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Prevalence and Mechanisms of Partial Migration in Ungulates

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Partial migration, a phenomenon wherein only some individuals within a population migrate, is taxonomically widespread. While well-studied in birds and fish, partial migration in large herbivores has come into the spotlight only recently due to the decline of migratory behavior in ungulate species around the world. We explored whether partial migration in ungulates is maintained at the population level through frequency-dependence, an environmental-genetic threshold, or a conditional strategy. Through a review of studies describing individual variation in migratory behavior, we then addressed how density-dependent and -independent factors such as social constraints, competition for forage, and escape from predators or pathogens, alone or together, could lead to occurrence of both migrants and residents within a population. We searched for evidence that intrinsic and extrinsic factors could combine with genetic predispositions and individual differences in temperament or life experience to promote migratory tendencies of individuals. Despite the long-held assumption for ungulates that migration is a fixed behavior of individuals, evidence suggested that flexibility in migratory behavior is more common than previously thought. Partial migration maintained by a conditional strategy results in changes in movement tactics as state-dependent responses of individuals. Data are needed to empirically demonstrate which factors determine the relative costs and benefits to using migratory vs. resident tactics. We outline what types of long-term data could address this need and urge those studying migration to meet these challenges in the interest of conserving partially migratory populations.

Keywords: ungulate, partial migration, density-dependence, frequency-dependence, condition, review

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INTRODUCTION

Dramatic declines in populations of migratory ungulates and the disappearance of migratory behavior in many ungulate species are now recognized as a global conservation challenge (Berger, 2004; Bolger et al., 2008; Tucker et al., 2018). Population reductions have been well-documented in migratory species ranging from antelope (*Antidorcas marsupialis*, Child and Le Riche, 1969; *Saiga tatarica*, Milner-Gulland et al., 2001) and buffalo (*Syncerus caffer caffer*, Bennitt et al., 2016) to wildebeest (*Connochaetes taurinus*, Gasaway et al., 1996) and zebra (*Equus burchelli antiquorum*, Bartlam-Brooks et al., 2013). Loss of migratory behavior in ungulates is attributed primarily to human-induced changes to landscapes, which may be exacerbated by climate change (Lendrum et al., 2013). Loss of migration can have significant ecological impacts, potentially resulting in collapse of whole ecosystems, extending from alteration of plant composition and ecosystem processes such as grassland production and nitrogen mineralization (McNaughton et al., 1988; Frank, 1998; Holdo et al., 2006), to declines in other species including apex predators (Packer et al., 2005; Lee et al., 2016), to loss of wildlife tourism-based dollars normally used for environmental protection of Africa's most iconic species (Harris et al., 2009; Holdo et al., 2011). Given the potential severity of these ecological impacts and their associated economic consequences, identifying the processes that lead to migratory behavior should be a primary focus of biodiversity research and conservation efforts to address the loss of migration in ungulate populations (Bolger et al., 2008).

Migratory movements of individuals are expected to arise in variable environments wherein ungulates migrate to enhance lifetime reproductive fitness by gaining access to critical resources such as nutrients or water, reduce their likelihood of predation, or escape parasites (Fryxell and Sinclair, 1988a; Mysterud et al., 2011, 2016; Qviller et al., 2013). However, anthropogenic disturbances and environmental changes have sometimes altered the relative benefits of migrating in large herbivores to make residency more profitable (Berger, 2004; Hebblewhite et al., 2006; Jones et al., 2014). Partial migration is a population-level phenomenon in which a population is comprised of both resident and migrant individuals (Chapman et al., 2011a). Partial migration has become a focus for studies on ungulates only recently, and is presumed to result from trade-offs between the costs and benefits of migration (Eggeman et al., 2016). Although several studies have described the pattern of partial migration, the underlying ecological processes, which we review below, for maintaining partial migration are theoretical or empirically correlative. Experimental manipulations needed to identify mechanisms driving migratory tendency in large mammals may be unethical and are difficult (but see below), which creates an urgent need to better synthesize existing information on partial migration in ungulates. A better understanding of the worldwide decline in migratory behavior of ungulates will offer directions for future studies and inform associated conservation actions (Bolger et al., 2008).

We explore this topic with a review that begins by defining migrant and resident behavior in the context of partial migration. We then review the evidence for population-level mechanisms described by others to explain why partial migration occurs and is maintained in diverse populations of ungulates that inhabit variable environments. We explain how changes in proportions of migrants and residents within populations might occur both across generations, through either a frequency- or density-dependent fitness equilibrium, and within generations, via behavioral switching between migrant and resident behavior by individuals. Then we review the factors operating on individuals that might promote migration vs. residency. We focus primarily on genetic variability, social interactions and cultural inheritance, intrinsic factors such as age and nutritional condition, and extrinsic or environmental factors such as forage and predation risk. We conducted the review by searching the published literature for all ungulate species listed in Ultimate Ungulate (Huffman, 2018) and by Groves and Grubb (2011) within the orders Perissodactyla (odd-toed ungulates) and Cetartiodactyla (even-toed ungulates). We used "Web of Science" and "Google Scholar" search engines to find articles by the common and Latin name and/or genus in combination with "migra*," "resid*," "partia* migra*," "facultative migra*," or "conditional migra*." In particular, we retained any article that described partial migration (i.e., the article needed to state that a portion of the population remained resident/sedentary, and another portion of the population migrated, irrespective of the form of migration observed) and addressed or speculated on the reasons behind the observed differences in migratory behavior. We chose not to include gray literature due to variability in data types and rigor. The hypotheses we evaluated are not mutually exclusive and two or more proximate mechanisms for migration are likely to operate simultaneously (Ketterson and Nolan, 1983; Smith and Nilsson, 1987; Avgar et al., 2014). The review focused on migration in female ungulates because adult female survival is thought to have the greatest influence on large ungulate population dynamics (Gaillard et al., 1998; Raithel et al., 2007) and because few articles concentrated on males or compared factors affecting migratory behavior between the sexes; we included migratory tendency in males if new mechanisms arose and there were adequate data (see **Supplementary Tables 1**, **2**). We end by challenging researchers to collect the long-term data necessary to test the mechanisms underlying maintenance of partial migration to bring us closer to conserving ungulate populations in the face of ongoing environmental change.

WHAT IS A MIGRANT?

