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FORUM

Do irrigation and predator control reduce the productivity of migratory ungulate herds?

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Introduction

Migration in ungulates is thought to have evolved as a strategy to increase seasonal access to high-quality forage and to decrease predation risk. Where migratory and nonmigratory ungulates coexist, migrants can outnumber nonmigrants by an order of magnitude. However, migratory ungulates are now in decline worldwide due to anthropogenic factors. Middleton et al. (2013; hereafter referred to Middleton et al.) suggest that the productivity of migratory elk (*Cervus canadensis*) in the Greater Yellowstone Ecosystem, USA, is declining because of increased predation pressure and a contraction of the growing season in their high-altitude summer range. As an alternative hypothesis, we propose that irrigation and predator control at low elevations have increased the benefits of a nonmigratory strategy. We show that while migratory elk calf : cow ratios decline in drought years, resident elk calf : cow ratios do not respond to drought. This is likely because resident elk increase forage utilization on irrigated landscapes during drought years. Low-altitude nonmigratory elk now outnumber the migratory segment of the population. We hypothesize that the resulting increase in competition for winter range is responsible for the decline in the productivity of the migratory elk herd. Our hypothesis is equally plausible to Middleton et al.'s and is supported by data. We suggest that this debate is best resolved using experimental or meta-analytical approaches where multiple hypotheses are tested against one another. Wildlife managers should consider the potential impacts on migratory elk of predator control and elk irrigation programs.

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Background

Many of the world's most impressive wildlife displays are those of migratory ungulates. These animals enrich local communities by attracting tourists (Dobson 2009), are an important food source for local peoples (Gordon 2005), and play a dominant role in ecosystem function (McNaughton 1976). Many migratory ungulates have declined or are threatened, however, by anthropogenic disturbances such as overhunting, habitat loss, and migration barriers (Berger 2004, Bolger et al. 2008). Still other populations are, or might be, in decline for reasons that are unknown (Hebblewhite et al. 2006).

The evolution of migration in ungulates is thought to have arisen as a way to maximize the intake of high-quality forage and minimize the impacts of predation (Fryxell and Sinclair 1988). Most migratory ungulates inhabit ranges where food resources vary spatially in quality over the course of the year. By tracking changes in food quality, migrants have access to more easily digestible calories, proteins, and nutrients than residents and so can grow to larger population sizes. In areas where migratory and resident species coincide, such as wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*) in the Serengeti, migrants outnumber residents by 10–16:1 (Fryxell et al. 1988). In temperate environments, such as those that occur in the Rocky Mountains of North America, migrating species, such as elk (*Cervus canadensis*), track vegetation green-up

(Hebblewhite et al. 2008) by migrating to higher elevations in spring and summer and returning to lower elevation winter ranges in the fall.

In addition to gaining access to higher quality food, migration also allows ungulates to escape strong top-down control because predators cannot respond numerically to increases in migrant herd sizes. To do so, predators such as lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) in Africa, or wolves (*Canis lupus*) and pumas (*Puma concolor*) in North America would need to follow migrants year round, but are unable to do so because of altricial young (e.g., Heard and Williams 1992). Theory suggests that the ultimate factors driving migration alternate between predation and resource acquisition (Fryxell and Sinclair 1988). At small population sizes, resident ungulates are unlikely to be food limited, and so escaping predation is more likely to drive migratory behavior. At larger population sizes, however, food becomes limiting, and so seeking out higher quality food resources is more likely to drive migratory behavior.

Middleton et al. propose that an observed decline in the productivity of Yellowstone elk might be due to novel circumstances for a migratory ungulate: increased calf predation on their summer range relative to their winter range, and a contraction in the temporal availability of high-quality forage brought on by changes in climate. They focused their analysis on the Clark's Fork (CF) elk herd, which has a migratory component that winters in low-elevation areas to the east of Yellowstone National Park (YNP) and migrates to higher elevation lands in and around YNP during summer, and a resident component that resides year round at lower elevations. To support their hypothesis, Middleton et al. provide data showing decreased calf : cow ratios and pregnancy rates of migratory elk relative to resident elk. They also provide evidence showing that grizzly bear (*Ursus arctos*) and wolf populations have increased on the migratory population's summer range due to wolf reintroduction and grizzly bear population recovery.

