individuals use various physiological, morphological, and behavioral adaptations to conserve energy and promote survival (Moen 1976, Mautz 1978).

Parker et al. (2009) proposed that behavioral strategies for large herbivores are based on lessening the primary detriment to fitness and that the basis of the strategies is nutritional. Mule deer in the Sierra Nevada may be capable of sequestering better forage resources on summer range in autumn by delaying migration to winter range; however, the primary detriment to adult females in poor nutritional condition may be mortality if they encounter deep snow that increases energetic costs and nutritional loss. We hypothesize that the lower energetic buffer against the potential loss of forage and energetic costs of locomotion in deep snow were responsible for the negative relationship between the daily probability of autumn migration and nutritional condition in mule deer (Table 3; Fig. 10). Similarly, bison (*Bison bison*) arrived earlier to low-elevation winter range as population density increased in Yellowstone National Park, USA, likely in response to negative effects of density dependence on nutritional condition (Plumb et al. 2009).

For spring migration, Garrott et al. (1987) hypothesized that deer must improve their physiological condition prior to incurring the energetic costs associated with migration, which aligns with predictions based on the somatic control of avian migration (Mitrus 2007, Pulido 2007). Contrary to that hypothesis, we observed no relation between date of departure from

winter range and nutritional condition, and documented the opposite pattern in autumn. Indeed, no life-history characteristic that we measured was strongly associated with the timing of spring migration (Table 4). Likewise, White et al. (2010) reported little support for effects of age or pregnancy status on timing of spring migration in North American elk. Winter foraging conditions for most large herbivores act as an equalizer by lowering the level and variability of nutritional condition of all deer by spring (Mautz 1978, Barboza et al. 2009, Parker et al. 2009), which likely reduces individual variability in timing of migration and lessens the flexibility in advantageous strategies between individuals during spring migration. Our results indicate that spring migration likely is caused by a direct response to seasonal stimuli of receding snow and new plant growth, and is equally advantageous for female mule deer regardless of age, destination (summer residency), fetal rate, or nutritional condition.

Climate

Phenological traits of both plants and animals are sensitive to climatic processes, with several characteristics advancing in chronology in response to climate change. For example, avian migration is related to plant and invertebrate phenology, with earlier spring migrations corresponding to earlier arrival of spring (Forchhammer et al. 2002, Sparks et al. 2005, Jonzén et al. 2006, Carey 2009). Indeed, the ability of species to advance or recess their timing of migration may have a direct effect on their ability to persist in the face of a changing climate (Walther et al. 2002, Møller et al. 2008, Carey 2009). Mule deer in our study adjusted their timing of seasonal migration to correspond with climatic conditions and plant phenology (Fig. 6, Fig. 8), which may enhance fitness when climate change alters seasonal dynamics of forage quality and availability, so long as that change is not too severe.

In some instances, timing of parturition by large herbivores may respond rapidly to effects of climatic warming on plant phenology (Rachlow and Bowyer 1991, Loe et al. 2005). Timing of migration and parturition by caribou in West Greenland, however, has failed to keep pace with the advancement of the plant-growing season; consequently, recruitment of young has declined fourfold during a single decade (Post and Forchhammer 2008). Plasticity in timing of migration may allow large herbivores to partially compensate for trophic mismatches between seasonal peaks in resource availability and peak energetic demands for reproduction, when phenological patterns of reproduction are less plastic (Post and Forchammer 2008). Plasticity in migration may be an adaptive trait (Gotthard and Nylin 1995), because it likely holds fitness consequences in a changing climate. For example, Møller et al. (2008) reported that populations of migratory birds that failed to exhibit a phenological response to climate change were declining. Species that coordinate life-history phenomena with patterns that remain unaffected by climate change, such as photoperiod, are more likely to encounter trophic mismatches because they fail to synchronize with food supplies that are affected by climate (Carey 2009). Our data indicate, however, that large herbivores may be capable of buffering negative effects of shifts in climate, because patterns of migration are flexible and individuals are responsive to environmental conditions.

Despite clear relationships between the phenological patterns of migration and local weather, timing of autumn migration by mule deer in the Sierra Nevada was influenced by life-history characteristics. Failure to consider effects of nutrition and other life-history traits on phenological patterns of mammals may confound relationships associated with outcomes expected from climate change. For example, progressive changes in nutritional condition or age within a particular population, as a result of density-dependent feedbacks (McCullough 1979, Kie et al. 2003), may yield directional shifts in the timing of migration, even in the absence of a shift in climate (e.g., Plumb et al. 2009). Even in a stochastic environment, fluctuations in population size with bottom-up underpinnings yield dramatic fluctuations in nutritional condition and age structure (Kie et al. 2003, Bowyer et al. 2005), both of which influenced phenological patterns of autumn migration for mule deer (Table 5, Fig. 10). Consequently, climatic change may affect phenological patterns of migration directly, through seasonal weather patterns (Table 1), and indirectly when climatic effects on migration are mediated through life-history

characteristics (Fig. 10).