Migration as a phenomenon is not easy to define because of variation in both terminology and types of animal movement among taxa (Sinclair, 1983; Fryxell et al., 2011). The term migration is also used differently when it is applied to individuals vs. populations (Dingle and Drake, 2007; Dingle, 2014b). In either context, associating migration with a trait or a behavioral syndrome (*sensu* Sih et al., 2004) requires that migration responds to natural selection (Dingle, 2014b), but it may do so as part of a correlated suite of behavioral, physiological, or life history traits (Réale et al., 2010). In this review, we define migration as a behavioral tactic (*sensu* Dominey, 1984; Gross, 1996; Dawkins, 1999) describing a movement type that is exhibited by individuals (**Table 1**). We call it a tactic, rather than assume it is a genetically fixed strategy (*sensu* Maynard Smith, 1982) because of the information we synthesized during our review (below). Consistent with this definition as a tactic, the migratory tendency of an individual could be rigid and result from conditions during a key developmental window (i.e., phenotypic plasticity or reaction norm) or change over time (i.e., ongoing behavioral flexibility; Piersma and Drent, 2003). We explore the evidence for these mechanisms below.

Additional confusion about the meaning of migration stems from spatial definitions. Ungulates are among the taxa for which migration is thought to be movement, most commonly, but not always, as a round-trip between discrete seasonal ranges (Sinclair, 1983; Fryxell and Sinclair, 1988a). The spatiotemporal separation between ranges and the emphasis on return movement makes migration different from: (1)

TABLE 1 | Definitions of words used in discussion of migration in ungulates.

Dispersal	Movement of individuals between populations, primarily for reproduction-related purposes (McPeek and Holt, 1992)
Frequency-dependence	A phenotype's fitness depends on its frequency and those of the other phenotypes within the population
Migratory	Individuals that undertake regular movements between discrete seasonal ranges, usually (but not always) as round-trips, and often in systems with predictable spatiotemporal variation in resources; even in cases when migration is considered relatively short (<10–50 km), areas used in different parts of the year do not overlap or are not adjacent, as occurs in range residency (see below)
Net squared displacement	Distinguishes migration from other movement by measuring the straight line distance between animal's point of departure and subsequent locations (Börger et al., 2011; Bunnefeld et al., 2011; Singh et al., 2016)
Nomadism or roaming	Broad-scale, temporally unpredictable landscapes (Mueller et al., 2011; Singh et al., 2012) support animals roaming, moving through, or occupying different ranges with no distinct pattern; Mongolian gazelles take advantage of changing conditions through lack of consistent range use (Olson et al., 2010)
Partial migration	Demonstrated by within-population behavioral dimorphism in migratory tendency, so one fraction of the population is migratory while the other is sedentary (Lundberg, 1988; Chapman et al., 2011a)
Residency	Individuals reside in areas that are relatively small compared to the overall range of the larger population (Mueller et al., 2011); areas used throughout the year overlap or are immediately adjacent and cannot be subdivided into seasonal ranges
Strategy	Set of rules or adaptations governing a range of behaviors an organism may employ; a ***pure strategy*** uses a single tactic without any alternative (e.g., only migrate, never resident); a ***mixed strategy*** can use more than one probabilistically preset tactic (e.g., either genotype determines migration 70% of time and residing 30%, or 70% of a species always migrates, while 30% always resides); an organism's environment and conditions determine the tactic used in a ***conditional strategy***
Tactic	Individual action or behavior (e.g., migrate or reside) used within a strategy

TABLE 2 | The different forms of migration in ungulates.

Seasonal	Perhaps the most documented form of migration, seasonal migration is often described as a round trip between non-overlapping ranges, although individuals may sometimes switch between different ranges instead of always returning to the same seasonal range. Temperate cervids, such as elk, mule deer, and red deer are well-known for migrating seasonally between discrete, high-elevation summer ranges and low-elevation winter ranges; hypothesized triggers are snow and lowering temperatures in fall (Sabine et al., 2002; Brinkman et al., 2005), and competition avoidance and phenological tracking in spring (Albon and Langvatn, 1992; Hebblewhite et al., 2008)
Altitudinal	Some mountainous herbivores use different elevations in different times of the year. We differentiate altitudinal from short-distance seasonal migration because in this case, migration is still achieved through movement across an "ecological distance" (LeResche, 1974; Peters et al., 2017), but may have no relationship with horizontal movement, as in mountain goats (Rice, 2008) and bighorn sheep (Spitz, 2015)
Short- and long-distance	These definitions may be subjective, dependent on species or population and life histories, but some suggest long-distance migration includes movements that are >10–20 km (Berger, 2004) or 50 km (Poor et al., 2012). Others suggest <50 km is short, 50–150 km is moderate, and >150 km is long (Sawyer et al., 2016). The best-known examples of long-distance migrators are barren-ground caribou and wildebeest

Note that populations exhibiting these non-exclusive forms may also be described as partially migratory.

dispersal, a relatively short-term, one-time movement to a new population or a new range primarily for the purpose of reproduction; (2) *nomadism* or *roaming*, where animals follow resource pulses with little spatial predictability; and (3) *residency*, where there is continuous, overlapping use of the same range (McPeek and Holt, 1992; Hjeljord, 2001; Abrahms et al., 2017). Distinguishing between migratory tactics using seasonal ranges becomes challenging when individuals exhibit more idiosyncratic or mixed movements, such as returning to a seasonal range soon after leaving it (Dingle and Drake, 2007; Dingle, 2014b). Describing migration as a round-trip is problematic when individuals switch among multiple ranges and do not return to the same seasonal range they used the summer or winter before (e.g., Eggeman et al., 2016). Variation in the spatial extent of migratory movement reinforces that partial migration is not the simple dichotomy that is implied by terms like migrant vs. resident or short-distance (<10–50 km) vs. long-distance migrant (>50–150 km; **Table 2**). Indeed, some authors consider the choice to migrate as one point in a continuum of movement responses that occur over multiple scales of spatiotemporal variability (Cagnacci et al., 2011).

Greater latitude in the way migration is defined, behaviorally and spatially, may lessen the need for several quantitative methods used to distinguish migration from other types of movements and to classify variation in migratory movements (Cagnacci et al., 2016; Singh et al., 2016; Abrahms et al., 2017; Peters et al., 2019). Migrants are often distinguished from residents based on criteria such as the amount of seasonal home range overlap (Mysterud, 1999; Ball et al., 2001; Fieberg and Kochanny, 2005), trajectory segmentation (Buchin et al., 2013), or algorithms that cluster seasonal locations (Cagnacci et al., 2011, 2016; Damiani et al., 2016). A second approach is based on Correlated Random Walk (CRW) models (Bergman et al., 2000), including the increasingly popular Net Squared Displacement (NSD), measured as the cumulative squared displacement from a starting point (Turchin, 1998;

Nouvellet et al., 2009; Bunnefeld et al., 2011). The drawback to NSD is that it can be computationally complex and often requires *ad hoc* reclassification of the migratory status of an individual (Spitz et al., 2017). On the other hand, this method is capable of quantifying different types of movement along a continuum, overcoming the problem of simplistic dichotomies (Singh et al., 2016). Despite the limitations in methodologies, quantifying animal movements as migratory behavior is a first step in exploring how partial migration is maintained.

