

The Value of Experimental Approaches in Migration Biology

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ABSTRACT

The past several decades have ushered in a golden age in the study of migration biology, leading to a wealth of descriptive articles that characterize various aspects of migration and its implications for individuals, populations, and ecosystems. However, relatively few studies have adopted an experimental approach to the study of migration, and fewer still have combined lab and field experiments to glean insights into the mechanisms underlying variation in migration behavior and success. Understanding the proximate and ultimate causes of migration timing, energy allocation and optimization, migration success, and fitness is important to aid the conservation and management of wildlife populations by establishing appropriate protections or managing environmental conditions that influence migration. With recent technological advances and miniaturization of animal-borne electronic tracking devices, as well as

ground-, water-, and space-based telemetry infrastructure, researchers have the tools necessary to experimentally test hypotheses central to the mechanics of migrations and individual variation therein. By pairing physiological measurements, molecular analyses, and other approaches within an experimental framework, there is the potential to understand not only how animal migrations function but also what differentiates successful migrations from failed migrations and the associated fitness implications. Experimental approaches to migration biology are particularly important, as they will help us to better comprehend and hopefully predict animal responses to environmental and anthropogenic changes by isolating confounding variables that challenge inferences from observations.

Keywords: experiments, laboratory, migration, proximate causes, treatments, ultimate causes.

Introduction

Animal migration is one of the great themes in organismal biology and ecology (Bowlin et al. 2010), and by understanding the proximate and ultimate drivers of migration behavior, insights into many fundamental questions in biology can be gleaned (Mayr 1961; Schwenk et al. 2009). These include the response of organisms to their environments, the functional diversity of migratory strategies and tactics, how physiological pathways underlie variation in migratory phenotypes, and how organisms cope with the trade-offs inherent to migration (e.g., between investment in locomotion vs. reproduction). Migratory animals exhibit a high degree of taxonomic and behavioral diversity, ranging from short- to long-distance migrations, partial migrations, altitudinal migrations, and more (Bowlin et al. 2010). Animals must therefore integrate physiological, morphological, behavioral, and genetic aspects of their biology with the environmental factors to which they are exposed (Åkesson and Hedenström 2007; Kunz et al. 2008). Migrations represent some of the most fascinating and awe-inspiring phenomena observed in the natural world.

Not surprisingly, some iconic migrations (think salmon, wildebeest, terns, sea turtles, and some land crabs) have also captured the imagination of the public, with them being routinely featured in documentaries and even popular movies (e.g., *Turtle Tale*, *The Lion King*). Migration is also a sufficiently important and interesting topic that it is covered (either as a chapter or through case studies) in almost every ecology, behavior, and animal physiology textbook from the past (e.g., the first major text

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on ecology; Allee et al. 1949) to the present (e.g., the classic *Eckert Animal Physiology* series and Alcock's *Animal Behavior* series, among many others) and now even has a dedicated journal (i.e., *Movement Ecology*).

Migration biology reveals when, where, why, and how animals undertake their often synchronized, cyclic, and predictable movements across land- and seascapes (Alerstam et al. 2003; Wilcove 2008; Bowlin et al. 2010). Answering these questions can inform both the management and the conservation of migratory species and their habitats by allowing researchers to predict how animals respond to disturbances (Newton 2008; Wilcove and Wikelski 2008; Altizer et al. 2011). From field observations of migrations at varying spatial and temporal scales and among a diversity of species, the general nature of organismal biology and animal migration has been fairly well described. Data from such observations allow us to build predictive models, but these have limited power to explain the proximate and ultimate mechanisms underlying migration. Experimental approaches to the study of migration in which specific variables can be controlled or manipulated in the lab or field are therefore needed to isolate causative factors differentiating migrants from nonmigrants and, from a fitness perspective, successful from unsuccessful migrations.

We contend that experimental approaches are needed if we are to provide answers to the key questions about migration biology, especially the *hows* (mechanistically) and *whys* (evolutionarily). These approaches must integrate multiple scientific disciplines and include both traditional and novel techniques in studies across multiple taxonomic groups that span laboratory and field-based settings (Bowlin et al. 2010). A

search of the Web of Science Core Collection database revealed that within the field of zoology, 6,850 migration studies (search: Topic = Migrat* NOT Topic = cell* to avoid false positives related to cell migration) were conducted between 1900 and 2019 (as of April 8, 2019). Within those, experimental studies (search: Topic = experiment* OR manipul* OR treat*) comprised just 13% (855 hits) of the studies, suggesting that experimental approaches within the realm of migration biology are somewhat uncommon. Manual screening of a subset ($N = 20$) by abstract revealed that false positives for experimental studies were common (7/20), such that this number of 13% is inflated. Although we acknowledge that this search is not fully comprehensive, it supports the perspective that experimental approaches, where either the organisms or environmental contexts are manipulated, are relatively uncommon in migration studies.

Kennedy and others (Kennedy and Booth 1963, 1964; Dingle 1965, 1966) are credited with some of the earliest research concerning the proximate drivers of migration biology. Experiments with insects revealed physiological pathways stimulating the onset of migration and the determinants of migration as a distinct behavior. Such experiments have contributed to a definition of migration to differentiate it from other movement behaviors observed in animals (Dingle 2006; Dingle and Drake 2007). In this review, we draw representative examples from the literature to highlight the potential that experimental approaches to migration biology have for revealing the many drivers of animal migrations (fig. 1). Whether under controlled laboratory conditions or in field contexts, experimental studies are useful for determining the proximate drivers, or causes, of migratory behaviors

