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How plastic is migratory behavior? Quantifying elevational movement in a partially migratory alpine ungulate, the Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*)

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

Abstract: 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 behaviors. 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, the Sierra Nevada bighorn sheep (*Ovis canadensis sierrae* Grinnell, 1912). We used nonlinear modeling to quantitatively describe migratory behavior, analyzing 262 animal-years of GPS location data collected between 2005 and 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 4 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.

Key words: Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*, altitudinal migration, behavioral plasticity, Caprinae, elevational migration, partial migration.

Résumé : Les espèces migratrices connaissent des baisses planétaires bien documentées, mais les causes de ces déclins ne sont pas bien établies. Un des obstacles à une meilleure compréhension de ce phénomène est l'incertitude concernant les causes du maintien du comportement de migration. La plupart des populations migratrices sont partiellement migratrices, présentant des comportements migratoires et résidents. La théorie ne fournit que deux explications possibles pour la coexistence de comportements de migration et de résidence, à savoir que ces comportements sont fixés au niveau individuel ou que les deux comportements font partie d'une même stratégie conditionnelle dans laquelle l'état migratoire d'un individu (l'adoption d'un comportement migratoire ou résident) est plastique. Nous vérifions l'existence de plasticité de l'état et des tactiques migratoires (moment, distance et durée de la migration) chez un capridé de montagnes figurant sur la liste fédérale américaine des espèces menacées, le mouflon de la Sierra Nevada (*Ovis canadensis sierrae* Grinnell, 1912). Nous utilisons la modélisation non linéaire pour décrire de manière quantitative le comportement migratoire, en analysant 262 années-animaux de données de positionnement par GPS recueillies de 2005 à 2016 pour 161 femelles issues de 14 sous-populations. Les tactiques migratoires et la prévalence de la migration variaient selon la sous-population. En moyenne, les individus de populations partiellement migratrices changeaient d'état migratoire tous les 4 ans. Nos résultats appuient l'hypothèse selon laquelle la migration partielle est maintenue par une stratégie conditionnelle unique. La compréhension de la plasticité dans le comportement de migration améliorera les efforts de surveillance et fournira une base rigoureuse pour l'évaluation des menaces, notamment celles qui sont associées aux changements climatiques. [Traduit par la Rédaction]

Mots-clés : mouflon de la Sierra Nevada, *Ovis canadensis sierrae*, migration altitudinale, plasticité comportementale, caprinés, migration en élévation, migration partielle.

Introduction

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.,

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individual adoption of migrant versus 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, 1817)) 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 that 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. 2014; 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, then 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, then 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 with other ungulates, the migratory behavior of caprids has remained largely unquantified, 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 with 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* Grinnell, 1912; hereafter Sierra bighorn), 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 is 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 toward recovery have focused on intensive monitoring, as well as 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, then 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, then threats to migrants and residents are connected and evaluating the rate of switching between migrant and resident behaviors is crucial to inform 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, then matching candidate individuals to habitat of the appropriate type should be a major focus of these efforts (U.S. Fish and Wildlife Service 2007).