MAINTENANCE OF PARTIAL MIGRATION IN UNGULATE POPULATIONS

Historically, partial migration was simply described as a kind of within-population variation in movement behavior in which just a part of the population migrates (Lack, 1943) with speculation about causation (e.g., Lack, 1943; Lundberg, 1988). Modern assessments have since evolved to developing theoretical frameworks for hypotheses that need to be tested with empirical data (Kokko, 2007, 2011; Lundberg, 2013). Both past and modern interpretations assume that migration results from natural selection such that the occurrence of partial migration requires the long-term balancing of Darwinian fitness between migrant and resident tactics under different ecological conditions. Such polymorphisms in life history tactics are maintained over evolutionary time only if fitness varies with population densities, environmental conditions, or similar phenomena (Swingland and Lessells, 1979). More specifically, natural selection could favor the maintenance of partial migration within a population via: (1) a *frequency-dependent mixed evolutionarily stable strategy* (ESS; Swingland, 1983; Dingle, 2014b), (2) an *environmental-genetic threshold*, a variant of a gene-environment interaction that accommodates changing environments (Pulido, 2011), or (3) a *conditional strategy* in which an individual's choice of migratory tactic varies with other aspects of phenotype, individual state, or the behavior of other individuals in the population (Lundberg, 1987; Chapman et al., 2011b, 2012; Pulido, 2011). Each of these mechanisms might prevail under different environmental conditions.

A frequency-dependent evolutionarily stable state (ESSt) assumes that migratory behavior is fixed, and residents are favored when migrants are at a high frequency and vice versa. At some specific equilibrium frequency, the migratory and non-migratory alternatives should have the same average pay-off; that is, if one alternative increases in frequency, its

TABLE 3 | Reported rates of switching between migratory tactics in partially migratory populations of large ungulates.

Species	Study years	Study location	Tot. # animals	Rate of switching	Study
African buffalo (*S. caffer*)	2007, 2009, 2010	Namibia	11	0%	Naidoo et al., 2012
Elephant (*L. africana*)	2001–2016	Africa	67	16%	Purdon et al., 2018
Elk (*C. elaphus*)	2002–2012	Canada	223	15%	Eggeman et al., 2016[a]
Elk (*C. elaphus*)	1989–2009	USA	90	0%	Middleton et al., 2013a
Impala (*A. melampus*)	2002–2003	Zimbabwe	61	11%	Gaidet and Lecomte, 2013
Moose (*A. alces*)	2004–2010	USA	67	21%	White et al., 2014
Moose (*A. alces*)	2006–2008	Norway	82	6%	Rolandsen et al., 2017
Moose (*A. alces*)	1980–1987	Sweden	36	0%	Sweanor and Sandegren, 1988
Mule deer (*O. hemionus*)	1999–2009	USA	297	<1%	Monteith et al., 2011
Mule deer (*O. hemionus*)	1989–1991	USA	23	17%	Nicholson et al., 1997
Mule deer (*O. hemionus*)	2007–2017	USA	312	0%	Sawyer et al., 2018
Pronghorn (*A. americana*)	1999–2005	USA	44	10%	White et al., 2007
Red deer (*C. elaphus*)	1999–2014	Europe	264	<1% of females 23% of males	Peters et al., 2019
Roe deer (*C. capreolus*)	1999–2014	Europe	273	8% of females 9% of males	Peters et al., 2019[b]
Sierra Nevada bighorn sheep (*O. c. sierrae*)	2005–2013	USA	70	33%	Spitz, 2015
Svalbard reindeer (*R. t. platyrynchus*)	1998–2000	Norway	34	35%	Hansen et al., 2010
Svalbard reindeer (*R. t. platyrynchus*)	2009–2013	Norway	27	41%	Meland, 2014
White-tailed deer (*O. virginianus*)	1994–1998	USA	54	39%	Sabine et al., 2002
White-tailed deer (*O. virginianus*)	1994–1998	USA	51	8%	Sabine et al., 2002[c]
White-tailed deer (*O. virginianus*)	2001–2002	USA	77	35%	Brinkman et al., 2005[c]
White-tailed deer (*O. virginianus*)	2000–2007	USA	149	20%	Grovenburg et al., 2011[c]
White-tailed deer (*O. virginianus*)	1992–1995	USA	83	7%	Van Deelen et al., 1998
White-tailed deer (*O. virginianus*)	1975–1996	USA	97	7%	Nelson, 1998

[a] *See also (Hebblewhite and Merrill, 2011).*

[b] *See also (Gurarie et al., 2017; Peters et al., 2017).*

[c] *Considered conditional migrants: migrating at least once, but failing to migrate during any 1 season, or migrating briefly within 1 season.*

pay-off should decrease (i.e., fitness is negatively frequency-dependent; Swingland, 1983; Dingle, 2014a). The evolution of partial migration has been examined using frequency-dependent ESS modeling especially in birds (Lundberg, 1987; Kaitala et al., 1993; Kokko, 2011). However, empirical support for frequency-dependent ESSts in most species is lacking (Chapman et al., 2011b; Lundberg, 2013), perhaps because negative frequency-dependence may be observable only when the population is at or above the carrying capacity.

In partially migratory ungulates, many authors assume that migration is a fixed trait (Hebblewhite and Merrill, 2011; Gaillard, 2013; Middleton et al., 2013b). Fixed migration would necessarily mean that the ratio of migrants and residents in a population would need to be balanced by density- or frequency-dependence in a mixed-ESS at the population level (Lundberg, 1988; Kaitala et al., 1993), as described above. That is, individuals are not able to change their behavior, but the relative demographic success of each separate tactic determines the relative fitness of each behavior, which then changes in some stabilizing way as densities or frequencies change. Without such a stabilizing mechanism, a population would be expected to reach fixation for a single behavior. The rarity of "pure" migrant or resident populations itself rejects this notion. Further, partial migration through an ESSt could not happen if there is switching between tactics, which has been reported in deer (*Odocoileus virginianus*, Nelson, 1995), elk (*Cervus elaphus*, Eggeman et al., 2016), impala (*Aepyceros melampus*, Gaidet and Lecomte, 2013), moose (*Alces alces*, White et al., 2014), pronghorn (*Antilocapra americana*, White et al., 2007), Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*, Spitz, 2015), and Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Hansen et al., 2010; Meland, 2014; **Table 3**). In these studies, the average annual rate of switching was ∼20%, although most studies had limited ability to detect switching due to inadequate sample size or infrequent monitoring over the course of entire lifetimes. If the results of these few switching studies are representative of the many long-lived ungulates with lifespans >10 years, the evidence suggests that individuals may switch tactics several times during their lifetime.

