The Scientific Naturalist

Broadening the migratory portfolio of altitudinal migrants

Kristin Denryter [iD],[1,4,5] Thomas R. Stephenson[2] and Kevin L. Monteith[3]

[1]Haub School of Environment and Natural Resources, University of Wyoming, 804 East Fremont, Laramie, Wyoming 82072 USA.
[2]Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Wildlife, 787 North Main Street, Suite 220, Bishop, California 93514 USA.
[3]Haub School of Environment and Natural Resources, Department of Zoology and Physiology, and Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, 804 East Fremont, Laramie, Wyoming 82072 USA.
[4]E-mail: kristin.denryter@wildlife.ca.gov

Movement is among the most important adaptations of animals living in seasonal environments. Movement allows animals to exploit spatially and temporally variable resources; these resources in turn influence individual fitness and demographic rates of populations (Fryxell et al. 1988, Bolger et al. 2008, Mueller and Fagan 2008, Hebblewhite and Merrill 2009). A diverse movement portfolio, wherein a variety of movement behaviors are represented across space and time and among individuals in a population, likely is important for population persistence in the face of environmental change (Lowrey et al. 2020) and may be especially important for managers to re-establish in populations of endangered species. Diverse movement portfolios include some combination of movement behaviors such as range residency (single, year-round range), migration (movement between two nonoverlapping ranges using the same route at regular time intervals), and nomadism (movements across the landscape that do not follow the same route; Mueller and Fagan 2008), although other intermediate behaviors may occur (e.g., abbreviated migration [Courtemanch et al. 2017]; commuting between ranges [Cagnacci et al. 2011]). Diverse migratory portfolios are associated with large, robust populations of large herbivores (Fryxell et al. 1988, Sawyer et al. 2016) and greater resilience with respect to population persistence. Further, movement behaviors have ever-increasing prominence in evolutionary ecology and conservation (Lowrey et al. 2020). Here, we report a novel movement behavior for altitudinal migration observed in Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; hereafter Sierra bighorn), which we suspect could have important demographic and fitness consequences.

Sierra bighorn are a federally endangered subspecies of bighorn sheep, endemic to the Sierra Nevada mountains of California. Since their federal listing in 1999, the California Department of Fish and Wildlife has monitored their population with the use of with VHF and GPS collars. Sierra bighorn are partially migratory and frequently switch between migration and residency among years (Spitz et al. 2018). Typically, Sierra bighorn occupy high-elevation (≥3,300 m) ranges during summer, with migrants moving to lower elevations (<2,500 m) during winter, though some individuals remain at higher elevations year-round (Spitz et al. 2018). We used migrateR to fit linear and nonlinear mixed-effects models of altitudinal migration to 632 animal years of GPS location data of male and female Sierra bighorn to determine movement behavior (Spitz et al. 2018); this sample included results for some previously published data (Spitz et al. 2018), which we included for comparison. Altitudinal movement models are similar to net-squared displacement models of animal movement (Bunnefeld et al. 2011), but they also account for a third dimension of vertical (altitudinal) movement. MigrateR allows for automation of model fitting of three potential models for altitudinal movements (i.e., migrant, double-sigmoid; resident, horizontal-linear; or disperser, single-sigmoid), and estimates parameters for mean elevation of initial range, vertical distance separating seasonal ranges, midpoint of departing movement, duration of movement between seasonal ranges, and duration of occupancy of the secondary range, and ranks models using Akaike information criterion (Spitz et al. 2018).

Upon visual inspection of profiles of elevational movements of Sierra bighorn, we identified three known patterns of movement behavior: (1) traditional migration—migrations characterized by a single round-trip movement between seasonal ranges (*n* = 261; 41%; Figs. 1A, 2A); (2) residency—remaining on the same

range year-round ($n = 136$; 22%; Figs. 1B, 2B); and (3) residency with abbreviated migration (sensu Courtemanch et al. 2017)—migrations characterized as short-duration movements of ~2 weeks to low-elevation ranges in late spring before returning to high elevations ($n = 60$; Fig. 2C). During visual inspection, we also identified a fourth movement behavior characterized by ≥ 2 (2–4, $\overline{x} = 2.3$) round trips between seasonal ranges between 1 November and 31 May that we termed "vacillating migration" ($n = 175$; Figs. 1C, 2D–F). Vacillating migrations also differed from traditional migration in that vacillating migrants had a lower coefficient of variation in elevation during winter than traditional migrants (indicating less variance in elevational movements when adjusted for differences in elevation among herds; Appendix S1: Fig. S1A; $P < 0.001$). Additionally, primary and secondary ranges of vacillating migrants were separated by less distance than in traditional migrants (Appendix S1: Fig. S1B; $P < 0.001$). The vacillating migrations we documented may have allowed Sierra bighorn to realize benefits experienced by traditional migrants (e.g., increased access to forage) and residents (e.g., reduced risk of predation), without committing to a single strategy for the entire winter, as in traditional migration, residency, and residency with abbreviated migration.

