

Human-induced reversal of fortunes for migratory ungulates?¹

Animal migrations link different ecosystems, with important consequences for nutrient cycling, trophic webs, and disease transmission over very large scales. Migratory populations usually reach much greater numbers than nonmigratory populations of the same or similar species, and many have substantial economic impacts. Many migratory populations of birds, fishes, reptiles, insects, and mammals are declining. These declines are usually attributed to two causes, which often interact: habitat alteration and climate change. This Forum discusses how environmental changes, particularly those driven by human activities, may affect the population dynamics of migratory and nonmigratory elk in the Greater Yellowstone Ecosystem, USA (GYE). It originated from the paper “Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd” by Art Middleton, Matt Kauffman, Doug McWhirter, John Cook, Rachel Cook, Abigail Nelson, Michael Jimenez, and Robert Klaver, published in this issue of *Ecology*.

Migratory populations of ungulates are thought to benefit from predator avoidance and access to forage of greater quantity and quality. That expectation rests upon two assumptions: migrating ungulates move out of range of most predators, and they exploit seasonal gradients in high-quality growing vegetation. Atle Mysterud points out that both assumptions may no longer hold in many ecosystems where ungulates migrate along altitudinal gradients. That is because of spatial changes in predation risk and the complex effects of climate change on the duration of snow cover and on the timing and speed of spring green-up at different altitudes.

The data presented in the focal paper by Middleton et al. show diverging trends in calf recruitment for migratory and resident elk, but the interpretations of those trends rests on correlative evidence. Jean-Michel Gaillard insists upon the importance of examining temporal changes in all seasonal ranges, and he underlines the limitations of studies not based on monitoring marked individuals. Recent research on long-lived mammals has emphasized the effects of temporal changes in sex–age structure on population dynamics. A complete understanding of elk population dynamics would ideally account for changes in both recruitment and age-specific adult survival.

Chris Wilmers and Taal Levi discuss how irrigation and predator control outside Yellowstone Park may have beneficial consequences for nonmigratory elk. Several contributions to this Forum underline the need for long-term monitoring of individuals to understand both population dynamics and ecosystem functioning. Jack Massey, Sarah Cubayes, and Tim Coulson suggest that, in the absence of detailed individual-level data or of experimental manipulations, we are left with many unanswered questions about the relative importance of changes in multiple predator species and in phenology of seasonal habitats. They end an entertaining contribution with a lament for their ecologically diminished island home and a plea for long-term monitoring. John Fryxell and Robert Holt attempt to provide some possible answers by modeling how environmental changes may lead to changes in numbers of migrant and resident elk.

The final response by Art Middleton and collaborators emphasizes the complexities faced by animals that migrate across jurisdictions, an increasingly important issue in conservation biology. Ecosystem functioning remains stubbornly independent of jurisdictional boundaries. The ecological consequences of jurisdictional fragmentation are compounded by other human-caused changes. In the GYE, those changes include reintroduction of wolves, a summer warming trend well above the continental average, and changes in agricultural practices outside the park. Many others could be added to this list, from increasing nutrient deposition to altered fire regimes, to changes in abundance, distribution, or sex/age structure of other species of plants and animals. Interacting changes over multiple fronts make predicting the future a difficult challenge for ecologists.

The Forum points to several unanswered questions. One is whether in the future more elk may switch between strategies, an event that so far has been extremely rare. Yet, theory predicts that switching should occur if one strategy becomes more beneficial than the other. A complete

¹ Reprints of this 44-page Forum are available for \$10 each, either as PDF files or as hard copy. Prepayment is required. Order prints from the Ecological Society of America, Attention: Reprint Department, 1990 M Street, N.W., Suite 700, Washington, D.C. 20036 (esaHQ@esa.org).

abandonment of the migratory strategy appears unlikely over the medium term. Another remaining question is why migratory females have lower fecundity than resident ones, despite similar preconception fat levels. Rather than being a fixed response to fat reserves, conception may be part of a reproductive strategy that takes into account multiple environmental variables. Elk may be more likely to reproduce when the cost of reproduction is compensated by its expected benefits, which may differ for migratory and resident females independently of autumn fat levels.

What happens in Yellowstone matters. Research conducted there has implications for conservation policy in and near other large protected areas. The Forum focuses on how spatial and temporal variability of human influences affect the dynamics of migratory and nonmigratory elk, and by extension the functioning of the GYE. It sheds light on the unpredictability of short-term ecological consequences of reintroducing large predators, a practice that is both controversial and highly jurisdictionalized. Similarly to genetic pollution or exotic species, however, reintroduced predators do not respect jurisdictional boundaries. In the GYE, elk demography appears mostly affected by changes in recruitment rather than in adult survival. Although bears are more important than wolves as calf predators, attention in the popular press is focused on wolves.

Faced with multiple interacting variables, scientists normally proceed by experiment. Unfortunately, calls for controlled experiments in the GYE are akin to calls for controlled experiments in planetary climate: They are not going to happen. Alternative approaches to understanding this system include long-term monitoring of the consequences of spatial and temporal changes in management strategies and judicious application of experiments performed on simpler systems to provide theory and predictions.

Short time series will provide neither reliable interpretations of what drives elk population dynamics nor solutions to the many real or perceived economic and social problems related to large mammals in the GYE. Although much of the Forum discussion is centered on what we are not sure about, it is encouraging that much ongoing research in the GYE can count on a long time series of ecological variables. Continuation of ongoing research programs, and more “long-term thinking” by both ecologists and managers, is required to understand this ecosystem and minimize the impacts of both climate change and conflicting jurisdictional mandates.

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