We find the Middleton et al.'s hypothesis enticing, for it suggests two novel mechanisms that might increasingly influence the dynamics of migratory ungulates, but we remain skeptical because Middleton et al. do not consider alternate hypotheses to explain their data. Here we examine one alternative hypothesis in depth: That use by resident elk of irrigated landscapes, and predator control on resident ranges have led to an increase in resident elk that now compete with migrants over winter access to forage. We hypothesize that increased winter range competition with the growing resident elk herd has resulted in migratory elk in worse condition during and after winter, which has caused the observed declines in pregnancy rates and calf : cow ratios that Middleton et al. report. The availability of forage to elk in Yellowstone declines during the winter, causing elk to lose valuable fat reserves (Houston 1982). As such, winter range conditions can strongly limit elk population growth by reducing overwinter survival and/or reproduction (Delgiudice et al. 1991, 2001, Singer et al. 1997). Competition among resident and migratory elk for winter forage might thus represent a significant factor causing the decline of migratory elk calf : cow ratios. The resident and migratory components of the CF elk herd summer apart, but have overlapping ranges in the winter. Middleton et al. report that ~10–15% of their collared migratory elk commingled with residents during winter. In addition, the nonoverlapping portions of wintering resident and migratory elk are immediately adjacent to each other suggesting that migratory elk might use resident winter range, were it not already occupied by resident elk.

Here we used a simple resident–migrant competition model with predation to provide a conceptual framework for understanding both Middleton et al.'s and our hypotheses. The model captures the multiple interacting ecological factors influencing these elk, such as conditions on the summer range of each sub-herd, competition for winter forage, and varying levels of predation on migrant and resident ranges. By including these in a conceptual model, we can more formally understand the range of possible ecological drivers consistent with the data observed by Middleton et al. While herd-specific data on carrying capacities and predator attack rates are not currently available to parameterize the model, we show that the data collected by Middleton et al. on calf : cow ratios are consistent with both their hypothesis and ours. We then examine empirical evidence in support of our hypothesis. We conclude by suggesting that either a hypothesis testing or model selection framework across many elk herds with variable levels of irrigation and predator control is needed to resolve this debate.

Conceptual framework

To incorporate the distinct elk summer ranges and shared winter ranges into our model, we assume that the total carrying capacity, K, of each herd component is the harmonic mean of their summer and winter range carrying capacities given by

$$K_{\mathrm{R}} = \frac{K_{\mathrm{W}} + K_{\mathrm{RS}}}{K_{\mathrm{W}} K_{\mathrm{RS}}} \tag{1}$$

and

$$K_{\mathrm{M}} = \frac{K_{\mathrm{W}} + K_{\mathrm{MS}}}{K_{\mathrm{W}} K_{\mathrm{MS}}} \tag{2}$$

where K_{R} is the total carrying capacity of resident elk, K_{RS} is the summer carrying capacity of residents, K_{M} is the total carrying capacity of migratory elk, K_{MS} is the summer carrying capacity of migrants, and K_{W} is the winter carrying capacity, which is common to both herd components. We choose the harmonic mean because it emphasizes the influence of the season whose carrying capacity is most limiting and thus is more realistic for