Migration should evolve when gains to fitness through increased access to forage and reduced predation risk in the different ranges overcome costs such as energy expenditures and increased predation risk while moving between ranges (Bolger et al. 2008). Greatest fitness benefits should be realized by animals that are best able to respond to environmental conditions, which can manifest through migration that is facultative—occurring only under specific conditions (Newton 2012). A relatively large proportion of Sierra bighorn migrate facultatively, switching between migration and residency among years (Spitz et al. 2018). Vacillating migration may be the ultimate, most flexible form of facultative migration in altitudinal migrants.

Vacillating migration may represent a conditional strategy for risk tolerance, depending on what endogenous (e.g., body fat, reproductive status) and exogenous (e.g., winter severity) cues influence decisions about migration. For example, resident Sierra bighorn that remain at higher elevations year-round are at lower risk of predation but greater risk of starvation, whereas animals wintering at lower elevations face lower starvation risk but greater predation risk (Spitz et al. 2020). Vacillating migration could allow animals to switch the range they occupy actively to balance the risks they face in response to real-time cues associated with predator presence, snowfall, or patterns of green up, illustrating a high level of plasticity. Moreover, changes in the nutritional state of the animal as winter progresses likely interact with other factors to produce an array of risk-tolerance
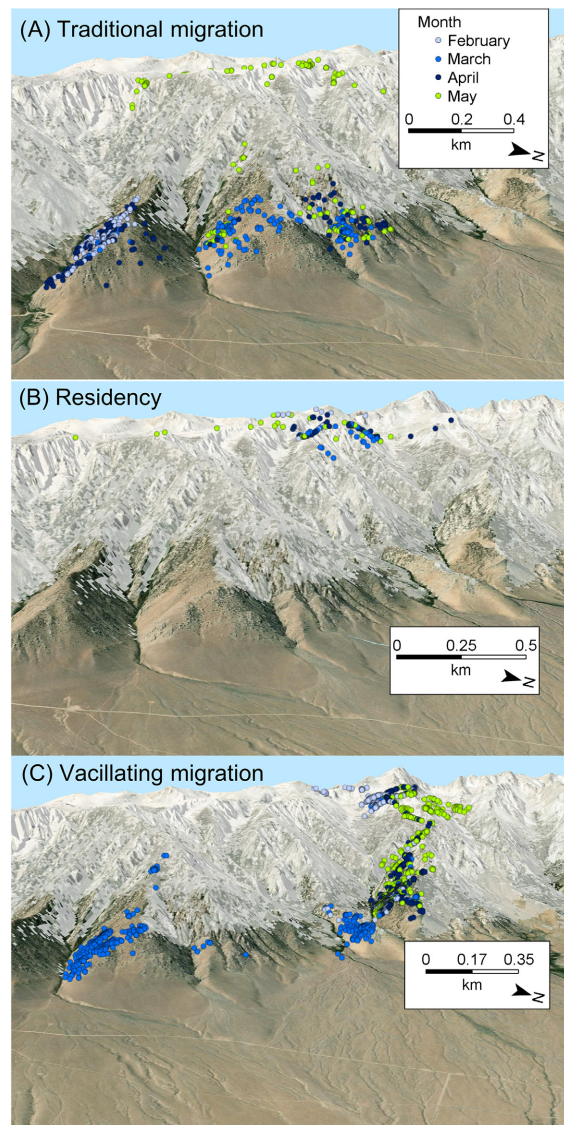

Fig. 1. Examples of movement patterns of individual Sierra Nevada bighorn sheep between January and June; Sierra Nevada bighorn sheep were collared between October 2006 and May 2019 in the Sierra Nevada mountains, California, USA. (A) Traditional migration (migrated from high- to low-elevation range ~9 November; returned to high-elevation range ~26 April); (B) residency (no movement between high- and low-elevation ranges); and (C) vacillating migration (first migration from high- to low-elevation range ~25 January; first returned to high-elevation range ~25 February; second migration from high- to low-elevation range ~5 March; second return to high-elevation range ~18 March; third migration from high- to low-elevation range ~5 April; third return to high-elevation range ~6 May).

