

Rejoinder: challenge and opportunity in the study of ungulate migration amid environmental change

ARTHUR D. MIDDLETON,^{1,2,8} MATTHEW J. KAUFFMAN,^{2,3} DOUGLAS E. MCWHIRTER,⁴ JOHN G. COOK,⁵
 RACHEL C. COOK,⁵ ABIGAIL A. NELSON,^{1,9} MICHAEL D. JIMENEZ,⁶ AND ROBERT W. KLAVER⁷

¹Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA

²Program in Ecology, University of Wyoming, Laramie, Wyoming 82071 USA

³U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA

⁴Wyoming Game and Fish Department, Cody, Wyoming 82414 USA

⁵National Council for Air and Stream Improvement, Forestry and Range Sciences Laboratory, La Grande, Oregon 97850 USA

⁶U.S. Fish and Wildlife Service, Jackson, Wyoming 83001 USA

⁷U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit and Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011 USA

Increasingly, animals that migrate long distances to exploit seasonal habitats must traverse political boundaries capable of altering the very ecological gradients that promote migratory behavior. This transboundary aspect of migration presents many new challenges and opportunities for research and conservation (e.g., Bolger et al. 2008, Taillon et al. 2012). Work to date has often focused on physical barriers to movement (roads, fences, and housing and energy development) that can threaten migratory populations to varying degrees (Holdo et al. 2011, Sawyer et al. 2013). However, even in the absence of conspicuous barriers, political and jurisdictional boundaries can bring dramatic differences in land use and conservation policy. What happens to migratory populations when these boundaries alter the resources and refuges that they seek on their seasonal journeys?

It was this subtler question we confronted as we tried to understand the divergent productivity of migratory and resident elk (*Cervus elaphus*) in a population that occupies relatively undeveloped habitats of the Greater Yellowstone Ecosystem, USA (GYE). Over two decades, the recruitment rate of migratory elk has declined, while that of resident elk has remained stable, and recently increased. Over the same period, resident elk have grown more abundant, and the population's winter distribution has shifted ~18 km further away from the wilderness core of the GYE (Fig. 1). These changes have emerged without any physical obstruction of migration,

and without migratory individuals “staying behind” to remain resident (Middleton et al. 2013). Gaillard (2013) points out that (1) calf:cow ratios are an imperfect index of recruitment, (2) that we could have failed to detect a low rate of individual switching between the two subpopulations, and (3) that we could not account for the full suite of fitness components in this population. Nevertheless, our comparative approach revealed important contrasts that suggest the population's ongoing transition has been largely brought about by changes in calf recruitment (Middleton et al. 2013), with residents outperforming migrants. Similar patterns have emerged in and around Banff National Park in Alberta, Canada, where wolf (*Canis lupus*) recovery and agriculture (factors also at play in the GYE) have been associated with declines in the recruitment and abundance of migratory elk (Hebblewhite et al. 2005, 2006). These trends pose challenges for conservation and management. Migratory ungulates can be ecologically and economically important, but are broadly threatened (Bolger et al. 2008), whereas resident ungulates that commingle with domestic livestock can increase risks of disease transmission (Cross et al. 2009), crop damage, and human–carnivore conflict (Nelson et al. 2012).

As the evidence for these changes has accumulated in our study area, it has been challenging to understand the likely causes, as the commentaries on our work make clear. Much has changed for migratory elk in the GYE over the past two decades (Mech 2012, Kauffman et al. 2013). Wolf reintroduction is often seen by ecologists, wildlife managers, and the public as a “natural experiment” (e.g., Estes et al. 2011, Ripple and Beschta 2011), implying that recent changes in this system can be interpreted as a consequence of wolf predation. However, other important changes coincided with wolf reintroduction, including the recovery and expansion of grizzly bears (*Ursus arctos*; see Plate 1) (Barber-Meyer

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⁸ Present address: Yale School of Forestry and Environmental Studies, 370 Prospect Street, New Haven, Connecticut 06511 USA. E-mail: arthur.middleton@yale.edu

⁹ Present address: Montana Fish, Wildlife, and Parks, Livingston, Montana 59047 USA.

et al. 2008) and severe drought and pronounced warming (Barnett et al. 2008, Shuman 2011). These factors might not only confound the natural experiment; they could conceivably combine to limit elk populations more strongly than wolves do. For these reasons, it is imperative that we consider the potential effects of predation by reintroduced wolves within a broader context.

