

# On the adaptive benefits of mammal migration<sup>1</sup>

T. Avgar, G. Street, and J.M. Fryxell

**Abstract:** Migration is well developed among mammals, but there has been little attempt to date to review common ecological constraints that may guide the evolution of migration among mammals, nor to consider its prevalence across different taxa. Here we review several alternate hypotheses for the evolution of migration in mammals based on improvements in energetic gain and mate-finding contrasted with reduction in energetic costs or the risk of predation and parasitism. While there are well-documented examples of each across the order Mammalia, the available evidence to date most strongly supports the energy gain and predation risk hypotheses in the terrestrial realm, whereas a combined strategy of reducing energetic costs in one season but improving energetic gain in another season seems to characterize aquatic mammal species, as well as bats. We further discuss behavioral and physiological specialization and provide a taxonomic cross section of mammalian migration.

**Key words:** movement ecology, adaptive behavior, competing hypotheses, partial migration, seasonal migration, resource gradient, habitat suitability.

**Résumé :** Si la migration est répandue chez les mammifères, peu d'ouvrages ont tenté d'établir une synthèse des contraintes écologiques communes qui pourraient guider l'évolution de la migration chez les mammifères ou d'examiner sa prévalence chez les différents taxons de ce groupe. Nous examinons plusieurs hypothèses proposées pour expliquer l'évolution de la migration chez les mammifères, qui reposent sur l'amélioration des gains énergétiques et de la quête d'un compagnon par opposition à la réduction des coûts énergétiques ou du risque de prédation ou de parasitisme. S'il existe des exemples bien documentés de chacun de ces cas chez les mammaliens, les données disponibles à ce jour appuient le plus fortement les hypothèses concernant les gains énergétiques et le risque de prédation pour ce qui est des mammifères terrestres, alors qu'une stratégie combinée de réduction des coûts énergétiques durant une saison jumelée à l'amélioration des gains énergétiques pendant une autre saison semble caractériser les espèces de mammifères aquatiques ainsi que les chauves-souris. Nous abordons plus en détail la spécialisation comportementale et physiologique et présentons une synthèse taxinomique de la migration chez les mammifères. [Traduit par la Rédaction]

**Mots-clés :** écologie du déplacement, comportement d'adaptation, hypothèses concurrentes, migration partielle, migration saisonnière, gradient de ressources, adéquation de l'habitat.

## Introduction

Migration, along with nomadism and range residency, is a distinct class of annual movement behavior (Mueller and Fagan 2008), in which animals alternate at periodic intervals between disjunct home ranges used on a regular basis. From an evolutionary adaptive perspective, animal movement is motivated by attraction to fitness enhancing localities (offering improved access to, e.g., food or mates) and avoidance of localities with unfavorable conditions (e.g., intense competition or predation). Hence, movement is an adaptive behavioral response to spatiotemporal ecological patterns (Nathan et al. 2008; Avgar et al. 2013). It is the scale and repeatability of these spatiotemporal patterns that dictate the class of movement they give rise to (Mueller and Fagan 2008; Mueller et al. 2011). According to this view, migratory behavior should arise if occupying specific ranges at specific times of the year results in higher fitness gains than range residency (occupying the same range year-round) or nomadism (occupying different ranges with no annual pattern).

A minimalist view of the evolution of migration that is particularly applicable to most mammals has been formalized recently (Holt and Fryxell 2011; Fryxell and Holt 2013). According to this view, migration should be an evolutionarily stable strategy so

long as there are at least two different source habitats available that exhibit seasonal variation in fitness. Interestingly, this model predicts the common coexistence of two or more strategies (i.e., residency in part of the range yielding similar fitness as migration) under a broad range of conditions. Their general conclusion is that in a seasonally fluctuating world, migration or partial migration should be the rule rather than the exception. Migratory behavior is accordingly expected to evolve under a wide variety of ecological conditions. Why then, do some species or populations not exhibit such behavior? The obvious answer to this question is that, under certain conditions, the costs of migration exceed its benefits (Holt and Fryxell 2011; Fryxell and Holt 2013). It is by examining these costs and benefits that we may gain deeper understanding of the ecology and evolution of migration.

Before discussing these costs and benefits in more detail, it is helpful to remember that observed behavioral strategies are not necessarily optimal. Sedentary behavior may persist even if migration or partial migration are superior under current conditions, simply because of the challenging odds that may exist against the emergence and establishment of a complex trait such as migration. Sedentary animals may be limited by lack of cognitive, physical, and physiological preadaptations to long-distance movement. Even if such preadaptations exist, migration may

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require information (whether genetically acquired or learned) regarding the whereabouts and quality of suitable habitats—information that sedentary ancestors might not possess. It is thus crucial to consider cognitive and physiological limitations, as well as realistic eco-evolutionary time scales, when studying the evolution of migratory behavior.

Balanced against this point of view is growing recognition that collective behavior can emerge in groups of animals that do not all share the same cognitive abilities. Indeed, migration can evolve even if a small number of individuals learn how to efficiently exploit spatial gradients in resource availability while others simply choose to stay close to conspecifics (Guttal and Couzin 2010).

## Why migrate?

Possible costs and benefits of mammal migration that have received attention in the literature tend to fall under four major headings: energy intake, energy expenditure, vulnerability to predation, and mate finding (Table 1). Note that in many systems, however, these putative fitness components covary so that in practice it is often difficult to identify a single factor as the driver, or inhibitor, of migratory behavior.