strategies in altitudinal migrants. Lactation status influences body fat available for energy catabolism, and winter severity determines the adequacy of body-fat reserves
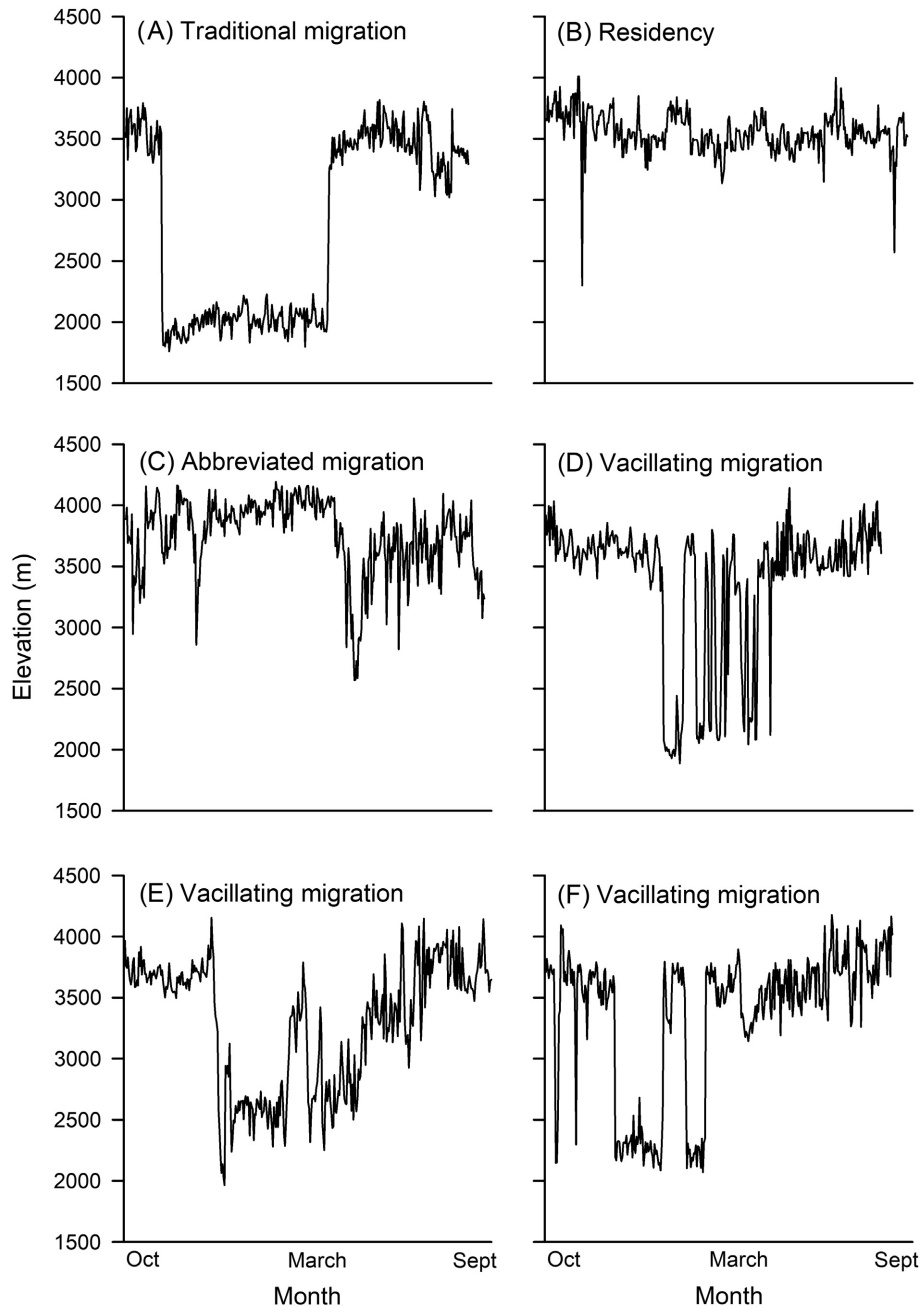
FIG. 2. Examples of annual movement patterns (elevation profiles) of individual Sierra Nevada bighorn sheep collared between October 2006 and May 2019 in the Sierra Nevada mountains, California, USA: (A) traditional migration, (B) residency, (C) residency with abbreviated migration, and (D–F) various forms of vacillating migration.

(Stephenson et al. 2020), yet flexibility in movement behavior afforded by vacillating migration may allow individuals to compensate for nutritional inadequacies that could otherwise have consequences to demographic rates and fitness.

Although movement behaviors often are categorized as migration, residency, or nomadism, movement behavior is a continuum (Cagnacci et al. 2011, Sawyer et al. 2016). Our results reinforce the need to move toward a broadened classification for migration (Berg et al. 2019) and to develop a continuous metric to describe migration; the latter promises to be a daunting task given substantial variability in movement parameters, even within a single movement behavior (Spitz et al. 2018, 2020).

Vacillating migration, as we describe it, represents a particularly unique challenge in the efforts to quantify migration. Movement patterns of vacillating migrants share attributes of movement patterns of traditional migrants and residents, but they do not fit the definition of either. Because vacillating migrants experienced a different environment than individuals with other movement behaviors in the same area, we expect their demography also may differ. Hence, we emphasize the importance of identifying vacillating and other atypical migratory strategies, particularly for demographic studies (Lowrey et al. 2020). An alternative explanation for vacillating migration is that it represents seasonal habitat use or forays rather than a type of migration; however, high- and low-elevation ranges were separated by hundreds to thousands of meters in elevation (Appendix S1: Fig. S1B) and ~4–12 km—distances that were ~3–12 times greater than the high end of the 95% confidence interval (CI) of daily movements of Sierra bighorn during winter (Denryter et al. 2021). Regardless of whether vacillating migration is a true migratory behavior or seasonal habitat use, it differed significantly from other types of movement behavior in our study area. Lumping vacillating migration with other types of movement behavior could limit our understanding of potential fitness consequences of this intermediate behavior. Broadening classifications of altitudinal migration creates opportunities to discover potentially important, and perhaps previously overlooked, evolutionary adaptations of animals to seasonal environments and may further expand our understanding of the evolution and maintenance of partial migration.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3321/suppinfo