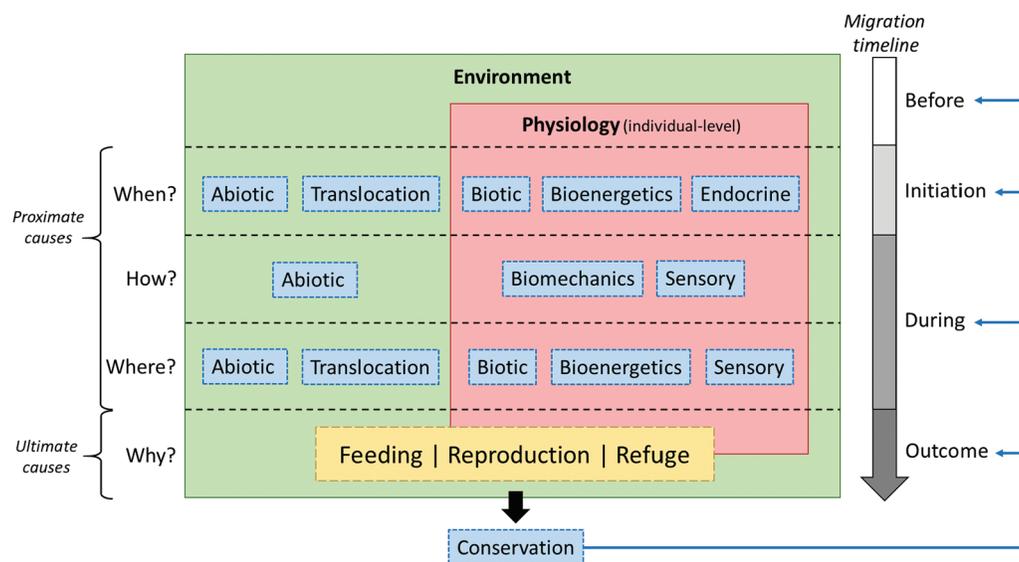


Figure 1. Conceptual framework of experimental biology in migration. Migration is the result of and/or is affected by an organism's physiology and the environment it lives in. Physiology (red) dictates an individual's internal state, which can be impacted either directly or indirectly by the surrounding environment (green). This interaction between physiology and the environment affects individuals throughout the entirety of the "migration time line" by determining when an individual is ready to initiate migration, how and where an individual will migrate, and finally, why an individual ultimately migrates (yellow). The blue boxes represent the types of experiments that can be performed at different stages along the migration time line to understand both the proximate and the ultimate causes of migration.

(Underwood 1990; Cooke et al. 2017). Here, we advocate for experimental approaches to migration biology and explore several thematic areas of migration biology research that should be testable with experimental methods. We then discuss the aspects of migration where experiments are currently lacking but which would greatly benefit our understanding of how, why, when, and where animals migrate.

What Can Experimental Biology Bring to the Study of Migration?

Experimental studies can be conducted in either laboratory or field settings to reveal the underpinnings of various aspects of migration. In both settings, environmental (e.g., temperature, oxygen availability), behavioral (e.g., predation, competition), or physiological (e.g., hormones, energetic substrates, disease) variables can be isolated by physical interventions. Experiments related to interspecific interactions are more challenging to perform but are highly relevant to explore, given that species or conspecific interactions may be an important force driving the evolution of migratory behaviors (Furey et al. 2018).

Field experiments are useful for generating in situ data related to the migration of animals at ecologically relevant scales that are not easily simulated in a laboratory (though we acknowledge that some mesocosm experiments can simulate nature fairly accurately, though mostly on a small scale). Frequently, these field studies require some method of remote observation to track the spatial and temporal progress of animals in the migratory arena. Methods include passive techniques such as photo identification and mark-resight/recapture, both of which rely on the identification of uniquely marked individuals. For example, photo identification techniques were used to track the movement patterns of individual white sharks and revealed site fidelity in at least 78% of individuals around Guadalupe Island, Mexico (*Carcharodon carcharias*; Domeier and Nasby-Lucas 2007). Active techniques include various forms of electronic tracking, such as biotelemetry or biologging, and can include satellite, radio, or acoustic transmitters that communicate position (and other) data to receivers or log it onboard for later retrieval. These active methods provide accurate information about individual migratory progress, which can be used to define discrete experimental treatment groups (Cooke et al. 2008).

However, not all questions about migration biology can be addressed using field studies. For example, when addressing uncertainty about the potential migration behavior of genetically engineered animals in nature, contained laboratory or mesocosm experiments must be used (e.g., Sundström et al. 2010), as the release of such animals to the wild is legally prohibited by most countries (Devlin et al. 2006; Kapuscinski et al. 2008). In cases when animals are too small or too sensitive to be tagged, laboratory studies have proven quite useful. Furthermore, because most field studies require some form of tagging to identify individuals, there is no possibility for true (untagged) migratory controls. Laboratory approaches also allow more direct observation and control over the environment to which animals are exposed. This is especially important as behavioral observations can be lost

during field studies when electronic tags are shed or if animals alter their behavior in unexpected ways (Hazekamp et al. 2010). In such cases, preliminary studies in the lab may help to guide field approaches.

One powerful, yet seldom used, way to address the inherent limitations of both laboratory and field studies is to conduct both types of studies in parallel or in succession to address the same question. Proof of concepts developed in a laboratory, which provide evidence that manipulations can effectively isolate variables that influence animal behavior, can then be scaled to field settings where behavioral manipulations can be tested in a natural context. Hellström et al. (2016) performed such an experiment to study the effects of a GABA_A receptor agonist on Atlantic salmon (*Salmo salar*) smolt migration, revealing that the agonist increased migration intensity of smolts first in a circular pool mesocosm, then in the Ume River in Sweden. These combined approaches are powerful for providing data at both relevant scales to isolate mechanisms and reveal applications and can make significant contributions to our understanding of animal migration.

Understanding the natural limits and regulations imposed on migratory populations is of crucial importance to adequately conserve and manage migratory species. Estimates of density dependence are especially relevant to develop predictive population models (Sutherland and Norris 2002; Norris and Taylor 2006; Taylor and Norris 2010). This is particularly salient for partially migratory species that are sensitive to density dependence and for which the expression of migration may depend on conspecifics (Griswold et al. 2010; Chapman et al. 2011). These estimates can be obtained from time series studies but lack proper controls. As such, experiments are key to advance this area of study (Flockhart et al. 2012) and can help us understand the mechanisms underpinning various aspects of migration (fig. 1). In the following sections, we highlight key experimental approaches that have provided valuable insights for understanding various aspects of migration. We acknowledge that these sections are not exhaustive, but we provide clear examples of the use of experiments in migration biology in various taxa and highlight their utility for elucidating migration processes.