### Energy intake

An increase in energy intake may be the result of migrating into a range that supports either higher quantity of food, higher food quality, or both (Fryxell and Sinclair 1988; Hebblewhite et al. 2008). Food quantity is likely a major limiting factor for specialists relaying on a narrow range of resources undergoing seasonal fluctuations. Plausible examples include baleen whales (Mysticeti) tracking spatiotemporal patterns of krill (Gaskin 1982; Corkeron and Connor 1999), nectivorous bats in Central America migrating along with the agave flowering season (Moreno-Valdez et al. 2000), and large carnivores (gray wolves, *Canis lupus* L., 1758; cheetahs, *Acinonyx jubatus* (Schreber, 1775); and spotted hyenas, *Crocuta crocuta* (Erxleben, 1777)) following the migration of their prey (Parker 1973; Durant et al. 1988; Hofer and East 1993; Walton et al. 2001).

For many large herbivores, however, food quality also plays a major role (Fryxell and Sinclair 1988; Fryxell 1991). For herbivorous mammals, the quality of food degrades with plant maturity due to the buildup of indigestible structural compounds such as lignin and cellulose (Langvatn and Hanley 1993; Wilmshurst et al. 1999). Hence, it seems reasonable to assume that any energy intake-driven migration of herbivorous mammals depends on some combination of the spatiotemporal patterns of food abundance and nutritional value, a process sometimes termed the “forage maturation” hypothesis (Fryxell 1991). Forage quality tends to decline over the growing season (i.e., the wet season in the tropics or spring in temperate regions), whereas absolute food abundance is actually increasing (Hebblewhite et al. 2008). By tracking locations with vegetation growing at a fast rate, a migrating animal could better obtain a continuous supply of young nutritious regrowth. This pattern of habitat use is consistent with migratory behavior in many large herbivores (Fryxell and Sinclair 1988), having been shown to well explain seasonal patterns of wildebeest (species of genus *Connochaetes* Lichtenstein, 1812) and Thomson's gazelle (*Eudorcas thomsonii* (Günther, 1884)) movement in the Serengeti system (McNaughton 1976; Fryxell et al. 1988, 2004; Holdo et al. 2009). Recently, Bischof et al. (2012) have elegantly demonstrated that some migrating red deer (*Cervus elaphus* L., 1758) in Norway follow the wave of vegetation green-up as it moves from the coastal regions to the mountains, whereas others “jump ahead” of the wave, reaching their summer ranges well before the arrival of spring.

Energy intake is often a function of local consumer density. The intensity of both inter- and intra-specific competition is largely density-dependent and hence so are the energetic benefits of migration (Mysterud et al. 2011). Intraspecific competition may be

particularly intense where aggregation serves as a predator avoidance strategy, resulting in rapid local depletion of resources. Under such conditions, consumer groups may need to perpetually move away from regions that have been depleted (Hopcraft 2010). In systems with predictable resource renewal, such dynamics may lead to synchronized migratory movements, whereas unpredictable patterns of resource renewal is more likely to encourage nomadism (Mueller and Fagan 2008).

Alternatively, it is possible that migration is driven by conspecific avoidance, such that migrants space themselves out to reduce resource depletion (Mysterud et al. 2011), in which case migration or nomadism are likely to be diffuse and uncoordinated among individuals (Mueller and Fagan 2008; Mueller et al. 2011). Either way, the particular shape of density dependence may be an important determinant of the profitability of migration and the frequency-dependent balance between migrants and residents in a population, or community, of consumers (Griswold et al. 2010; Holt and Fryxell 2011; Fryxell and Holt 2013).

Under certain conditions, migration may actually result in reduced energy intake compared with a resident strategy. Such reductions in energy gain could be caused directly by migrating through forage-poor areas or caused indirectly due to missed-opportunity costs. The latter includes time spent moving (rather than feeding) and inefficient utilization of local resources while migrating through (or into) relatively unfamiliar environments (i.e., spending more time searching for food than required by an experienced resident). A migratory individual would obviously find itself at a significant disadvantage if territoriality is required to defend critical resources, as is the case for many terrestrial predators. Whereas missed-opportunity costs are almost always the rule in avian migration, mammals often migrate through habitats that are suitable for foraging and can thus satisfy at least part of their nutritional needs during migration.

### Energy expenditure

Moving fast and for extended periods are hallmarks of migration. Movement is energetically costly and its cost is expected to vary with the mode of locomotion and the fuel load of the animal (Hedenström 2003a, 2003b). Movement costs are generally lower for swimmers and flyers compared with runners (Alerstam et al. 2003). Metabolic scaling predicts that the energetic costs of long-distance movement should decrease with body mass among swimmers and runners (Alerstam et al. 2003; Hein et al. 2012). Conversely, migratory behavior can also serve as a strategy to reduce annual energy expenditure through two mechanisms: aiding in thermoregulation and escaping ectoparasites.

Maintaining adequate body temperature may be energetically costly for endotherms, especially where there is a large difference between body temperature and environmental temperatures. It is thus most reasonable to expect the evolution of migratory behavior in mammals residing in seasonally fluctuating thermal environments. Thermal costs are often difficult, however, to tease apart from other factors, such as food availability, due to the inherent covariation between productivity and climate. One clear example of thermoregulatory costs on migration is the annual migration of tree-dwelling insectivorous bats from their northern breeding ranges to spend the winter in milder southern climates (Fleming and Eby 2003; Rodrigues and Palmeirim 2008; Popa-Lisseanu and Voigt 2009). Like nonmigratory bats, these migratory bats spend most winter in torpor hibernation. Hence, it is safe to conclude that their movement south is not motivated by food availability but rather by thermoregulation. Other possible examples of thermoregulatory migration include West Indian manatees (*Trichechus manatus* L., 1758) migrating along the Atlantic Coast of the US in response to water temperature (Deutsch et al. 2003), humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) wintering off Central America (Rasmussen et al. 2007; Rizzo and Schulte 2009), and