In contrast, the environmental-genetic threshold describes a mechanism in which a number of additive, environmental variables may interact with a number of genes to contribute toward expression of an underlying phenotypic, behavioral liability (i.e., migratory tendency) or trait that is normally distributed within a population (**Figure 1**, Pulido, 2011). According to the environmental-genetic threshold model, individuals have a genetically determined propensity for migration that is triggered, or not, by environmental conditions. A threshold exists below which individuals are sedentary, whereas those above the threshold are migratory (Berthold, 1991; Pulido et al., 1996). Migratory traits may not be fixed, even under strong, directional selection, because as the distribution of migratory propensity shifts below the threshold, migratory traits will not be phenotypically expressed (Pulido, 2011). Environmental variables such as food, social dominance, or body condition may affect individuals with liability values close to the threshold, causing them to change migratory tactic. This conceptual model has not been used to address partial migration in ungulates, and testing its predictions would require long-term studies once the genetic basis or a correlate for migration propensity was identified. Even if further work identifies genetically controlled, regulatory pathways of complex traits linked to migration, monitoring the interaction of these traits with environmental conditions over a sufficiently long period in free-ranging ungulates remains a formidable challenge (Pulido, 2011).

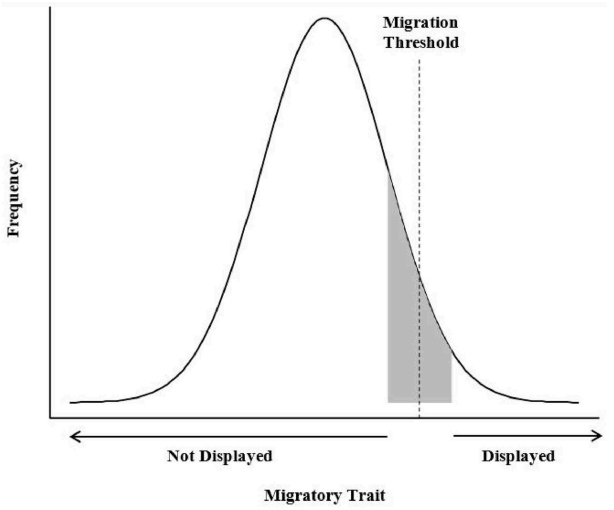

FIGURE 1 | The environmental-genetic threshold model assumes that a dichotomous trait is displayed as a result of an underlying continuous character or liability (i.e., migratory tendency) that is normally distributed within a population (Pulido, 2011). The combined effects of genetic influences and environmental effects on the threshold position can push a facultative migrant (represented in gray), with a liability close to the threshold, to either migrate or remain resident, depending on the direction of the environmental shift.

The alternative to genetically fixed traits or liabilities is the possibility that migration varies between individuals as a function of state, such as age, nutritional condition, or other circumstances. As we discuss below, state-dependent migration may be relatively fixed intrinsically (e.g., dependent on an individual's age or sex or personality), or highly plastic based on nutritional state (e.g., fat reserves or other physiological mechanisms of the metabolic, immune, or endocrine systems) or extrinsic conditions (e.g., predation risk, parasite loads, or climate). If fitness varies temporally with environmental conditions (Rolandsen et al., 2017), then fitness balancing is not necessary over the short term. In this case, a single condition-dependent strategy could produce 2 (or more) tactics. Each individual should adopt the migratory tactic that is best for it at the time (Swingland, 1983), in some cases, making the "best of a bad job" (Lundberg, 1987) and resulting in relative pay-offs that may not be equal across individuals. For example, dominant or more competitive individuals may optimize fitness by remaining resident, whereas less competitive or sub-dominant individuals may optimize fitness by trading the cost of migration in return for a habitat where there is less competition (Swingland, 1983; Lundberg, 1987; Chapman et al., 2011b).

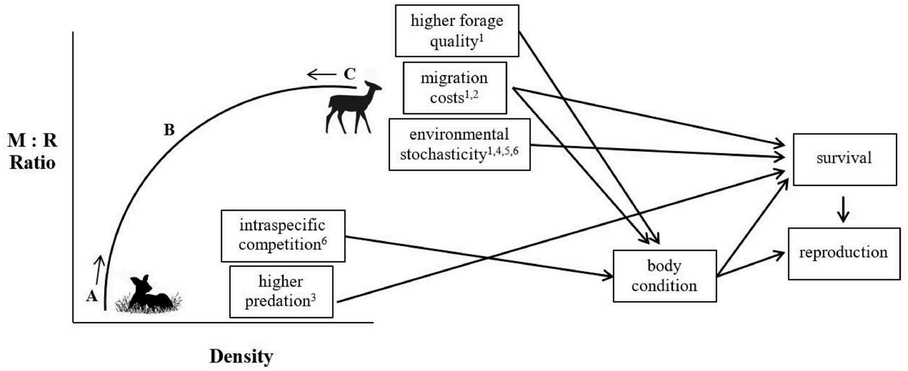

FIGURE 2 | Conceptual framework depicting how the density-dependent and density-independent factors may interact on the vital rates of migrants and residents to maintain partial migration within a population. Migrants (M) may do better in one vital rate at high density, but residents (R) will do better in another vital rate at low density. This "demographic balancing" may not happen every year, but will prevent fixation of the proportion of migrants at either 0 or 1, and provide the mechanism for the long-term average ratio of M:R in a population. (A) With each additional R individual, individual fitness for each R individual declines, and density dependence in predation or competition, or alternatively, stochastic climate events, shift the M:R ratio back toward (B), the point at which partial migration is maintained. (C) With each additional M individual, fitness for each M individual declines. However, very little empirical evidence to support demographic balancing is found in the partially migratory ungulate literature because most studies are not long-term, or examine only 1 or 2 vital rates. For examples, see (1) Nicholson et al. (1997) (2) Hebblewhite and Merrill (2011) (3) White et al. (2014) (4) Middleton et al. (2013a) (5) Fieberg et al. (2008) (6) Plumb et al. (2009).

