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Environmental change and the evolution of migration

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Perhaps the most difficult challenge in evolutionary biology is to "explain" existing patterns in light of environmental, genetic, and physical constraints (Gould and Lewontin 1979). The reason is obvious: Because we can only observe the resulting pattern, causes for the underlying process that produced that pattern will always prove elusive. Yet the mountains of data

accumulated by ecological and evolutionary studies linked with rapid environmental changes that have occurred over the past few decades now present a remarkable opportunity to witness evolution in action. Such is the opportunity hinted at by Middleton et al.'s (2013; hereafter referred to as Middleton et al.) paper comparing pregnancy rates and cow : calf ratios of resident elk (Cervus elaphus) living outside Yellowstone National Park (USA) to those of elk that migrate seasonally. The latter use montane areas during the summer months and lowland habitat similar to that of residents during the winter months. All other things being equal, their data suggests a substantial decline in

the rate of offspring recruitment of migratory elk, compared to that of residents, likely driven both by phenological changes and an upsurge in predation from large carnivores. This would suggest that there might be strong selection underway, disfavoring migration.

Here we present a minimalist demographic model intended to express the critical evolutionary elements that might apply to the Yellowstone elk. Our intent is to sketch out the essential features that might help to predict possible outcomes arising from the demographic patterns found by Middleton et al. As we argue in the *Discussion*, many of the underlying features that pertain to the Yellowstone elk recur in other migratory ungulates and a large fraction of other taxa, so our evolutionary arguments should apply more broadly.

THE MODEL

For simplicity, we considered the evolutionary dynamics of a generic ungulate species that lives in a world with two distinct habitats (termed A and B), and two distinct seasons in each habitat (winter and summer). Such conditions are common for many ungulate species, including elk. The model is deterministic, implying that we ignore the potential impact of both environmental and demographic stochasticity. The habitats are assumed to be far enough apart that an imposed perturbation in population density in one habitat does not at the same time alter fitnesses of individuals in the other habitat at the same time. We considered the relative fitnesses of morphs with different alternative movement "strategies," which are assumed to breed true. Moreover, we assumed that the fitness over a complete annual cycle of a morph is determined by the product of offspring recruitment in its summer habitat and survival in its winter habitat (and survival during migration for migrating morphs).

To explore the evolutionary consequences of changing conditions imposed by climate alteration or major changes in ecological interactions, we will use a simple, but not unrealistic, demographic model for a population of ungulates which we assume is naturally regulated by density-dependent recruitment of offspring. We also assumed that habitats vary in their intrinsic quality, as frequently observed in many studies of ungulates (Sæther 1997, Gaillard et al. 2000). Offspring recruitment in both habitats is given by a Ricker (1954) formulation, with density dependence arising from the summed density of all behavioral types that are found in a given habitat. We assumed that winter survival is insensitive to changes in density, which is also often the case for many long-lived ungulates (Sæther 1997, Gaillard et al. 2000). We can accordingly represent morph dynamics with the following system of equations:

$$N_1(t+1)$$
$$= N_1(t) \times \exp(r_A \times [1 - N_1(t) - N_3(t)] - s_A) \quad (1)$$

$$N_2(t+1) = N_2(t) \times \exp(r_B \times [1 - N_2(t)] - s_B) \quad (2)$$

$$N_3(t+1)$$
$$= N_3(t) \times \exp(r_A \times [1 - N_1(t) - N_3(t)] - c - s_B) \quad (3)$$

where $\exp(r_j)$ is the maximal per capita recruitment in habitat j during the summer, $\exp(-s_j)$ is the winter survival probability in habitat j (s_j is a measure of mortality), $\exp(-c)$ is the survival rate during migration (c is migration's demographic "cost"), and $N_i(t)$ is the population density of behavioral morph i at time t. In this formulation, morphs 1 and 2 are year-round residents of habitats A and B, respectively, and morph 3 individuals spend the summer in habitat A (assumed to be the most productive habitat), but migrate to spend the winter in habitat B (assumed to offer the highest survival). We have scaled density so that if survival is guaranteed through the winter, carrying capacity (viz., equilibrial density) is unity. Morphs that co-occur are competitively equivalent, as measured by density dependence in offspring recruitment.