Abiotic Challenges Experiments

There are a large number of environmental cues, such as temperature, photoperiod, river discharge, and lunar phase, as well as endogenous cycles, that can influence migratory activity of animals via effects on endocrine signaling (Bradshaw and Holzapfel 2008; Lennox et al. 2018). Experimental manipulation of the environment by controlling some of these abiotic factors has yielded insights into how these processes progress or change (e.g., Gwinner 2003; Farrell 2009; Müller et al. 2018; table 1). By manipulating the release date of red deer (*Cervus elaphus*) in Germany, Rivrud et al. (2016) showed that late-released individuals could compensate for having missed the peak plant maturity by migrating faster and to higher elevations than early-released individuals. These compensations are likely to involve extra energetic costs, demonstrating the importance of adequate

Table 1: Abiotic challenges experiments

Taxa	Species	Experimental approach	Reference
Birds	White-throated sparrow (<i>Zonotrichia albicollis</i>)	Sparrows did not exhibit migratory restlessness at the warmest temperature treatment (24°C), suggesting that migration phenotypes respond to temperature	Berchtold et al. 2017
Fish	Brown trout (<i>Salmo trutta</i>)	Trout exposed to a temperature challenge designed to instigate a stress response migrated earlier than control animals, suggesting that acute environmental stressors influence an individual's migration strategy	Peiman et al. 2017
Herptiles	Green turtle (<i>Chelonia mydas</i>)	Hatchling turtles were exposed to natural light or artificial light early in the marine migration, showing significant affinity for the artificial lights compared with individuals released on nights with only natural light	Thums et al. 2016
Invertebrates	Monarch butterfly (<i>Danaus plexippus</i>)	Monarchs were either held at control conditions or treated with longer photoperiod and warmer temperatures; treated monarchs displayed similar behavior to control individuals, suggesting that the manipulation had not altered their migratory preparedness	Perez and Taylor 2004
Mammals	Red deer (<i>Cervus elaphus</i>)	The forage maturation hypothesis was tested by manipulating the release date of red deer in Germany; deer released late missed the peak plant maturity and migrated more rapidly to elevation to compensate, whereas deer released early capitalized on peak vegetation production and migrated more slowly	Rivrud et al. 2016

environmental conditions during migration and highlighting the consequences that could result from a mismatch between these conditions and migration timing.

Environmental conditions can negatively impact the capacity for migratory animals to reach their breeding or non-breeding destinations. Energetic constraints imposed on migration by the environment can disrupt the timing and success of migrations. Experimental studies of the metabolic capabilities of migrants and the fuel-conversion efficiencies can be applied to estimate challenges to migration. Clark et al. (2011) compared the cardiorespiratory capabilities of Pacific salmon by manipulating temperatures in laboratory trials of swimming in respirometry chambers and revealed that maintenance of the aerobic scope of pink salmon (*Oncorhynchus gorbuscha*) at high temperatures would confer an advantage over thermally sensitive congeneric Pacific migrants. In this way, experimental manipulations can be useful to understanding how changing migration conditions will impact future reproductive output, survival, and the evolution of fitness-related traits.

Rearing organisms under various environmental conditions may also help to understand the underlying mechanisms that allow organisms to migrate. For example, Lague et al. (2016) reared bar-headed geese (*Anser indicus*)—some of the highest-flying migratory birds—at high altitude (3,200 m) in the Himalayas and at sea level and found that those reared at high altitude had lower metabolic rates and faster ventilation rates in hypoxic conditions compared with those reared at sea level. These findings suggest that high-altitude rearing enabled better capacity for high-elevation flight because of a reduced oxygen demand during resting and an increased oxygen uptake and

delivery during exercise. This adaptation is specifically what allows bar-headed geese to migrate through the Himalayas. It is also possible to use the natural variability or seasonality of environments to test how it shapes and affects movements in animals. In one study, Conenna et al. (2019) tracked yellow-winged bats (*Lavia frons*) in dry and rainy seasons and found that home ranges were larger during the dry season, when resources are scarce. These findings may suggest the presence of a coping mechanism, where bats cover larger areas and spend more time actively foraging to find food. These types of experiments not only help us to understand the drivers of migration but may also enable us to predict how these movements will change under various climate scenarios.

Biotic Challenges Experiments

Disease and parasitism have the potential to negatively affect the expression or success of migration. As animals move through the environment, their metabolism can be influenced by exposure to pathogens as well as by latent infections (Altizer et al. 2011). Experimental manipulations have identified several pathways through which infections can alter the physiology and movement of migrant individuals (table 2). Bradley and Altizer (2005) experimentally infected monarch butterflies (*Danaus plexippus*) with a protozoan parasite (*Ophryocystis elektroscirha*), which impaired flying capabilities and reduced the capacity for these insects to migrate. Sea louse (*Lepeophtheirus salmonis*) ectoparasitism of Atlantic salmon (*S. salar*) has similarly been demonstrated to decrease host swimming capabilities and cardiac performance compared with controls (Wagner