**Table 1.** Case studies of mammalian migration exemplifying specific hypothesis as described in the text.

Hypothetical benefit	Species	Migration type	References
Increase forage quantity	African and Amazonian manatee	Complete	Reeves et al. 1988; Arraut et al. 2010
	Frugivorous and insectivorous bats	Complete	Fleming and Eby 2003
	Humpback whale	Complete	Gaskin 1982; Rizzo and Schulte 2009
	Mexican long-nosed bat	Complete	Bernardo and Cockrum 1962; Moreno-Valdez et al. 2000
	Cheetah	Partial*	Durant et al. 1988
	Grey wolf	Partial	Parker 1973; Walton et al. 2001
	Lesser long-nosed bat	Partial	Rojas-Martínez et al. 1999
	Sperm whale	Partial*	Best 1969
Increase forage quality	Spotted hyena	Partial	Hofer and East 1993
	African elephant	Complete	Sikes 1971; Spinage 1994
	Caribou	Complete	Bergman et al. 2000
	Thomson's gazelle	Complete	Fryxell et al. 2004; Hopcraft 2010
	Wildebeest	Complete	Fryxell et al. 1988; Holdo et al. 2009
Avoiding conspecific resource depletion	Red deer	Partial	Bischof et al. 2012
	Thomson's gazelle	Complete	Hopcraft 2010
Thermoregulation	Red deer	Partial	Mysterud et al. 2011
	Humpback whale	Complete	Gaskin 1982; Rizzo and Schulte 2009
	Killer whale	Complete	Durban and Pitman 2012
	Schreiber's bat	Complete	Rodrigues and Palmeirim 2008
	Mexican free-tailed bat	Partial*	Bernardo and Cockrum 1962; Fleming and Eby 2003
Avoiding ectoparasitism	West Indian manatee	Partial*	Deutsch et al. 2003
	Reindeer	Complete	Folstad et al. 1991
Escape predation	Amazonian manatee	Complete	Arraut et al. 2010
	Zebra	Complete	Hopcraft 2010
	North American elk	Partial	Hebblewhite and Merrill 2007
Escape calf predation	Baleen whale (general)	Partial*	Corkeron and Connor 1999
	Bighorn sheep	Partial*	Festa-Bianchet 1988
	Caribou	Partial*	Bergerud et al. 1990; Heard et al. 1996
Mating	Bighorn sheep	Partial*	Bleich et al. 1997
	Bowhead whale	Partial*	Reeves et al. 1983
	Flying fox	Partial	Tidemann and Nelson 2004
	Harbor seal	Partial*	Parijs et al. 2000
	Harp seal	Partial*	Burns 1970
	Himalayan tahr	Partial*	Forsyth 1999
	North American elk	Partial*	Clutton-Brock et al. 1982
	Northern elephant seal	Partial*	Stewart and DeLong 1995; Van Den Hoff et al. 2002
	Sperm whale	Partial*	Best 1969
	Walrus	Partial*	Wiig et al. 1996

**Note:** Migration types are defined as complete (all individuals migrate) and partial (some but not all individuals migrate). An asterisk marks examples where partial migration could be predicted by individual characteristics (e.g., age, sex). The designation of migration type was dependent upon the specific hypothesis and example (e.g., humpback whales undergo partial migration in response to calf thermoregulatory needs, but complete migration in response to increased summer forage availability). Note that certain hypotheses could be included under multiple mechanisms (e.g., instances of sexual segregation leading to mating migration could be listed under energy intake if different nutritional requirements drive the separation).



killer whales (*Orcinus orca* (L., 1758)) making round-trip movements to subtropical waters (Durban and Pitman 2012).

An alternative route by which migratory behavior can serve to reduce energy expenditure is through its suppressive effect on parasite load (Alerstam et al. 2003). Parasites are known to inflict severe metabolic costs on their hosts, either directly (i.e., via consumption of nutrients and (or) tissue) or, in the case of some ectoparasites, indirectly through ear flapping, tail wagging, and reduction in time spent foraging or resting (Hughes et al. 2009). Moreover, mounting an immune defense to fight off parasites carries its own metabolic costs, which may be reduced if risk of infection is lower. Movement patterns of monkeys may be partially motivated by avoidance of intestinal parasites caused by local buildup of fecal contamination (Freeland 1980; Hausfater and Meade 1982). This idea has been extended to migratory movement in what has been termed the “migratory escape” hypothesis (Loehle 1995; Altizer et al. 2011). Some evidence suggests that migratory animals carry fewer parasites and that parasite load is negatively correlated with migration distance (Piersma 1997; Alerstam et al. 2003). Mammalian examples include reindeer (*Rangifer tarandus* (L., 1758)) in Finland (Folstad et al. 1991) and cave-dwelling bats in the Mediterranean (Rodrigues and Palmeirim 2008). Whereas parasites may play an important role in the energy budget of many marine mammals (Geraci and St. Aubin 1987), little is known about transmission dynamics and host density dependence and we know of no established links to migratory behavior.

From a mechanistic perspective, migratory escape from parasites may be possible because of the inability of most ectoparasites to adapt to different environmental conditions characterizing each seasonal range occupied by the host. Parasites relying on multiple host species (leading to apparent competition among hosts) or environmental transmission (leading to local buildups of parasite loads) may also struggle to persist on migratory hosts. Conversely, migration may increase parasite loads through exposure to a wider variety of parasites and pathogens along the migration route and in the migratory range (Alerstam et al. 2003; Altizer et al. 2011). Whatever the exact process might be, the temporal dynamics of local host densities could play a key role in determining parasite loads and virulence (Altizer et al. 2003, 2011) and hence the costs versus benefits of host migration. In practice, however, it will often be difficult to tease apart causal relationships between parasites and host migratory behavior because both are strongly influenced by seasonality (Altizer et al. 2006).