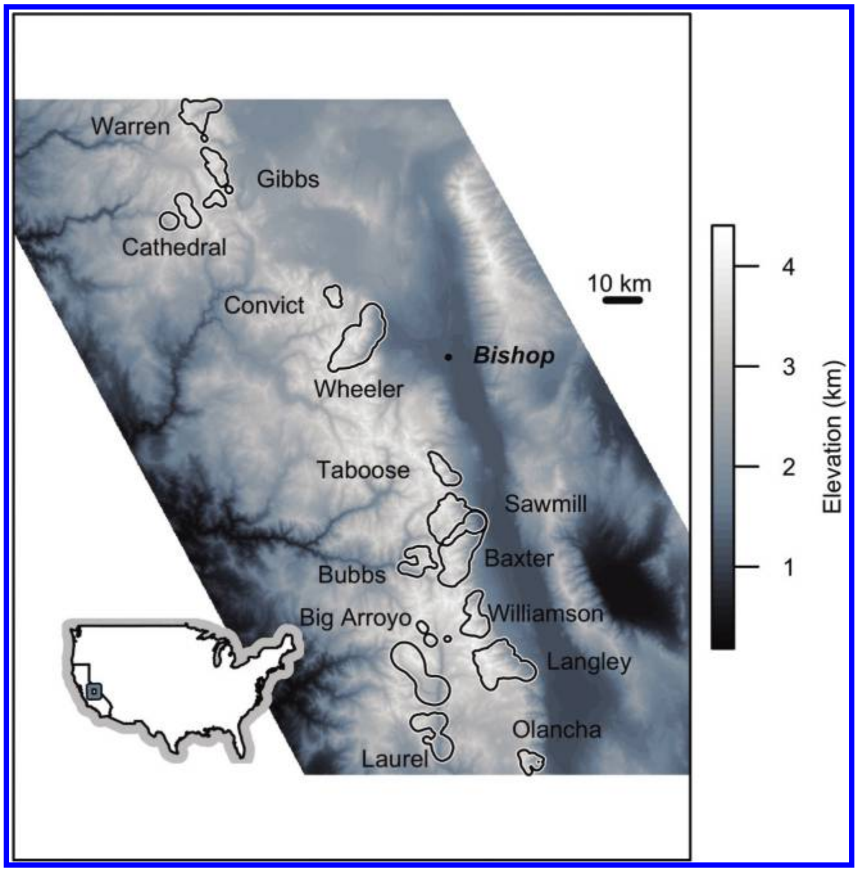
Here, we quantify female migratory status and tactics across 14 subpopulations of Sierra bighorn. We then test for (*i*) evidence of individual-level plasticity in migratory status (i.e., individuals changing between migrant and resident status among years); (*ii*) subpopulation-level differences in status prevalence; and (*iii*) interannual 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 300 m (in California's central valley) to a mean of over 3000 m, including numerous peaks over 4000 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 from November to April and the resulting deep banks of snow slowly melting from May to September (during 2005–2013, the mean 1 April snowpack at Mammoth Pass (elevation 2835 m) = 0.97 m, SD = 0.47 m; U.S. 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) are characterized by pinyon–juniper woodland, subalpine meadows, and forest; and low elevations (2500–1500 m) are characterized by sagebrush steppe vegetation. Winter storms in the Sierra Nevada are characterized by extreme

Fig. 1. Plot of elevation and Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) 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 terrain (above 4000 m; white) and low-elevation terrain (below 2000 m; dark gray).



winds that scour snow from alpine 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 that 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 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 Institutional Animal Care and Use Committee AUP 046-11, U.S. Fish and Wildlife Service Permit No. TE050122-4). The California Department of Fish and Wildlife conducted autumn captures from 2005 to 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 on 1 November to follow the completion of autumn captures. For further details on location data see Supplementary Table S1.[1]

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., ≤2 weeks after the beginning of a migratory year) and ending ≥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; we chose the 15 April end date to include the bulk of the period that we expect migrants and residents to occupy separate ranges. Thus, we restricted analyses to animal-years were at least 41% complete (mean = 90% complete). To improve model convergence, we also subsampled each animal-year to one location per day, choosing the point closest to the hour of 1600 (Bunnefeld et al. 2011; Spitz et al. 2017).

Modeling elevational movement

Nonlinear 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 a priori models, each representing a different movement behavior, that are then fit to animal location data. Movement behavior can then be classified by comparing the fit of 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 quantita-

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[1] Supplementary table is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0367.

tively 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 a priori models of animal movement behavior to 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's 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 that 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 that quantify movement behavior. The model for residency was parameterized as

$$\text{(1)} \qquad \text{elevation} = \gamma$$

where γ is a constant. The model for migration was represented as the double sigmoid:

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

where γ represents the mean elevation of the starting range, δ represents the difference in elevation between ranges, t represents time, θ indicates the midpoint in time of autumn migration, φ is the time required to complete half to three-quarters of the migration (representing the duration of migratory movements), and ρ is the length of time spent on the second (i.e., winter) range. Subscripts on φ differentiate parameter estimates for autumn and spring and the midpoint in time of spring migration (θ_{spring}) can be calculated as $\theta + 2\varphi + 2\varphi_{\text{spring}}$. Additionally, to account for animal-years with incomplete data (i.e., migration with autumn or spring movement absent due to either 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:

$$\text{(3)} \qquad \text{elevation} = \gamma - \delta/[1 + e^{(\theta - t)/\varphi}]$$

and we interpreted its parameters identically as in the migrant model. For each animal-year, we fit this a priori set of nonlinear models to elevation as a function of time. In fitting these models, we restricted the range of migratory start dates (θ, minimum = 1) and the duration of migratory movements (φ and φ_{spring}, 1–21 days; total duration of migration $\sim 4\varphi$). 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 $\theta_{\text{spring}} - \theta \geq 80$ 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 δ, ρ, and $\theta_{\text{spring}} - \theta$. We included the threshold based on separation of migratory movements ($\theta_{\text{spring}} - \theta$) to provide redundancy in cases where protracted migratory movements (i.e., large φ and φ_{spring}) appeared to cause our models to underestimate the duration of occupancy (ρ). We interpreted estimated range occupancy of <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 γ 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 ρ and θ_{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 cut-off by ±10%.

Based on extensive survey efforts, we further assumed that, like 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 migrations were reversed (e.g., due to misalignment of migratory movement to our definition of migratory year). We retained the classification of upward migration as "migrant", but we withheld these animal-years from our analysis of migratory tactics. To summarize the absolute fit of the models corresponding to our classifications, we calculated the root-mean-squared error, which represents the standard deviation of residuals and retains the same units as the response variable (i.e., elevation, in metres).

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 status 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 χ^2 test for equality of proportions.

Next, we used mixed-effect linear regression to test interannual and subpopulation-level differences in three migratory tactics: vertical distance traveled (δ), timing (θ and θ_{spring}), and duration

Fig. 2. Example classification plots from two individual Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) 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 solid lines and resident models are shown with broken lines. 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). In 2012, we classified individual s166 as a resident 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).