Table 2: Biotic challenges experiments

Taxa	Species	Experimental approach	Reference
Birds	Six species of passerine birds	Experimentally challenged the immune system of six passerine species during autumn migration; immune-challenged groups prolonged their stopover duration	Hegemann et al. 2018
Fish	Atlantic salmon (<i>Salmo salar</i>)	Experimental infection of postsmolt salmon with sea lice (<i>Lepeophtheirus salmonis</i>) impacted the ability of fish to maintain homeostasis and constrained migration success	Nolan et al. 1999
Herptiles	Cane toad (<i>Rhinella marina</i>)	Comparative field study of experimentally infected toads (with a lungworm) and uninfected controls using radiotelemetry revealed that lungworms did not modify rates of invasive toad dispersal	Brown et al. 2016
Invertebrates	Honey bee (<i>Apis mellifera</i>)	Comparative study of the flight activity of experimentally infected (with <i>Nosema ceranae</i>) and noninfected bees in small colonies using an electronic optic bee counter; infected bees showed precocious and elevated flight activity	Dussaubat et al. 2013
Mammals	Brush-tail possum (<i>Trichosurus vulpecula</i>)	Possums were experimentally infected with <i>Mycobacterium bovis</i> , and their movement and activity were compared with noninfected possums in New Zealand using radiotelemetry	Norton et al. 2005

et al. 2003). In songbirds, lipopolysaccharide injections used to simulate bacterial infection were shown by automated radio tracking to alter movements and prolong migratory stopovers (Hegemann et al. 2018). These experimental manipulations provide support for a role of infections in modulating the capacity of animals to migrate, which can alter host-pathogen coevolution dynamics (Nuismer et al. 1999; Teffer et al. 2018; Bass et al. 2019). As our ability to characterize infections among wild animals develops through the novel application of molecular tools (e.g., environmental DNA, gene sequencing), our understanding of how multiple infections and host responses interact to impact migration biology is growing rapidly (Satterfield et al. 2018).

Infectious agents have been shown to impact animals at multiple life stages, with effects relevant to the migrations occurring therein. For example, the long-distance migrations of Pacific salmon (*Oncorhynchus* spp.) can be physiologically and metabolically challenging but necessary for growth (e.g., juvenile migration to sea) and reproduction (adult spawning migration; Groot and Margolis 1991). Among juvenile sockeye salmon (*Oncorhynchus nerka*), viral response indexes were associated with reduced migration success from freshwater rearing lakes to marine feeding grounds (Jeffries et al. 2014); viral infection (infectious hematopoietic necrosis virus) has also been linked to predation susceptibility of juvenile sockeye in freshwater (Furey 2016) and marine habitats (Miller et al. 2014). Among adult sockeye, severe parasitic kidney infections (*Parvicapsula minibicornis*) were associated with reduced exercise recovery and swim speeds compared with controls but similar initial swim performance (Wagner et al. 2005). The conditions of the migration (e.g., water flow) may therefore regulate the role of infections on migration success. Collectively, these studies have identified behavioral associations that warrant further experimentation and also demonstrate strong regulatory roles of the

environment (e.g., stressors) and host biology (e.g., species, population, sex) on the degree to which infections influence survival and migration success.

Pathogens and infectious agents are pervasive in nature and can have deleterious effects on animal performance and migration biology (Dhabhar and McEwen 1997). Warming temperatures caused by climate change are projected to increase the virulence of infectious agents by increasing rates of replication and development, as well as suppressing the immune resistance of hosts (Altizer et al. 2013). This is especially true among ectotherms because body temperature and metabolic rate are determined by environmental temperatures, which in a warming climate can lead to accelerated pathological processes (Altizer et al. 2013). In one example, Crossin et al. (2008) intercepted homing adult sockeye salmon during their spawning migration in the Fraser River (Canada) and held them in experimental pools at different temperatures for several weeks. Sockeye were then released back into the river to complete migration. Via acoustic telemetry, the study revealed that fish held at ecologically realistic high temperatures (mimicking recent high temperatures in the river) had reduced migration success and enhanced *P. minibicornis* infections, highlighting the interacting effects of thermal stress and disease processes. Given that many animal populations are locally adapted to historic thermal conditions encountered at each life stage, including crucial migration periods (Eliason et al. 2011; Hoffman et al. 2013), temperature perturbations have the potential to alter host-pathogen relationships during migration. Our knowledge of host defenses against novel pathogen exposure during migration is still in its infancy, but understanding these relationships is important for conservation efforts that aim to improve landscape connectivity and enhance migratory (and subsequently, transmission) potential (Satterfield et al. 2018). Experiments that define the mechanisms of host-pathogen dynamics

and migration behavior in the context of climate change and environmental perturbation are urgently needed (Miller et al. 2014).

Bioenergetic and Biomechanical Experiments

Migration allows individuals to exploit fluctuating productivity among habitats (Alerstam et al. 2003; Buehler and Piersma 2008). However, there are substantial costs associated with migration that must be balanced against the benefits conferred by these long-distance movements. Experimental approaches to measuring the energy stores of migrants and the energetic costs of activity provide insight into the expression of migration (table 3). Rates of energy expenditure can be measured by doubly labeled water (Wikelski et al. 2003), wind tunnels in birds (e.g., Klaassen et al. 2000), or respirometry in small gill-breathing species (e.g., Lee et al. 2003; Clark et al. 2011). Experimental intervention to manipulate aerobic capabilities of animals has seldom been performed, but such studies could be important to evaluate how animals respond to energetic challenges before or during migration. One example of experimentally manipulating energetic effort on migration success and timing has been done via wing clipping or handicapping in migratory birds. Elliott et al. (2014) attached “handicaps” using tape to the lower back of thick-billed murres (*Uria lomvia*) to evaluate energy expenditure during a period of high energy demand (chick rearing) and found that energy expenditure did not differ between handicapped and nonhandicapped individuals because of behavioral adjustments, but this finding was dependent on age. In another experiment, Cohen et al. (2012) manipulated the energetic condition of migrating red-eyed vireos (*Vireo olivaceus*) and then radio tracked them to elucidate the importance of body condition on migration. Upon release, migrating vireos of lower condition moved faster and farther than

those of higher condition, perhaps as a means of accessing better or more food sources to replenish energetic fuels necessary to continue migration.

Experimental manipulation of feeding or food availability provides insight into energetic constraints on migration. White-throats (*Sylvia communis*) attracted to feeding sites weighed significantly more and showed higher rates of fuel deposition and energy stores just before migration than control individuals (Fransson 1998), suggesting that mass, fuel deposition, and fuel load were adjusted according to food availability in preparation for migration. Starvation of large milkweed bugs (*Oncopeltus fasciatus*) before migration influenced levels of juvenile hormone and the expression of migration-associated flight behavior (Rankin and Riddiford 1977). By manipulating the fatty acid composition of the diet of red-eyed vireos to test whether fatty acid composition enhances exercise performance, Pierce et al. (2005) found that the energetic cost of migration in birds is likely to be modulated by the fatty acid composition of the diet (see review in McWilliams et al. 2004). In brown trout (*Salmo trutta*), short-term food deprivation resulted in decreased expression of migration compared with control animals (Midwood et al. 2016). Food-deprived trout that did migrate were delayed by approximately 1 wk, suggesting that food availability and energetics are involved in dictating whether an individual migrates in this partially migratory species.

