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Regulation of Migration

MARILYN RAMENOFSKY AND JOHN C. WINGFIELD

Migration is a widespread and ancient phenomenon commonly involving a seasonal response to predictable changes in the environment. Such changes include the four seasons at the higher latitudes and wet–dry seasons in the tropics. In general, migrations are movements to breeding grounds followed by a postbreeding return to areas for nonreproductive activities. We focus on these seasonal migrations and summarize processes by which diverse organisms prepare and adjust to different phases of the migration life history stage, such as preparation, onset (actual traveling), and termination. This framework enables investigations of physiological and behavioral mechanisms involved in each phase, as well as studies of how environmental signals control this diverse and successful process across the taxa.

Keywords: common traits, control mechanisms, environmental conditions, endocrinology, migration life history stages

All organisms live in a changing environment and must adjust their morphology, physiology, and behavior to maximize fitness in any habitat configuration. The changes in environmental conditions to which organisms must respond fall into three major groups. The first includes predictable (seasonal) changes in the physical environment accompanied by successional changes in specific resources (e.g., food supply from plants). The second grouping involves unpredictable changes resulting from inclement weather, predator numbers, and, in recent years, human disturbance. The third group comprises social interrelationships (e.g., dominant–subordinant relations for access to resources such as food and mates), which play a crucial role at all stages of the life cycle. All three forms of environmental conditions can change dramatically such that organisms may be forced to move in order to breed or survive.

Migrations in response to predictable changes (seasons) are defined as movements between distinct habitats—usually one where breeding occurs and the other a nonbreeding or overwintering site. Organisms thus take advantage of available resources at each location to enhance fitness. An alternative example is the successional change in plant growth, in which specific resources may peak sequentially within a habitat, creating a series of available microhabitats upon which organisms rely. Thus, migratory-like movements would take place within a habitat from one spent patch to a more productive site, all within the breeding season; in insects, for example, such movements occur from one host plant to another.

In contrast, migrations that occur in response to unpredictable events or changes in social status (facultative migration) are generally less uniformly oriented, can occur at any time in the life cycle (whether breeding or not), and may be "one-way"—that is, there need not be a return component, resulting in a permanent change in an organism's home range.

Our focus here is on the first form of migration—predictable movements between breeding and nonbreeding areas. Mechanisms and preparations underlying this type of migration may have evolved multiple times in diverse organisms, from invertebrates to vertebrates. Key concepts are how organisms prepare for and adjust their physiology and behavior throughout migration, and how migratory traits are integrated into the rest of the life cycle.

Migration in the perspective of life cycles

Long-lived (> 1 year) species undergo repeating cycles of life history stages, each providing adaptation to environmental conditions at specific times of year and specialized for processes such as migration, molt, and breeding (phenotypic flexibility; Piersma 1998, Jacobs and Wingfield 2000, Piersma and Drent 2003, Wingfield 2004). Each life history stage has three phases—development, mature capability or onset, and termination—that involve differentiation of cells, tissues, and sometimes organs, as well as changes in physiology and behavior (Jacobs and Wingfield 2000, Ramenofsky et al. 2003, Wingfield 2004). In general,

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invertebrates (particularly insects) are short-lived and diverge from the vertebrate pattern in that life history stages are often expressed only once within an individual. Variations observed in morphology and physiology or phenotypic plasticity have been attributed to genetic differences, polymorphism, or proximate responses to diverse environmental conditions (polyphenism) (Dingle 1996).

Migratory movements can occur both during ontogeny and in adult life history stages, but distinctions exist. Among vertebrates, the timing of the migratory life history stage differs from that of ontogenetic movements because the latter occur once and are not repeated, whereas adult migrations are repeated, usually on an annual basis. The ontogenetic form is most evident among semelparous species (i.e., species that breed once and die). Some of the most common examples are found among diadromous species that migrate between fresh water and seawater, which include lampreys (Agnatha: *Petromyzon* and *Lampetra* spp.) and teleosts such as Pacific salmon (*Oncorhynchus* spp.) and eels (*Anguilla* spp.). Among these general examples, there is tremendous variation. For example, in Pacific salmon, the alevins hatch from fertilized eggs and develop into parr that remain in fresh water. After varying lengths of time, parr metamorphose into smolt, or saltwater-adapted fish. Fish at this stage then migrate to the sea (ocean-run form), where they grow in size until reproductive maturation begins. At this point, the fish migrate or "home" to their natal rivers to spawn and die (e.g., Dickhoff 1989, Quinn 2004). This is a true ontogenetic progression of stages, because none is repeated within the life span of an individual. Another example of an ontogenetic migration is reported in African black oystercatchers (*Haematopus moquini*) (Hockey et al. 2003). In these populations, the sedentary adults reside and breed along the southern coasts of Namibia and South Africa. Postfledgling juveniles migrate to distinct coastal locations (nurseries), where they reside for a period of years, then return to the breeding habitats and become sedentary.