If morph 3 is absent, equilibrium values for N_1 and N_2 can be found be setting $N_i(t+1) = N_i(t) = N_{i,eq}$ in Eq. 1 and Eq. 2, which give $N_{1,eq} = 1 - s_A/r_A$ and $N_{2,eq} = 1 - s_B/r_B$ (persistence of morph 1 requires $r_A > s_A$ and that of morph 2 requires $r_B > s_B$). At this equilibrium, morph 3 can increase when rare if and only if $c + s_B < s_A$ (the condition for the exponent in Eq. 3 to be greater than 0 with $N_1(t) = N_{1,eq}$ and $N_3(t) = 0$). If this is true, morph 3 eliminates morph 1 and reaches an equilibrium of $N_{3,eq} = 1 - (c + s_B)/r_A$, whereas density of morph 2 is unchanged.

If resident herbivores can stably persist in each habitat without movement between them, and those two habitats experience seasonal variation in conditions, then a mixture of resident and migratory strategies will always be the evolutionarily stable strategy (ESS; Holt and Fryxell 2011). To better understand this, consider an example, hypothetically framed around Middleton et al.'s elk study in Yellowstone. Let us assume that the montane environments of Yellowstone provide a higher maximum recruitment than do the lower elevation landscapes outside the park, possibly because of a better supply of high-quality vegetation with green-up at high elevations. This is commonly observed in montane ungulate species (Pettorelli et al. 2005). Such a scenario could be well depicted with the following demographic parameters, where A refers to Yellowstone and B refers the areas outside Yellowstone: $r_A = 0.45$ and $r_B = 0.30$. These values are roughly consistent with maximum recruitment rates observed in the neighboring Jackson Hole elk herd (Boyce 1989). Yellowstone elk probably experience higher predation risk due to higher carnivore densities inside than outside the park. We accordingly assumed decreased winter survival in the park relative to that in outlying areas, such that $s_A = 0.357$ and $s_B = 0.223$, implying survival rates of 70% vs. 80%, parameter values which should be realistic for a mix of adult and juvenile ungulates (Gaillard et al. 2000).
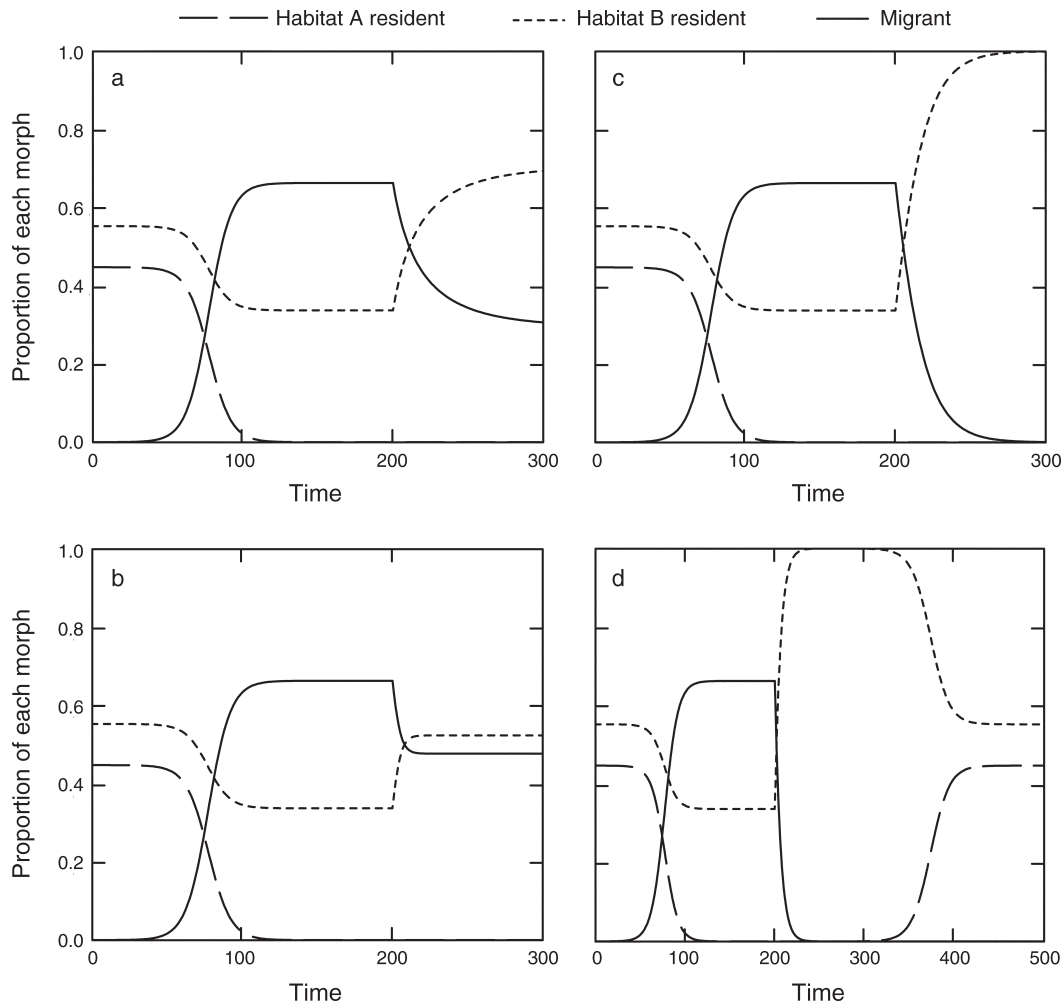
FIG. 1. Variation over time (unitless) in the relative frequency of behavioral genotypes in a model system with resident ungulates that live year-round in two distinct habitats (A and B) and migratory ungulates that shift seasonally between the habitats, spending summer in A and winter in B. Habitat A is initially best during the growing season, whereas habitat B is best during the nongrowing season. In all four simulations, conditions greater than time = 200 favor migratory behavior ($r_A = 0.45$, $r_B = 0.30$, $s_A = 0.357$, $s_B = 0.223$, $c = 0.0$). At time = 200, environmental conditions change. For panel (a), the maximum rate of offspring recruitment in habitat A declines slightly ($r_A = 0.25$), for panel (b), the maximum rate of offspring recruitment in habitat B increases slightly ($r_B = 0.50$), for panel (c), the maximum rate of offspring recruitment in habitat A declines severely ($r_A = 0.15$), and for panel (d), the cost of migrating between habitats increases severely ($c = 0.40$). Demographic rates expressed in exponential form are referred to as r, s, and c, such that $\exp(r_j)$ is the maximal per capita recruitment in habitat j during the summer, $\exp(-s_j)$ is the winter survival probability in habitat j (s_j is a measure of mortality), and $\exp(-c)$ is the survival rate during migration (c is migration's demographic "cost").

