How plastic is migratory behavior? Quantifying elevational movement in a partially-migratory alpine ungulate

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How plastic is migratory behavior? Quantifying elevational movement in a partially-migratory alpine ungulate

D. B. Spitz, M. Hebblewhite, T. R. Stephenson, David W. German

(Corresponding Author): spitzderek@gmail.com

Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA

Mark.Hebblewhite@umontana.edu

Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA

Tom.Stephenson@wildlife.ca.gov

Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Wildlife, 787 North Main St., Suite 220, Bishop, California 93514 USA

David.German@wildlife.ca.gov

Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Wildlife, 787 North Main St., Suite 220, Bishop, California 93514 USA

Current affiliation and address:
Oregon State University Department of Fisheries and Wildlife,
U.S. Forest Service Pacific Northwest Research Station
1401 Gekeler Lane, La Grande, OR 97850

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Migratory species face well-documented global declines, but the causes of these declines remain unclear. One obstacle to better understanding these declines is uncertainty surrounding how migratory behavior is maintained. Most migratory populations are partially migratory, displaying both migrant and resident behavior. Theory only provides two possible explanations for this coexistence of migration and residency: either these behaviors are fixed at the individual level or both behaviors are part of a single conditional strategy in which an individual’s migratory status (adoption of migrant or resident behavior) is plastic. Here we test for plasticity in migratory status and tactics (timing, distance, and duration of migration) in a federally-endangered mountain caprid, Sierra Nevada bighorn sheep (Ovis canadensis sierrae Shaw, 1804). We used non-linear modeling to quantitatively describe migratory behavior, analyzing 262 animal-years of GPS location data collected 2005 – 2016 from 161 females across 14 subpopulations. Migratory tactics and prevalence varied by subpopulation. On average, individuals from partially migratory subpopulations switched migratory status every four years. Our results support the hypothesis that partial migration is maintained through a single conditional strategy. Understanding plasticity in migratory behavior will improve monitoring efforts and provide a rigorous basis for evaluating threats, particularly those associated with changing climate.

**KEYWORDS:** Sierra Nevada bighorn sheep, Ovis canadensis sierrae, altitudinal migration, behavioral plasticity, caprinae, elevational migration, partial migration
Global population declines across numerous migratory taxa have renewed interest in the ecology of these populations (Wilcove and Wikelski 2008). Migration is a behavioral adaptation to temporal variation in resources, which can allow populations to grow by exploiting resources in areas incapable of supporting permanent habitation (Fryxell and Sinclair 1988). Recent research has revealed that most migratory populations are partially migratory, including an alternative resident behavior wherein individuals occupy a single range year round (Chapman et al. 2011).

There is, however, still disagreement over how partial migration is maintained. One hypothesis is that migratory status (i.e., individual adoption of migrant v. resident behavior) is fixed at the individual level and that migrants and residents function as separate populations (Lundberg 1988). Many studies appear to support the fixity of individual migratory status among large terrestrial herbivores including research by Monteith et al. (2011) on mule deer (*Odocoileus hemionus* Rafinesque, 1818), and work by Cole et al. (2015) on elk (*Cervus canadensis* Erxleben, 1777).

Consequently, ungulate biologists often continue to assume that migratory behavior is fixed at the individual level (e.g., Hebblewhite and Merrill 2007; Middleton et al. 2013), even though this assumption contradicts long-standing knowledge of plastic life history (Gaillard et al. 1998). This assumption even permeates the language we use to discuss migratory behavior; references to “migrant” or “resident” individuals represent the implicit assumption that these behaviors are fixed.

Alternatively, partial migration could be maintained through a single conditional strategy in which individual migratory status is plastic (i.e., capable of changing between years; Lundberg 1988). Research across a number of taxa has provided examples of individual-level plasticity in migratory status (e.g., Adriaensen and Dhondt 1990). Few studies have sought to explicitly test this hypothesis in ungulates, presumably due to the difficulty of collecting adequate data (Gaillard 2013). There have, however, been an increasing number of recent studies confirming that indeed, individual ungulates can...
switch status between years, supporting the need to better understand the extent of migratory plasticity in this taxon (Gaidet and Lecomte 2013; White et al. 2013; Eggeman et al. 2016).

The extent to which migratory behavior is plastic carries key implications for demography. Migration and residency expose individuals to conditions that may differentially affect survival and reproduction (e.g., Adriaensen and Dhondt 1990; Hebblewhite and Merrill 2007). If migratory status is fixed at the individual level, migrants and residents each represent a closed population whose vital rates can be estimated and interpreted in isolation. If, however, individuals frequently switch their migratory status, migrant and resident populations are instead open and interpreting either population’s demography may depend on understanding rates of immigration and emigration (i.e., status switching; Bolger et al. 2008). Plasticity in migratory behavior carries further demographic implications in that this plasticity constrains a species' capacity for behavioral adaptation to changing conditions. Still, in most taxa the prevalence of status switching remains poorly understood.