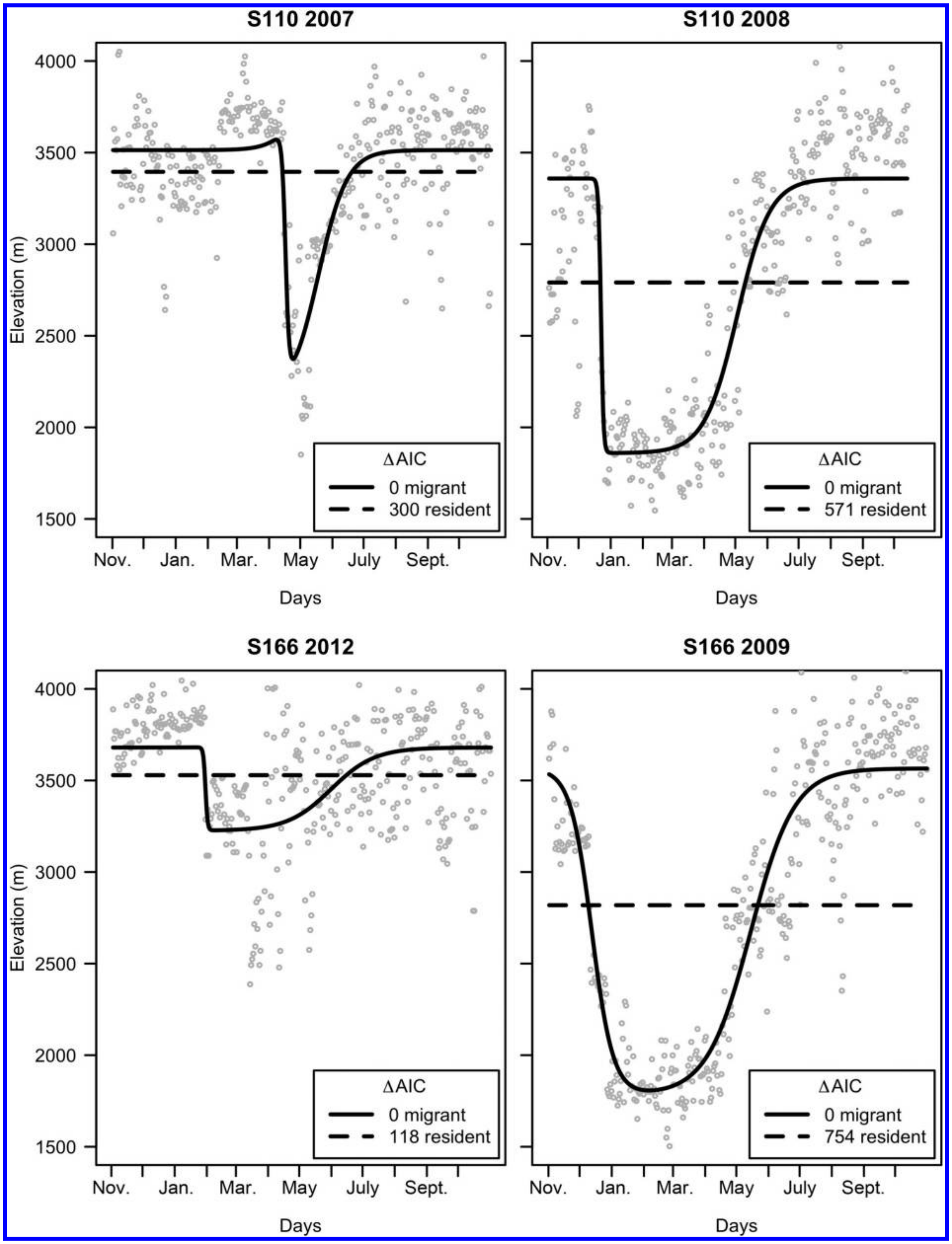
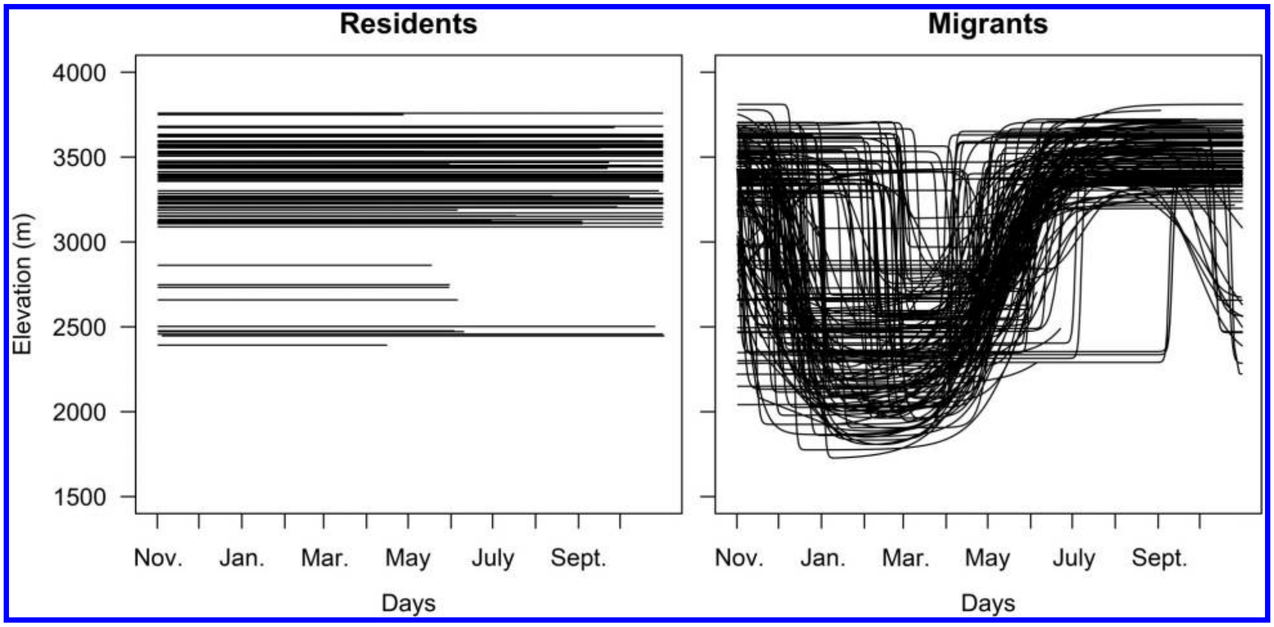