Consequently, both migratory and non-migratory tactics may be maintained within a population due to differential density-dependent regulation of vital rates that must counteract each other over the long term, such that any differences in reproductive success between migrants and residents must be countered by differences in survival (**Figure 2**). Hebblewhite and Merrill (2011) found that despite higher pregnancy rates and winter calf weights, migratory elk were more at risk during migration. In contrast, residents reduced predation risk by remaining in areas of human activity, which resulted in lower pregnancy and calf weights, but slightly higher adult and calf survival. Similarly, White et al. (2014) also found that calf survival was higher in migratory moose, but that there was no difference in body fat accumulation between residents and migrants. Both studies were suggestive of demographic balancing between the two tactics (Hebblewhite and Merrill, 2011; White et al., 2014). Peters et al. (2019) suggested that the probability of migrating should increase under high-density conditions; with increasing density, density-dependent or environmentally-driven switching between tactics would maintain partial migration within a population. Indeed, recent evidence from elk supports the notion of density-dependent migration being a potentially stabilizing mechanism regulating partial migration in populations (Eggeman et al., 2016). On the other hand, stochastic environmental events could cause mortality for the more successful tactic, independent of density, but if the increase in mortality is only to the level of survival of the alternative behavior, partial migration can be maintained (Grayson et al., 2011). The balance between these conflicting costs and benefits leads to individuals remaining in a range year-round, or moving to new areas. In the next section, we identify and assess the support for the most commonly hypothesized mechanisms shaping individual variation in migratory tendency in ungulates.

WHY DO SOME INDIVIDUALS MIGRATE?

In this section, we summarize results from a range of field studies focused on ungulate migration to address what factors promote migration in an individual animal. We summarize evidence for a genetic basis to migration, evidence for the role of learning and cultural transmission, and factors related to individual state or environmental conditions and/or their interactions (**Tables 4**, **5**).

Genetics

Evidence for a direct genetic basis for migration would require that behavioral traits of individuals were linked to specific alleles that differentiated groups or showed heritability, as demonstrated for migratory restlessness in captive birds (Berthold and Querner, 1982; Terrill, 1987; Berthold, 1991; Berthold and Pulido, 1994). Such experiments showing restless behavior related to migration have not been attempted and may not be feasible in ungulates, which are harder to hold in captivity and often express less spatial and temporal synchrony in their migration. Nonetheless, some authors have attempted more correlative approaches for exploring indirect genetic effects by using genetic surveys to distinguish individuals with different migratory tendencies. For example, authors used microsatellites to identify genetic differentiation between GPS-collared pronghorn antelope defined as migrants vs. residents in the Yellowstone Ecosystem (Barnowe-Meyer et al., 2013). Similar uses of microsatellites have revealed genetic structure in ungulates (e.g., Coltman et al., 2003; Colson et al., 2016), but inferences from microsatellite differentiation based on a few multi-loci (typically <20) were generally limited (**Table 5**). This scanning approach might better distinguish behavioral differences among individuals with new genomics approaches, such as amplified fragment length polymorphism (AFLP) markers in whole genome scans (Liedvogel et al., 2011).

TABLE 4 | State- or condition-dependent hypotheses to explain individual variation in migratory tendency within partially migratory ungulate populations.

Driver	References	Hypothesis	Prediction in ungulates
Terminal investment	Clutton-Brock, 1984	Age predicts migration to obtain resources for current reproduction at expense of survival	Increase in proportion of older migrants with higher density
Dominance; competitive release	Gauthreaux, 1982; Nelson, 1995; Mysterud et al., 2011	Intraspecific competition for food predicts subordinate individuals will migrate, while more dominant individuals remain sedentary	Increase in proportion of migrants with higher density on shared range
Social fence	Matthysen, 2005; Mysterud et al., 2011	Social constraints at high densities predict a decrease in migratory behavior	Less and shorter migrations with higher density
Forage maturation/High-quality forage	Fryxell and Sinclair, 1988b; Hebblewhite et al., 2008	Phenological gradients of plant development predict migration to maximize energy intake. Rainfall effects on vegetation predict migration	Increase in proportion of migrants in areas with altitudinal variation, with higher density, and following severe winters or during dry summers
Predation (or human) or pathogen risk	Bergerud et al., 1990; Barten et al., 2001; Skov et al., 2011	Seasonal predation/pathogen risk predicts animals should move to minimize the ratio of risk to potential growth	Individuals migrate to avoid predation/pathogens on vulnerable individuals, with higher predator density, but usually irrespective of intraspecific density. Alternatively, a predator swamping tactic results in residency because migration is costly (inverse density dependence)

Support for these hypotheses can be found in ***Table 5****.*

A second approach for identifying genes associated with migration could attempt to isolate aspects of mitochondrial genotypes. For example, the probability of being migratory in a hybrid swarm of caribou (*R. tarandus*) in the Canadian Rockies was higher in individuals carrying a Beringian–Eurasian haplotype, which was mainly associated with the migratory, barren-ground subspecies, compared to the typically non-migratory woodland caribou (McDevitt et al., 2009). Interestingly, these animals could not be distinguished with microsatellite data, perhaps owing to interbreeding between diverged lineages since the last glaciation (McDevitt et al., 2009). The promise of an mtDNA approach was amplified by the correlation reported by Northrup et al. (2014) between the timing of migration in mule deer (*O. hemionus*) from 4 distinct winter ranges in the Piceance Basin of Colorado. These authors attributed the correlation to differences in mitochondrial efficiency associated with metabolic demands of migration.

Two other classic approaches for identifying the genetic basis of any behavior would be to compare parent-offspring pairs in long-term studies with known individuals (e.g., Gaillard, 2013) or to conduct cross-fostering experiments. To our knowledge, no authors have applied either technique to address migration in ungulates. Perhaps measuring gene expression in a species with fixed migrants, fixed residents, and individuals that switch migratory tactics within their lifetime could shed some light. A further challenge would be to consider alternative explanations for genetic correlations. For example, in the case of timing of migration in mule deer, Northrup et al. (2014) were able to reject a causative effect of sociality by controlling for the source of the individual's winter range, which showed little spatial clustering of haplotypes. Clearly, it would be challenging to disentangle alternative explanations such as fat levels or physiological status and social or cultural factors, which we discuss next, in correlative studies to support a genetic component for migration. In many cases, particularly in species for which animals switch migratory tactics within their lifetime, it is likely that genetic tendencies are moderated by environmental circumstances.

Learning, Culture, and Personality

Being able to discriminate genetic mechanisms from learning and cultural transmission is difficult but could be possible via studying mother-offspring pairs for long periods. Within and beyond these pairs, it is likely that information about navigation and migratory routes are passed from more experienced, key individuals to those that are less experienced (Dodson, 1988; Couzin et al., 2005; Fagan et al., 2012). Nelson (1998) reported that white-tailed deer fawns mimicked the migratory behavior of their mothers. Particularly in the first year of life, residency or migration can be assumed to be dependent on the migratory status of the parent because of the offspring-parent bond (Andersen, 1991b). However, we found few studies that addressed the potential effects of early learning or cultural inheritance on migration beyond the first year in ungulate populations (Sweanor and Sandegren, 1988; Nelson, 1998), although it has been documented in whales (Valenzuela et al., 2009). Translocated bighorn sheep and moose learned to increase knowledge and exploit green waves of forage growth in new environments where they had no previous knowledge of the landscape; as knowledge increased, so did the propensity to migrate (Jesmer et al., 2018).