Compared to other ungulates, the migratory behavior of caprids has remained largely un-quantified, even as accelerating anthropogenic change to alpine ecoregions raises mounting concerns surrounding threats to montane migratory species (Beever et al. 2011). Mountain caprids have long been known to migrate, often along steep elevational gradients (Geist 1974), but although sexually dimorphic behavior is well documented in this taxon (e.g., sexual segregation), most research on caprid migration has focused exclusively on males, leaving a gap in our understanding of female migratory behavior. Compared to cervids, caprids often show an inverted pattern of migration; instead of migrants and residents sharing a single range during the season of scarcity, partially-migratory caprids share a summer range and occupy separate ranges in winter (Seip and Bunnell 1985; Dubois et al. 1992; Grignolio et al. 2004). Loss of migration has been documented in some caprid populations (Courtemanch et al. 2017). Among mountain ungulates, migratory behavior is assumed to provide greater access to forage as has been shown in other elevational migrants (Albon and Langvatn 1992),
but movement along elevational gradients may also determine individual exposure to severe weather and predation risk (Festa-Bianchet 1988).

Federally-endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804; Sierra bighorn hereafter), a partially-migratory alpine caprid, are one of North America’s rarest ungulates (U. S. Fish and Wildlife Service 2007). The species was nearly extirpated following mid-nineteenth century European settlement and consequently information on the species’ behavior and historic range are limited (U. S. Fish and Wildlife Service 2007). In summer Sierra bighorn occupy high-elevation ranges, but whereas some individuals remain year-round residents at high-elevation, others migrate to lower-elevation ranges for the duration of winter (Spitz et al. 2017). Recent efforts towards recovery have focused on intensive monitoring, and reintroductions to restore the subspecies' distribution to more of its historic range (U. S. Fish and Wildlife Service 2007).

Understanding the extent to which individual-level migratory status is plastic has crucial implications for evaluating demographic threats to partially migratory populations. A specific concern for Sierra bighorn management is heightened predation risk on the low-elevation winter ranges occupied by migrants, where productive mule deer herds have buoyed populations of cougar (*Puma concolor* Linnaeus, 1771), Sierra bighorn’s primary predator (Johnson et al. 2012). If migratory status is fixed at the individual level, threats to migrants can be considered in isolation and predation on low-elevation migratory winter ranges could threaten the persistence of migratory behavior, but not Sierra bighorn subpopulations per se (i.e., residents would remain unaffected). Conversely, if individual-level migratory status is plastic, threats to migrants and residents are connected and evaluating the rate of switching between migrant and resident behaviors is crucial to informing the evaluation of these threats. Finally, plasticity in migratory status is also an important consideration for translocations, one of the main management actions employed by the recovery program; if migratory status is fixed at the
individual level, matching candidate individuals to habitat of the appropriate type should be a major
focus of these efforts (U. S. Fish and Wildlife Service 2007).

Here, we quantify female migratory status and tactics across 14 subpopulations of Sierra
bighorn. We then test for 1) evidence of individual-level plasticity in migratory status (i.e., individuals
changing between migrant and resident status among years); 2) subpopulation-level differences in
status prevalence; and 3) inter-annual and subpopulation-level differences in migratory tactics (timing,
duration and separation of migratory movements). Based on life-history theory (e.g., Gaillard et al.
1998) and evidence for plasticity in migratory status from other taxa, we hypothesize that Sierra
bighorn are plastic in both status and tactics and that consequently the prevalence and tactics of
migration vary by subpopulation.

Materials and methods

Study Area The Sierra Nevada form the backbone of the state of California, USA, extending 650 km
and varying in width from 75 to 125 km (Hill 1975). The west side of the range rises gradually from
300m (in California's central valley) to an average of over 3,000 m, including numerous peaks over
4,000 m (Fig. 1). These high Sierra peaks create a rain shadow along the sheer east edge of the range
which is consequently more xeric (Hill 1975). Precipitation is strongly seasonal, mostly accumulating
as snow November-April and the resulting deep banks of snow slowly melting May-September (2005-
2013 mean 1 April snowpack at Mammoth Pass, 2835 m = 0.97 m, SD = 0.47; US Bureau of
Reclamation). The result is steep gradients of temperature, moisture, elevation and vegetation along the
eastern edge of the Sierra Nevada's crest. High elevations (>3300 m) are characterized by sparse alpine
vegetation interspersed with meadows; mid elevations (3300 – 2500 m) by pinyon-juniper woodland,
subalpine meadows, and forest; and low elevations (2500 – 1500 m) by sagebrush steppe vegetation.
Winter storms in the Sierra Nevada are characterized by extreme winds that scour snow from alpine

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ridges. The current distribution of Sierra bighorn is limited to the southern half of this range, which contains the bulk of the range's alpine habitat (U. S. Fish and Wildlife Service 2007).