Migration timing is essential for animals to reach their destinations at optimal times. The green-wave hypothesis posits that terrestrial migrants “surf” a wavelike dynamic of progressively budding plants to match their northward migration to appropriate weather and forage possibilities (Van der Graaf et al. 2006; Rivrud et al. 2016). However, climate change has led to measurably shorter migrations in birds (Visser et al. 2009) and has generated phenological mismatches at foraging stop-over sites (Kellermann and van Riper 2015). What effects this

Table 3: Bioenergetic and biomechanical challenges

Taxa	Species	Experimental approach	Reference
Birds	Cory's shearwater (<i>Calonectris diomedea</i>)	Increased workload by adding 45 g of extra weight to the birds, which led to extended foraging trips, lower rate of mass gain, and indication of muscular damage	Navarro et al. 2008
Fish	European eel (<i>Anguilla anguilla</i>)	Male eels were swum in groups and individually, and oxygen consumption was measured; swimming costs were reduced by one-third when in groups	Burgerhout et al. 2013
Herptiles	Green turtles (<i>Chelonia mydas</i>)	Turtles were swum at sustained speeds, and oxygen consumption was measured; the cost of transport is lower for turtles than for birds but higher than for fish of similar size	Prange 1976
Invertebrates	Honey bee (<i>Apis mellifera</i>)	Bees with experimentally trimmed wings foraged at similar rates but had reduced food delivery; may affect bees with damaged wings during seasonal migrations	Dukas and Dukas 2011
Mammals	Mountain goat (<i>Oreamnos americanus</i>) and bighorn sheep (<i>Ovis canadensis</i>)	Terrain conditions were altered using a treadmill to assess the energetic costs and efficiency of locomotion under different conditions (variable activity level, slope, and snow condition)	Dailey and Hobbs 1989

change will have on population dynamics may dictate whether a population persists or grows as a result of climate change (Reed et al. 2013). An artificial selection experiment suggests that residency will likely evolve rapidly in populations of migratory birds if selection for shorter migrations persists (Pulido and Berthold 2010). Similarly, the green-wave hypothesis (and other “surfing” hypotheses) is supported by ungulate migrations in savannahs, where animals attempt to balance the seasonality of rainfall and soil fertility gradients. Even shorter migrations, like that of elephants in the Marsabit protected area of Kenya, support this hypothesis (Bohrer et al. 2014). Given the occurrence of climate change and other human-induced changes, such as habitat alteration, experimental approaches are particularly needed to investigate how animals respond to changes and what consequences can be expected for migrants working to make it to the right place at the right time.

Endocrine and Signaling Pathways Experiments

Migration is regulated by endocrine signals that respond to exogenous cues and stimulate or suppress the migratory state. Seasonal changes to hormone levels or sensitivity are responsible for timing and synchronizing migration with the environment and food sources. Direct alterations of circulating hormone concentrations by injections or implants or by blocking receptors to attenuate effects of putative hormones are useful approaches to investigate the roles and relative importance of hormones or neurotransmitters (see Sopinka et al. 2014; e.g., Hedenström and Lindström 2017; Minter et al. 2018; table 4).

Glucocorticoid manipulation is a classic experimental approach used to reveal mechanisms of migration behavior. Glu-

corticoids are metabolic regulators involved in energy mobilization, as well as components of the stress response (Hau et al. 2016), and thus can yield information about the homeostatic status of an individual (Sopinka et al. 2015). Glucocorticoid hormone concentrations can be manipulated indirectly (e.g., induced reproductive failure; Ramos et al. 2018) or directly via implantation or injection. Glucocorticoid effects can also be modified by blocking the receptors (Sopinka et al. 2014). Downstream effects differ for acute and chronic stressors, with chronic stressors yielding tertiary responses such as compromised growth, immunity, reproduction, or migratory behavior that can be observed in animals that have experimentally altered stress states.

A variety of other hormones have been implicated in migratory behavior. In birds, experiments have demonstrated that gonadotropins are crucial for eliciting vernal migratory restlessness, although other hormones, such as thyroid hormones, appear to be more important in autumn (Ramenofsky and Wingfield 2007). Gonadotropin-releasing hormone (GnRH) may be manipulated by implantation, and Sato et al. (1997) and Kitahashi et al. (1998) observed more rapid homing by treated sockeye (*O. nerka*); however, Crossin et al. (2009) observed no differences in the migration of GnRH-treated sockeye compared with controls (though testosterone was related to migration timing in males). In amphibians, thyroxine treatment leads to a preference for terrestrial environments even during the aquatic phase of their life cycle (e.g., Tassava and Kuenzli 1979), and juvenile hormone stimulates migratory behavior of insects (Rankin 1978). In fish and birds, melatonin secreted in response to photoperiodic changes exerts influence over the expression of migratory restlessness and the onset of migration