Using these results, these parameters imply an equilibrium density of 0.21 for resident elk inside the park, compared to 0.26 for resident elk living outside the park. Under equilibrium conditions, seasonal fitness in habitat A would fluctuate between $\exp(r_A[1-N_{1,eq}]) = 1.43$ in the growing season and $\exp(-s_A) = 0.7$ in the nongrowing season, so fitness over the year would be the product of these two seasonal values ($1.43 \times 0.7 = 1$). Although offspring recruitment is lower at equilibrium in habitat B, such that $\exp(r_B[1-N_{2,eq}]) = 1.25$, animals residing there enjoy a more benign environment in the winter, such that $\exp(-s_B) = 0.8$, implying an annual fitness of $1.25 \times 0.8 = 1$.

A mutant migratory genotype that resided in habitat A in the summer, but moved outside the park into habitat B during the winter would have an annual growth rate when rare of $1.43 \times 0.8 = 1.14$ (assuming no cost of migration), so it would be selected and increase when rare ($t < 200$; Fig. 1). In other words, this mixture of habitats would favor the evolution of migration into and out of the park. By the same token, in this example, nonmigratory morphs still persist outside the park, leading to mixture of individuals, some that migrate to the best habitat available in the season without density dependence (in this example) and others that specialize on a single habitat ($t < 200$; Fig. 1). Such a mixed

strategy is inevitably favored unless both habitats are sinks for resident animals. This might be considered a reasonable, if crude, depiction of elk movement strategies up until the 1970s in and around Yellowstone.

We now consider how major ecological changes or climatic perturbation of the type described by Middleton et al. might influence future evolutionary changes. First, we consider the hypothesis that hotter summer temperatures reduce the nutritional benefits of foraging at high elevation. This would have the effect of reducing the maximum recruitment rate of Yellowstone (habitat A), while having little impact on the maximum recruitment rate at lower elevations (habitat B). Reduction in r_A would inevitably reduce equilibrium abundance of the morph that uses the montane habitat (the migrants in Fig. 1a). However, migrants should continue to tend to persist alongside an increased proportion of individuals resident outside the park.