By the late 1970s fewer than 50 Sierra bighorn females remained in the wild, surviving in three adjacent subpopulations. The 14 subpopulations we analyzed (Fig. 1) are all descendants of this stock. Although these subpopulations are demographically distinct (Johnson et al. 2010), we do not expect them to be genetically isolated, because the distances separating subpopulations are smaller than those routinely traveled by rams during the rut (T. R. Stephenson, California Department of Fish and Wildlife, unpublished data). Sierra bighorn were placed on the federal endangered species list in 1999 and the California Department of Fish and Wildlife (CDFW) has been the lead agency managing the species for recovery (U. S. Fish and Wildlife Service 2007).

Location Data We captured adult female Sierra bighorn by helicopter net-gun and outfitted them with global positioning system (GPS) collars (University of Montana IACUC AUP 046-11, Federal Fish and Wildlife Service Permit No. TE050122-4). CDFW conducted autumn captures from 2005 – 2015, concluding each year by 31 October. For analysis of migratory behavior, we divided GPS data for each animal into one or more biological years, defined as beginning 1 November to follow the completion of autumn captures. (For further details on location data, see Table S1.)

To maximize classification success, we confined our analysis to animal-years with complete winter data, which we defined *a priori* as beginning before 15 November (i.e., \( \leq \) two weeks after the beginning of a migratory year) and ending \( \geq \) 15 April of the following calendar year. We chose the 15 November cut-off to represent Sierra bighorn summer range and to precede the rut, and chose the 15 April end date to include the bulk of the period we expect migrants and residents to occupy separate ranges. Thus, we restricted analyses to animal-years were at least 41% complete (mean \( \approx \) 90% complete). To improve model convergence, we also subsampled each animal-year to one location per day, choosing the point closest to 1600hr (Bunnefeld et al. 2011; Spitz et al. 2017).
Modeling Elevational Movement Non-linear movement modeling (Bunnefeld et al. 2011) has recently risen in popularity as a method of quantifying and classifying movement behavior (Mysterud et al. 2011; Singh et al. 2012; Eggeman et al. 2016). This approach uses a set of \textit{a priori} models, each representing a different movement behavior, which are then fit to animal location data. Movement behavior can then be classified by comparing the fit of \textit{a priori} movement models to determine which movement behavior received the greatest support. This approach has the advantages of generating parameter estimates that have a direct biological interpretation, are quantitatively standardized, and are comparable across taxa (Bunnefeld et al. 2011). However, these methods are tailored to long-distance movements and have difficulty detecting short-distance migration, for example, across elevational gradients. In earlier work, we found that these models often had a poor visual fit to Sierra bighorn data (Spitz et al. 2017). We therefore adapted \textit{a priori} models of animal movement behavior to be fit to vertical distance (elevation), which better correspond to the ecology of our study species and consequently provide a better visual fit.

We classified each animal-year by movement status in two steps. First, we determined the best-supported model for each animal-year by comparing elevation-based movement models using Akaike Information Criterion (AIC; Burnham and Anderson 2002). Second, we used the parameter estimates from these movement models to further restrict classification to a biologically consistent definition of migration. We follow previous authors in defining migration as entailing fidelity to $> 1$ spatially separate seasonal ranges to distinguish this behavior from exploratory or opportunistic forays (Dingle and Drake 2007). Parameter-based decision rules thus allow us to compensate for some of the limitations of the modeling methods we employ, while remaining transparent about our assumptions and thereby also allowing others to replicate our approach.

We compared the fit of each animal-year of data to three elevation-based models, each representing a different movement behavior: residency, migration, and one-way movement. Where
possible, these models were parameterized to be directly comparable with previous approaches to quantifying movement behavior. The model for residency was parameterized as:

\[ \text{elevation} = \gamma \]  

Eqn 1.

where \( \gamma \) is a constant. The model for migration was represented as the double sigmoid:

\[ \text{elevation} = \gamma - \frac{\delta}{(1 + e^{((\theta - t)/\varphi)})} + \frac{\delta}{(1 + e^{((\theta + 2 \times \varphi + \rho + 2 \times \varphi_{spring} - t)/\varphi_{spring})})} \]  

Eqn 2.

where \( \gamma \) represents the average elevation of the starting range, \( \delta \) represents the difference in elevation between ranges, \( t \) represents time, \( \theta \) indicates the midpoint in time of autumn migration, \( \varphi \) is the time required to complete \( \frac{1}{2} \) to \( \frac{3}{4} \) of the migration (representing the duration of migratory movements) and \( \rho \) is the length of time spent on the second (here: winter) range. Subscripts on \( \varphi \) differentiate parameter estimates for autumn and spring and the midpoint in time of spring migration (\( \theta_{spring} \)) can be calculated as \( \theta + 2 \times \varphi + 2 \times \varphi_{spring} \). Additionally, to account for animal-years with incomplete data (i.e., migration with autumn or spring movement absent due either to GPS collar failure or misalignment of migratory movement to our definition of migratory year) we also included a “one way” model to quantify unidirectional elevational movements. This one-way model was parameterized as the single sigmoid:

\[ \text{elevation} = \gamma - \frac{\delta}{(1 + e^{((\theta - t)/\varphi)})} \]  

Eqn 3.

and we interpreted its parameters identically as in the migrant model. For each animal-year we fit this \( a \) priori set of non-linear models to elevation as a function of time. In fitting these models, we restricted the range of migratory start dates (\( \theta \), minimum = 1) and the duration of migratory movements (\( \varphi \) and \( \varphi_{spring} \), 1 to 21 days; total duration of migration ~ 4 \( \varphi \)). We then used AIC to determine which model was best supported for each animal-year. All models were fit using the “migrateR” package for the R programming language (Spitz et al. 2017).