Insects present a special case of semelparity, also with tremendous variation among the taxa. Many progress through the ontogenetic and adult life history stages only once within a life span. As adults, individuals either enter diapause (suspend activity) or migrate before reproducing; depending on the species, they may breed multiple times within a season before succumbing. Multivoltine species, such as the black bean aphid (*Aphis fabae*) or monarch butterfly (*Danaus plexippus*), produce multiple generations as the populations migrate north during the spring and summer months (Barker and Herman 1976).

Species in which the migratory periods of the breeding and nonbreeding life history stages are reiterated annually are called "iteroparous migrants" (typically most vertebrates; e.g., Quinn 2004, Wingfield 2004). Individuals reach the adult life history stages and then proceed to migrate annually.

Juvenile postnatal dispersal could also be considered an example of migratory movement during ontogeny of iteroparous species, as it occurs just once and is not reversible. Thus, we have included postnatal dispersal in the iteroparous migratory life history, but with the clear distinction that it is ontogenetic and thus likely to be controlled by different mechanisms. The various types of dispersal that serve to increase the mean distance between individuals do not fall into this category, as they may occur anytime during the life span of an individual.

The cycles of life history stages in iteroparous species can be complex (figure 1). Some show no migratory stages whatsoever. Some migrate toward and away from breeding locations, and others may also have a separate molt migration (figure 1; see also Wingfield 2005). Note that the progression of life history stages is one-way, has an invariant sequence, and is cyclic, usually on an annual basis (Jacobs and Wingfield 2000, Wingfield 2004). Each life history stage has a unique set of substages, and these are particularly complex for migration (figure 2). Substages can be expressed in various combinations, as required by local conditions, resulting in migratory movements or "stopover" periods for refueling. The state of an individual at any point in its life cycle is a function of the life history stage and the substages it expresses at that time (Wingfield and Jacobs 1999, Jacobs and Wingfield 2000). Thus the migratory state is a function of initial preparation, then multiple substages such as fueling and moving, and finally termination as the organism arrives at its destination (figure 2). These states involve different physiological and behavioral traits that must be regulated precisely in time and in relation to local environmental conditions. The control mechanisms involved are still largely unknown and present an urgent challenge for research. Given the rapid changes occurring globally from climate shifts and human disturbance, the potential for migration systems to be disrupted is very great, and yet relatively little is known about the proximate mechanisms.

Superimposed on this predictable (seasonal) cycle of life history stages are unpredictable events in the environment that may disrupt the normal progression. Such perturbations include severe weather, changes in predator numbers, and human disturbance (Wingfield 2004); they may result in major facultative changes in physiology and behavior, called the emergency life history stage (figure 1; Wingfield and Ramenofsky 1999, Wingfield and Romero 2000). In many cases, the emergency triggers facultative migration away from the disturbance, toward an alternate habitat or refuge. Some species that live in unpredictable environments, or depend on a food source that is spatially and temporally variable, may show nomadic movements (spatial opportunism) involving migratory activity but without regular timing and patterns (e.g. Hahn et al. 1995, Wingfield 2003).

We will not discuss further the facultative or nomadic types of migration, nor will we address ontogenetic movements such as dispersal. Our focus is on the life history stages of vernal and autumnal migrations of the predictable life cycle. These two migratory periods are often equated because they appear similar in aspects of mobility, energetics, and physiology. However, it should be noted that because the migrations occur at different times of year, when availability of resources and reproductive status are very different, the ways in which individuals prepare for and regulate the migratory process need not be the same (O'Reilly and Wingfield 1995).