There is a threshold level of r_A at which migrants cannot persist ($r_A < s_B + c$), because fitness over the entire annual cycle <1. As a result, continuing decline in maximum recruitment rate would lead to the disappearance of migration, with only resident elk continuing to persist (Fig. 1c). It is currently impossible to tell whether the Yellowstone elk situation has reached such a stage, but a simple litmus test would be to compare the product of rates of recruitment in the park and survival outside the park.

An alternative interpretation of the existing data, however, would be that the cost of migration has increased because of increased predator density along migration pathways. This is not implausible: Work conducted in Banff National Park has demonstrated that migrating elk are exposed to high rates of predation to and from their summer range at high elevations (Hebblewhite and Merrill 2007, 2011, Hebblewhite et al. 2008). This would of course impose an additional cost (c) on our calculation of Malthusian fitness. As in the previous case, a minor increase in costs would only alter the ratio of migrants to residents. At a point where $r_A < s_B + c$, however, a new ESS emerges, with migrants being replaced by residents in the better summer habitat A to match the continued residents in habitat B (Fig. 1d). That is, at a certain level of additional demographic cost, residency in each habitat yields the highest fitness. Such an outcome is possible because there has been no reduction in the intrinsic fitness of habitat A, only in the fitness of animals that have to traverse both ways through unfavorable matrix habitat. Whether this is an important possibility can only be answered by comparing the annual survival of migratory elk and resident elk outside the park. Since they spend the most challenging season of the year in the same habitat, any difference is most likely explained by escalating costs of migration.

Finally, there is another possible explanation hinted at by the demographic data gathered by Middleton et al. That is, novel agricultural subsidies may have improved the maximum recruitment rate of residents living outside the park (r_B). Comparable to a decline in recruitment rates inside the park, such a subsidy would increase the equilibrial ratio of residents to migrants (Fig. 1b), but would not threaten the long-term viability of migration as a behavioral strategy (which requires only that $r_A > s_B + c$). If agricultural subsidies simply improved winter survival rates, this would have little impact on the existence of a mixed ESS. If this increase in reproduction translated into an increase in the density of resident elk in the winter, this could magnify density dependence experienced by the migratory elk, and help contribute to their ongoing continued decline. Such density dependence outside the breeding season is not included in our model, but is likely to occur in some migratory systems, and would provide an additional realistic mechanism helping to disfavor migration in this system.

DISCUSSION

Migration is ubiquitous in the natural world. It has evolved multiple times in multiple taxa throughout evolutionary history (Dingle 1996, 2006, Cresswell et al. 2011). While each system offers variations on the same fascinating theme, at least two obvious commonalities emerge: All migratory populations are exposed to substantial variation in environmental conditions both on a seasonal basis, and across broad geographic gradients. As a consequence, any model of evolutionary dynamics of migration requires a specification of both seasonality and spatial structure, and density dependence (Lack 1968, Cohen 1976, Lundberg 1987, 1988, Kaitala et al. 1993, Parvinen 1999, Heino and Hanski 2001, Kokko and Lundberg 2001, Griswold et al. 2010). The model we use here is stripped of all but the barest of essentials: two habitats and two seasons, with simple demographic rules of change imposed in each season. Nonetheless, this minimalist representation is consistent with the characteristics of herbivore migration in many instances (Fryxell and Sinclair 1988a, Schick et al. 2008, Mueller and Fagan 2008).

For example, seasonal migrations of barren-ground caribou encompass a vast annual range, but within their annual circuit, caribou demonstrate repeated patterns of use of summer and winter ranges (Mueller et al. 2011). Migratory wildebeest in the Serengeti ecosystem travel from open grasslands used during the peak of the wet season to more heavily wooded savannahs used during the dry season (Maddock 1979, Holdo et al. 2009). White-eared kob in the Sudan exhibit similar seasonal shifts between wet and dry season ranges (Fryxell and Sinclair 1988b). In more mountainous regions, a similar dichotomy is retained. North American mule deer (*Odocoileus hemionus*), elk, and pronghorn antelopes (*Antilocapra americana*) often migrate between lowland winter ranges and montane pastures favored during the summer (Berger et al. 2006, Hebblewhite and Merrill 2007, 2011, Hebblewhite et al. 2008, Monteith et al. 2011, Sawyer and Kauffman 2011). Reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), and moose (*Alces*

alces) often exhibit similar migrations across elevation gradients in Scandinavia (Albon and Langvatn 1992, Mysterud et al. 2001, Mysterud 2011), with traditional summer and winter ranges used on a periodic basis. In other words, two habitats in two seasons is often not far off the mark.