**Decision Rules** We assumed that within a given year all Sierra bighorn were either resident or migrant and imposed a series of additional constraints on our model results to restrict our classification of migratory behavior to a consistent biological meaning. To ensure our definition of migration included
fidelity to multiple seasonal ranges, we defined minimum thresholds of elevational separation ($\delta > 500$ m) and duration of occupancy ($\rho \geq 30$ days or $\theta_{spring} - \theta \geq 80$ days). We classified as resident any animal-year for which migration was the best supported model but failed to meet either of these thresholds (Fig. 2). These thresholds were chosen post hoc based on local minima in the distributions of $\delta$, $\rho$ and $\theta_{spring} - \theta$. We included the threshold based on separation of migratory movements ($\theta_{spring} - \theta$) to provide redundancy in cases where protracted migratory movements (i.e., large $\phi$ and $\phi_{spring}$) appeared to cause our models to underestimate the duration of occupancy ($\rho$). We interpreted estimated range occupancy of less than 30 days and migratory movements separated by < 80 days as representing opportunistic or exploratory forays rather than migration (i.e., lacking station keeping behavior typical of home range maintenance). For animal-years including forays, we retained the $\gamma$ estimate from the migratory model for descriptive purposes, because it better represented mean elevation of the resident winter range. Because we were unable to apply these decision rules to animal-years that showed strongest support for models of one-way movement (these models lacked $\rho$ and $\theta_{spring}$), we withheld these animal-years ($n = 23$) from further analysis. To test the robustness of our decision rules to the choice of specific thresholds, we compared consistency of animal-year classifications after individually altering each cutoff by ±10%.

Based on extensive survey efforts, we further assumed that, similar to other caprids, Sierra bighorn do not travel to higher elevations to winter (Seip and Bunnell 1985; Dubois et al. 1992; Grignolio et al. 2004). Consequently, we interpreted all upward migration ($\delta > 0$) as cases in which the order of autumn and spring migration were reversed (due, for example, to misalignment of migratory movement to our definition of migratory year). We retained the classification of upward migration as “migrant”, but withheld these animal-years from our analysis of migratory tactics. To summarize the absolute fit of the models corresponding to our classifications, we calculated root-mean-squared error
(RMSE) which represents the standard deviation of residuals and retains the same units as the response variable (here elevation, in meters).

**Statistical Analyses** We used mixed-effect logistic regression (Hosmer et al. 2013) to estimate the frequency of status switching and to test for subpopulation differences in the prevalence of migration. First, we used a model with no fixed effects to quantify the across-subpopulation rate of status switching. To test for directional switching, we ran a second model that also included a single fixed-effect term for an individual's starting status (the individual's last observed stratus preceding each opportunity to switch). This parameter allowed us to test whether animals were more likely to switch strategies in a particular direction (either migrant-to-resident or vice versa). We evaluated the statistical significance of these terms based on their associated p-values. Throughout we included individual as a random effect (to account for individual variation in repeated measures; Gillies et al. 2006) and excluded data from subpopulations where we only observed one status (because both outcomes are required for successful parameter estimation with logistic regression; Hosmer et al. 2013). To test for differences in the prevalence of migration by subpopulation, we used a $\chi^2$ test for equality of proportions.

Next, we used mixed-effect linear regression to test inter-annual and subpopulation-level differences in 3 migratory tactics: vertical distance traveled ($\delta$), timing ($\theta$ and $\theta_{spring}$), and duration ($\phi$ and $\phi_{spring}$). We modeled estimates of each parameter separately, beginning with a full model containing terms for year and subpopulation, and then sequentially removing the least supported term through backwards-stepwise regression (Hocking 1976). Backwards-stepwise regression was halted after reaching a term whose removal resulted in a change in model fit $> 2 \Delta AIC$ (Burnham and Anderson 2002). The Baxter subpopulation and 2015 migratory year were held as reference categories and, to limit model complexity, we only included data from subpopulations and years for which we had at least 3 animal years classified as migrant ($n = 123$). As above, individual was held throughout as a
random effect to account for individual variation. All analyses were performed in program R (R Core Team 2014).