Social learning that promotes migration does not need to be heritable to evolve (Boyce, 1991), although the ability to learn and mimic migratory behavior is likely partially hereditary (Nelson, 1998). Indeed, behavioral flexibility itself appears to be highly heritable (Laughlin et al., 2011) and might be especially important for partial migration. In the Canadian Rockies,

TABLE 5 | Support (+ positive/likely, ? potentially but untested/suppositional, – negative/evidence against) for mechanisms explaining individual variation in migratory tendency within partially migratory ungulate populations, including genetics, learning, personality or cultural transmission, and state- or condition-dependence.

					State- or condition-dependent?				
Family	**Scientific name**	**Common name**	**Genetic?**	**Learning, personality, cultural?**	**Dominance/ competitive release**	**Forage maturation/ high-quality forage**	**Predation/pathogen risk**	**Social fence**	**Terminal investment**
Antilocapridae	*Antilocapra americana*	Pronghorn	+ (Barnowe-Meyer et al., 2013)	+ (Barnowe-Meyer et al., 2013)	? (Kolar et al., 2011)	? (Hoskinson and Tester, 1980)	– (White et al., 2007) ? (Barnowe-Meyer et al., 2010)		? (White et al., 2007)
Bovidae	*Aepyceros melampus*	Impala				+ (Gaidet and Lecomte, 2013)			
	Antidorcas marsupialis	Springbok			? (Child and Le Riche, 1969)				
	Bison spp.	Bison			+ (Bruggeman et al., 2008; Kowalczyk et al., 2013)				
	Budorcas taxicolor	Takin				+ (Guan et al., 2013)			
	Connochaetes taurinus	Gnu, wildebeest				? (Morrison and Bolger, 2012)			
	Hemitragus jemlahicus	Himalayan tahr			+ (Forsyth, 1999)				
	Ovis canadensis	Bighorn sheep				? (Spitz et al., 2018)	+ (Festa-Bianchet, 1988)		
	Ovis dalli stonei	Stone's sheep				+ (Seip and Bunnell, 1985)			
	Rupicapra spp.	Chamois, isard		? (Crampe et al., 2007)	+ (Clarke and Frampton, 1991; Crampe et al., 2007)	? (Crampe et al., 2007)			
	Syncerus caffer	African buffalo				+ (Naidoo et al., 2012)			
	Taurotragus oryx	Common eland			– (Hillman, 1988)	+ (Hillman, 1988)			
Camelidae	*Lama guanicoe*	Guanaco			? (Moraga et al., 2015)				
Cervidae	*Alces alces*	Moose		+ (Sweanor and Sandegren, 1988; Andersen, 1991b) ? (Histol and Hjeljord, 1993; Singh et al., 2012)	? (Singh et al., 2012)		+ (White et al., 2014)		– (Singh et al., 2012)
	Capreolus capreolus	Roe deer		? (Lamberti et al., 2004)	? (Wahlström and Liberg, 1995; Mysterud, 1999)	? (Ramanzin et al., 2007)	? (Wahlström and Liberg, 1995; Lamberti et al., 2004)		

(Continued)

TABLE 5 | Continued

Family	Scientific name	Common name	Genetic?	Learning, personality, cultural?	State- or condition-dependent?				
					Dominance/ competitive release	**Forage maturation/ high-quality forage**	**Predation/pathogen risk**	**Social fence**	**Terminal investment**
	Cervus elaphus	Elk/red deer		+ (Jones et al., 2014; Found and St. Clair, 2016, 2017)	? (Barker et al., 2018)	+ (Albon and Langvatn, 1992; Hebblewhite et al., 2008; Bischof et al., 2012; Jones et al., 2014; Barker et al., 2018)	+ (Pruvot et al., 2016) ? (Mysterud et al., 2016)	? (Mysterud et al., 2011)	+ (Eggeman et al., 2016)
	Cervus nippon	Sika deer		+ (Sakuragi et al., 2003)	? (Sakuragi et al., 2003; Takii et al., 2012)	+ (Sakuragi et al., 2003) ? (Takii et al., 2012)			
	Odocoileus hemionus	Mule deer	- (Nicholson et al., 1997)		? (Sawyer et al., 2016)	+ (Nicholson et al., 1997) ? (Sawyer et al., 2016; Schuyler et al., 2019)	+ (Nicholson et al., 1997)		
	Odocoileus virginianus	White-tailed deer	– (Nelson, 1998)	+ (Nelson, 1998)		? (Brinkman et al., 2005)	? (Grovenburg et al., 2011)		
	Rangifer tarandus	Caribou/reindeer	+ (McDevitt et al., 2009)	? (Hansen et al., 2010)		+ (Hansen et al., 2010)	? (Folstad et al., 1991)		
Elephantidae	*Loxodonta africana*	Elephant				? (Purdon et al., 2018)			
Equidae	*Equus burchelli*	Zebra		– (Bartlam-Brooks et al., 2013)		+ (Bartlam-Brooks et al., 2013)			
Giraffidae	*Giraffa camelopardalis*	Giraffe				? (Le Pendu and Ciofolo, 1999)			
Suidae	*Sus scrofa*	Boar		+ (Singer et al., 1981)		+ (Singer et al., 1981)			

resident elk exhibited bolder personalities that included greater exploration of novel objects relative to migratory individuals (Found and St. Clair, 2016). Bolder elk also exhibited lesser lateralization of hoof preferences when pawing the snow to forage, which potentially signals greater cerebral flexibility (Found and St. Clair, 2017). The same authors suggest that less lateralized animals had genetically determined temperaments that made them more responsive to environmental stimuli, which resulted in greater likelihood of them realizing the increasing benefits of residency and abandoning previous histories of migration (Found and Clair, in review). Similar metrics for studying personality traits in wild animals have proliferated in recent years (reviewed by Dingemanse et al., 2010 and Sih et al., 2012), creating much potential to explore their correlations with both migratory tactics and genotypic variation.