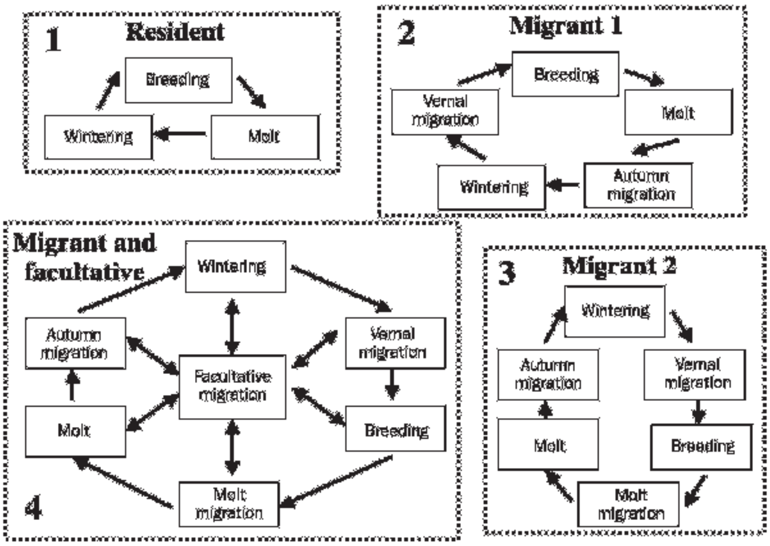

Figure 1. Illustration of the concept of life history stages in residents and migrants, using birds as examples. (1) Resident birds show breeding, wintering, and molt life history stages but no migration. (2) A typical migrant has two additional life history stages, vernal and autumnal migration. Some may be partial migrants, in which some individuals migrate and others do not. (3) A migratory bird with an additional specialized molt migration. (4) Facultative migration (in response to unpredictable events) can be triggered from any life history stage. It is common to all species, regardless of whether they are resident or migratory, as part of their normal life cycle (1, 2). Once the unpredictable event has passed, the individual returns to an appropriate life history stage in the normal life cycle.

Common migratory traits across taxa

It is not surprising that there are recurring themes in terms of the regulation of migration, although it should be kept in mind that migration as a process has evolved independently numerous times across varied taxa. Thus, common themes may represent parallel or convergent responses to the environmental demands of migratory life histories (Piersma et al. 2005). Note also that many migratory traits are found in nonmigrants as well: Both migrants and nonmigrants need muscles to move, a source of energy to fuel that movement, and mechanisms to navigate to find food. However, migrants have effectively amplified the morphology and physiology of these traits in species-characteristic ways to support movements over extended distances.

An engine to power movement. Some form of locomotion is required, usually involving wings, fins, legs, tails, and so on, and the muscles to power them. In long-distance migrants, the size of this machinery fluctuates throughout the migratory period (phenotypic flexibility; Klassen 1996, Piersma and Drent 2003). In preparation for departure, many long-distance avian migrants develop hypertrophy of the organs that support flight (Piersma 1998). These organs include the heart, flight muscles, and skeletal muscle attached to the tibiotarsus (Driedzic et al. 1993, Jehl 1997, Bauchinger and Biebach 2005).

In insects, variation in the morphology of wings is associated with flight distance and migratory activity. Various environmental conditions, including day length, crowding, food availability, and humidity, have been shown to affect both wing structure and the attendant musculature that supports long-distance flight (Dingle 1996). In a number of migrants, including "true bugs" of the genus *Dysdercus,* the flight apparatus is maintained during the migratory period, but once flight is completed, the muscles are broken down by histolysis and the wings discarded. This also occurs in ants (Hymenoptera) and termites (Isoptera), in which the wings of the sexual forms of the insects are lost at the end of the migratory flight. The advantage of this is that the proteins garnered from the attendant muscles are catabolized and deposited in oocytes for reproduction (Dingle and Arora 1973, Nair and Prabhu 1985).

Fuel. Some form of energy is required to support sustained flight. The main sources include lipid (fat), protein, ketone bodies, and carbohydrate. In birds, biochemical alterations that enhance the accumulation and delivery of fuels to metabolically active tissues (e.g., heart, skeletal muscle, and brain) are associated with fueling (Jenni-Eiermann and Jenni 1992, Ramenofsky et al. 1999, Guglielmo et al. 2002, Bauchinger and Biebach 2005). Organs that support feeding, including the stomach, gut, gizzard, liver, and kidneys, enlarge during fueling but decrease in size with takeoff and flight, when intake and digestion are inactive (Landys-Ciannelli et al. 2003, Piersma and Drent 2003). Energy recaptured from these quiescent and reduced structures can serve as a potential source of fuel. In other cases, heart, muscles, and attendant organs hypertrophy before the onset of movement and are reduced in size by catabolism throughout the journey. This decreases wing loading and provides fuel in terms of essential intermediates derived from amino acid deamination and degradation (Jenni and Jenni-Eiermann 1998). In addition, soluble proteins stored in the sarcoplasmic reticulum of flight muscle provide available sources of amino acids used for catabolism and as intermediates for fatty acid oxidation (Bauchinger and Biebach 2005).