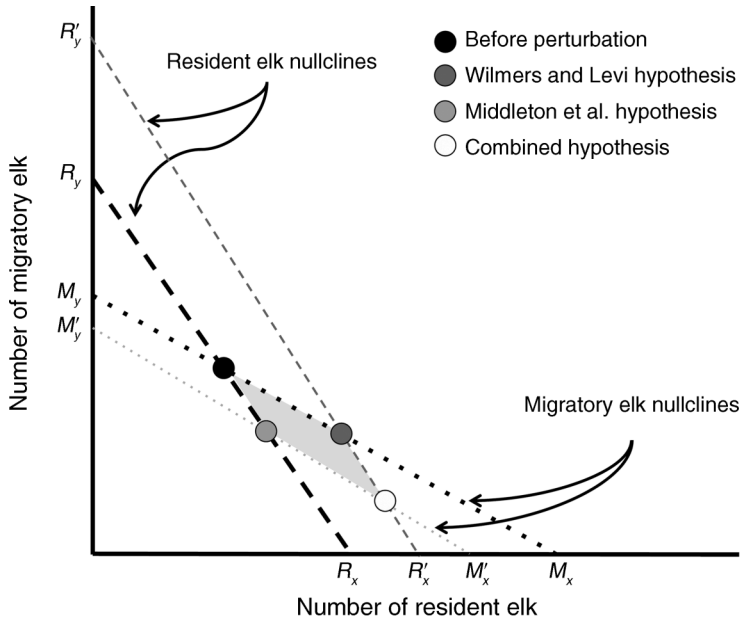

FIG. 1. Conceptual figure illustrating competition between resident and migratory elk based on the model described in Eqs. 3 and 4. If predation pressure increases and/or the summer carrying capacity of migratory elk decreases (Middleton et al. [2013] hypothesis), this results in a shift of the migratory elk nullcline down and to the left. Conversely, if the carrying capacity of the resident elk increases and/or predation pressure on resident elk decreases (Wilmers and Levi hypothesis), the resident elk nullcline shifts up and to the right. Both processes result in new equilibria with fewer migratory elk. The gray shaded area displays all possible combinations of the Middleton et al. (2013) hypothesis and our hypotheses. Axis intercepts are given by $R_x = [K_{RS}/(K_W + K_{RS})] \times (r - a_R P_R)$, $R_y = [K_{RS}/(K_W + K_{RS})] \times [(r - a_R P_R)/\alpha_{RM}]$, $M_x = [K_{MS}/(K_W + K_{MS})] \times [(r - a_M P_M)/\alpha_{MR}]$, and $M_y = [K_{MS}/(K_W + K_{MS})] \times (r - a_M P_M)$. Variable and parameter definitions are as described for Eqs. 1–4. The inclusion of a prime symbol (′) after the intercept indicates a shift in the nullcline due to implementation of one of the hypotheses.

modeling elk carrying capacity across the year than the arithmetic mean. The population growth rates of the resident and migratory components of the elk herd are modeled using logistic growth with Lotka-Volterra style (Lotka 1925, Volterra 1926) competition, but with predators also added to the model to allow for differential predation rates between migratory and resident ranges. The dynamics of resident and migratory elk are given by

$$\frac{dN_R}{dt} = rN_R\left(\frac{K_R - N_R - \alpha_{RM}N_M}{K_R}\right) - a_R N_R P_R \quad (3)$$

and

$$\frac{dN_M}{dt} = rN_M\left(\frac{K_M - N_M - \alpha_{MR}N_R}{K_M}\right) - a_M N_M P_M \quad (4)$$

where r is the intrinsic growth rate, N_R and N_M are the number of resident and migratory elk, α_{RM} and α_{MR} are the competitive effect on residents by migrants and vice versa, a_R and a_M are the predator attack rate on residents and migrants, and P_R and P_M are the number of predators in the resident and migratory ranges, respectively. We assume a linear functional response by predators to increasing prey for simplicity, but the qualitative results of our model are robust to a saturating functional response.

After solving for the nullclines of each model, it can be shown (Fig. 1) that the following conditions are necessary for coexistence of resident and migratory elk:

$$\frac{K_{RS}}{K_W + K_{RS}} \times (r - a_R P_R) < \frac{K_{MS}}{K_W + K_{MS}} \times \frac{(r - a_M P_M)}{\alpha_{MR}} \quad (5)$$

and

$$\frac{K_{RS}}{K_W + K_{RS}} \times \frac{(r - a_R P_R)}{\alpha_{RM}} > \frac{K_{MS}}{K_W + K_{MS}} \times (r - a_M P_M). \quad (6)$$

Data are not currently available to fully parameterize the model, but we can see graphically that, as the terms on the left hand side of Eqs. 5 or 6 increase and/or the terms on the right hand side of Eqs. 5 or 6 decrease, the equilibrium number of elk shifts towards more resident elk and fewer migratory elk (Fig. 1). This can occur because the carrying capacity K_{MS} of the migratory summer range decreases and/or the predation pressure $a_M P_M$ on the migratory range increases (the Middleton et al. hypothesis), or because the carrying capacity K_{RS} of the resident summer range increases and/or the predation pressure $a_R P_R$ on the resident range decreases (our hypothesis). These hypotheses are not mutually exclusive since all of these factors may be driving the reduced relative productivity of the migratory herd, but either hypothesis is sufficient to explain the data.