Recently, Barnett et al. (2008) provided evidence of anthropogenic effects on the changes in snow pack and the hydrological regime in the western United States. Between 1950 and 1999, precipitation in montane regions in the western US exhibited a general shift from snow to rain (Knowles et al. 2005), declining snow pack (Hamlet et al. 2005), and snowmelt occurred progressively earlier (Hamlet et al. 2005, Mote et al. 2005). If the occurrence of heavy snowfall wanes with the changing climatic regime, risk of delaying departure from summer range lessens and the nutritional benefits of remaining on summer range increase. Hence, individuals that exhibit risk-prone behavior by delaying departure from summer range will sequester more and higher-quality resources, likely yielding greater fitness than individuals arriving on winter range early. As a result, differences in nutritional condition among individuals within a population may inherently determine the direction of selection with respect to migratory strategies. Likewise, the relation between nutritional condition and the timing of migration, as well as the fitness consequences of that timing, are well documented in birds (Newton 2006, Pulido 2007). Although delayed arrival to and early departure from winter range could bear the cost of encountering inclement weather conditions, individuals employing such tactics may benefit from greater abundance and diversity of food (Albon and Langvatn 1992), yielding higher fitness in the face of a warming climate. Partial migration is common in some populations of large herbivores and, if a warming climate does not compel migration to winter range, we hypothesize that differential selection among individuals employing such strategies will favor the evolution and maintenance of partial migration with permanent residents on summer range (Kaitala et al. 1993).

Phenological relationships for autumn migration also are less conclusive in other taxa compared with spring migration (Walther et al. 2002, Adamik and Pietruszkova 2008, Carey 2009), perhaps because patterns of autumn migration are confounded by life-history characteristics. Thus, we recommend obtaining long-term data on the timing of spring migration to assess the effects of climate change on those phenological patterns because patterns of spring migration may be less confounded by individual life-history characteristics and provide more definitive patterns with respect to climate change. Furthermore, effects of nutritional condition on the timing of migration and how that timing, in turn, influences nutrition and selective pressures among various strategies, requires further investigation across other species of large herbivores.

Conclusions

The persistent movement of thousands of animals across large spatial scales on a seasonal basis is among the most spectacular and well-recognized phenomena of the natural world. Nevertheless, long-distance migrations are being altered by burgeoning human populations and ensuing disturbance and barriers to movement, including habitat loss (Berger 2004, Bolger et al. 2008). In addition, phenological patterns of seasonal migration are likely to be affected by climate change (Walther et al. 2002, Stenseth et al. 2003, Bolger et al. 2008). The need for effective conservation of animal migration warrants a more complete understanding of the biology of this complex behavior (Bolger et al. 2008, Wilcove 2008). We employed an extension of an analytical approach used for survival analyses (Dinsmore et al. 2002, Fieberg and DelGiudice 2008) to consider the distribution of migratory events among individuals and assess the effects of life-history characteristics on timing of migration, which has heretofore received little attention. This methodology should be useful for assessing questions related to timing in most migratory species. We documented that autumn migration of mule deer in the Sierra Nevada was highly variable and associated with patterns of winter weather (cold and snow), whereas spring migration was coincident with decreasing snow depth and advances in plant phenology (Table 5). Although we did not observe directional changes in chronology of spring or autumn migration during our 11-year study, the association between seasonal migration and environmental conditions provides convincing evidence that those migratory patterns may be altered by global climate change. Nevertheless, the close association of the phenology of seasonal migration with environmental conditions may reduce

the potential for migratory patterns to be mismatched (sensu Post and Forschhammer 2008) with food availability as climate change alters seasonal patterns of plant growth.

The response of individual mule deer to environmental conditions during autumn was influenced by their life-history characteristics, which may conceal expected relationships with climate change. The risk-prone strategy of delaying autumn migration, which was exhibited by older females, lends support to both the terminal-investment hypothesis, and an experiential explanation (Fig. 10a), and the effects of summer residency on autumn migration indicate that individuals respond to fine-scale patterns of weather within their local environment (Fig. 10b). We demonstrated that unlike birds, mule deer did not accumulate a threshold of fat reserves prior to initiating migration during either season, but in contrast, delayed autumn migration when fat reserves were abundant (Table 3), and yet were unaffected by fat reserves in spring (Table 4). Clearly, our results illustrate the potential problems with extending models developed for avian taxa to large herbivorous mammals (sensu Ralls 1977). Nutritional underpinnings of the timing of autumn migration for mule deer support the hypothesis that behavioral decisions by large herbivores are based on lessening the primary detriment to fitness (Parker et al. 2009), and that those decisions may be underpinned by current nutritional state. We emphasize the importance of considering the influence of individual life-history characteristics on behavior of large herbivores and the underlying effects of nutrition on their life-history strategies. For large herbivores, failure to consider the effects of life-history characteristics when attempting to elucidate relationships between phenological patterns of life-history events and climate may, at best, lead to equivocal relationships or, at worst, be entirely misleading.