### Predation risk

Migrating animals may be more vulnerable to predation, particularly when traveling from one seasonal range to another (Hebblewhite et al. 2008; Middleton et al. 2013). This vulnerability stems from greater exposure to predators and increased detectability when traveling via narrow movement corridors at high densities and with little protective cover. If such short-term elevation in predation risk is sufficiently high to balance energetic advantages of seasonal habitat shifts, it could lead to the evolution of resident rather than migratory behavior (Fryxell and Holt 2013). Alternatively, moderate levels of risk en-route should still allow the evolution of migratory behavior if there is sufficient reduction in predation pressure or increase in energy gain over the entire annual cycle.

Predation has been elegantly demonstrated as the main driver of diel vertical migration in zooplankton (Gliwicz 1986), but less is known about its role in shaping seasonal migratory behaviors in mammals. Fryxell et al. (1988) employed simulation modeling to test the logical basis of several different hypotheses regarding the prevalence of migratory herbivores in the Serengeti. Their models suggest that migration could provide sufficient refuge from predation that Serengeti herbivore populations are no longer regulated from above. Hebblewhite and Merrill (2007) demonstrated that, at the seasonal-range scale, migratory North American elk

(*Cervus elaphus canadensis* Erxleben, 1777) experience lower predation risk from wolves than do resident elk occupying the same winter range. On the other hand, there is evidence that the opposite is true of elk in eastern parts of Yellowstone (Middleton et al. 2013). Arraut et al. (2010) suggest that Amazonian manatees (*Trichechus inunguis* (Natterer, 1883)) annually migrate into resource-poor environments to reduce predation risk associated with seasonal changes in water levels. Finally, neonate predation has been implicated as a major driver of calving migration (migratory movement to specific calving areas) in bighorn sheep (*Ovis canadensis* Shaw, 1804; Festa-Bianchet 1988), caribou (*Rangifer tarandus* (L., 1758); Bergerud et al. 1990; Heard et al. 1996), and baleen whales (Corkeron and Connor 1999; Connor and Corkeron 2001; Ford and Reeves 2008).

Under the most typical scenario, migratory escape from predation is enabled because predators are unable or unwilling to follow their migratory prey over the entire annual circuit. Among terrestrial predators, range residency seems to be common, even for carnivores that rely heavily on migratory prey. The most often quoted explanation for this is that species at higher trophic levels have complex social structure, such as territoriality (Fryxell et al. 1988). Alternatively, predators may not be able to follow prey along their migratory routes because of specialized metabolic and anatomical adaptations for hunting (requiring short bursts of rapid, high-energy locomotion) that are incompatible with efficient movement over long distances at regular intervals. Whatever the explanation for their different movement strategies, predators that are exposed to high densities of prey for only part of the annual cycle cannot appropriately respond numerically and thus inflict lower predation pressure even when prey are present (Fryxell et al. 1988). This numerical effect would obviously depend on the relative availability and profitability of nonmigratory prey (whether of the same or different species as the migrants) and could accordingly contribute to apparent competition among migrants and residents.

### Mate finding

The probability of encountering a mate, and particularly a high-quality mate, obviously depends on the local density of conspecifics. In contrast, animals often tend to avoid areas of high conspecific density outside the breeding season to reduce the adverse effects of competition. Such dynamics could conceivably lead to seasonal migration into a common breeding site, followed by dispersive movement following the breeding season, and may be especially prevalent among large aquatic mammals that must traverse the oceans to satisfy their nutritional needs. Alternatively, if males and females differ in their ecological needs (Barboza and Bowyer 2000), or aggregate in family groups with high kinship, potential mates may be spatially segregated outside of the mating season, leading to migratory movements by one sex only. Either way, mating would be the major driver for migration, with aggregation in the breeding season relatively brief and timed to coincide with female sexual receptivity.

Because of relatively long gestation periods, many mammals have distinct breeding and calving seasons, and migratory mammals may spend these in distinct migratory ranges. Thus, unlike avian migration, the mating success hypothesis may be considered independently of seasonal and environmental factors affecting the success of offspring rearing (including energy balance and predation avoidance discussed above). That said, the mate-finding hypothesis has received little-to-no attention in the mammal migratory literature. Limited evidence suggests that male harbor seals (*Phoca vitulina* L., 1758) return to the same acoustic display area year after year (Van Parijs et al. 2000) and that migratory movements by flying foxes (species of the genus *Pteropus* Erxleben, 1777) may be motivated by mate search (Tidemann and Nelson 2004; Sugita et al. 2009). More research is needed, however, into

the prevalence and relative importance of mating success as a driver of migratory behavior.

## Behavioral and physiological specialization

Whereas migration seemingly requires a complex array of adaptive traits, its frequent appearance and disappearance within and among mammal species, as well as the prevalence of mixtures of migratory and resident subpopulations in migratory species, suggest that mammalian migration requires little more than a minor extensions of typical physiological characteristics (Alerstam et al. 2003). Almost without exception, migratory mammals are highly mobile even outside of the migration season. In this respect, mammal migration differs markedly from avian, fish, or insect migrations, where mobility often increases by an order of magnitude when entering the migratory phase. Hence, unlike other taxa, long-distance migration in most mammals probably requires only minor phenotypic modification in body plan.

Migrating among distinct seasonal ranges may, however, require more substantial changes in cognitive and other behavioral traits. A successful migrant needs to “know” when to leave its current range, where to move, and when to stop. This knowledge may be genetically inherited or culturally transferred (e.g., from parent to offspring or among conspecifics). To date, little evidence exists to support one or the other. In the mid-1980s, a large fraction of elk in Banff National Park were migratory, classically moving from valley bottoms in the winter to alpine areas in the summer (Woods 1991). Within a decade, however, migration had largely ceased. Intriguingly, this change in space use coincided with the reinvasion by gray wolves into the Bow Valley in 1986, following extermination earlier in the century, which led to rapid decline in elk fitness throughout the Bow Valley (Hebblewhite et al. 2005). This case history clearly suggests that perceived changes in predation pressure might have led to facultative alterations in behavior, which seems most consistent with a culturally flexible trait rather than a genetically mediated change in behavior. Interestingly, recent evidence suggests that similar demographic changes may be occurring in response to the rapid range expansion of gray wolves throughout the Yellowstone ecosystem. Migratory elk in the eastern part of Yellowstone show evidence of reduced offspring recruitment compared with resident animals living outside the park in the winter range occupied by both behavioral types (Middleton et al. 2013). If cultural selection is involved in maintaining migration, one might predict just such rapid change in response to alterations in predation risk across the Yellowstone landscape, whereas changes in genetic makeup could take much longer.