Insects also rely on amino acids, carbohydrates, and lipids to support flight in general and, like other aerial species, use lipid as the primary fuel for long-distance migrations (Kent and Rankin 2001). Carboyhydrate derived from nectar is converted to lipid and used to support long-distance migration and overwinter survival in monarch butterflies (Alonso-

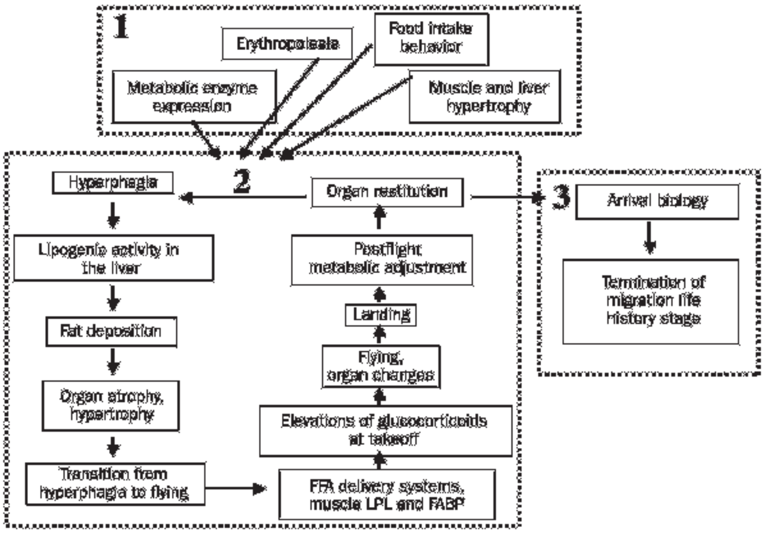

Figure 2. Divisions (substages) of the three phases of vernal and autumnal migration life history stages in birds. Phases of migration are defined in large boxes with dotted lines. Substages are defined in smaller boxes with single solid lines. (1) Substages of the development phase include changes in morphology, physiology, and behavior. (2) In the mature capability phase of migration, the individual can initiate hyperphagia and fat deposition (fueling), leading to migratory flight. During this phase, there may be multiple bouts of fueling (stopover; boxes on the left) and flight (boxes on the right). (3) The termination phase (arrival biology) begins as the individual approaches its destination. Once the individual has actually settled, final termination of the migration life history stage occurs. Abbreviations: FABP, fatty acid binding protein; FFA, free fatty acid; LPL, lipoprotein lipase.

Mejía et al. 1997). A remarkable distinction among insects is the use of the amino acid proline as a primary fuel for flight. Proline is synthesized in the fat body from alanine and triglyceride in the potato beetle (*Leptinotarsa decemlineata*), tsetse fly (*Glossina morsitans*), and others (Bursell 1963, Brouwers and De Kort 1979, Zebe and Gäde 1993, Gäde 1997). Once synthesized, proline is oxidized to glutamate, which serves as a precursor for α-ketoglutarate before entering the Krebs cycle for oxidation to pyruvate. The energy gained approaches that from lipid oxidation, and the process can provide metabolic water.

Flight duration influences the types of fuel utilized. For short flights, carbohydrate is the primary fuel for most Diptera, Hymenoptera, and a few Lepidoptera (Rankin and Burchsted 1992). Relatively little carbohydrate is stored as glycogen in tissues; most of it resides as a ready store of energy in the hemolymph as the disaccharide trehalose, which can be easily taken up by flight muscles. For longer flights, the energy source shifts from carbohydrates to lipids, where lipase activity is present in flight muscle (Sappington et al. 1995, Dudley 2000). For some species, long-distance flights can easily reduce stored fuel supplies to such an extent that reproductive capacity is impaired (Rankin and Burchsted 1992). However, this is not the case for colonizing species such as the migratory grasshopper (*Melanoplus sanguinipes*) (Min et al. 2004). Long-distance flight allows access to novel locations and rapid colonization of new resource-dense habitats (Dingle 1996, Min et al. 2004). Here flight activity enhances reproduction by influencing the timing of oogenesis and yolk deposition, thus increasing the number of eggs produced and the fitness of offspring (McAnelly and Rankin 1986, Min et al. 2004).