**Results**

Elevation models generally provided a good visual fit to Sierra bighorn location data (e.g., Fig. 2). Our decision rules were robust to changes in threshold values; decreasing the $\delta$ threshold by 10% changed 2.7% of animal year classifications (i.e., 7 of 262), while all other threshold values we tested changed $\leq$ 1.1% of classifications. We identified 150 migrant and 89 resident animal-years between 2005 and 2016 (63% and 37% of total animal years, respectively, representing 157 unique individuals; Fig. 3). Models fit to migrant animal-years included parameter estimates for 133 round-trip migratory movements. Approximately half of resident animal-years ($n = 44$) included non-migratory facultative movements in spring, which we term “forays”. The mean RMSE from migrant and resident models were 303 m and 289 m, respectively.

Spring migratory movements were more synchronous and ≥ 2 times the duration of autumn movements (Table 1). The mean date of autumn migration was 27 December (95% CI: 20 Dec—3 Jan) and the mean date of spring migration was 15 May (95% CI: 10 May—20 May). Vertical distances migrated varied from 519 to 1893 m (mean = 1174 m), the duration of migratory-range occupancy varied from 20 to 309 days (mean = 108) and the separation of migratory movements ranged from 53 to 313 days (mean = 140; Table 1). Mean estimates of year-round resident elevation and summer migrant elevation differed by less than 90 m and had overlapping 95% confidence intervals.

We observed both resident and migrant behaviors in 11 of 14 subpopulations and found that the prevalence of migration varied among subpopulations ($\chi^2_{13} = 82.56$, $p < 1 \times 10^{-5}$). In one population, we observed resident behavior exclusively (Gibbs), while in two other populations we observed exclusively migrant behavior (Wheeler and Laurel; Fig. 4). We estimated the rate of individual-level status switching across partially migratory subpopulations of Sierra bighorn at 0.25
switches/opportunity (Table 2) Thus, on average these individuals changed status every four years (95% CI: 0.15-0.39). We also found moderate evidence (p-value = 0.05) that individuals were more likely to switch from resident to migrant status rather than vice versa.

Our results also indicate plasticity in migratory tactics. The vertical distance, timing and duration associated with migratory movements all changed both as a function of subpopulation and year (Table 3). Our model for the vertical change associated with migration ($\delta$) retained one term for subpopulation and two for year, indicating the importance of both factors in explaining the vertical separation of seasonal ranges. Each model of migratory timing retained four subpopulation terms, but although there was some overlap the terms retained by these models differed. Similarly, the model for departing movement ($\theta$) also retained two terms for year, while the model for return movement ($\theta_{spring}$) retained a single year term; there was no overlap in retained year terms for timing models. Models of migratory duration ($\varphi$ and $\varphi_{spring}$) each retained only a single subpopulation term that differed between models. We interpreted these results as indicating that in most years, subpopulation played a greater explanatory role than did inter-annual variation in determining the timing and duration of migratory movements, but that vertical distance traveled tended to be better explained by inter-annual differences.

Discussion

Our results support the hypothesis that partial migration in Sierra bighorn is maintained through a single conditional strategy. We found Sierra bighorn to be plastic in migratory status and variable in tactics both at the individual and subpopulation levels. Migratory propensity and all three tactics we examined—the timing, duration and elevational distance of migration—varied both by subpopulation and year. To our knowledge, the rate of status switching we observed is the highest so far recorded for any ungulate and the first such estimate for a caprid. In comparison, switching rates have been estimated 0.15 in elk, another mountain ungulate (Eggeman et al. 2016), 0.1 in white-tailed deer ($Odocoileus virginianus$ Zimmerman, 1780; Nelson 1995), and 0.12 to 0.08, respectively in impala.
(Aepyceros melampus Lichtenstein, 1812; Gaidet and Lecomte 2013) and wildebeest (Connochaetes taurinus Burchell, 1823; Morrison and Bolger 2012), two tropical migrants whose movements are not elevational. Our observations encompassed the extremes of migratory prevalence, including populations in which we observed no migration, migration as the minority behavior, migration as the majority behavior, and exclusively migratory behavior. Like migratory prevalence, rates of switching may vary geographically, with specific subpopulations experiencing higher and lower rates than the population mean we report. Population-level differences in migratory prevalence and tactics have been described in a number of other ungulates including moose (Alces alces Linnaeus, 1758; Singh et al. 2012), white-tailed deer (Fieberg et al. 2008) and roe deer (Capreolus capreolus Linnaeus, 1758; Cagnacci et al. 2011). Unlike these study systems, our populations showed no obvious relationship between migratory prevalence and latitude, emphasizing the importance of other ecological or behavioral gradients within our study system (Fig. 3). Our description of migratory tactics in bighorn is otherwise largely consistent with descriptions of migratory behavior from other ungulates. For example, similar to mule deer and roe deer, we found that migration was more synchronous in spring than autumn (Cagnacci et al. 2011; Monteith et al. 2011).