A recent study of zebra (*Equus burchelli* (Gray, 1824)) in Botswana recorded migratory movements retracing a historical migratory route that had been blocked by fences during the previous 36 years prior to the study (Bartlam-Brooks et al. 2011). As culturally transferred knowledge is unlikely over such an extended period, these findings suggest that zebra migration has at least some genetically inherited component. Alternatively, exploratory behavior could have encouraged rapid identification of fitness-improving patterns of range use once the barrier was removed, allowing zebra to rapidly “re-learn” a culturally transmitted trait.

For some migratory mammals, migration may emerge from a simple behavioral response to seasonally changing environmental gradients. Such might be the case for some large ungulates following the landscape pattern of vegetation green-up in spring (wildebeest migration across the Serengeti plains: Boone et al. 2006; Holdo et al. 2009; red deer migration in Norway: Bischof et al. 2012) and northern ungulates, such as white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780); Sabine et al. 2002), mule deer (*Odocoileus hemionus* (Rafinesque, 1817); Russell 1932), moose (*Alces alces* (L., 1758); Ball et al. 2001), roe deer (*Capreolus capreolus* (L., 1758); Ramanzin et al. 2007), and sika deer (*Cervus*

*nippon* Temminck, 1838; Igota et al. 2004), that conceivably track the continually changing margin of the snow distribution in alpine areas. Simple gradient tracking is similarly plausible in nectar-seeking Mexican long-nosed bats (*Leptonycteris nivalis* (Saussure, 1860); Moreno-Valdez et al. 2000) and warmth-seeking West Indian manatees (Deutsch et al. 2003). In each of these examples, migration could conceivably arise without any obvious behavioral change—the animal simply follows continuously shifting environmental conditions, in essence climbing gradients of habitat suitability. As appealing as this view of animal migration may be, there is plausible evidence that higher cognitive abilities are involved. For example, some migrating red deer actually jump ahead of the environmental gradient, arriving at their summer ranges weeks before the spring green-up (Bischof et al. 2012). In Serengeti wildebeest, patterns of habitat selection (Wilmschurst et al. 1999) and seasonal changes in population distribution over the annual range (Holdo et al. 2009) strongly suggest an ability to respond to changes in resource conditions over large spatial scales (80–100 km) in the surrounding landscape, larger than would be expected based on sensory information alone. Further study of cognitive limitations on migration is definitely a fruitful area for future empirical and theoretical research.

One practical implication of the ambiguity characterizing our understanding of the process and patterns of mammal migration is the challenging nature of quantifying migration. The high degree of mobility, large annual home ranges, responsiveness to local conditions (e.g., gradient following), and inconsistencies among individuals (e.g., partial migration) make it difficult to determine whether, when, and where an animal should migrate. One formal approach, developed by Bunnefeld et al. (2011), is based on a nonlinear regression of the animal's net squared displacement over time. It is designed to both distinguish migration from other types of movements and quantify different aspects of the migratory behavior such as departure time, distance between ranges, and residence time in each range. Whereas this methodology represents a significant step forward in the quantitative analysis of animal migration, successfully applying it necessarily depends on details about the migratory pattern (e.g., stopovers, occupancy of multiple ranges). Part of the value in trying to develop general formal approaches for the quantification of migration lays in the necessity to refine definitions and be explicit about what does and does not qualify as migratory behavior. Overall, we see the identification of useful analytical tools a fruitful field of future migration study.

In avian migration, it is fairly common to observe complex migratory networks with a mixture of multiple wintering and (or) breeding sites (Webster et al. 2002). While migratory networks are not common in mammalian systems, they certainly do occur. Perhaps the best-known examples are traditional migration routes used by mule deer and pronghorn antelope (*Antilocapra americana* (Ord, 1815)) in montane regions of western North America (Sawyer et al. 2005, 2009; Berger et al. 2006). Ungulate migratory routes along river valleys can be quite narrow, and therefore vulnerable to inadvertent creation of barriers, such as from oil wells, housing developments, or other anthropogenic environmental modifications. Maintaining the integrity of migratory networks would seem one of the most important conservation needs.

In birds, migratory networks are thought to have a strong suppressive effect on local adaptations because of substantial gene flow among subpopulations. The typical delay between copulation and parturition in mammals means that such gene-flow effects could only operate if subpopulations share common wintering grounds. At any rate, migratory networks should reduce localized speciation through the exposure of multiple subpopulations to the same ecological condition through at least part of the year.



## Taxonomic variation in migration

We provide here a taxonomic cross section of mammalian migration. Table 1 maps many of these case studies to the set of hypotheses reviewed above.