Oriented movement. All organisms that move from one location to another need mechanisms first to locate the correct direction (orientation) and then to move while maintaining that direction (navigation). There are four general modes by which migrants orient. The first is compass orientation, or movement in a fixed direction or heading, relying on the ability to perceive cues that denote the orientation of the desired destination. Examples include Earth's magnetic field and sun or star compasses (Wiltschko and Wiltschko 2003). The second is piloting, or locating a direction to a goal using local reliable cues, which may include permanent landmarks or characteristic cues or odors specific to the migration path (Dittman and Quinn 1996). Third is true navigation, involving the determination of position relative to a destination that may be unfamiliar to the migrant, relying on a cognitive map established genetically or through experience (Able 1993). Fourth is "homing," or migrating to a specific destination, which is usually the natal location for a breeding or roosting site (as in homing pigeons; Waldvogel 1989). Mechanisms that organisms use to home or to reach the general location involve piloting. However, once the general location of the destination is reached, finely tuned mechanisms come into play to identify the specific qualities of a particular breeding site. For example, in sockeye salmon (*Oncorhynchus nerka*), selection of a particular redd (nest) site in the stream or lake is contingent on water flow, sediment qualities, and possibly dissolved elements such as nitrogen and phosphorus (Moore 2004, Quinn 2004). Olfactory cues provided by bile acids from larval sea lampreys (*Petromyzon marinus*) serve as olfactory signposts of productive breeding streams for migrating adults (Bjerselius et al. 2000).

From the foregoing, it is evident that orientation mechanisms rely on a host of environmental cues. To be effective, cues must be relevant, reliable, and persistent. In most cases, migrants do not depend on a single factor to navigate but utilize a battery of cues as backup systems in case one is obscured at the time of movement (Able 1993, Wiltschko and Wiltschko 2003, Cochran et al. 2004). Some of these include Earth's magnetic field, celestial and solar cues, olfactory signals, physical landmarks, and atmospheric conditions (Drake and Farrow 1988, Bjerselius et al. 2000, Åkesson et al. 2005). To use any of these cues, organisms must possess specific sensory systems and be able to interpret the information accurately.

A timing mechanism or clock. As migration occurs on both a seasonal (figure 1) and a daily basis (figure 2), accurate timing is paramount. Regardless of whether species travel over short or long distances, they require a timekeeping mechanism or biological clock (Gwinner 1996). It is critical to accurately assess predictable changes in the environment at the immediate location, along the migratory route, and at the destination in order to take advantage of ephemeral food sources, arrive on time to breed or find a good home range, and avoid inclement weather. Moreover, progression through the migratory life history substages (figure 2) must be timed on a daily basis to enhance fuel loading and utilization and to track both celestial and solar cues for orientation en route (Cochran et al. 2004). Without a clock, determining location precisely in relation to environmental cues is severely hampered. Such problems faced early sailors navigating great distances, particularly across longitudes, without the aid of a reliable clock. It wasn't until the 18th century, when John Harrison developed a clock that could maintain precise time at sea, confronted by variations in motion, temperature, and humidity, that longitude could be determined accurately (Sobel 1995). Endogenous biological rhythms allow organisms to time day length, the onset and orientation of migration to and from any location in a specific season, and the progression of migratory substages (e.g., refueling, flight) within a matter of days.

Much has been written about the biological clocks underlying migration, especially in birds. Many transequatorial species, such as old world warblers (*Sylviidae*), use endogenous circannual clocks to time migratory life history stages at the right season and to integrate them with other life history stages, such as breeding, molt, and winter (Gwinner 1996, Berthold 1999, Helm and Gwinner 2006). Daily switches between refueling and migratory movement are probably under the control of circadian rhythms, as shown in the monarch butterfly (Sauman et al. 2005), garden warbler (*Sylvia borin;* Bartell and Gwinner 2005), white-throated sparrow (*Zonotrichia albicollis;* McMillan 1972), and white-crowned sparrow (Coverdill et al. 2005). In other species, a circannual clock may be less strong, and the effects of photoperiod (changing day length over the year) may drive migratory processes (Gwinner 1996).

Physiological traits for migration across taxa

Migratory species are found in diverse taxa. These species not only live in diverse environments but migrate through different media and may be exposed temporarily to severe environments and various social systems. Several additional traits that are apparent, but not necessarily ubiquitous, in migrants deserve consideration.

Osmoregulation. In cases in which individuals migrate long distances without drinking, osmoregulatory adjustments are required to conserve water. The oxidation of lipids produces carbon dioxide and water, the latter of which may contribute to water balance. Protein catabolism also supplies water, but it contributes to negative nitrogen balance unless mechanisms are in place to reduce toxic nitrogen by converting it to uric acid through the uricolytic pathway. This involves production of a purine ring from glycine, aspartate, and glutamine. The end product is uric acid, a thick precipitate that requires little urinary water.