Migrant-resident status switching can be conceptualized as a special case of home-range selection wherein individuals chooses annually between two overlapping alternatives: the continuous resident or the disjointed migrant home range (Gaudry et al. 2015). In contrast to the high rate of switching we observed, Dalerum et al. (2007) found a long-distance migrant, caribou, to have high range fidelity even in the face of extreme habitat alteration. These authors suggest that large home-range sizes allowed caribou to avoid negative demographic consequences of habitat alteration by concentrating within-home-range patterns of habitat selection in areas of consistently high quality. Thus an individual's ability to compensate for changes in within-home-range conditions likely depends both on home range size and environmental stochasticity, with changes in migratory status occurring when...
compensation within the resident range is no longer possible or when the additional resources afforded
by the migrant range are non-essential. We should therefore expect rates of status switching to vary
along a continuum, with elevated rates in populations that, like Sierra bighorn, occupy small ranges
with high inter-annual variation.

Shorter migration distances may also contribute to plasticity in migratory behavior. As the cost
of moving between seasonal ranges approaches zero, we should expect the relative costs and benefits
associated with migration to be determined by the differences in resources accessible to individuals
adopting migrant and resident behavior (e.g., differences in climate, forage and predation risk; Fryxell
and Sinclair 1988; Mysterud et al. 2011). In elk, however, Hebblewhite and Merrill (2007) showed that
the risk of predation during migration exceeded the risk experienced by elk on migrant or resident
ranges, making the migratory transition between ranges the most vulnerable state for this species. High
cost of movement can force partial migrants to make the annual decision between migration and
residency before information on the quality of the migratory range is available (Dingle and Drake
2007). In contrast, short-distance migrants like Sierra bighorn may be capable of directly assessing
conditions on both migrant and resident ranges before annually determining their status. For example,
individuals may visit the migrant range before deciding whether to remain resident or adopt the migrant
range for the remainder of winter. Where travel and information are inexpensive, we should expect
greater plasticity in migratory status as individuals pursue ideal-free distribution (Fretwell and Lucas
1969).

Our results also underline differences in partial migration among ungulates, suggesting a
taxonomic division. For cervids moving along an elevational gradient, partial migration typically
consists of a shared low elevation winter range, with some individuals migrating to high elevation for
summer while others remain resident at low elevation (“low-elevation resident”; red deer Cervus
deer...
deer: Monteith et al. 2011). We observed the opposite of this pattern in Sierra bighorn where summer is
the shared range, only migrants retreat to lower elevations for winter and residents remain at high
elevations year-round (“high-elevation resident”). Although information on partial migration in caprids
is still relatively limited, the pattern of high-elevation residency we observed in Sierra bighorn is
consistent with other studies of ovids (Seip and Bunnell 1985; Dubois et al. 1992) and of caprids more
generally (Grignolio et al. 2004). The similarities among migratory behavior in caprids suggest higher
rates of status switching among these species as compared to cervids.

We may further expect the drivers of high-elevation and low-elevation residency to differ.

Residents have often been shown to experience higher predation rates than migrants (e.g., Fryxell and
Sinclair 1988; Hebblewhite and Merrill 2007), but this pattern is reversed in systems with high-
elevation residents. Upward elevational movement is broadly acknowledged as an ungulate predator-
avoidance strategy (Hebblewhite and Merrill 2007; Monteith et al. 2011), especially for caprids, where
elevation is assumed to have a central role in predator avoidance (Geist 1974; Festa-Bianchet 1988).

Sierra bighorn face the highest predation risk on low-elevation winter range, where they overlap
spatially with more abundant mule deer capable of supporting predators at higher densities (Johnson et
al. 2012). Thus, in contrast to low-elevation residency, high-elevation residency may reduce predation
risk in our system. This avoidance of predation risk, however, requires high-elevation residents to incur
alternative costs; lower temperatures and higher snow levels shorten the growing season, limit access to
forage and increase the cost of movement (Telfer and Kelsall 1984; Albon and Langvatn 1992). Sierra
bighorn migratory status therefore appears to represent a choice between two inversely related costs:
predation risk and the energetic expense of harsher winters (i.e., the combined cost of reduced foraging
opportunity and increased metabolic demands imposed by severe weather).

Spatial differences in these costs and benefits likely underlie the differences we observed in
migratory prevalence among subpopulations and through time. Resource requirements of migrants and
residents, however, remain little explored (Bolger et al. 2008). In winter, resident Sierra bighorn are thought to be limited to wind scoured slopes while migrants are expected to depend on rugged terrain below snow line (U. S. Fish and Wildlife Service 2007). A lack of access to snow-free areas at low elevation may explain the relative absence of migration in the two northernmost Sierra bighorn subpopulations. Similarly, the observation of “all-migrant” subpopulations may be due to the local absence of sufficient snow-free patches at high elevation. Consequently, variation in winter severity could lead to temporal shifts in the prevalence of migratory behavior. This provides an alternative interpretation to past observations of purported winter range abandonment by Sierra bighorn (Wehausen 1996). Future studies should investigate potential causes of the flexibility in migratory status and tactics displayed here by ovids.