### Ungulata

Migration is well developed among ungulates of both orders Perissodactyla (odd-toed) and Artiodactyla (even-toed). It is widely believed that ungulate migration (and ruminants in particular) is driven primarily by changes in forage availability across seasons, effectively tracking high-quality forage and habitats across time and space. This may manifest simply as minor changes in elevation as populations track snow depth and changes in microclimate in mountainous regions, as in North American bison (*Bison bison* (L., 1758); Plumb et al. 2009), black-tailed deer (*Odocoileus hemionus columbianus* (Richardson, 1829); Loft et al. 1984), mule deer (Brown 1992), white-tailed deer (Nelson 1998), North American elk (Boyce 1991; Hebblewhite et al. 2008), and red deer (Albon and Langvatn 1992; Bischof et al. 2012), or long migrations across essentially flat landscapes, as observed in temperate populations of caribou (Bergman et al. 2000), tropical populations of white-eared kob (*Kobus kob leucotis* (Lichtenstein and Peters, 1853)), tiang (*Damaliscus korrigum korrigum* (Ogilby, 1837)), zebra, Thomson's gazelle, and wildebeest (Fryxell et al. 2005; Holdo et al. 2009), although often there are meaningful gradients in rainfall or primary productivity at such enormous spatial scales. Ungulates may also benefit from reduced predation pressure while migrating (Fryxell and Sinclair 1988; Hebblewhite and Merrill 2007). The potent combination of increased foraging success and decreased predation risk is common across many terrestrial ecosystems, so it is perhaps not surprising that migration has evolved accordingly in numerous ungulate species across all continents (Fryxell and Sinclair 1988).

Sexual differences in nutritional demands often produces seasonal patterns of sexual segregation in ungulates (Clutton-Brock et al. 1982). In systems where environmental conditions substantially restrict resource availability, sexual segregation may produce sex-biased partial migration in ungulates with nonoverlapping seasonal ranges. For example, resident populations of Himalayan tahr (*Hemitragus jemlahicus* (C.H. Smith, 1826)) exhibit fluctuating seasonal abundance of males, with subadult and often adult males migrating to distinct summer grounds when female densities become too extreme (Forsyth 1999). Similar patterns are often observed in other large ungulates such as elk (Clutton-Brock et al. 1982) and bighorn sheep (Bleich et al. 1997).

### Cetacea

As in ungulates, migration is decidedly common in both toothed (Odontoceti) and baleen (Mysticeti) whales. Migratory behavior is primarily influenced by seasonal trade-offs between optimal environmental conditions for breeding and feeding, with tropical waters favored for calf thermoregulation during the winter, and arctic regions favored because of dramatic increase in food availability during the spring and summer (Gaskin 1982; Corkeron and Connor 1999). This has led most migratory cetaceans to return to distinct breeding grounds at low latitudes. This is particularly true of baleen whales, whose migratory behavior is clearly defined and predictable (Gaskin 1982). For example, humpback whales reliably breed at approximately 20° latitude regardless of hemisphere, then return to subarctic waters to feed after fasting throughout the breeding season (Rasmussen et al. 2007; Rizzo and Schulte 2009). Fin whales (*Balaenoptera physalus* (L., 1758); Mizroch et al. 2009), gray whales (*Eschrichtius robustus* (Lilljeborg, 1861); Killingley 1980), and blue whales (*Balaenoptera musculus* (L., 1758); Mate et al. 1999) provide additional examples of such distinct seasonal ranging in the baleen suborder, though this is by no means exhaustive.

Similar migrations between breeding and feeding grounds are not uncommon in toothed whales, including sperm whales (*Physeter macrocephalus* L., 1758; Best 1969) and beluga whales (*Delphinapterus leucas* (Pallas, 1776); Shpak et al. 2010), and Pacific humpback dolphins (*Sousa chinensis* (Osbeck, 1765); Karczmarski 2000). These migrations tend to be less predictable than those of the baleen whales, and may be influenced by factors other than female nutrition and calf reproduction (Gaskin 1982; Durban and Pitman 2012). For example, a recent study found that killer whales routinely migrate into subtropical waters during the winter to improve skin regeneration, a benefit of warm-water habitats that may extend to other cetaceans (Durban and Pitman 2012). Whether such benefits are a primary driver or secondary benefit of migration remains to be determined, and adaptive advantages stemming from improved foraging and calf production remain the most well-known and supported hypotheses concerning cetacean migration.

Partial migration is decidedly common across all migratory cetaceans (Gaskin 1982). Female humpback whales may remain in winter feeding grounds if they are unburdened by calves (Brown et al. 1995), and new mothers are often the last to leave the summer breeding grounds (Rizzo and Schulte 2009). Female and juvenile bowhead whales (*Balaena mysticetus* L., 1758) may use alternate southward migratory routes compared with males (Reeves et al. 1983). Sperm whale pods observed at high latitudes are often composed of bachelor males (Best 1969; Gaskin 1982), and females are known to travel more slowly and shorter distances when burdened with young (Gaskin 1982). Indeed, partial migration in cetaceans is frequently linked to sexual differences in nutrition and parental care. It has been suggested, however, that a reduction in predation risk by killer whales may drive female cetaceans to migrate to warmer waters (Corkeron and Connor 1999). Still, most explanations for this behavior rely on calf thermoregulation and female nutrition as the primary driver of sex-biased migration in cetaceans (Gaskin 1982; Reeves et al. 1983; Rizzo and Schulte 2009).

### Chiroptera

The migratory behavior of bats seems to be primarily driven by seasonality, due to changes in either abiotic environmental conditions or resource availability (Fleming and Eby 2003). The former is particularly true for bats occurring in temperate climates, where migratory behavior consists primarily of movement between warmer regions during the breeding and birthing seasons, and cooler regions for hibernation and torpor (Rodrigues and Palmeirim 2008; McGuire et al. 2012). Seasonal temperature is obviously linked to changes in resource availability. Roost-site temperature is often the best predictor of migratory behavior in temperate bats, however, suggesting that the metabolic advantages of selecting migratory destinations (such as winter hibernacula) for their thermal properties far outweigh any energetic benefits associated with resource availability (Fleming and Eby 2003; Rodrigues and Palmeirim 2008). Conversely, bats inhabiting tropical regions are less driven to migrate than those occupying temperate latitudes, owing to the absence of seasonal changes in temperature and productivity, and those that do migrate typically do so in response to changes in resource availability (Rojas-Martínez et al. 1999; Moreno-Valdez et al. 2000). Insectivorous tropical species experience relatively little temporal variation in prey abundance. Frugivorous and nectivorous species may suffer extreme variation in resource abundance due to plant phenology and are therefore expected to undergo seasonal range shifts that track shifting spatial inflorescence patterns (Fleming and Eby 2003).