Table 4: Endocrine and signaling pathways experiments

Taxa	Species	Experimental approach	Reference
Birds	Mountain white-crowned sparrow (<i>Zonotrichia leucophrys oriantha</i>)	Endogenous corticosterone manipulation and radiotelemetry used to examine interactions between locale climate, hypothalamo-pituitary-adrenal axis activation (via corticosterone manipulation), migration arrival timing, and prebreeding behavior at high-elevation sites in the Sierra Nevada	Breuner and Hahn 2003
Fish	Brown trout (<i>Salmo trutta</i>)	Endogenous cortisol manipulation coupled with electronic tracking used to examine the timing and success of seaward migration in trout smolts	Midwood et al. 2014
Herptiles	Tiger salamanders (<i>Ambystoma tigrinum</i>)	Laboratory-based experiments used thyroxine manipulations to investigate land- and water-drive behaviors; results explained known salamander migration behaviors in the wild	Duvall and Norris 1980
Invertebrates	Milkweed bug (<i>Oncopeltus fasciatus</i>)	Milkweed bugs were given a juvenile hormone mimic and flight tested; more males and females receiving the treatment made long, presumably migratory flights	Caldwell and Rankin 1972
Mammals	Belding's ground squirrels (<i>Spermophilus beldingi</i>)	Used food-provisioning experiments and testosterone manipulations to examine the dispersal behavior of free-living juvenile male and female squirrels	Nunes et al. 1999

at stopover sites (Bradshaw and Holzapfel 2007). Experimental manipulation of melatonin levels via manipulations of light cycles led to the expression of migratory restlessness in bramblings (*Fringilla montifringilla*) during cool light to warm light cycles but not during blue light to red light cycles (Phol 2000). The findings suggest that melatonin cycles are involved in regulating migratory restlessness by granting or inhibiting nocturnal activity (Phol 2000). Garden warblers (*Sylvia borin*) injected with ghrelin (a hormone regulating physiological and behavioral aspects of foraging) exhibited diminished food intake and increased migratory restlessness (Goymann et al. 2017). Food intake must therefore regulate at least some of the hormones that control migratory behavior, an inference made possible by an experimental approach to investigate migration. There are likely still more hormonal pathways contributing to migration of different species (and taxa beyond fish and birds) that can be investigated by applying these experimental approaches.

Sensory, Navigation, and Orientation Experiments

There is a long history of experimental laboratory and field studies directed at understanding how migrating animals orient and navigate (e.g., Åkesson 2003). Animals orient using a variety of means from visible landmarks to cues associated with the sun, stars, and Earth's magnetic field (Åkesson and Hedenström 2007). Isolating the critical components of compasses is challenging and requires experimentation (table 5). Compasses that depend on decoding geophysical features of the environment, such as magnetic field polarity, inclination, or strength and skylight polarization, require sensory organs and neural processing of the information to be accurate. Evolutionary analysis is needed to establish the origin of such adaptations, but evidently, there is strong selection toward accuracy that has permitted the evolution of finely tuned sen-

sory organs for orientation and navigation. Characterizing and understanding them remains a major challenge.

Sensory manipulations in the field have contributed to our understanding of animal navigation. Sensory manipulations may be applied by direct intervention of the animal's senses or by altering the individual's environment and monitoring its integration of the stimuli. By depriving juvenile loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) turtles of visual cues under laboratory conditions and subsequently displacing them between 30 and 167 km away from their site of capture, Avens and Lohmann (2004) found that turtles oriented toward feeding areas between May and September but toward their migration route during October and November. The findings suggest that turtles can assess their position relative to their ultimate destination using local cues and, as such, can navigate using a sensory "map." Ablation of vision, smell, and magnetoreception has been used to isolate senses and compare the progress of fish toward their destination to reveal the phases of homing and the sensory foundation that these animals rely on for finding their way (Barbin 1998; Ueda et al. 1998; Mitamura et al. 2005). In another example, Kishkinev et al. (2016) surgically ablated either the magnetic or the olfactory sensory systems of experienced (individuals that have migrated successfully at least once) white-throated sparrows (*Zonotrichia albicollis*) in Ontario and radio tracked them after the birds were displaced 2,200 km away in Saskatchewan. Both the ablated and the nonablated individuals demonstrated an inability to reorient once translocated to an unknown area, suggesting that this species does not display compensatory behavior required for true navigation. In an experiment altering the sensed environment of butterflies, monarch butterflies (*D. plexippus*) were exposed to simulated magnetic fields: under control conditions, the insects oriented southwest (typical for migrants); under a reversed magnetic field,

Table 5: Sensory, navigation, and orientation experiments

Taxa	Species	Experimental approach	Reference
Birds	Homing pigeons (<i>Columba livia domestica</i>)	Pigeons were displaced and various sensory modalities (e.g., vision, smell, magnetic compass) were manipulated to assess return rates	Walcott 1996
Fish	Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	Smolts were introduced into a large flume and exposed to LED lights in an effort to guide them to safe migratory paths	Hansen et al. 2018
Herptiles	Red-sided garter snakes (<i>Thamnophis sirtalis parietalis</i>)	Snakes were exposed to pheromones from conspecifics to investigate trailing behavior; demonstrated that both sexes trail the other sex for mating	LeMaster et al. 2001
Invertebrates	Monarch butterfly (<i>Danaus plexippus</i>)	Monarchs were exposed to simulated magnetic fields (control, reversed, and nonmagnetic); demonstrated that the species relies on magnetic cues to orient	Etheredge et al. 1999
Mammals	American black bears (<i>Ursus americanus</i>)	Used extensive tracking data sets from over 200 bears to test alternative hypotheses regarding migration path choice (e.g., landscape morphology, olfaction, instinct, etc.); revealed social interactions mediated by chemical communication as likely driver	Noyce and Garshelis 2014

individuals oriented in the opposite direction (i.e., northeast); and last, under a nonmagnetic condition, monarchs showed no orientation at all (Etheredge et al. 1999). Similarly, in birds, experimental cue conflict and surgical manipulations followed by radio tracking have been used to study compass orientation and navigation mechanisms (e.g., Cochran et al. 2004; Holland et al. 2009; Kishkinev et al. 2016). These experiments have been powerful in exhibiting the importance of orientation senses as investigators work toward understanding how animals migrate accurately over large distances.

