Assessing fitness consequences of migratory tactics requires long-term individually based monitoring

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Migration is a behavioral response of individuals to the spatiotemporal variability of their environment across large spatial scales (Fryxell and Sinclair 1988). Migration has been reported in many vertebrate species living in seasonal environments and is interpreted as a tactic to maximize Darwinian fitness (Swingland and Greenwood 1983). By migrating, ungulates can both benefit from greater access to high-quality forage and escape from predators. For instance, Fryxell et al. (1988) observed that migratory ungulates outnumbered residents in savanna ecosystems of Africa mostly by escaping predation by large carnivores, while Hebblewhite et al. (2008) found that migrant elk (*Cervus elaphus canadensis*) had higher fecal nitrogen levels than residents. If such benefits indeed translate into fitness advantages, migrating should be the rule among ungulate populations in seasonal environments. However, in most populations of large herbivores studied so far, only a proportion of individuals migrate, whereas others remain resident. The role of environmental factors and individual attributes in shaping such partial migration is currently attracting attention among ecologists (Chapman et al. 2011). During the last decade, several studies have reported increasing threats to migrants. These threats include overhunting and restricted access to water or forage generated by habitat loss, competition with livestock, or fencing (Harris et al. 2009). Both a marked decrease in the propensity to migrate and rapid population collapse have been reported (Bolger et al. 2008).

Middleton et al. (2013; hereafter referred to as Middleton et al.) studied an elk population where migrants winter in wilderness areas and summer 40–60 km away in Yellowstone National Park (USA), all areas not subject to human disturbance. Despite the lack of habitat degradation or physical barriers caused by human activities, the proportion of migrants decreased from 81% in the late 1970s to the early 1980s to 47.5% in recent years. In parallel, the productivity of migratory females decreased over the last 20 years. Compared to resident females, young and lactating females engaging into migration had a lower reproductive output than their nonmigratory counterparts in recent years. The authors concluded that deterioration of summer range habitat induced by climate change and high predation by wolves (*Canis lupus*) and grizzly bears (*Ursus arctos horribilis*) in summer range account for the patterns observed. While this case study improves our understanding of ungulate migratory tactics by providing clear evidence for lower pregnancy rates of migrants compared to residents in the absence of human disturbance, it fails to either quantify fitness differences between migrant and residents or identify the contribution of factors involved in such differences. Three major limitations, common to most studies of fitness consequences of migratory tactics in ungulates, likely account for these shortcomings: high heterogeneity in data quality and temporal scale, strong assumptions, and the lack of long-term individually based data.

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*Heterogeneous data prevent the assessment
of the relationships among population productivity,
migration rate, and the relative performance
of migrant and resident elk*

Middleton et al. measured productivity from calf : cow ratios from aerial counts between 1989 and 2009. Assuming this rough index does provide a reliable picture of yearly variation in recruitment (but see Bonenfant et al. 2005 for potential problems related with this measure) and that a reliable identification of migrants vs. residents is possible, recruitment decreased through time and was similar in migrants and residents up to 2002. That pattern remains unexplained. Yearly variations in either vegetation index or predation pressure seem unrelated to the change in recruitment between the early nineties and 2002 (see Figs. 2 and 4 in Middleton et al.). From 2002 onwards, recruitment of migrants remained quite constant (~15 calves per 100 cows from 2002 to 2009), but recruitment of residents increased from 20 to 40 calves per 100 cows. That pattern seems to exclude maximum Normalized Difference Vegetation Index (NDVI) increment or green-up duration displayed in Fig. 4 of Middleton et al.'s paper as an explanatory factor, because these variables only changed for migrants, contrary to recruitment. Therefore, from the data available, there is no support to Middleton et al.'s interpretation that changes in vegetation phenology influenced the temporal variation of recruitment observed in either migrant or resident female elk. While predation pressure could account for the low recruitment of migrants, as discussed by Middleton et al., the twofold increase of recruitment between 2002 and 2009 for resident female elk cannot be explained by predation. Moreover, whether the marked decreased recruitment of migrants over two decades was associated with decreasing migration rates cannot be assessed from the data available. Indeed, the decreasing migration rate is simply deduced by comparing a study performed about 10 years before starting the recruitment monitoring (in 1979–1980) with the migration rate observed in recent years (2005–2009).

*Strong assumptions need to be relaxed
for a more comprehensive analysis
of migratory tactics*

In their study, Middleton et al. made two strong assumptions to assess the cause of migration. First, they excluded a priori any effect of winter range conditions and only focused on differences between the summer ranges of migrants and residents. Although the authors provided some justification for that assumption, previous studies of ungulates in northern temperate areas indicate that winter ranges should also be considered. For instance, a deterioration of winter range quality led to decreased calf production in migratory moose (*Alces alces*) in Norway (Andersen 1991). Likewise, poor quality and low abundance of winter forage reduced parturition rate and birth mass in caribou, *Rangifer tarandus* (Sharma et al. 2009). In the focal elk population, the spatial distribution of GPS locations of elk in Middleton et al.'s Fig. 1 clearly shows spatial differences in winter ranges between migratory and resident elk. Importantly, migratory elk seem to winter at higher elevation than residents. A test of whether winter habitat differences between migrants and residents were associated with contrasted patterns of variation in recruitment between migratory types would have been informative.