State and Physiological Condition

In reviewing potential intrinsic factors promoting migration, we found studies primarily addressed one specific hypothesis related to age, and very few studies directly tied physiological mechanisms to partial migration. The *Terminal Investment Hypothesis* states that older (past their prime) individuals are more likely to devote more resources toward ensuring successful reproduction than younger (yearling or prime-aged) individuals because they anticipate fewer future reproductive events (Clutton-Brock et al., 1982; Clutton-Brock, 1984; Bercovitch et al., 2009). When applied to migration, this hypothesis predicts that ungulates might have a propensity to remain resident while young so as to prioritize their own survival by avoiding risks that can occur during migration (e.g., from predation or anthropogenic factors; Nicholson et al., 1997; Hebblewhite and Merrill, 2011; Schuyler et al., 2019); as they age, they might accept greater risks to migrate to increase access to resources for investment in their terminal offspring (Fryxell and Sinclair, 1988a; Albon and Langvatn, 1992). The age at which this hypothesis might occur in ungulates could be quite old; indeed, Eggeman et al. (2016) showed potential evidence that elk became more likely to migrate with age in Alberta, Canada, but migrants rarely switched to a resident tactic after aging (>15 years old). However, the opposite pattern appears to occur in both pronghorn antelope, which became non-migratory as they aged (White et al., 2007), and moose, which migrated when young but were less likely to migrate as they aged (Singh et al., 2012). Evidence to support predictions of the terminal investment hypothesis could be confounded with other factors. For example, increasing costs of movement are associated with age-related changes in physiological condition (Ericsson and Wallin, 2001), and home ranges may become smaller with age due to experience gained (Allen et al., 2016).

Migration may also be state-dependent (Visscher and Merrill, 2018). If individuals were able to meet their nutritional demands satisfactorily without migrating, there may be no need to migrate if an individual were to incur additional costs or stress related to movement, predation risk, or social conflict (but see below). Because ungulate survival and reproductive efforts are closely tied to body fat reserves (Cook et al., 2004, 2016; Monteith et al., 2014), we would expect to see the propensity to migrate closely linked to nutritional state if condition buffers consequences (Spitz, 2015). Other physiological mechanisms differing between migratory tactics might include metabolic, immune, and endocrine systems, or oxidative stress associated with intense physical activity or fatigue (Jachowski and Singh, 2015; Hegemann et al., 2019). Although Jachowski et al. (2018) found individual mule deer occupying areas closer to peak forage quality during migration had decreased levels of fecal glucocorticoid metabolites, to our knowledge, there have been no studies comparing these mechanisms as related to partial migration in ungulates. Experiments would most likely be needed to identify the specific physiological mechanism, but even then, these could differ among species and environments (Hegemann et al., 2019). Further, recent evidence shows that transfer of the nutritional benefits that are normally associated with migration to residents, as can occur when irrigated agriculture supplements elk feeding, can promote resident behavior (Jones et al., 2014; Barker, 2018). In fact, reproducing and migrating every other year (Morrison and Bolger, 2012) may be a better tactic for ensuring survival and lifetime reproduction, and decisions surrounding migration in ungulates might be driven almost primarily by nutrition and reproductive status (e.g., Festa-Bianchet, 1988, described below).

Competition, Forage, Predation, and Pathogens

Competition may promote migration but how and where competition influences the tendency for an individual to migrate may vary. The *Dominance or Competitive Release Hypothesis* (Ketterson and Nolan, 1976; Fudickar et al., 2013) is based on intraspecific competition, with an individual's propensity to migrate expected to increase at higher density on sympatric range. Although competition for food on high-density, sympatric range is likely, it is difficult to demonstrate directly, but might be inferred. For example, white-tailed deer have shown flexible migratory behavior in which they do not remain after fall arrival on sympatric winter ranges, and instead move back to summer ranges during years of little snow and mild weather, suggesting avoidance of competition on the less nutritional winter ranges (Nelson, 1995). Similarly, the distance migrated by elk and red deer in summer has been shown to increase with density, suggesting avoidance of competition on seasonal ranges (Mysterud et al., 2011; Eggeman et al., 2016). Sawyer et al. (2016) also showed that long-distance migrants spent more time migrating and may have initiated spring migration 3 weeks earlier than moderate- or short-distance migrants to escape intraspecific competition by lessening time spent on winter range. In contrast to competition that occurs on sympatric winter ranges, if population densities also increase on allopatric summer ranges, leading to occupation of all the summer areas, migration tendency can be restricted due to competition and social aggression according to the *Social Fence Hypothesis* (Matthysen, 2005). For example, Mysterud et al. (2011) reported that a lower proportion of red deer migrated at high density during summer, consistent with this hypothesis. However, the authors only contrasted areas of differing densities and did not measure variation in habitat quality, which is needed to determine the level of competition (Fretwell and Lucas, 1969). Because fall migration was delayed at high density, Mysterud et al. (2011) further suggested that a combination of the competitive release and social fence hypotheses were needed to explain migratory tendency in ungulates. Constraints on distribution and changes in sociality and aggressive behaviors of individuals would need to be documented on both sympatric and allopatric ranges as ungulate densities increased to support these hypotheses.

In seasonal environments, the *Forage Maturation Hypothesis* predicts that spatiotemporally varying resources promote migration to maximize nutrient intake where there are phenological gradients of plant development (Fryxell and Sinclair, 1988a; Fryxell et al., 1988; Albon and Langvatn, 1992; Hebblewhite et al., 2008). Whereas the classic example may be the Serengeti wildebeest following new green growth to the plains during the wet season (Holdo et al., 2009), many cervids in temperate systems show migrations tied to elevational gradients in plant green up (Sawyer and Kauffman, 2011; Bischof et al., 2012; Merkle et al., 2016; Aikens et al., 2017). If migrants "surf" or "jump" an altitudinal green wave, they are predicted to enter winter with heavier masses and in better body condition than residents as a consequence of higher-quality forage (Albon and Langvatn, 1992; Hebblewhite et al., 2008). Only a handful of studies focused on partially migratory ungulates have demonstrated that females or their young were fatter when they were migratory (e.g., Mysterud et al., 2001; Hebblewhite et al., 2008; Hebblewhite and Merrill, 2011). Yet, this conclusion for elk in the Greater Yellowstone Ecosystem was driven largely by non-lactating females with no data on calf survival and whether release from nutritional costs associated with calf loss contributed to their better condition; in addition, an influence of surfing on autumn fat levels was not detected for lactating elk so results remained somewhat inconclusive (Middleton et al., 2018). Even fewer efforts have linked the tactic of migration to life-time reproductive success. Such studies would require not only long-term studies but additionally evaluating other costs or benefits of migration.