Translocation Experiments

Rather than simulating an environment for migrants, they can be relocated to a new venue where their responses to the novel environment can be monitored. Experimental displacement of wild animals is a widespread approach to study navigation and orientation mechanisms (table 6). One of the first experimental displacement studies ever performed was on green sea turtle hatchlings, in which the newly emerged turtles were translocated from the east coast to the west coast of Central America (Carr and Ogren 1960). This was the first indication that hatchlings likely use lighting cues rather than an innate preference for direction to migrate to the ocean (i.e., their sea-finding phase). Experimental displacements of adults between islands have highlighted that local cues are important in the final phase of homing during breeding (reviewed in Lohmann et al. 2008). In migrating Manx shearwaters (*Puffinus puffinus*), clock shifting (where animals are exposed to artificial photoperiods in captivity) coupled with experimental displacement also revealed the importance of the sun as a navigation tool (Padget et al. 2018). In Scopoli's shearwaters (*Calonectris diomedea*), displacement and sensory ablation (magnetically dis-

turbed and anosmic groups) revealed the importance of olfaction and visual integration of topography to navigation (Pollonara et al. 2015). These Mediterranean seabirds appeared to use olfactory cues over open water but then relied on topographical cues from the coastline to orient neritic zones. In another study, Skov et al. (2010) investigated the influence of environmental cues, migration history, and habitat familiarity on the roach (*Rutilus rutilus*), a partially migrant fish species. Roach from populations with different migratory routes to lakes were translocated to unfamiliar habitats. The study found that translocated fish abandoned their previous migration tactic (i.e., partial migration) and adopted migration patterns similar to local fish, suggesting that partial migration is a phenotypically plastic trait triggered by local environmental cues.

Translocation experiments are not only useful for understanding the mechanisms used to orient and navigate but they can be used to understand energy allocation processes and migratory costs. In a common-garden rearing experiment, Kinnison et al. (2003) raised two populations of chinook salmon (*Oncorhynchus tshawytscha*) from two different river systems (i.e., spawning areas 17 km inland and 17 m elevation vs. 100 km inland and 430 m elevation) and then experimentally released the adults into the nonnatal river. By so doing, each locally adapted population experienced a new spawning migration, and upon completion, differential energy allocations and costs were measured in spawning adults. The study showed that males exhibited different reproductive morphologies as a result of the new migration costs they experienced, which indicated reallocation of limited energy to a new locally adapted form. When displaced from the short-distance migration to the longer migration, they had smaller dorsal humps and kypes, with reduced tissue energy reserves, suggesting that longer migrations reduce available energy for spawning competition. Similarly, female chinook salmon

Table 6: Translocation experiments

Taxa	Species	Experimental approach	Reference
Birds	Gray catbird (<i>Dumetella carolinensis</i>)	Veteran migratory catbirds displaced from Illinois to New Jersey had migration orientation similar to controls except when their sense of smell was ablated, suggesting a role of smell interacting with experience in orientation	Holland et al. 2009
Fish	Roach (<i>Rutilus rutilus</i>)	Roach from populations with different migratory opportunities to a lake were translocated; translocated fish showed migration patterns more similar to local fish than to their home location, suggesting that partial migration is phenotypically plastic and triggered by local environmental cues	Skov et al. 2010
Herptiles	Sea turtle (<i>Chelonia mydas</i>)	Hatchlings were translocated from the east to the west coast; demonstrated that hatchlings use light and not innate preferences to find their way to sea	Carr and Ogren 1960
Invertebrates	Monarch (<i>Danaus plexippus</i>)	Monarch flight orientation was compared in their capture site and in a site 2,500 km away to show that they did not compensate for the change in position, suggesting that they are not true navigators	Mouritsen et al. 2013
Mammals	Egyptian fruit bats (<i>Rousettus aegyptiacus</i>)	Even when translocated, Egyptian fruit bats have cognitive maps supported by visual cues that allow them to commute successfully between foraging sites and home	Tsoar et al. 2011

were found to have smaller ovarian mass when translocated from the short to the longer migration (Kinnison et al. 2001). These findings highlight the importance of migration to the evolution of locally adapted forms in species operating under a fixed energy budget (capital breeding).

Conservation-Related Experiments

Migrating animals are exposed to a gamut of stressors, including naturally occurring ones as well as anthropogenic challenges (Boonstra 2013), which can include barriers to migration, fisheries interactions, noise disturbance, light pollution, and exposure to contaminants, among others. Understanding how anthropogenic activities are affecting migrations is a pressing issue for the conservation and management of many migratory species (Martin et al. 2007). By experimentally exposing migrant animals to relevant single and/or cumulative stressors, the mechanisms underlying individual variation in behavior, success, and survival can be investigated. In some instances, the effects of anthropogenic activities or infrastructure on migrations can be investigated without experimental intervention per se but rather as a result of the occurrence of anthropogenic stressors in nature (table 7). One such example, by Gula et al. (2009), showed that wolves (*Canis lupus*) were able to migrate to find mating partners through densely populated areas with high densities of roads. Although this example does not provide insight into the mechanisms that underlie migration, it suggests that wolves may face multiple nonnatural threats during their migration, which may in turn affect their success in reproduction. Similarly, in freshwater fish, dams act as barriers to migration. Using existing dam infrastructure, much can be learned about the costs of overcoming these

human-made structures in a semiexperimental approach. A study using 18,286 radiotagged adult chinook salmon and steelhead trout (*O. mykiss*) that had to migrate passed eight Columbia and Snake River dams to reach spawning areas found that unsuccessful migrants had longer passage times at nearly all the dams (Caudill et al. 2007). These findings may suggest the presence of delayed negative effects or condition-dependent effects of dam passage, which may vary across individuals, and highlight the need for a mechanistic understanding of the factors that influence migration success.