Fig. 3. Combined plots of nonlinear models fit to elevation for Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) migrant and resident animal-years divided by migratory status. Line length (on x axis) corresponds to date range of available data in each animal-year. All low-elevation residents were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



(φ and φ_{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 ΔAIC (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 δ threshold by 10% changed 2.7% of the animal-year classifications (i.e., 7 of 262), while all other threshold values that we tested changed ≤1.1% of the animal-year 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 nonmigratory facultative movements in spring, which we term “forays”. The mean root-mean-squared errors from migrant and resident models were 303 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% confidence interval (CI): 20 December – 3 January) and the mean date of spring migration was 15 May (95% CI: 10–20 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 days), and the separation of migratory movements ranged from 53 to 313 days (mean = 140 days; Table 1). Mean estimates of year-round resident elevation and summer migrant elevation differed by <90 m and had overlapping 95% CI.

We observed both resident and migrant behaviors in 11 of 14 subpopulations and found that the prevalence of migration varied among subpopulations ($\chi^2_{[13]} = 82.56$, $p < 0.00001$). 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 4 years (95% CI: 0.15–0.39). We also found moderate evidence ($p = 0.05$) 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 (δ) 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; however, although there was some overlap, the terms retained by these models differed. Similarly, the model for departing movement (θ) also retained two terms for year, whereas the model for return movement (θ_{spring}) retained a single year term; there was no overlap in retained year terms for timing models. Models of migratory duration (φ and φ_{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 interannual variation in determining the timing and duration of migratory movements, but that vertical distance traveled tended to be better explained by interannual differences.

Discussion

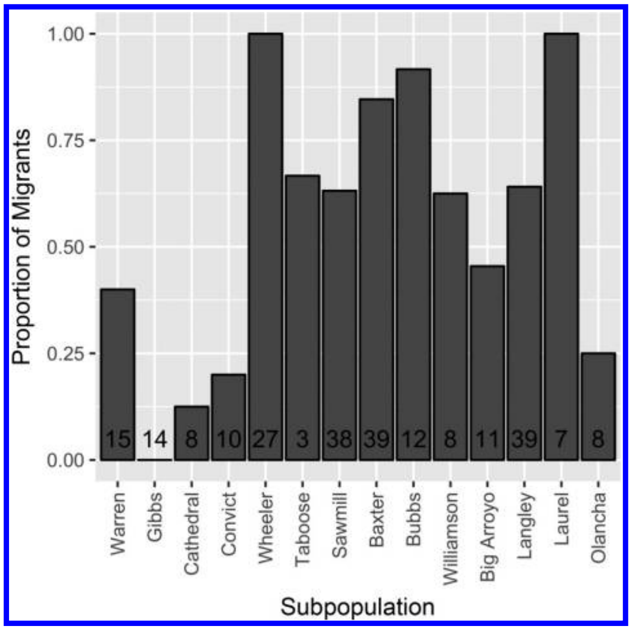
Our results support the hypothesis that partial migration in Sierra bighorn is maintained through a single conditional strategy. We found Sierra bighorn to be plastic in migratory status and variable in tactics both at the individual and subpopulation levels. Migratory propensity and all three tactics that we examined — the

Table 1. Across-subpopulation summary statistics of parameter estimates for migrant and resident Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*).

Variables	Term	Units	Mean	Minimum	Maximum	SD
Mean annual elevation	$\gamma_{\mathrm{resident}}$	m	3394.25	2352.07	3857.3	322.31
Mean summer elevation	γ	m	3482.08	2973.8	3810.94	158.09
Elevational movement	δ	m	–1173.59	–1892.61	–519.12	325.37
Winter range residency	ρ	m	107.65	20	308.51	50.46
Separation of movements	$\theta_{\mathrm{spring}} - \theta$	days	140.25	52.65	312.91	49.93
Timing of autumn migration	θ	days	57.3	1	161.2	40.4
Timing of spring migration	θ_{spring}	days	197.55	115.89	315.21	30.75
Duration of half autumn migration	φ	days	4.87	1	21	6.09
Duration of half spring migration	$\varphi_{\mathrm{spring}}$	days	11.43	1	21	7.73

Note: The mean, minimum, maximum, and standard deviation (SD) 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_{spring} represent the respective midpoints of autumn and spring migrations, with $\theta_{\mathrm{spring}} - \theta$ interpreted as the time separating migratory movements. Similarly, φ and $\varphi_{\mathrm{spring}}$ indicate the duration of autumn and spring migratory movements (calculated as the time required for each movement to progress from half to three-quarter completion).