Diadromous organisms migrating from freshwater to marine systems, and vice versa, must be able to accommodate the changes in salt and water balance, especially during the transition phases. Excellent examples are Pacific salmon passing from fresh to salt water during the smolt migration and then back from seawater to fresh water in the breeding migration (Dickhoff 1989). Major changes in salt transport in the gills, skin, and gastrointestinal tract must occur before and during this transition. Many amphibians, too, make major adjustments in the water permeability of their skin when moving from a terrestrial environment to the freshwater pools where they breed. The mechanisms include thickening of the skin to make it more impermeable (e.g., Norris 1997).

Insulation. Some endothermic migrants enter regions where temperatures become extreme (e.g., high latitude and altitude). Changes in the hair or feather covering, fat layers, and so on may be needed to reduce the amount of energy used for thermoregulation so that more can be used for the migration itself. Hyperthermia can be a problem, as can the increased heat production from persistent muscle contraction. To avoid overheating, many terrestrial organisms pant, and aerial species may increase their flight altitude to reach cooler conditions (Biebach 1990). But size plays a critical role: Small passerines are unable to cross the Sahara Desert fast enough for a nonstop flight, and so must land during the heat of the day and rest in shaded areas to avoid overheating and dehydration (Carmi et al. 1992).

Social behavior. Migration in many animals involves a major change in social behavior. For example, individuals that were territorial before migration form large social groups to migrate. The formation of such social groupings is widespread in both vertebrates and invertebrates. Some examples are the mass migrations of sharks in the Gulf of Mexico; ungulates in East Africa; family parties of cranes, geese, and swans throughout the Northern Hemisphere; and such agricultural pests as desert locust (*Schistocerca gregaria*) and African armyworm (*Spodoptera exempta*) in Africa and the Middle and Far East. In other species, social groups may form in several life history stages but break down in migration as group members migrate separately. Virtually nothing is known about the mechanisms underlying such social adjustments associated with migration.

Respiration efficiency. Prolonged migratory activity at extreme high altitude may require adjustments in blood hemoglobin, erythropoiesis, and muscle myoglobin, among other changes. Migratory white-crowned sparrows (*Zonotrichia leucoprhys gambelii*) show increases in hematocrit in both vernal and autumnal migratory periods, which are thought to accommodate the increased energetic and aerobic demands during migration (Wingfield and Farner 1980).

The processes of migration: What needs to be regulated?

Morphological, physiological, and behavioral traits that are expressed during migration have many common themes across taxa, including characteristic substages within the migratory life history stages (figure 2). The three phases of migration (figure 2) may also be ubiquitous: (1) a development phase in which gene expression is regulated, resulting in morphological, physiological, and behavioral changes leading to the second phase; (2) the mature capability phase (i.e., onset), when characteristic substages can be expressed that mark the initiation of migration (including stopovers for refueling and migratory movement itself); and (3) the termination phase, in which the expression of genes associated specifically with migration may be turned off (Jacobs and Wingfield 2000, Wingfield 2005, Ramenofsky and Wingfield 2006).

The development phase for migration involves morphological changes, such as muscle and liver hypertrophy, and physiological changes including the expression of enzymes involved in anabolic and catabolic metabolism (figure 2, section 1). Also, changes in erythropoesis are associated with increased hematocrit and with behavioral alterations, including hyperphagia and decreased territoriality before departure, all leading to the mature capability phase when actual migratory activity can begin (figure 2, section 2).

The mature capability phase is very complex, but it can be divided into migratory movement (i.e., locomotor function that persists for prolonged periods and is oriented; Dingle 1996) and stopover, when the individual stops oriented locomotion to rest, refuel, and make other adjustments before the next leg of migration. Stopover biology—an area of intense study, especially in birds (Landys-Ciannelli et al. 2003, Moore et al. 2005)—involves increased food intake for refueling, fat deposition, and associated changes in enzymes. Hyperphagia may be followed by aphagia before the onset of locomotion. Organs such as the gut may hypertrophy during refueling and then atrophy before flight—all within a few hours (Piersma and Drent 2003). There is often a quiescent phase just before migratory movement, when metabolic enzymes and hormones are adjusted from an anabolic (refueling) to a catabolic (burning fuel during migration) state (Landys-Ciannelli et al. 2002, Ramenofsky et al. 2003). The movement itself, whether flying, walking, or swimming, may require further adjustments associated with changes in the endogenous and environmental conditions encountered en route. At the end of a migratory bout, metabolic adjustments aid the transition back to stopover biology.