The major hypothesis posed as an alternative to ungulate migration as a response to forage maturation is the *Predation Risk Hypothesis*, which states that ungulates migrate to escape or minimize predation or other risk factors, such as human hunting or parasites (Fryxell and Sinclair, 1988a; Bergerud et al., 1990; Hebblewhite and Merrill, 2007). Evidence we found to support this hypothesis focused on ungulates moving outside of predator ranges and denning territories (Bergerud, 1988) or by using terrain where predators travel less frequently (Bergerud and Page, 1987). For example, pregnant bighorn sheep in Alberta moved from relatively higher-quality forage to rugged high-elevation summer range earlier than non-pregnant ewes and before plant growth started, which Festa-Bianchet (1988) argued was to avoid predation on vulnerable newborn lambs. On the coast of Alaska, migrant moose showed almost 3 times higher neonatal calf survival by migrating to avoid predation but did not obtain nutritional benefits through accumulation of body fat (White et al., 2014). Recent theoretical work suggests that parasites and pathogens could be drivers of partial migration, either as escape from infected areas or individuals, through loss of infected individuals during migration, or as recovery from infection when parasites cannot adjust to environmental changes that occur during migration (Altizer et al., 2011; Fritzsche McKay and Hoye, 2016; Shaw and Binning, 2016). In support of these mechanisms, Pruvot et al. (2016) showed that migratory elk herds in Canada were potentially less likely to be infected with giant liver flukes (*Facioloides magna*) when compared with resident elk, and lower intensities of warble fly larvae (*Hypoderma tarandi*) were found in reindeer the farther they migrated post-calving (Folstad et al., 1991).

While comparing the costs and benefits of migratory tactics represents an important first step to understanding what promotes the tendency to migrate, explaining migration by only 2 hypotheses (predation risk avoidance vs. forage maturation, which tend to be the focus of many studies) limits the possibility that other intrinsic or extrinsic factors could also be influential as we've described above. However, results do demonstrate that there may be no straightforward, easy answer because the top-down benefits of avoiding risk through migration may be complicated by life history trade-offs (the cost of rearing offspring to subsequent fecundity), or which may be at times compete with, or modulate, the bottom-up effects of increased access to forage.

CONCLUSIONS AND FUTURE DIRECTIONS

We have shown that flexibility in migratory behavior by ungulates is more common than previously appreciated, amplifying the suggestion by others that migration should evolve under widely varying environmental conditions in response to the advantages and disadvantages of different life-history strategies (Holt and Fryxell, 2011; Fryxell and Holt, 2013; Avgar et al., 2014). Migration is a complex phenomenon (Alerstam et al., 2003) determined by a number of traits, in turn affected by several genes with pleiotropic effects (Sutherland, 1998). We conclude that migration is not determined by a direct mapping of genotype to phenotype, making it a flexible tactic adopted within a broader strategy. Establishing that partial migration is common in ungulates, and that it appears to respond to diverse genetic, environmental, and demographic correlates, increases the range of techniques that might be applied to study it. Achieving these advances will require use of clear, universal definitions (Avgar et al., 2014; Cagnacci et al., 2016) and classification methods (e.g., Bunnefeld et al., 2011; Naidoo et al., 2012). In fact, the longer individual white-tailed deer were monitored, the more likely they were to be classified by researchers as conditional migrants as opposed to fixed migrants or residents (Fieberg et al., 2008).

Limitations of past studies of migration might be overcome with an understanding that migration is often flexible. Very few of the studies we found were set up to examine how density could lead to a long-term demographic balancing of migrants and residents within a population, but viewing migration as a conditional tactic in a broader strategy to maximize forage intake increases the range of experimental studies that might be applied to this problem. For example, related hypotheses might be tested by manipulating forage or ungulate access to it in protected areas (e.g., Most et al., 2015) or in managed herds (Rivrud et al., 2016). Similarly, few studies have tested explicitly for a genetic basis for differences in migratory and resident individuals within partially migratory populations. The few studies that mentioned learning or cultural inheritance (Singer et al., 1981; Sweanor and Sandegren, 1988; Andersen, 1991a; Barnowe-Meyer et al., 2013) did not conduct them with detailed behavioral observations or controlled experiments to test related hypotheses. A broader view of the genetic and environmental correlates of migratory tactics increases the relevance of many associated metrics.

The decision to migrate or not is made by individuals, but rarely do studies examine individual decision-making in migratory populations (Ball et al., 2001). Nonetheless, some authors attempt such an approach, as with the characterization of multiannual movement patterns by more than 300 moose in 10 different populations (Allen et al., 2016). But many authors whose studies we reviewed characterized migration dichotomously at the level of single populations. Emerging is the view that migration may be a continuum (Ball et al., 2001), both as a behavior (e.g., individuals may exhibit intermediate tactics or variability in timing and distance) and as a population metric (i.e., 1 to 99% of the population may be migratory). Based on our review, migration as a continuum means the reasons for migration were often hard to detect and characterize (Cagnacci et al., 2016). In particular, instances in behavioral switching between migratory tactics should be explored for their potential intrinsic and extrinsic correlates.

Unfortunately, it is difficult to link multiple, interacting intrinsic and extrinsic variables to the occurrence of migration when there is strong environmental variation (Fieberg et al., 2008). In contrast to fixed migrants in other species that show predictable movements as a result of physiological processes (neuroendocrine and endocrine systems), linking environmental cues (day length, photoperiod) to the mechanisms controlling facultative migration in highly variable environments is challenging (Ramenofsky et al., 2012). We found speculative support for state- or condition-dependent migration in ungulates in our review, but relatively little experimental data, despite several indirect lines of evidence. We know that differences in habitat quality can lead to corresponding differences in physiology, nutritional condition, and reproductive success in ungulates, and that these can be modified by density (Weber et al., 1984; Becker et al., 2010). More studies are needed that relate habitat use to resulting nutritional acquisition, and measures of body condition and reproductive success, to identify the fitness consequences of migratory tactics. Given new advances in remote monitoring of physiological traits in free-ranging animals, studies on not only how body fat at time of capture, but also physiological mechanisms, differ between migrants and residents and contribute to switching between tactics are warranted (Hegemann et al., 2019). Further, studies that track migratory traits of mothers and their offspring could separate the genetic and learned components of migratory behavior from environmental effects.

Current knowledge of partial migration in ungulates is sometimes limited by their large size, long lives, and wide-ranging use of habitats, but these traits also confer advantages of observability, long-term study, and generalization across spatial scales. These advantages will be further amplified by using methodologies that are increasingly cost-effective and tractable over the long term in space and time, and in remote environments, to test the relative fitness-related consequences of partially migratory behavior (Bolger et al., 2008; Gaillard, 2013). Long-term, demographic studies and population models tracking the life-history traits of co-existing individuals along the resident-migrant gradient through the year will allow for calculating the costs and benefits of their migration patterns (Bolger et al., 2008). Given the potential ecological and evolutionary significance of partial migration, and that ever-increasing anthropogenic disturbance and environmental change may alter or eliminate the benefits of migration altogether (Bischof et al., 2012), understanding the genetic, environmental, and density-driven trade-offs underlying partial migration is of the utmost importance.

AUTHOR CONTRIBUTIONS

JB designed and wrote the first draft of the manuscript. All authors contributed to manuscript revision and read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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