The high synchrony and prolonged duration we observed in spring migration is consistent with the expectations of the forage maturation hypothesis, where migrants may attempt to maximize forage quality by riding the “green wave” of phenology as it advances upslope in spring (Bischof et al. 2012). The importance of phenology in driving these movements is also suggested by the presence of a similar movement pattern among resident forays. The resident forays we documented are similar to those observed in other elevational migrants, most notably bighorn sheep (Courtemanch et al. 2017), stone sheep (Ovis dalli stonei Nelson, 1884; Seip and Bunnell 1985), roe deer (Cagnacci et al. 2011) and red deer (Mysterud et al. 2011). These excursions suggest that residents may be able to reap some of the nutritional benefits of migration while minimizing migration's costs (e.g., increased predation risk). In other systems, however, bighorn are expected to be obligate long-distance migrants (summarized in Singer et al. 2000). This expectation could result from a detection bias against short-distance migration, but may also indicate that the ecological gradients driving bighorn migration are rarely as horizontally compressed as in the Sierra Nevada. The ability of the migrant model to capture foray movements indicates that our elevation-based models are flexible and capable of handling a wide range of
behaviors, including some we did not anticipate. This flexibility, however, also highlights the importance of clearly defining behaviors of focal interest (e.g., through parameter-based constraints), because a single model may be capable of representing multiple behaviors whose ecology is important to distinguish.

The conditional nature of migration among Sierra bighorn challenges the assumptions conventionally applied to the analysis of partially-migratory populations, especially among large herbivores. The comparatively high rate of switching we observed suggests that it is inappropriate to assume migrants and residents can be treated conceptually as separate populations with separate vital rates. Unless the demographic consequences of migration and residency are identical, understanding the demography of conditional migrants like Sierra bighorn requires identifying not only the demographic consequences specific to each status, but also the rates at which individuals switch status and the ecological drivers of these transitions. The data required to address questions of this complexity remain a major challenge in the study of migration. Consequently, improving our understanding of migration continues to depend on increasing collection of long-term individual-based data (Bolger et al. 2008; Wilcove and Wikelski 2008; Gaillard 2013).

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References


Fig. 1 Plot of elevation and Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804) subpopulations in the eastern Sierra Nevada Mountains, California, USA. Subpopulation boundaries shown are 95% kernel density estimates based on the location data included in our analysis. Even though they tend to be relatively small, most subpopulations include significant portions of high-elevation (above 4,000 m, white) and low-elevation (below 2,000 m, dark gray) terrain.

Fig. 2 Example classification plots from two individual Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804) observed switching migratory status between years. The movement models shown were fit to elevation values from an individual's location data (in gray; see text for details). Migration models are shown with a solid line and resident models with a dashed line. In 2007 we classified individual s110 as a resident because although the migrant model received the greatest support, this model's estimate for the duration of migratory-range occupancy failed to meet our minimum threshold (>30 days residency on secondary range or >80 days between midpoints of movements, top left). We classified individual s166 as a resident in 2012, because the migrant model failed to meet our minimum threshold for vertical separation between ranges (500 m, bottom left). Both of these individuals were classified as migrants in other years (right panels).

Fig. 3 Combined plots of non-linear models fit to elevation for Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804) migrant and resident animal-years, divided by migratory status. Line length (on x-axis) corresponds to date range of available data in each animal-year. All low-elevation residents were from the Big Arroyo (*n* = 5, *γ* < 2500m) and Bubbs subpopulations (*n* = 1, *γ* = 2626m).