Several of the commentaries on our work indicated the need for experiments and long-term, individual-based studies. We agree that these would strengthen our inference. However, experiments are rarely feasible on the vast (and often highly protected) landscapes roamed by large mammals (but see Bilyeu et al. 2008, Kauffman et al. 2010), and there is not currently enough individual-based information to directly quantify long-term fitness and demographic changes among migratory elk in the GYE (but see Garrott et al. 2009). Meanwhile, wildlife managers in this system are under intense public pressure to make important decisions involving complex ecological questions. For example, the states of the GYE (Idaho, Montana, and Wyoming) have recently implemented plans that give wildlife managers the flexibility to increase wolf harvests in areas where wolves are associated with low elk population performance. If other factors such as bear predation and habitat quality are limiting elk, however, wolf harvests may not substantially ameliorate these declines. Relatedly, wolves are widely perceived to be causing behaviorally mediated shifts in elk distribution away from core areas of the GYE (e.g., Fig. 1), but if these distribution shifts are instead mediated by demography, and mainly by factors other than wolf predation, how relevant is wolf management? These questions, and many others, are not academic to the people charged with managing ecosystems that include recovering populations of large carnivores. Ecologists can play an important role in this process. For our part, though we do not have a complete understanding of these dynamics, we are confident that our observations and analyses have advanced our knowledge of the factors affecting migratory elk in the GYE. We join in the call for new experiments and long-term, individual-based studies in the GYE; but in the meantime, like many applied ecologists, we seek to interpret the system we study on a time scale that is relevant to current management efforts.

In this context, we considered a number of mechanisms that might help explain the patterns we observed. We focused much of our effort on understanding the low calf:cow ratios of migratory elk, already strikingly low (0.15) just three months after calving. Through biannual recaptures of migratory elk, we found evidence for a low pregnancy rate (0.71), driven partly by infrequent reproduction of young and lactating females. Poor summer nutrition can limit the reproduction of young and lactating females (Crête and Huot 1993, Cook et al. 2004, Tollefson et al. 2010, Cook 2011). Many areas of the western United States have experienced relatively