Fig. 4. Proportion of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) observed migrating by subpopulation (ordered from 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.



timing, duration, and elevational distance of migration — varied both by subpopulation and year. To our knowledge, the rate of status switching that 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 to be 0.15 in elk, another mountain ungulate (Eggeman et al. 2016), 0.1 in white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) (Nelson 1995), 0.12 in impala (*Aepyceros melampus* (Lichtenstein, 1812)) (Gaidet and Lecomte 2013), and 0.08 in blue wildebeest (*Connochaetes taurinus* (Burchell, 1823)) (Morrison and Bolger 2012); note that the impala and blue wildebeest are 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 that 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 Sierra bighorn is otherwise largely consistent with descriptions of migratory behavior from other ungulates. For example, like 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 choose 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 that we observed, Dalerum et al. (2007) found a long-distant migrant, the woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788), 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 nonessential. 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 interannual 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 behaviors (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

Table 2. Opportunities to observe individual changes in migratory strategies among years in Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) between 2006 and 2014.

	Subpopulation								
	Warren	Convict	Taboose	Sawmill	Baxter	Bubbs	Williamson	Big Arroyo	Langley
Migrant to resident	1	0	0	1	1	1	1	0	2
Resident to migrant	0	2	1	1	1	0	0	0	3
Remaining migrant	1	0	0	10	12	4	0	2	6
Remaining resident	1	0	0	3	1	0	1	1	3

Note: 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 3. Wald statistics for significant terms remaining in models of migratory tactics of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) following backwards-stepwise selection.

		Timing		Duration	
Variables	Distance (δ)	θ	θ_{spring}	φ	φ_{spring}
Warren	3.58	4.56	3.64		
Wheeler		2.72	2.31		
Sawmill					2.98
Bubbs			2.38		
Big Arroyo		−2.18			
Langley		3.09		−3.73	
Laurel			5.56		
2008		3.64			
2012	2.28		−2.77		
2014	2.88	4.37			

Note: 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 (for further details see eq. 2). We interpret these results as suggesting that the local geography associated with specific populations is more important in determining the phenology of migration, but that interannual variation (e.g., in winter severity) can also play a role in determining the vertical distance traveled. Subpopulations are listed from north to south and Baxter in 2015 was chosen as the reference category.

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 elaphus* Linnaeus, 1758): Albon and Langvatn 1992; roe deer: Mysterud 1999; elk: Hebblewhite and Merrill 2007; mule 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 that 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 compared with cervids.

We may further expect the drivers of high-elevation residency 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 that 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, whereas migrants are expected to depend on rugged terrain below the 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 that 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 that we documented are similar to those observed in other elevational migrants, most notably bighorn sheep (Courtemanch et al. 2017), Stone's sheep (*Ovis dalli stonei* J.A. Allen, 1897) (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 it 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 that 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 that 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

Adriaensen, F., and Dhondt, A.A. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. J. Anim. Ecol. **59**(3): 1077–1090. doi:10.2307/5033.

Albon, S., and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos, **65**(3): 502–513. doi:10.2307/3545568.

Beever, E.A., Ray, C., Wilkening, J.L., Brussard, P.F., and Mote, P.W. 2011. Contemporary climate change alters the pace and drivers of extinction. Glob. Change Biol. **17**(6): 2054–2070. doi:10.1111/j.1365-2486.2010.02389.x.

Bischof, R., Loe, L.E., Meisingset, E.L., Zimmermann, B., Van Moorter, B., and Mysterud, A. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? Am. Nat. **180**(4): 407–424. doi:10.1086/667590. PMID:22976006.