Termination of migration—that is, arrival biology (figure 2, section 3; Wingfield et al. 2004)—involves some flexibility for the migrant that cannot predict the environmental conditions at the destination. For example, migrant birds that breed on the arctic tundra arrive in May, when local conditions may be extremely severe, with deep snow cover, high winds, and temperatures well below freezing. In other years, migrants arrive to find the tundra snow free and temperatures above freezing. Because the high-latitude summer is short, migrants have one opportunity to breed and must be extremely flexible in physiology and behavior so that they can respond quickly to the frequent storms and adverse conditions of the arctic spring. Thus, transitions from the migration life history stage to the next life history stage require considerable preparation to maximize fitness (Wingfield et al. 2004, Ramenofsky and Wingfield 2006).

Although this scheme of life history stages and substages may seem complex, it provides a useful framework to form hypotheses about control mechanisms that regulate the migration process in general. The migratory state of an individual is a combination of phase in the life history stage and substages expressed at any point in the migratory period (figures 1, 2; Jacobs and Wingfield 2000, Ramenofsky and Wingfield 2006). This kind of detail is important in that it pinpoints the state of an individual or species throughout the migration life history stage, which allows for an accurate assessment or comparison of the responses or preparatory mechanisms involved.

Very little is known of the natural history, not to mention the mechanisms, of different phases of migration in comparative contexts. Much work needs to be done here, especially in species in which the timing of migration onset and termination is variable, and particularly in the face of global climate change, when environmental conditions around the migratory periods may be increasing in variability from year to year.

Control mechanisms

Much remains to be explored concerning the environmental cues that influence the timing of migration life history stages, when and how substages are expressed, the sensory modalities by which this information is perceived, the neural pathways by which it is transduced, and, finally, the neural, neuroendocrine, and endocrine mechanisms by which the morphological, physiological, and behavioral effects are manifest. What is known tends to be focused on migration in insects, fish and birds, but even then the data are scattered, with little in common in terms of possible shared mechanisms. We hope that the framework proposed above (figures 1, 2) may prove useful to develop specific hypotheses that allow experimental tests of what the mechanisms might be. Because the current literature is quite diverse, we focus on a few examples.

Environmental cues. What are the signals from the world in which organisms live that provide information for the regulation of the development, mature capability, and termination of life history stages? There are two major categories of predictive information (e.g., Wingfield 2004): (1) initial predictive information, which triggers the first transition from one life history stage to another and sustains the life cycle; and (2) local predictive information, which provides for adjustments to local conditions. Behavioral processes called synchronizing and integrating information are also important; they include the social interactions that enable an individual to synchronize its migratory patterns with conspecifics.

An example of initial predictive information is the annual change in day length that can act as a driver of the life history stage or as a zeitgeber for an endogenous circannual rhythm (Gwinner 1986, 1996, Berthold 1999). For the migration life history stages, such mechanisms trigger the development phase and sustain the mature capability phase. They then precipitate the termination phase so the next life history stage can develop. Such may not be the case for some insects, such as aphids, in which the expression of mature capability—migratory flight—precipitates the termination of migration and onset of breeding (Kennedy and Booth 1963). Mechanisms by which initial predictive information acts at each phase differ markedly; much more work is needed to understand this fully, especially in diverse taxa.

Once initiated, the development phase can also be regulated by local predictive information, such as atmospheric conditions, rainfall, temperature, and food supply (for a review in birds, see Wingfield et al. 1990). These factors act in two ways: Inhibitors can slow down effects of initial predictive information, or accelerators can speed it up. In this way, the individual can fine-tune the development of the migration life history stage according to local conditions. Local predictive information also acts to trigger the onset of migration itself (in the mature capability phase) or inhibit it (i.e., individuals may not show migratory movement every day). Finally, local predictive cues can inhibit or accelerate the termination phase through interactions with initial predictive information.

Another type of environmental cue, synchronizing and integrating information, includes all the social interactions involved in coordinating departure and arrival within a group, as well as transitions from migratory movement to stopover and arrival biology—that is, this information affects all phases of migration life history. The mechanisms of social interactions involved in migration are virtually unknown and could be a rich area of future research.