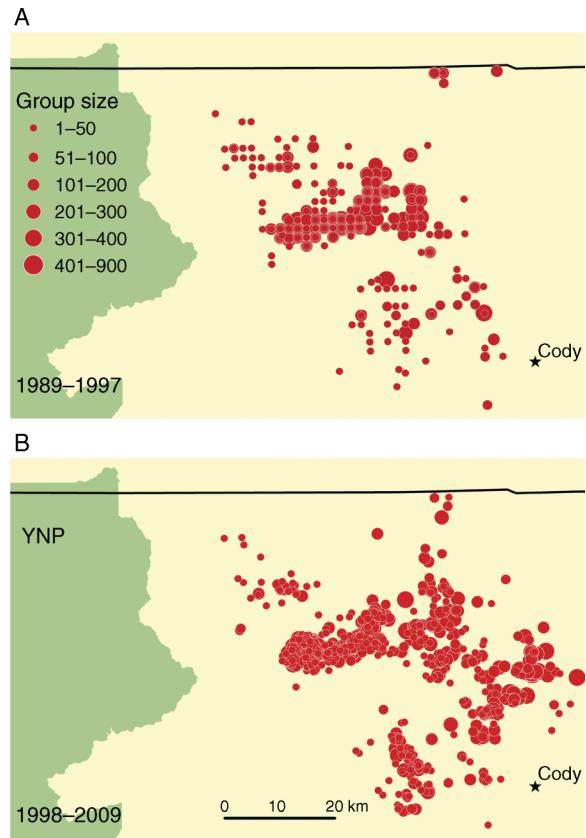


FIG. 1. Long-term spatial and group size distribution of the study population of elk (*Cervus elaphus*) as observed during winter recruitment surveys from (A) 1989–1997 and (B) 1998–2009. Linear regression of the weighted mean easting of each year's observations indicates an eastward distribution shift of ~ 18 km over 21 years ($F_{1,21} = 14.73$, $P < 0.01$). Note that the gridded appearance of the observations in panel (A) is a result of earlier observations being tied to the center of 1.6-km (one-mile) grids, prior to the use of GPS technology.

harsh summer conditions in the past decade or so (e.g., Barnett et al. 2008, Shuman 2011); for instance, during the latter half of our study period (1999–2008), severe drought was associated with a reduction from 1.7 to 1.3 million cattle supported on Wyoming rangelands (Associated Press 2009). When we saw evidence for a compressed vegetation green-up on the high-elevation summer ranges of migratory elk inside Yellowstone National Park (YNP), an area lately experiencing reductions in both elk density (Eberhardt et al. 2007) and winter severity (Wilmers and Getz 2005), we connected the low pregnancy rate of migratory elk partly to a drought-induced reduction in summer habitat quality.

Several of the commentators (Gaillard 2013, Wilmers and Levi 2013) were skeptical of our inference about the role of summer conditions, suggesting that we ignored a potential winter influence on elk condition, pregnancy, and recruitment. We did not present late-winter body fat data in our paper largely because of strong evidence that

summer conditions (not winter conditions) are the primary limitation on elk pregnancy rates (Cook et al. 2004, Cook 2011) and have recently grown more severe in the GYE. We did, nevertheless, collect late-winter body fat data. After accounting for autumn body fat (and individual effects) using generalized linear mixed models, we found that migratory and resident elk lost a similar amount of fat over the winter (migrants $8.4\% \pm 0.97\%$ [shown are mean \pm 95% CI], $n = 20$; residents $7.2\% \pm 1.14\%$, $n = 18$; $\chi^2 = 0.47$, $P = 0.49$; A. D. Middleton, M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, J. G. Cook, R. C. Cook, S. E. Albeke, H. Sawyer, and P. J. White, *unpublished manuscript*). By late winter, migrants were fatter (7.4%) than residents (5.1%) ($n = 78$, $t = 3.9$, $P < 0.001$). The late-winter body fat of migrants was high, and that of residents was average, relative to 19 other populations in the western United States (see Cook 2011, White et al. 2011). Further, the late-winter fat of migrants was well above levels associated with reproductive limitations (Cook et al. 2004). These data do not support the suggestion by Gaillard (2013) and Wilmers and Levi (2013) that winter conditions might explain differences in reproductive performance between the two subpopulations.

Two of the commentaries (Massey et al. 2013, Myrsterud 2013) discussed another alternative explanation for low elk pregnancy rates: a nonconsumptive effect (NCE) of wolves (Creel et al. 2007, 2009). However, empirical support for this mechanism has been contested by recent field study (White et al. 2009, 2011) and synthesis (Boonstra 2012). In our own study population (A. D. Middleton, M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, J. G. Cook, R. C. Cook, S. E. Albeke, H. Sawyer, and P. J. White, *unpublished manuscript*), neither fat levels nor pregnancy status were associated with the risk of wolf predation even though individual elk experienced 20-fold variation in their rate of encounter with wolves. Instead, strong carryover effects of autumn fat levels largely determined late-winter fat levels and pregnancy status (A. D. Middleton, M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, J. G. Cook, R. C. Cook, S. E. Albeke, H. Sawyer, and P. J. White, *unpublished manuscript*). The notion of a wolf-induced NCE is also at odds with evidence from other prey taxa that wide-ranging, coursing predators as the wolf do not induce strong NCEs on prey demography (Preisser et al. 2007, Schmitz 2008, Thaker et al. 2011). Multiple lines of evidence are at odds with the notion that wolves limit elk pregnancy rates in the GYE.