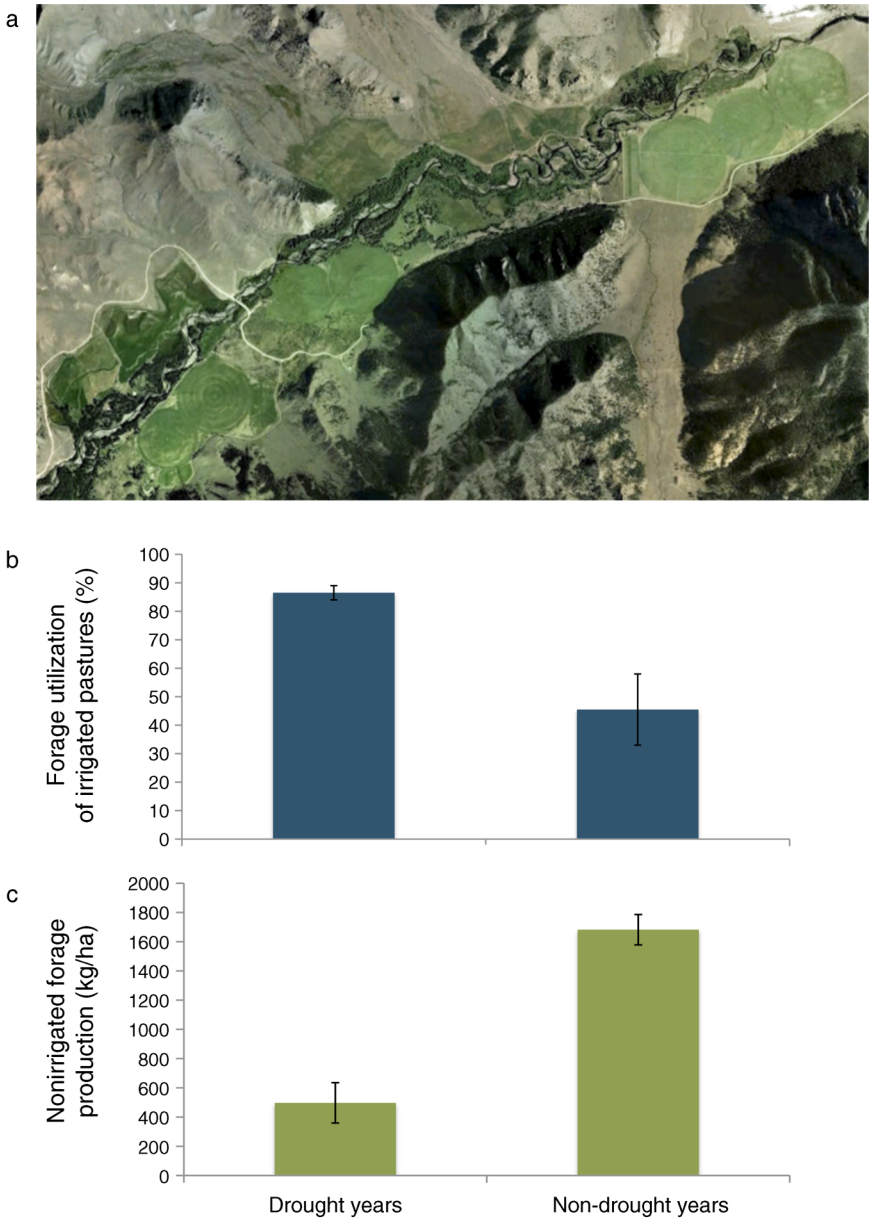

FIG. 2. Irrigation in the Greater Yellowstone Ecosystem is increasingly used as a management strategy to increase elk populations. (a) Areal image of the Sunlight Basin Wildlife Habitat Management Area, which is irrigated to increase forage production for elk. (b) Elk use this forage in all years, but particularly in drought years when (c) forage production from nonirrigated meadows declines dramatically (McWhirter 2009).