Contaminants and other forms of pollution are ubiquitous in nature, even in the most remote locations on the planet. Even at sublethal levels of exposure, environmental contaminants may pose threats to migratory animals. For example, an experimental lab study showed that methylmercury impaired flight performance of migratory yellow-rumped warblers (*Setophaga coronata*) in a wind tunnel (Ma et al. 2018), and a subsequent dosing and field release showed that mercury exposure altered the activity behavior of warblers at a migratory stopover site, causing them to depart sooner than controls (Seewagen et al. 2019). Similarly, exposure to neonicotinoid and organophosphate pesticides disrupted migratory orientation, and neonicotinoids also reduced body mass in short-term captive white-crowned sparrows (*Zonotrichia leucophrys*; Eng et al. 2017), and a field manipulation and radio tracking study showed that neonicotinoid insecticides suppress fueling, reduce body mass, and delay migration in free-living sparrows (Eng et al. 2019). In western sandpipers (*Calidris mauri*), experimental oiling of feathers reduced escape flight performance and increased endurance flight energy costs (Maggini et al. 2017a, 2017b), effects that were predicted to impair migration ability. If sublethal effects of contaminants at environmentally relevant exposures

Table 7: Conservation-related experiments

Taxa	Species	Experimental approach	Reference(s)
Birds	Western sandpipers (<i>Calidris mauri</i>)	Experimental oiling of feathers reduced escape flight performance and increased endurance flight energy costs	Maggini et al. 2017a, 2017b
Fish	Sockeye salmon (<i>Oncorhynchus nerka</i>)	Salmon were implanted with accelerometer transmitters and released in different locations to quantify and contrast the impacts of dam water releases and fish passage in a fishway on anaerobic energy expenditure and migration success to inform dam operations ^a	Burnett et al. 2014
Herptiles	Three anuran species	Behavioral choice experiments were used to determine whether several anurans had preferences for different tunnel types intended to serve as safe crossing sites at roads	Lesbarrères et al. 2004
Invertebrates	Rocky Mountain apollo butterfly (<i>Parnassius smintheus</i>)	Nectar abundance was manipulated in a meadow, which influenced the dispersal behavior of butterflies assessed via mark recapture, thus informing meadow restoration strategies	Matter and Roland 2002
Mammals	Wolf (<i>Canis lupus</i>)	Used trapped or dead wolves to demonstrate that they could migrate through densely populated areas with high road densities ^a	Gula et al. 2009

^aStudies where the approach was not purely experimental but rather made use of the presence of anthropogenic activities/infrastructure to evaluate their effects on migrations.

are demonstrated in the laboratory setting, then experimental field studies should be used to determine fitness consequences for migrants under natural conditions. Given the increasing number of threats that migratory organisms face in the Anthropocene (Wilcove 2008), there are growing opportunities to use experimental approaches to understand the consequences of threats and to identify and test potential strategies for mitigating them (Lennox et al. 2016).

Seasonal Carryover Effects, the Need for Experimental Approaches to Address Conservation of Migrants, and Prospects for the Future

As individuals migrate, they may carry with them the experiences that occurred during previous periods of the annual cycle (Harrison et al. 2011; O'Connor et al. 2014). These may affect future survival and alter migration routes and timing, as well as population dynamics (Norris and Marra 2007). Much of these so-called carryover effects have been ascribed to habitat and diet (Norris 2005; Conklin and Battley 2012), both of which can be significantly impacted by humans (Birnie-Gauvin et al. 2016), but there is evidence that other factors may impose delayed consequences on migration (Midwood et al. 2014; Peiman et al. 2017). For example, how does variation in population density (i.e., number of individuals within a given area) in one season affect recruitment and reproduction rate the following season (Betini et al. 2013)? How do inter- and intraspecific interactions alter migratory behaviors? How does habitat loss affect habitat selection and migratory routes in subsequent periods? How do stressors influence variation in reproductive investment and thus breeding decisions, breeding success, and population processes (O'Connor et al. 2014)? How do stressors affect the number of migrant individuals from a partially migratory species? These are only a few of the questions that future research should aim to address, but we argue that experimental studies provide an important approach for doing so. Comparing migratory and nonmigratory species in an experimental setup could provide one way to investigate some of these questions.

At present, anthropogenic structures and stressors are abundant and widespread. Experiments to understand applied issues and their potential impacts on animal migrations will help conserve and manage species by answering key questions, such as the following: How do dams affect migratory fish species? How do wind turbines affect birds and bats during migration? How do landscape characteristics, including urbanization and agriculture, affect migration patterns and success? Whereas the immediate and direct impacts of these human-originated issues have been studied (e.g., Jepsen et al. 1998; Norberg et al. 2002; Donaldson et al. 2011; Keefer et al. 2011; Minderberg et al. 2012; Silva et al. 2012; Spoelstra et al. 2015), their carryover effects on future aspects of individual success have seldom been the focus of research. For example, wind turbines may affect bird feeding outside of their migratory period, which could influence migration success by limiting the energy storage and stress status of the animal. These long-term effects must emerge

as a focal point of studies to develop a more holistic, lifetime-scale perspective on animal migration.

Conclusions

Given the importance of migratory species to biodiversity, ecosystem function, and human culture and economies, an understanding of where, when, how, and why animals migrate is critical for their conservation and for the sustainability of the ecosystem services they provide. Observational studies, where animals are not manipulated, will continue to play a fundamental role in expanding our knowledge of animal migrations (e.g., identifying pathways and timing patterns) and the effects of various extrinsic and intrinsic factors on individuals and populations. Experimental approaches, with animals in the laboratory, in the field, or in combination, provide an avenue through which many crucial observations can be tested to establish mechanism and cause. Indeed, experiments provide strong inference and may in some cases be the only way to definitively test hypotheses. Experimental approaches are not without limitations. For example, it is much easier to manipulate large numbers of insects and fish than birds and mammals. There is a noticeable dearth of experimental studies on mammals (likely for ethical and logistical reasons) and herptiles. Many long-distance migrants are also small (especially insects), making tracking with telemetry devices for long durations and distances a challenge (Wikelski et al. 2007). However, technological improvements and miniaturization of electronics, sensors, computer memory, and batteries, driven particularly by innovations for portable communications, personal computing, and gaming, are rapidly expanding capabilities to deploy powerful telemetry and geolocation devices on small migratory animals (Bridge et al. 2011). Combining these new tagging devices with large-scale, collaborative land-, sea-, and space-based tracking platforms, such as GLATOS (Krueger et al. 2017), the Ocean Tracking Network (Cooke et al. 2011), the European Tracking Network (Abecasis et al. 2018), the Motus Wildlife Tracking System (Taylor et al. 2017), ATLAS (Toledo et al. 2016), and ICARUS (Wikelski et al. 2007), will provide unparalleled opportunities for experimental migration biology.

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