In numerous species of bats, migratory behavior differs substantially both between and within populations. For example, the Brazilian free-tailed bat (*Tadarida brasiliensis* (I. Geoffroy, 1824)) has sedentary populations in the western US, whereas southwestern US populations migrate long distances between Oklahoma and

Texas in the summer and western Mexico in the winter (Bernardo and Cockrum 1962). Moreover, migratory populations of Brazilian free-tailed bats may not occupy the same winter and summer grounds each year and individuals (usually males) may remain in the wintering grounds. Glass (1982) concluded that this behavior may be attributed to individual failure to locate and follow established roosting sites using olfactory cues; however, sex-biased partial migration has also been documented in the Mexican long-nosed bats (species of the genus *Leptonycteris* Lydekker, 1891), the hoary bat (*Lasiurus cinereus* (Beauvois, 1796)), and the little-collared fruit bat (*Myonycteris torquata* (Dobson, 1878); Cockrum 1991; Rojas-Martínez et al. 1999; Fleming and Eby 2003).

It is noteworthy that bat migratory behavior is heavily influenced by wing morphology. Migratory bats often possess wings adapted to long-distance travel: long and narrow, with decidedly pointed wing tips (Norberg and Rayner 1987). These adaptations also restrict in-flight maneuverability, however, limiting the capacity to hover and travel at low velocities. Wing morphology of bats is thus believed to have developed in response to foraging strategy, where species that rely on speed and ambush tactics have evolved wing morphology that is equally suited to high velocity and energetic efficiency (Norberg and Rayner 1987). Migration in many bats may therefore be a secondary benefit of specific morphological adaptations enhancing foraging success.

### Proboscidea

The migratory behavior of elephants is well documented, with records of their migrations going back as far as the 18th century (Spinage 1994). Although their seasonal movements coincide with rainfall patterns, elephants do not typically migrate between predictable areas or regions, but rather between predictable habitat types. For example, African elephants (*Loxodonta africana* (Blumenbach, 1797)) track primary productivity and forage quality as influenced by rainfall (Coe et al. 1976; Eltringham 1977; Sukumar 1989), often moving into forested habitat during the dry season to mate and rear young, then returning to more open foraging areas when primary productivity increases at the onset of the rainy season (Sikes 1971; Spinage 1994). Such migrations rarely involve the entire population, often being limited to family units. Records exist of elephant family units regularly traveling 160 km between Uganda and Sudan, and accounts suggest that they may travel from Mount Kilimanjaro to the Lorian Swamp in Kenya and back, a distance of 480–640 km (Sikes 1971).

The mechanism driving migration in Asian elephants (*Elephas maximus* L., 1758) seems less certain. Although there is some evidence suggesting that Asian elephants are driven by forage quality during migration (Eltringham 1982; Sukumar 1989), others have found that water availability and climatic conditions, rather than forage quality alone, influence seasonal range shifts in Asian elephants (Daniel 1998). However, such studies still note that habitat quality is an important factor in determining seasonal ranges, suggesting that forage quality should be considered in any discussion of Asian elephant migration.

### Carnivora

There is little evidence to suggest that terrestrial carnivores migrate with any predictability. Members of this order often establish and maintain or defend territories for the purposes of hunting and mating, which precludes the possibility of migrating (Ballard et al. 1987; Fryxell and Sinclair 1988). Certain exceptions to this have been noted in terrestrial carnivores whose primary prey typically migrate long distances. For example, packs of wolves may abandon their territories in favor of following barren-ground caribou during their annual migration (Parker 1973; Walton et al. 2001). Female and nonresident male cheetahs track herds of Thomson's gazelles (Durant et al. 1988). Finally, spotted hyenas may leave their clan territory to prey upon migratory herds

within 90 km or so, but seemingly cannot track migratory ungulates around the entire seasonal cycle (Hofer and East 1993).

Conversely, migratory behavior is decidedly common in marine carnivores. All extant families of suborder Pinnipedia (walruses, Odobenidae; eared seals, Otariidae; earless seals, Phocidae) contain at least one migratory species. In seals, this behavior often coincides with distinct foraging and breeding areas (i.e., rookeries), as in northern elephant seals (*Mirounga angustirostris* (Gill, 1866); Stewart and DeLong 1995; Burton and Koch 1999), southern elephant seals (*Mirounga leonina* (L., 1758); Van Den Hoff et al. 2002), northern fur seals (*Callorhinus ursinus* L., 1758; Burton and Koch 1999; Ream et al. 2005), and harp seals (*Pagophilus groenlandicus* (Erxleben, 1777); Burns 1970; Nordøy et al. 2008). In the case of northern elephant seals, these feeding sites are spatially separate for males and females (Stewart and DeLong 1995). Male walruses (*Odobenus rosmarus* (L., 1758)) also separate from the female population on Franz Josef Island, Norway, and migrate to Svalbard during the winter (Wiig et al. 1996). Additionally, a recent study on sea otters (*Enhydra lutris* (L., 1758)) revealed predictable movement coinciding with fluctuations in solar activity between the Commander Islands, Russia (Zagrebel'nyi et al. 2008).

### Sirenia

Both extant genera of this order—manatees (species of the genus *Trichechus* L., 1758) and dugongs (*Dugong dugon* (Müller, 1776))—are migratory. Movements by Amazonian and African manatees (*Trichechus senegalensis* Link, 1795) are seemingly influenced by seasonal changes in water depth, effectively trading off areas of high resource density vs. low predation pressure that are used equally by both sexes (Reeves et al. 1988; Arraut et al. 2010). This contrasts well with West Indian manatees occurring at the northern extent of their range along the east coast of the US. West Indian manatees often follow a north–south migration route based on water temperature and exhibit sexual differences in migration velocity and site preference (Deutsch et al. 2003). Populations of West Indian manatees at the southern extent of their range, however, exhibit migratory behavior similar to that displayed by African and Amazonian species (Castelblanco-Martínez et al. 2009).