Hormonal control of migratory processes. There is surprisingly little information on the hormonal regulation of migratory processes in any organism. Birds have been frequent subjects of such research, but the literature tends to be contradictory and lacking specific hypotheses and predictions (see Wingfield et al. [1990] for a review of the historical literature). A few trends are emerging. At least in birds and fish, vernal migration is clearly regulated by androgens in both males and females (e.g., Dickhoff 1989, Wingfield et al. 1990). This perhaps is not surprising, because vernal migration in vertebrates tends to be associated with reproductive development before the onset of breeding. On the other hand, autumnal migration is not androgen dependent and may be regulated by thyroid hormones, at least in part (Dickhoff 1989, Wingfield et al. 1990). In addition, thyroid hormones have been shown to influence the development of the aerobic capacity of muscle in preparation for migration in barnacle geese (*Branta leucopsis*) (Deaton et al. 1997), and glucocorticoid secretion is elevated in association with flight and arrival, suggesting similarities of underlying mechanisms (Landys-Ciannelli et al. 2002).

In insects, the hormonal control of migration and breeding life history stages are regulated largely by juvenile hormone (JH), but other players include the adipokinetic hormone (AKH) and a neurohormone, parsin (Gäde 1997, Zera and Cisper 2001, Min et al. 2004, Zera and Zhao 2004). Environmental factors influence the endocrine system to regulate expression of reproduction, migration, and overwintering stages. For example, in monarch butterflies, long photoperiods are associated with circulating levels of both forms of JH (I and II) that promote rapid growth of the reproductive system, leading to breeding (Barker and Herman 1976). The shorter photoperiods of autumn correspond with decreased levels of JH and a diminished reproductive tract. At this time, the fat bodies hypertrophy in preparation for long-distance migration to the overwintering site for diapause (Herman 1985). Similar findings have been identified in the migratory armyworm moth (*Pseudaletia unipuncta*) (Cusson and McNeil 1989). Furthermore, in the wing-polymorphic cricket *Gryllus firmus,* the temporal pattern of JH secretion determines the degree of lipid and carbohydrate storage that is related to life history trade-offs of flight versus reproduction (Zera and Zhao 2004). In the migratory grasshopper, long-distance flight increases titers of JH, which in turn enhance oogenesis and previtellogenic growth of the follicle that may also be affected by parsin (Min et al. 2004). Regulation of fuels, particularly lipid and proline, appears to be controlled by AKH, a family of peptides synthesized in the corpus cardiacum (e.g., Auerswald et al. 1998, Min et al. 2004). AKH has been shown to increase hemolymph levels of diacylglycerol in the migratory grasshopper (Kent and Rankin 2001) and to stimulate migratory flight in monarch butterflies when injected along with JH (Rankin and Burchsted 1992). Thus, the effect of these hormones on the metabolic machinery and flight itself is apparent, but the actual mechanisms are unresolved.

Another important issue for scientists studying migration in insects is the tremendous diversity of life histories apparent in this taxon. Attempting to pinpoint common themes among this group is probably unrealistic, given the complexity and plasticity of its life-forms. This should not dissuade researchers from attempting to analyze the multitude of systems, but encourage an appreciation of the broad scope for study of the tremendous diversity of adaptations among this highly successful and prolific group.

Although there are numerous clues concerning the hormonal regulation of migratory processes, much work remains to be accomplished. Given the emerging appreciation for the frameworks of what the migratory process actually involves, more specific hypotheses on control mechanisms are likely for the diverse migratory species.

Conclusions

To understand how animals prepare for migration and then regulate the complex shifts of physiology and behavior during migration itself, the concept of life history stages, phases of those stages, and substages may provide an heuristic framework. As this framework makes clear, vernal and autumnal migratory life history stages are part of a temporal sequence of life history stages (at least in vertebrates) that contribute to the life cycle as a whole. Although these migration life history stages appear similar, they have a very different position in the temporal sequence, may be regulated by different environmental cues, and may also differ in actual substage physiology. How the common traits of an "engine," fuel, oriented movement, and the biological clock fit into these schemes remains to be seen, but more common patterns and mechanisms may come to light, especially when invertebrate and vertebrate migration systems are compared.

Overall, scientists' understanding of the physiological, cellular, and molecular mechanisms underlying the regulation of migration from development to movement to termination has not progressed far in the past 50 years (at least compared with understanding of other life history stages, such as breeding). This is, in part, a reflection of the complexity of the migratory process across vertebrate and invertebrate taxa, as well as the diversity among terrestrial, aquatic, and aerial modes of movement. We hope that this framework will have value in pinpointing the processes with sufficient accuracy and clarity to enable critical experiments to be performed.

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