All these observations point back to a summer nutritional limitation as the most likely explanation for the low pregnancy rate of young and lactating migratory elk, but we recognize that the lack of a significant difference in the autumn body fat of lactating migratory ($10.5\% \pm 0.6\%$) and resident ($10.7\% \pm 0.5\%$) ($P = 0.76$) females is puzzling (Gaillard 2013). These levels of body fat are near a threshold below which failure to breed is more likely, and above which high pregnancy rates can

be expected (Cook et al. 2001, 2004). Given adequate summer nutrition, elk are capable of achieving 17–20% body fat by autumn in spite of lactation costs; thus, the autumn body fat of both subpopulations suggests marginal summer nutrition (Cook et al. 2004, Cook 2011). There is also evidence that short-term energy balance can have an important influence on pregnancy, independently of or in combination with body fat levels (Gerhart et al. 1997, Tollefson et al. 2010). Although body fat is widely assumed to be a direct physiological driver of ovulation in mammals and may play a “permissive” role (as modulated by the hormone leptin; Zieba et al. 2005), energy balance from three days to three weeks prior to breeding evidently drives ovulation (Bronson and Manning 1991, Molle et al. 1995, Scaramuzzi et al. 2006). In contrast, body fat levels result from cumulative energy balance over a longer time period, such as the previous one to four months. We observed a compressed period of green-up recently on the summer range of migratory elk, and hypothesize that a negative energy balance in late summer preceding the autumn rut reduced the conception (and pregnancy) rates of migratory elk, while resident elk were buffered by the availability of high-quality forage in irrigated fields. Future studies of climatic influences on migratory ungulates may benefit from considering a potential influence of energy balance on conception and early pregnancy, alongside better studied climatic effects on other life history events such as migration timing and parturition (e.g., Post and Forchhammer 2008).

As Myrsterud (2013) noted, climatic changes can influence the timing, duration, and spatial heterogeneity of the spring green-up on which migratory ungulates depend. Previous work by Post and Forchhammer (2008) suggested that the timing of spring migration and parturition in a caribou population had not advanced to match an earlier green-up, whereas our study suggests the potential for an overall shortening of the green-up period for migratory elk. Both patterns could be largely driven by changes in the spatial heterogeneity of spring snowmelt and plant emergence (Post et al. 2008), a mechanism that will be important to explore in the GYE. Although these localized studies point to mechanisms by which particular changes in the “green-up curve” might influence the reproduction of migratory ungulates, Myrsterud’s (2013) overview makes it clear that new research is needed to understand (1) whether migratory ungulates will face some forms of phenological change more generally than others; (2) which aspects of ungulate behavior (e.g., migration, parturition) and demography (e.g., fecundity, juvenile survival) will be most sensitive to phenological changes; and (3) to what extent behavioral flexibility will allow migratory ungulates to cope with those changes. A better predictive understanding of these issues will likely require longer term studies at larger spatial scales. The work of Post and Stenseth (1999) provides a classic example, primarily focusing on how winter climatic



PLATE 1. A grizzly bear in the Greater Yellowstone Ecosystem, USA. Wolves were reintroduced to Yellowstone National Park (YNP) in 1995, and wolf predation is widely perceived as the driver of elk population declines. Recent studies, however, indicate that grizzly bears are a much more frequent predator of neonatal elk in YNP. Grizzly numbers have grown substantially over the course of wolf recovery. Photo credit: Mark Gocke.

variation affects resident ungulate populations; our work (along with several of the commentaries) suggests a need for new research to evaluate the relative influence of summer phenology and winter climate on migratory populations.