Bolger, D.T., Newmark, W.D., Morrison, T.A., and Doak, D.F. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecol. Lett. **11**(1): 63–77. doi:10.1111/j.1461-0248.2007.01109.x. PMID:17897327.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J., and Ericsson, G. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. J. Anim. Ecol. **80**(2): 466–476. doi:10.1111/j.1365-2656.2010.01776.x. PMID:21105872.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York.

Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A.J.M., Morellet, N., Kjellander, P., Linnell, J.D.C., Mysterud, A., Neteler, M., Delucchi, L., Ossi, F., and Urbano, F. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos, **120**(12): 1790–1802. doi:10.1111/j.1600-0706.2011.19441.x.

Chapman, B.B., Brönmark, C., Nilsson, J.-Å., and Hansson, L.-A. 2011. The ecology and evolution of partial migration. Oikos, **120**(12): 1764–1775. doi:10.1111/j.1600-0706.2011.20131.x.

Cole, E.K., Foley, A.M., Warren, J.M., Smith, B.L., Dewey, S.R., Brimeyer, D.G., Fairbanks, W.S., Sawyer, H., and Cross, P.C. 2015. Changing migratory patterns in the Jackson elk herd. J. Wildl. Manage. **79**(6): 877–886. doi:10.1002/jwmg.917.

Courtemanch, A.B., Kauffman, M.J., Kilpatrick, S., and Dewey, S.R. 2017. Alternative foraging strategies enable a mountain ungulate to persist after migration loss. Ecosphere, **8**(6): e01855. doi:10.1002/ecs2.1855.

Dalerum, F., Boutin, S., and Dunford, J.S. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. Can. J. Zool. **85**(1): 26–32. doi:10.1139/z06-186.

Dingle, H., and Drake, V.A. 2007. What is migration? BioScience, **57**(2): 113–121. doi:10.1641/B570206.

Dubois, M., Gerard, J.-F., and Maublanc, M.-L. 1992. Seasonal movements of female Corsican mouflon (*Ovis ammon*) in a Mediterranean mountain range, southern France. Behav. Processes, **26**(2–3): 155–165. doi:10.1016/0376-6357(92)90010-B. PMID:24924325.

Eggeman, S., Hebblewhite, M., Bohm, H., Whittington, J., and Merrill, E.H. 2016. Behavioural flexibility in migratory behaviour in a long-lived ungulate. J. Anim. Ecol. **85**: 785–797. doi:10.1111/1365-2656.12495. PMID:26790111.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia, **75**(4): 580–586. doi:10.1007/BF00776423. PMID:28312434.

Fieberg, J., Kuehn, D.W., and DelGiudice, G.D. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. J. Mammal. **89**(6): 1529–1539. doi:10.1644/07-MAMM-A-277.1.

Fretwell, S.D., and Lucas, H.L., Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. **19**(1): 16–36. doi:10.1007/BF01601953.

Fryxell, J.M., and Sinclair, A.R.E. 1988. Causes and consequences of migration by large herbivores. Trends Ecol. Evol. **3**(9): 237–241. doi:10.1016/0169-5347(88)90166-8. PMID:21227239.

Gaidet, N., and Lecomte, P. 2013. Benefits of migration in a partially-migratory tropical ungulate. BMC Ecol. **13**: 36. doi:10.1186/1472-6785-13-36. PMID:24079650.

Gaillard, J.-M. 2013. Assessing fitness consequences of migratory tactics requires long-term individually based monitoring. Ecology, **94**(6): 1261–1264. doi:10.1890/12-0710.1. PMID:23923487.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol. Evol. **13**(2): 58–63. doi:10.1016/S0169-5347(97)01237-8. PMID:21238201.

Gaudry, W., Saïd, S., Gaillard, J.-M., Chevrier, T., Loison, A., Maillard, D., and Bonenfant, C. 2015. Partial migration or just habitat selection? Seasonal movements of roe deer in an alpine population. J. Mammal. **96**(3): 502–510. doi:10.1093/jmamma/gyv055.

Geist, V. 1974. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, Ill.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., and Jerde, C.L. 2006. Application of random effects to the study of resource selection by animals. J. Anim. Ecol. **75**(4): 887–898. doi:10.1111/j.1365-2656.2006.01106.x. PMID:17009752.