Dugongs follow migratory patterns similar to those of manatees: at high latitudes (e.g., southern Australia) dugong populations tend to track seasonal changes in water temperature, whereas dugongs at low latitudes typically respond to changes in water depth and the hydrological cycle (Sheppard et al. 2006). However, there is also suggestive evidence that dugong migratory behavior may be induced by habitat degradation caused by tropical cyclones (Gales et al. 2004). If so, it follows that there may exist a heretofore unidentified trade-off in high-latitude sirenian populations between ambient water temperature and habitat quality.

### Lagomorpha

The lone migratory species of this order is the black-tailed jackrabbit (*Lepus californicus* Gray, 1837), which migrates to distinct wintering grounds southwest of its normal feeding grounds (Smith et al. 2002).

### Primates

There is anecdotal evidence to suggest that gorillas (*Gorilla gorilla* (Savage and Wyman, 1847)) use regular migration routes while searching for foraging grounds (Casimir 1975). However, the vast majority of literature on primate migration describes emigration–immigration of individuals between groups and semi-nomadism.

Migration was a well-developed life-history strategy in several different preindustrial human societies. Several Indian tribes living on the Great Plains of North America relied on the Plains bison for a large fraction of their meat protein. The Sioux were particularly renowned for their ability to track buffalo migrations for extended periods, developing an entire economy around



bison-derived goods. Indeed, the government-sponsored slaughter of bison was intended as to harm the Sioux and other First Nations people as much as to open the Great Plains for commercial livestock operations.

Inuit people in the areas fringing the Arctic Ocean also migrated from inland areas occupied during the winter to the sea-side during the brief summer. This presumably allowed them to take maximum advantage of the rich assortment of fish and sea mammals available in Arctic waters during the ice-free period, but shifting back onto the tundra to hunt caribou, moose, and other terrestrial mammals during the winter. Similar migrations are well documented across Siberia.

Pastoralist societies often migrated with their herds in a manner remarkably similar to that of wild ungulates (Behnke et al. 2012). Some transhumant migrations persist to this day, such as the Saami people of Scandinavia and Finland, who migrate with their reindeer to high montane pastures during the summer, taking advantage of the travelling wave of nutritious forage used by many wild ungulates, but migrating back to lower elevations during the winter period, presumably to reduce thermal stress and to gain access to lower quality, but abundant food resources to tide them over the winter.

Similar pastoralist migrations were adopted by many peoples, such as the Tuareg and Fulani tribes, across the Sahel region of sub-Saharan Africa. These movements allowed them to track the same green wave of vegetation growth triggered by movement of the Inter-Tropical Convergence Zone north and back south across the equator each year that funds the great migrations of Serengeti and Boma. Misguided efforts by development agencies to encourage large commercial livestock ranches replete with watering points discourage such transhumant pastoralist migration, having the unintended consequence of reducing the ability of pastoralist peoples to adapt to changing rainfall from year to year, as well encouraging unsustainable levels of grazing and browsing of semi-arid vegetation, and thereby exacerbating famine conditions (Sinclair and Fryxell 1985).

## Conclusions

Migration is a common life-history strategy in mammals. Theory suggests that this is to be expected, because vast parts of the globe are capable of sustaining large mammals (i.e., source habitat is common) and seasonality in demographic rates is commonly experienced by mammals (Holt and Fryxell 2011; Fryxell and Holt 2013). Indeed, there are well-documented examples of migration in many mammalian families. The most prominent exception is terrestrial carnivores, among which there are relatively few true migrants. The reasons for this are rather unclear, but likely stem from spatial restrictions imposed by social structure, such as territoriality and exclusive home-range use.

There is also seemingly a lower limit on migration strategies in mammals, in that few rodents, lagomorphs, or small carnivores are migratory. This probably stems from the limited ability of small mammals to move extended distances, required to advantage of seasonal variation in habitat quality. Hence, there would be a pronounced cost to switching habitats, making migration no longer an evolutionarily stable strategy. The exception to size limitation is bats, for which there are numerous examples of migratory behavior. Given that bats are obviously more mobile and movement comes at far lower cost than in the terrestrial realm, perhaps this is to be expected.

Of the many possible selective advantages of migration, the most common among herbivores is taking advantage of regional variation in resource abundance and (or) quality. In a sense, migration resembles rotational grazing. Accordingly pastoral societies often have transhumant pastoralist strategies, strongly resembling those of wild herbivores. In both cases, movement is rarely engineered to secure maximum food resources, but rather to

more efficiently exploit a shifting mosaic of sites whose combinations of abundance and quality yield the highest energy returns. There is also growing evidence that herbivore migration can reduce predation risk, at least in systems with top carnivores with territorial social systems. Most of the examples of this come from terrestrial ecosystems, but then again there are few aquatic herbivorous mammals in the first place.

Among mammalian carnivores, variation in food quality is undoubtedly a minor concern because their prey species are nutritionally identical to themselves, at least in a crude sense. Under these circumstances, there seem to be two alternative pathways to the evolution of migration. First, some terrestrial predators have seemingly evolved the ability to migrate to track their migratory prey. Second, aquatic predators seem to trade off energetic costs against benefits of feeding in resource-rich environments. Hence, marine mammals commonly feed in arctic waters teeming with food, but retreat to tropical waters to rear offspring to independence.

Other potential benefits of mammalian migration that have been discussed in the literature include improvement in mate-finding and reduction in parasite loads. While both are intriguing, supporting evidence is rather fragmentary at best.

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