Acknowledgments

We thank fixed-wing pilots R. Anthes, T. Evans, and G. Schales of California Department of Fish and Game (CDFG), and G. Pope (Black Mountain Air Service), and R. Nixon for their dedication and interest in this project. Landells Aviation was largely responsible for the helicopter capture and survey work, especially, S. deJesus, and C. Pickrell, who worked closely with CDFG capture specialists R. Teagle and T. Glenner to ensure safe and efficient handling of hundreds of mule deer. We are also privileged to have worked with numerous dedicated field assistants including, P. McGrath, J. Augustine, D. Spitz, A. Howell, T. Swearingen, W. Allsup, A. Stephenson, M. Kiner, T. Branston, C. Schroeder, H. Johnson, M. Leonard-Cahn, K. Monteith, R. Long, S. Monteith, and especially P. Partridge who committed much of his own time and resources to maintain deer monitoring. We are indebted to volunteers C. Baker, R. Noles, N. Partridge, and D. deJesus for their selfless dedication to mule deer research in Round Valley. We thank D. German, L. Konde, and K. Knox, for their assistance with the Round Valley deer project. Support for capture work was provided by numerous individuals including, J. Villepique, J. McKeever, T. Taylor, B. Clark, and B. Adams. Additional capture support was provided by personnel from the CDFG Wildlife Investigations Lab including S. Torres, K. Jones, A. Hunter, B. Gonzales, P. Swift, J. Schultz, and H. Zurawka. We also are thankful to other CDFG employees and other volunteers who aided in the completion of this long-term research project. The bulk of the funding and logistical support for this long-term investigation was provided by the CDFG Deer Herd Management Plan Implementation Program through the efforts of E. Loft, S. Mastrup, K. Mayer, R. Mohr, and C. Stowers; additional funding was provided by the California Deer Association, Mule Deer Foundation, Granite Bay Chapter of Safari Club International, and Idaho State University. We dedicate this paper to the memory of our friends and colleagues Clu Cotter, Mike Donovan, Kevin O'Connor, and Tom Stolberg who died in a tragic helicopter accident while conducting an aerial survey on summer range used by mule deer from Round Valley. This is a contribution from the CDFG Deer Herd Management Plan Implementation Program, and is Professional Paper 084 from the Eastern Sierra Center for Applied Population Ecology. We thank R. Long, E. Andersen, M. Kauffman, J. Jenks, A. Mysterud, and an anonymous reviewer for their comments that improved previous versions of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States Government.

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Appendix

Table A1. Summary statistics for daily temperature, daily snow depth during winter (November–March), total annual snowfall and precipitation for Mammoth Lakes, California, USA, and annual mean of the southern oscillation index (SOI), 1999–2009.

Weather variable	Mean	SD	Range
Maximum temperature (°C)	13.6	9.2	−13.3–32.8
Average temperature (°C)	5.9	8.0	−20.0–23.3
Minimum temperature (°C)	−1.7	7.3	−26.7–16.7
Snow depth (cm)	39.4	39.1	0–167.6
Annual snowfall (cm)	469.4	163.1	152.4–714.2
Annual precipitation (cm)	49.5	14.9	13.6–66.5
SOI	0.08	0.6	−0.7–1.0

Table A2. Loadings for principle components (1–5) for daily weather variables included in principle components analysis. Weather variables are daily measurements and daily change (Δ) in weather relative to the mean for the previous 2 weeks, Mammoth Lakes, California, USA, 1999–2009.

	Principle component				
Weather variable	1	2	3	4	5
Maximum temperature (°C)	−0.180	−0.021	0.568	−0.083	0.183
Average temperature (°C)	−0.155	0.001	0.518	−0.004	0.198
Minimum temperature (°C)	−0.129	0.024	0.468	0.076	0.212
Snowfall (cm)	0.071	0.191	0.008	0.623	−0.007
Snow depth (cm)	0.945	−0.188	0.242	−0.012	0.110
Precipitation (cm)	0.005	0.015	0.000	0.051	0.000
ΔMaximum temperature (°C)	−0.013	−0.144	0.222	−0.012	−0.612
ΔAverage temperature (°C)	−0.011	−0.110	0.196	0.072	−0.520
ΔMinimum temperature (°C)	−0.010	−0.076	0.170	0.157	−0.429
ΔSnowfall (cm)	0.012	0.193	0.007	0.702	0.076
ΔSnow depth (cm)	0.171	0.922	0.119	−0.265	−0.187
ΔPrecipitation (cm)	0.005	0.015	0.001	0.058	0.007