While simplistic, it is also not unrealistic to decompose annual growth rates of many herbivore species into summer or wet-season episodes of offspring recruitment and winter or dry-season survivorship. There is substantial evidence of density-dependent patterns of offspring recruitment in large herbivores (Sæther 1997, Gaillard et al. 2000), including Soay sheep (Coulson et al. 2001), wildebeest (Mduma et al. 1999), and elk (Coughenour and Singer 1996). It is far less common to find evidence of pronounced density-dependent survival of individuals older than young of the year, although it certainly can occur in some cases (Mduma et al. 1999). Hence, our choice of seasonal alternation between density-dependent recruitment and density-independent survival perhaps is not too violently out of line with the usual circumstances.

Our model predicts that if both habitats are sources (i.e., resident populations would be sustainable, at least in principle) and both have different fitnesses, then a mixture of resident and migratory genotypes (termed "partial migration") should often occur (Holt and Fryxell 2011). There are numerous examples of this, including Serengeti wildebeest (Maddock 1979), pronghorn antelope (White et al. 2007), and elk (Hebblewhite and Merrill 2007, 2011, Hebblewhite et al. 2008). Indeed, the conditions favoring partial migration are so general that it should be regarded as the norm rather than the exception.

In light of this, Middleton et al.'s study provides a fascinating glimpse into the circumstances under which herbivore migration might unravel. Their finding that migratory elk in eastern Yellowstone have experienced declines in reproductive rates and offspring recruitment relative to resident elk outside the park suggests that recent changes in demography may signal major evolutionary changes. Such examples of novel evolutionary challenges to migratory herbivores are not unheard of (Cresswell et al. 2011). For example, Hebblewhite et al. (2005) showed how reinvasion of gray wolves into the Bow Valley in Banff National Park led to substantial changes in elk spatial distribution, with a large fraction of the elk population becoming resident in the Banff town site, rather than migrating up and down the elevation gradient as they had just a decade before.

Our model suggests that the kinds of demographic changes observed by Middleton et al. could indeed result in the long-term disappearance of migratory elk. The evolutionary outcome, however, might well depend on the precise demographic cause for the observed changes. For example, our model predicts that enhanced recruitment of the population resident outside the park via agricultural subsidies is unlikely to make pure residency the ESS. This can only happen if it is accompanied by severe decline in recruitment in the park, either because of reduction in maximum recruitment via declining feeding opportunities or increased cost of migration due to higher predator densities en route. If resource shortage is responsible for the observed changes, it is conceivable that migration would disappear as a behavioral strategy, provided the decline is severe enough that Yellowstone becomes a strong sink for elk, in which case, resident elk would not be viable either within the park. On the other hand, elevated costs of migration due to increased predator densities could shift the evolutionary outcome to resident, but viable, elk populations inside as well as outside the park. The viability of these resident subpopulations depends in turn on the stability of local predator–prey interactions.

A full evolutionary model of the shifting pattern of migration in Yellowstone elk would, of course, be considerably more complex than the one we have sketched here. For instance, one would want to make more realistic assumptions about the genetic basis of migratory behaviors, incorporate assumptions about the reproductive linkages and demographic exchanges between migratory and nonmigratory subpopulations, and consider the implications of shifting age structure. One would also want to examine continuous rather than discrete spatial structures for the landscape, and density-dependence occurring in both seasons (as may pertain to elk; M. Boyce, *personal communication*). It might well prove fruitful to consider partial migration of elk as a facultative decision, with individuals choosing sometimes to migrate and other times to remain resident (Middleton et al. 2013), depending on environmental variables, population density, and internal condition relative to genetically determined thresholds (Chapman et al. 2011, Mysterud 2011, Pulido 2011). Nonetheless, our model results, and the stimulating study by Middleton et al., suggest that altered migration patterns are likely to be ubiquitous features of our rapidly changing world.

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