Low pregnancy rate could explain only a fraction of the decline in recruitment among migratory elk. Assuming that the March pregnancy rate (0.71) carries forward to calving time around June 1, then the September calf:cow ratio (0.15), based on recent trend counts of migratory elk, suggests that >900 calves disappear over the summer months. Where do they go? Fortunately, two studies (Singer et al. 1997, Barber-Meyer et al. 2008) have

described patterns of elk calf mortality in a study area that included the summer range of the migratory elk, in study periods roughly spanning our own (late 1980s vs. mid-2000s). Predation by bears on elk calves more than tripled from the first to the second study, and bears (mainly grizzlies) became the leading cause of elk calf mortality. This increase in predation by grizzly bears matched a tripling of grizzly bear numbers over the same period on the range of the migratory elk. Thus, we inferred that grizzly bears (even in the midst of the “natural experiment” of wolf recovery) played the primary role in reducing migratory elk calf recruitment. Having reached this inference, we are not sure why

Massey et al. (2013) feel that “proponents of large elk herds in the vicinity of Yellowstone will use the results reported [by Middleton et al. 2013] as evidence that wolves are responsible for the decline of elk.” Bears are the primary predators of neonatal ungulates in many landscapes (Zager and Beecham 2006), and more than wolves, are thought to exert an additive influence on elk calf survival (e.g., Griffin et al. 2011), a key driver of elk population growth (Raithel et al. 2007). Our work adds to the number of studies that highlight a strong and growing influence of grizzly bears on migratory elk in the GYE (Barber-Meyer et al. 2008, Griffin et al. 2011, Fortin et al. 2013).

Though we focused primarily on understanding the decline in calf recruitment among migratory elk, we also noted that resident elk benefit from irrigated fields and relatively low numbers of grizzly bears and wolves. The commentary of Wilmers and Levi (2013) posits that growing competition from resident elk for winter forage causes poor nutrition, reproduction, and calf recruitment among migrants. However, the growth in resident elk numbers involved a dramatic eastward expansion into previously unoccupied habitat (Fig. 1). The winter ranges occupied by migrants and residents are ~20 km apart, and GPS collar data indicate only 10–15% overlap when some of the migrants move onto the resident elk range in mid-late winter. Thus, a key assumption in the model of Wilmers and Levi (2013), that of a shared carrying capacity on winter range, is not appropriate for our study population. Wilmers and Levi (2013) also show heavier use of irrigated fields during drought years as evidence for a competitive advantage of resident elk, but these data and analyses (see Fig. 2 in Wilmers and Levi 2013) center on a small area (~220 acres) located on the winter range of *migratory* elk that is not used by resident elk. Wilmers and Levi (2013) predict that competition from resident elk leaves migratory elk in worse condition by late winter, but migratory elk are in *better* condition by late winter, and we have documented a strong effect of autumn body fat on late-winter body that leaves little room for an effect of winter competition (A. D. Middleton, M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, J. G. Cook, R. C. Cook, S. E. Albeke, H. Sawyer, and P. J. White, *unpublished manuscript*; see also Cook 2011). Since there is no evidence for a competitive effect of resident elk on migrants, we suspect that the negative correlation between resident elk abundance and migratory elk recruitment presented by Wilmers and Levi (2013) simply tells us that resident elk numbers grew while migratory elk recruitment declined. Wilmers and Levi (2013) also assume in their model that the comparative absence of bears and wolves strongly benefits resident elk. We agree, but ultimately our inference relies simply on the direct costs to migratory elk of those same predators, rather than an indirect cost to migrants mediated by an unquantified degree of competition between residents and migrants. The model of Wilmers

and Levi (2013) will be useful where there is evidence that resident and migratory ungulates compete on winter range, but we see no evidence that this factor is currently important in our study area.