Grignolio, S., Rossi, I., Bassano, B., Parrini, F., and Apollonio, M. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. Ethol. Ecol. Evol. **16**(3): 255–264. doi:10.1080/08927014.2004.9522636.

Hebblewhite, M., and Merrill, E.H. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia, **152**(2): 377–387. doi:10.1007/s00442-007-0661-y. PMID:17287955.

Hill, M. 1975. Geology of the Sierra Nevada. University of California Press, Berkeley.

Hocking, R.R. 1976. A Biometrics Invited Paper. The analysis and selection of variables in linear regression. Biometrics, **32**(1): 1–49. doi:10.2307/2529336.

Hosmer, D.W.J., Lemeshow, S., and Sturdivant, R.X. 2013. Applied logistic regression. John Wiley & Sons, Inc., New York.

Johnson, H.E., Mills, L.S., Stephenson, T.R., and Wehausen, J.D. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecol. Appl. **20**(6): 1753–1765. doi:10.1890/09-1107.1. PMID:20945773.

Johnson, H.E., Hebblewhite, M., Stephenson, T.R., German, D.W., Pierce, B.M., and Bleich, V.C. 2012. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia, **171**(1): 295–307. doi:10.1007/s00442-012-2397-6. PMID:22791131.

Lundberg, P. 1988. The evolution of partial migration in birds. Trends Ecol. Evol. **3**(7): 172–175. doi:10.1016/0169-5347(88)90035-3. PMID:21227194.

Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Cook, J.G., Cook, R.C., Nelson, A.A., Jimenez, M.D., and Klaver, R.W. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology, **94**(6): 1245–1256. doi:10.1890/11-2298.1. PMID:23923485.

Monteith, K.L., Bleich, V.C., Stephenson, T.R., Pierce, B.M., Conner, M.M., Klaver, R.W., and Bowyer, R.T. 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.

Morrison, T.A., and Bolger, D.T. 2012. Wet season range fidelity in a tropical migratory ungulate. J. Anim. Ecol. **81**(3): 543–552. doi:10.1111/j.1365-2656.2011.01941.x. PMID:22256947.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. J. Zool. (Lond.), **247**(4): 479–486. doi:10.1111/j.1469-7998.1999.tb01011.x.

Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. 2011. Partial migration in expanding red deer populations at northern latitudes — a role for density dependence? Oikos, **120**(12): 1817–1825. doi:10.1111/j.1600-0706.2011.19439.x.

Nelson, M.E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Can. J. Zool. **73**(6): 1069–1076. doi:10.1139/z95-127.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org.

Seip, D.R., and Bunnell, F.L. 1985. Foraging behaviour and food habits of Stone's sheep. Can. J. Zool. **63**(7): 1638–1646. doi:10.1139/z85-243.

Singer, F.J., Papouchis, C.M., and Symonds, K.K. 2000. Translocations as a tool for restoring populations of bighorn sheep. Restor. Ecol. **8**(4S): 6–13. doi:10.1046/j.1526-100x.2000.80061.x.

Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N., and Ericsson, G. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecol. Appl. **22**(7): 2007–2020. doi:10.1890/12-0245.1. PMID:23210316.

Spitz, D.B., Hebblewhite, M., and Stephenson, T.R. 2017. 'MigrateR': extending model-driven methods for classifying and quantifying animal movement behavior. Ecography, **40**: 788–799. doi:10.1111/ecog.02587.

Telfer, E., and Kelsall, J. 1984. Adaptation of some large North American mammals for survival in snow. Ecology, **65**(6): 1828–1834. doi:10.2307/1937779.

U.S. Fish and Wildlife Service. 2007. Recovery plan for the Sierra Nevada bighorn sheep. U.S. Fish and Wildlife Service, Sacramento, Calif.

Wehausen, J.D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildl. Soc. Bull. **24**(3): 471–479.

White, K.S., Barten, N.L., Crouse, S., and Crouse, J. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology, **95**(1): 225–237. doi:10.1890/13-0054.1. PMID:24649661.

Wilcove, D.S., and Wikelski, M. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biol. **6**(7): e188. doi:10.1371/journal.pbio.0060188. PMID:18666834.