Empirical evidence

If irrigated landscapes are augmenting populations of resident elk, we would expect: (1) irrigation to increase browse production, (2) that elk use this resource, and (3) that it increases the productivity of their populations. Indeed, the evidence appears to support these expectations. While we did not evaluate its exact spatial extent within the Clark's Fork elk herd, irrigation for elk range improvements appears to be widespread in the greater Yellowstone ecosystem (GYE), including within the resident range of the CF elk herd (e.g., Fig. 2a). Elk are also known to feed in irrigated rangelands and fields intended for commercial crop production, though the extent to which they do so has not been quantified. Irrigation statistics from the Sunlight Basin Wildlife Habitat Management Area (SBWHMA), which provides irrigated and fertilized rangeland for the Clark's Fork herd, reveal that between 2006 and 2009, irrigated sites produced 1484–2597 more kg/ha of herbaceous matter than nonirrigated sites (McWhirter 2009).

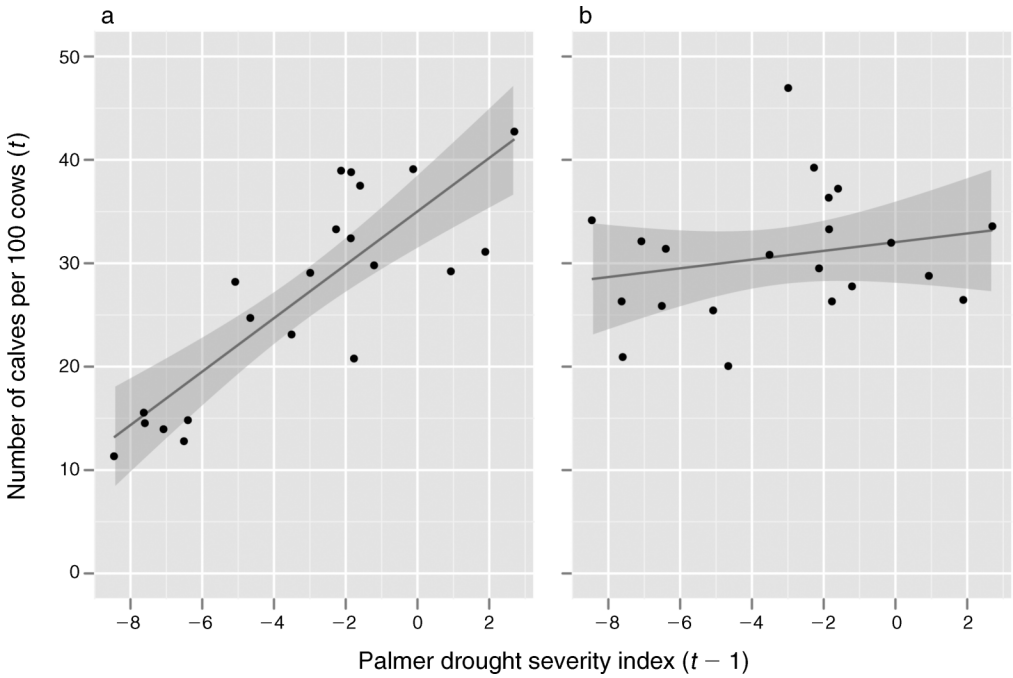

FIG. 3. Drought impacts in year $t-1$ on (a) migratory elk ($P < 10^{-5}$, $R^2 = 0.70$) and (b) resident elk ($P = 0.34$, $R^2 = 0.05$) calves per 100 cows in year t as indicated by linear regression (solid lines) and associated 95% confidence intervals (shaded area). The availability of irrigated meadows allows resident elk to largely avoid the negative impacts of drought relative to migratory elk.

In the SBHMA, elk utilized between 33% and 89% of the production from irrigated meadows in the four years reported (McWhirter 2009). Utilization of irrigated herbaceous production was much higher in the two drought years of 2006 and 2007 (84% and 89% utilization, respectively), when nonirrigated site production averaged only 691 and 415 kg/ha, respectively, than in the non-drought years of 2008 and 2009 (58% and 33% utilization), when nonirrigated site production averaged 1579 and 1786 kg/ha of forage, respectively (McWhirter 2009). Elk are thus utilizing irrigated herbaceous production in all years, while in drought years, they increase use of irrigated sites in order to offset reduced availability of forage in nonirrigated sites (Fig. 2 b, c).