Ecologists understand migration as a strategy to gain high-quality resources while avoiding predation (Fryxell and Sinclair 1988, Fryxell et al. 1988). Our study is informative in this context because it suggests that transboundary differences in land use and large-carnivore conservation policy may effectively transfer the benefits of migration to residents (similar to Hebblewhite et al. 2005, 2006). Though partial migration with a fluctuating migrant:resident ratio is common among ungulates (Fryxell and Holt 2013, Gaillard 2013, Mysterud 2013), a long-term tendency for environmental change to favor residents (similar to what we have observed) could complicate the conservation and management of migration (Fryxell and Holt 2013). In their commentary, Massey et al. (2013) ask the provocative question, “Will central Wyoming elk stop migrating to Yellowstone, and should we care?” The model of Fryxell and Holt (2013) predicts that GYE elk will not stop migrating, but could be undergoing a long-term reduction in their relative abundance, whose extent will partly depend on the magnitude of declines in elk calf recruitment (Fryxell and Holt 2013). We cannot currently foresee whether ecological changes in the GYE will deepen declines in the recruitment of migratory elk, or how low recruitment might combine with other demographic changes to reduce the abundance of migratory elk. The migratory northern herd of Yellowstone has declined by >70% since 1995 (Northern Yellowstone Cooperative Wildlife Working Group, *unpublished manuscript*), which is more than many biologists expected in light of wolf reintroduction and human harvest alone (Barber-Meyer et al. 2008). Because YNP’s elk populations caused adverse ecosystem impacts for much of the late 20th century, many welcome elk declines as a return to a historical baseline. For example, Massey et al. (2013) “enjoy visiting areas where predators roam free and where ungulate numbers are low.” At the same time, the effect of predation on migratory elk may be increasing as anthropogenic disturbances including invasive species and potentially climate change deprive grizzly bears of other key diet items, such as cutthroat trout and whitebark pine seeds (Fortin et al. 2013), and we do not yet know if more frequent and severe drought will limit the reproductive rates of migratory individuals in the long term. Thus, while we expect migratory elk to persist in the GYE, it may be important to consider the possibility that migratory populations are not simply receding to their historical abundance and distribution.

Ecologists began to reveal the fitness benefits of ungulate migration a quarter-century ago, in the classic work of Fryxell and Sinclair (1988) and Fryxell et al. (1988). In the decades since, a number of important studies have elucidated how, and to what extent, animals

derive foraging benefits from migration (Albon and Langvatn 1992, Mysterud et al. 2001, Hebblewhite et al. 2008, Sawyer and Kauffman 2011). Our work demonstrates that even in a relatively undeveloped wilderness ecosystem, changing resource distributions and the partial recovery of large carnivores can combine to alter the benefits of migration. While these perturbations warrant conservation and management attention, close observation of their impacts can also enhance our understanding of the ecology of migration (see also Hebblewhite et al. 2005, 2006). Fryxell and Holt (2013) make it clear that current declines in migrant productivity portend a lower relative abundance, but not the loss, of migrants from the system. Wilmsers and Levi (2013) have provided a useful conceptual model to explore interactions among migrants and residents when their fates are linked via competition on shared seasonal ranges. Gaillard (2013) reminds us that individual fitness is the ultimate currency of migration's benefits, and that our work will be strengthened when we estimate all fitness components in migratory systems: A goal that can be more fully realized through the new long-term, individual-based studies sought by Massey et al. (2013). Mysterud (2013) has identified a critical need for progress in understanding how changes in vegetation phenology may affect migration. Collectively, these commentaries emphasize a singular challenge faced by all who study or manage migratory animals: To understand the effects of environmental change on a single population, we must integrate the nutrition, demography, and behavior of individuals across entirely distinct seasonal ranges and the migratory corridors that connect them (Bolger et al. 2008). Clearly, there remains a great deal of work to be done in the GYE and other systems, but these commentaries have highlighted many promising avenues forward.

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