Fig. 4 Proportion of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804) observed migrating, by subpopulation (ordered north to south). We observed both strategies in all but three subpopulations: Gibbs, Wheeler and Laurel (exclusively resident, migrant and migrant, respectively). Numbers indicate the total count of classified animal-years analyzed from each subpopulation.
Table 1. Across-subpopulation summary statistics of parameter estimates for migrant and resident Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804). The mean, minimum, maximum, and standard deviation are given for each parameter estimated. “γ” represents the estimated elevation of the resident or high-elevation migrant range. “δ” is the change in elevation between migratory ranges. “ρ” is the duration of residency on the winter range. “θ” and “θ<sub>spring</sub>” represent the respective midpoints of autumn and spring migration, with θ<sub>spring</sub> - θ interpreted as the time separating migratory movements. Similarly, “φ” and “φ<sub>spring</sub>” indicate the duration of autumn and spring migratory movements (calculated as the time required for each movement to progress from ½ to ¾ completion).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Term</th>
<th>Units</th>
<th>Mean</th>
<th>Min.</th>
<th>Max.</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Annual Elevation</td>
<td>(γ&lt;sub&gt;resident&lt;/sub&gt;)</td>
<td>m</td>
<td>3394.25</td>
<td>2352.07</td>
<td>3857.3</td>
<td>322.31</td>
</tr>
<tr>
<td>Mean Summer Elevation</td>
<td>(γ)</td>
<td>m</td>
<td>3482.08</td>
<td>2973.8</td>
<td>3810.94</td>
<td>158.09</td>
</tr>
<tr>
<td>Elevational Movement</td>
<td>(δ)</td>
<td>m</td>
<td>-1173.59</td>
<td>-1892.61</td>
<td>-519.12</td>
<td>325.37</td>
</tr>
<tr>
<td>Winter Range Residency</td>
<td>(ρ)</td>
<td>m</td>
<td>107.65</td>
<td>20</td>
<td>308.51</td>
<td>50.46</td>
</tr>
<tr>
<td>Separation of Movements</td>
<td>(θ&lt;sub&gt;spring&lt;/sub&gt; - θ)</td>
<td>days</td>
<td>140.25</td>
<td>52.65</td>
<td>312.91</td>
<td>49.93</td>
</tr>
<tr>
<td>Timing of Autumn Migration</td>
<td>(θ)</td>
<td>days</td>
<td>57.3</td>
<td>1</td>
<td>161.2</td>
<td>40.4</td>
</tr>
<tr>
<td>Timing of Spring Migration</td>
<td>(θ&lt;sub&gt;spring&lt;/sub&gt;)</td>
<td>days</td>
<td>197.55</td>
<td>115.89</td>
<td>315.21</td>
<td>30.75</td>
</tr>
<tr>
<td>Duration of ½ Autumn Migration</td>
<td>(φ)</td>
<td>days</td>
<td>4.87</td>
<td>1</td>
<td>21</td>
<td>6.09</td>
</tr>
<tr>
<td>Duration of ½ Spring Migration</td>
<td>(φ&lt;sub&gt;spring&lt;/sub&gt;)</td>
<td>days</td>
<td>11.43</td>
<td>1</td>
<td>21</td>
<td>7.73</td>
</tr>
</tbody>
</table>
Table 2. Opportunities to observe individual changes in migratory strategies among years in Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804) 2006-2014. Instances in which an individual's status remained consistent are divided by status (“migrant to migrant” vs. “resident to resident”). These data only include partially migratory subpopulations (i.e., subpopulations in which we observe both migrant and resident strategies). We observed 15 switches in status out of a possible 60 opportunities for a status-switching rate of 0.25 animals per opportunity (SE = 0.072).

<table>
<thead>
<tr>
<th>Sub Population</th>
<th>Migrant to Resident</th>
<th>Resident to Migrant</th>
<th>Remaining Migrant</th>
<th>Remaining Resident</th>
</tr>
</thead>
<tbody>
<tr>
<td>Warren</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Convict</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Taboose</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sawmill</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Baxter</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bubbs</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Big Arroyo</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Williamson</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Big Arroyo</td>
<td>0</td>
<td>2</td>
<td>6</td>
<td>3</td>
</tr>
</tbody>
</table>


Table 3. Wald statistics for significant terms remaining in models of migratory tactics of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Shaw, 1804) following backwards-stepwise selection. Population- and year-differences were both important in explaining differences in the vertical distance (δ) traveled, but only population-differences were significant in explaining the timing (θ) and duration (ϕ) of migratory movements (see Eqn 2. for further details). We interpret these results as suggesting that the local geography associated with specific populations is more important to determining the phenology of migration, but that inter-annual variation (e.g., in winter severity) can also play a role in determining the vertical distance traveled. Subpopulations are listed north to south and Baxter in 2012 was chosen as the reference category.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Distance (δ)</th>
<th>Timing (θ)</th>
<th>(θ&lt;sub&gt;spring&lt;/sub&gt;)</th>
<th>Duration (ϕ)</th>
<th>(ϕ&lt;sub&gt;spring&lt;/sub&gt;)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Warren</td>
<td>3.58</td>
<td>4.56</td>
<td>3.64</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wheeler</td>
<td>2.72</td>
<td>2.31</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sawmill</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.98</td>
</tr>
<tr>
<td>Bubbs</td>
<td></td>
<td></td>
<td></td>
<td>2.38</td>
<td></td>
</tr>
<tr>
<td>Big Arroyo</td>
<td>-2.18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Langley</td>
<td>3.09</td>
<td>-3.73</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Laurel</td>
<td></td>
<td></td>
<td></td>
<td>5.56</td>
<td></td>
</tr>
<tr>
<td>2008</td>
<td></td>
<td>3.64</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2012</td>
<td>2.28</td>
<td></td>
<td>-2.77</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2014</td>
<td>2.88</td>
<td>4.37</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Fig. 1
Fig. 2

![Graphs showing elevation changes over time for different years and species.](https://mc06.manuscriptcentral.com/cjz-pubs)
Fig. 3

[Graph showing data for Residents and Migrants]
Fig. 4

![Bar chart showing proportions of migrants in different sub-populations.]

- Proportion of Migrants
- Sub-Population
- Values for each sub-population are listed on the chart.