By reducing natural variation in forage availability, the irrigated landscape insulates resident elk from the effects of drought. Under natural conditions, we would expect some elk to forgo reproduction during drought years because they lack the fat reserves to support pregnancy and/or a nursing calf. For our hypothesis to be supported, we would therefore expect migratory elk (but not resident elk) to display lower calf : cow ratios in drought years than in non-drought years. To test this, we regressed the number of calves/100 cows against the Wyoming Climate Division 1 Palmer Drought Severity Index (a regional index that uses temperature and rainfall information to determine levels of dryness) for both the migratory and resident components of the CF elk herd. As predicted, the calf : cow ratio of the migratory herd is severely impacted by drought (Fig. 3a), while the calf : cow ratio of the resident herd is not (Fig. 3b).

In addition to benefitting from the irrigated landscape, resident elk also appear to increasingly benefit from predator control programs. Since 2003, the year in which calf : cow ratios for the resident and migrant herds began to diverge (Middleton et al.), the per capita number of wolves killed in depredation actions in Wyoming increased dramatically (Fig. 4a; Jimenez et al. 2010) from an average of 7% of wolves killed per year in the years up to 2002, to 28% in the following years ($P < 0.01$), creating a differential in predation pressure between the two herds. Wolf removal rates (wolves killed/remaining wolves alive) of adult wolves in the Hoodoo, Sunlight, and Absaroka packs, which are sympatric with the CF elk herd, have reached levels as high as 23%, 71%, and 67%, respectively, from 2009 to 2011 (although annual mortality rates are highly variable). We did not evaluate trends in grizzly bear removals; however, parts of the resident range of the Clark's Fork elk occur within a hotspot of grizzly bear–human conflict, from which bears are frequently removed (Gunther et al. 2011).

As resident elk populations, maintained at high abundance by irrigation and predator control programs, increase, competition with migratory elk over the winter range is also likely to increase. This can occur if resident

elk either colonize whole areas that would otherwise be used by migratory elk, or if they reduce herbaceous biomass in areas currently used by wintering migratory elk. The most effective way to test this would be with large-scale manipulative experiments. In the absence of such a large-scale study, correlational evidence can be brought to bear. As food availability declines in large mammals, juvenile survivorship is the first life history stage to experience declines (Eberhardt 1977, Wilmers et al. 2007). Reduced access to winter forage for migratory elk due to competition with residents is thus expected to result in lower pregnancy rates and/or lower birth weight calves that are more vulnerable to predation. The result is a lower calf : cow ratio for migratory elk during summer. As hypothesized, resident elk population size has a highly significant negative effect on migratory elk calf : cow ratios ($P = 0.01$, $r^2 = 0.58$; Fig. 4b). This suggests that increasing competition among resident and migratory elk herds for winter range might be increasing across the ecosystem.

If a contraction of the growing season in the migratory range of the CF elk herd is a major cause of their declining pregnancy levels, as Middleton et al. suggest, then we would expect to find similar results for the Northern Range (NR) elk herd (Houston 1982), which has an overlapping summer range with the CF migratory herd. Yet we find the opposite to be the case. White et al. (2011) compared pregnancy rates and body condition of NR elk during a similar time period (2000–2006) as Middleton et al. to an eight-year period prior to wolf reintroduction, and found no decline in either pregnancy rates or body condition post wolf reintroduction. Importantly, the NR elk herd does not compete with a large resident herd as the CF migratory herd does. A very small resident herd does live in the Mammoth Hot Springs tourist area, where they forage extensively on irrigated lawns (T. Levi and C. C. Wilmers, *personal observations*), but the scale of irrigation is too small to support many elk.