Second, as commonly done in analyses of migration, female elk were classified as either migrant or resident. However, migration, either from winter to summer ranges or from summer to winter ranges cannot be reduced to a single one-way movement. Advanced GPS-based technology (Cagnacci et al. 2010), reveals that movements between seasonal ranges include a continuum of movement patterns, from remaining in the same range (i.e., residence) to moving straight from one range to the next (i.e., migratory), separated by a gradient of movements from one seasonal range to the other. For instance, stopover sites on the migration route have been found in migratory mule deer (*Odocoileus hemionus*) in Wyoming (Sawyer and Kauffman 2011). Mule deer spent, on average, three weeks on stopover sites. Spending so much time in high-quality sites outside the summer range might influence the body condition of migrants, and thereby their reproductive performance, independently of resource available in summer ranges. Similarly, red deer (*Cervus elaphus*) in Norway used stopover sites when migrating (Bischof et al. 2012) from winter to summer ranges, and whether, or to what extent, elk in the population studied by Middleton et al. did the same might change the expected contribution of summer range conditions to reproductive performance of females. The use of stopover sites by female elk in Yellowstone could account for the constant reproductive output displayed by migrant elk despite deteriorating summer range quality between 2002 and 2009.

*Impossibility of assessing fitness consequences
of migratory tactics without long-term
individually based monitoring*

To my knowledge, there has been no quantification of the relative payoffs of migratory and resident tactics in terms of individual fitness. Only a few studies have addressed the link between fitness and habitat use or selection (see Gaillard et al. 2010 for a review). Several studies used metrics other than fitness to compare the relative benefits of migrating or not. For instance, population abundance, habitat quality, body mass, and reproductive performance all have been compared between migrant and resident ungulates (Fryxell et al. 1988, Hebblewhite and Merrill 2011, Middleton et al. 2013). Unfortunately, such metrics have not been monitored for long enough during the lifetime of focal individuals to provide reliable estimate of Darwinian fitness. Middleton et al.'s study is no exception, because

it used two short-term measurements of individual performance: age- and reproductive status-dependent pregnancy rates, and body fat. While pregnancy rates were markedly lower in migrants than in residents, especially for young and lactating females, lactating females had same body fat independently of migratory status, and non-lactating migratory females had higher body fat than non-lactating resident females. As possible among-year variation in performance of migratory and resident female elk was not accounted for, these conflicting patterns of variation between reproductive output and body condition do not allow any firm conclusion about the relative fitness of migrants and residents. Clearly, the covariation among reproductive output, body condition, and survival should be analyzed to assess the relative benefits of migrating or not. To do that, data on survival are required. For instance, in a recent analysis of another elk population, Hebblewhite and Merrill (2011) found that residents had higher survival, but lower pregnancy rates than migrants. A simple demographic model showed that population growth rate of migrants would be similar to that of residents. As the population growth rate corresponds to the average fitness of individuals (Fisher 1930), we can interpret these results as a first estimation of relative fitness of migratory and resident individuals. However, the possibility of a switch between migratory tactics for a given female was excluded. While neglecting within-individual variation in migratory tactic was justified by the data (<2% of cases; Hebblewhite and Merrill 2011, and no switch in Middleton et al.), this does not mean that all individuals have fixed migratory tactics. From an evolutionary viewpoint, we would expect individuals to adjust migration to the spatiotemporal distribution of resources by either tracking high-quality resources (Bischof et al. 2012) or avoiding poor-quality resources (Stien et al. 2010). Whether female elk switch between migratory tactics during their lifetime is a question that needs to be investigated to fully capture the evolutionary significance of migration tactics. While GPS monitoring offers highly detailed information on movements, it does not yet allow long-term monitoring of individuals. Most elk included in both Middleton et al. (2013) and Hebblewhite and Merrill (2011)'s studies were monitored for only a couple of years, yet most females in non-hunted populations could migrate 10 times or more during their lifetime. Duration of GPS monitoring closer to the lifetime of females is required to assess reliably the switching rate between migratory and residence and its evolutionary meaning for a given individual, especially in long-lived species like elk.

Migration is a crucial response to spatial variations of the environment, allowing individuals to "escape in space" (sensu Wiener and Tuljapurkar 1994) from variable environments in addition to other ways to "escape in time" (by, for instance, delaying development or reproduction; Tuljapurkar and Wiener 2000). While the fitness consequences of escaping in time have been investigated in long-term studies based on observations of recognizable individuals monitored over their entire life (Clutton-Brock and Sheldon 2010), we still lack such detailed monitoring for assessing fitness consequences of escaping in space by seasonal migrations. I call for such studies in the near future to fill the gap.

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