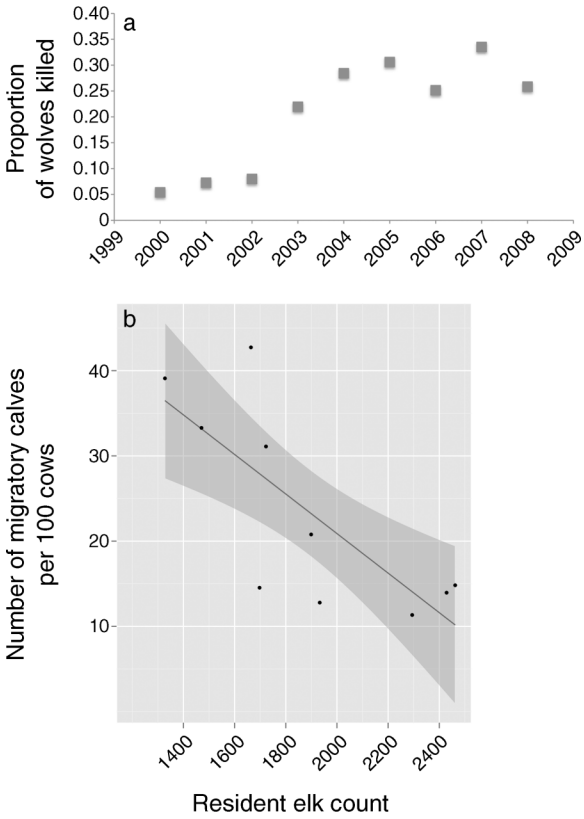

FIG. 4. (a) Proportion of wolves killed from 2000 to 2008 in management actions in Wyoming, USA. The dramatic increase in wolf control actions on elk resident ranges after 2002 coincides with the timing of diverging calf : cow ratios of migratory and resident elk reported by Middleton et al. (2013). (b) Linear regression (solid line) and associated 95% confidence interval (shaded area) showing the negative relationship between resident elk population size and migratory elk calf : cow ratios ($P = 0.01$, $r^2 = 0.58$).

CONCLUSION

We have presented an alternative hypothesis to Middleton et al. to explain the reduced productivity of the CF migratory elk herd. Namely, that increased competition with resident elk over access to winter range is primarily responsible for the decline in the productivity of the migratory component of the CF elk herd. This competition is likely fueled by increased irrigation and predator control at low elevation that supports an expanding resident elk population. We present a conceptual model to frame our ideas and provide support for our hypotheses by analyzing existing data. While our personal bias is to believe in our hypothesis over that of others, we are no more persuaded scientifically by our analysis than we are by that of Middleton et al. Other hypotheses might also explain the decline in productivity of the CF elk herd. For instance, differential responses to drought or predation alone might respectively explain the decline in productivity of the migratory herd relative to the resident one. We are reminded of Gould and Lewontin's (1979) cautionary paper in which they warn of the perils of telling "just so" stories that support one's own view of the world without considering alternative hypotheses. Like Middleton et al., we have presented persuasive correlational data in support of our hypothesis, but neither of us has formally tested one hypothesis against the other (or any other informative hypothesis for that matter). We can think of at least two ways, however, that these ideas could be scientifically tested. The first would be by experimentally manipulating each of the proposed causes of declining migratory elk productivity. This could be achieved by stopping irrigation and/or predator control in the range of resident elk, or by implementing predator control in YNP and/or irrigating high-altitude meadows used by summer migrants in drought years. Alternatively, and perhaps more realistically, a meta-analysis could be conducted on data from multiple elk herds that have different combinations of irrigation and predation

within their home ranges. Model selection could then be used to identify the best set of predictor variables or the relative model weight associated with each predictor (Burnham and Anderson 2002).

While elk herds throughout the Yellowstone Ecosystem (including the CF, but with the notable exception of the Northern Range herd) have mostly increased since wolf reintroduction (Cross et al. 2010), it is not well understood whether it is the resident or migratory components of these herds that are increasing. Given that migratory ungulates are critical to ecosystem function (Frank and McNaughton 1992, Holdo et al. 2009) and that irrigation and/or predator control programs might augment resident elk that compete with migratory elk, future research should examine whether expanding the policy of natural regulation (Huff and Varley 1999), whereby artificial nutritional support and predator control are reduced, from YNP alone to the whole ecosystem would benefit migratory elk.

Acknowledgments

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