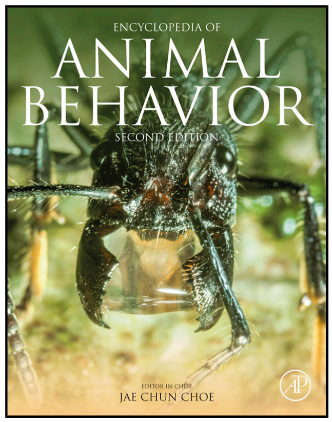




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# Behavioral Endocrinology of Migration☆

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## Glossary

**Adult life history stages** Stages of behavior, physiology and morphology an adult expresses that cycle on an annual basis.
**Anadromy** Migratory pattern of fish that hatch and develop in fresh water then migrate to saltwater for adult development and return to fresh water to breed.
**Catadromy** The migratory pattern of fish that hatch and develop in saltwater then migrate to fresh water for adult development and then return to the sea to breed.
**Corticosterone/cortisol** Two glucocorticoids produced by the adrenal cortex in vertebrates that act in concert with other hormones to affect metabolism, energy balance and reproductive and migratory behavior and physiology.
**DHP or 7α,20β-dihydroxy-4-pregnen-3-one** A prominent progesterone metabolite in teleost fish that promotes germinal breakdown of the ovarian follicles during folliculogenesis prior to ovulation.
**Diapause** A condition of dormancy in insects when development growth or other life stage processes are interrupted, metabolic rate drops and usually induced by adverse environmental conditions.
**Estradiol-17ß** A major estrogen synthesized by the ovary to ovarian growth and development during breeding.
**Hypertrophy** Growth and enlargement of tissues and organs without cell division.
**Iteroparity** The repeated or iterated cycles of reproduction of the adult before succumbing.
**Multivoltine** Refers to species that are short lived but have multiple broods within a year.
**One-way migration** Movement of an organism from a location where it develops to where it breeds without returning to the natal habitat before succumbing.
**Ontogenetic life history stages** The developmental stages from gamete to completion of growth to the adult form. Progression of the stage is only forward and does not repeat.
**Phase-dependent polyphenism** A form of plasticity in which an individual alters its phenotype under specific environmental conditions.
**Phenology** The repetitive sequence of events of the complete life cycle of plants and animals.
**Phenotypic flexibility** Variable phenotypes or traits expressed by an organism that function optimally at specific times or stages of the annual cycle.
**Phenotypic plasticity** The variable expression of alternative phenotypes arising from a single genotype with exposure to diverse environmental conditions.
**Rheotaxis** Maintaining a stationary position in space.
**Semelparity** Ontogenetic form that develop to and adult stage, reproduce once before succumbing.
**Serotonin (5-HT)** A monoamine neurotransmitter that is derived from tryptophan. It is synthesized in the gut, pineal and CNS. In the brain, 5-HT influences learning and memory as well as appetite, sleep and muscle contraction.
**Smoltification** The transformation or metamorphosis of anadromous salmonids from the parr to smolt stages including changes in morphology, endocrinology and behavior in preparation for saltwater entry. Some of these include increased plasma levels thyroid hormones and cortisol as well as deposition of guanine in the skin giving the fish a silvery appearance. This impedes water loss and with the increase of $Na+/K+$ ATPase pumps in the gills and gut osmoregulatory function improves as the fish enters the hyperosmotic conditions for seawater. Behaviorally, smolts leave the natal streams and migrate to open water.
**Testosterone** A major androgen produced primarily by the Leydig Cells of the testis granulosa and thecal cells of the ovary, and adrenal glands of both sexes. The steroid is integral to reproductive physiology and behavior.


## Abstract

On an annual basis many organisms travel to distinct geographical locations each offering seasonal resources that increase overall fitness and survival. Each trip requires dramatic changes in behavior, morphology and physiology to prepare for and complete outward and return legs of the journey. Predictability of resources serves as a selective agent molding the diverse patterns of migration as exemplified by the 5 case studies of insects and vertebrates. Migration has evolved numerous times


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across phyla creating varied patterns and thus providing a rich platform for investigating the diverse strategies for this adaptation and their underlying mechanisms.

**Keywords**

Anadromy; Environmental conditions; Iteroparity; Metamorphosis; Migration; Migration life history stages; Phase-stage polyphenism; Phenotypic flexibility; Phenotypic plasticity; Semelparity

## Introduction

The term migration has many meanings in modern culture. It can refer to the repositioning of subatomic particles within a molecule, to the movements of charismatic mega fauna – whales and elephants – or the monumental treks of ancient human populations across continents to the current heart-wrenching tales of people seeking political asylum. The underlying thread of all these definitions is movement from one location to another to locate either molecular stability or resources requisite for survival and reproduction. Migration, as intended here, is the movement of organisms between distinct geographical locations. In some cases these movements are seasonal and include regular outward and return journeys, one for breeding and the other for survival during the non-breeding period, each offering access to seasonal and predictable resources. In other cases the movements are more irregular in timing, duration and destinations related to the unpredictability of locating required resources. The migration life history has evolved many times across phyla creating numerous distinct movement patterns and striking parallels, all providing a rich platform for investigating multiple pathways for a variety of adaptations to environmental conditions.

## Migration: A Response to Environmental Conditions

Environmental conditions fluctuate to varying degrees on a daily and seasonal basis. To survive and reproduce successfully, organisms alter their behavior, physiology and morphology to best match demands of the current environmental conditions. Migratory species that rely on seasonal and predictable resources in the environment show regular or calendar movements between locations that provide support for breeding and survival. In such cases species will schedule movements according to seasonal cues that are predictive of resource abundance. In general, these are referred to as obligate or calendar migrants, since the pattern of migration is fixed and individuals show little variation in timing and strategy. However, if resources are irregularly and/or unpredictably available, movement patterns tend to be more facultative, and rely to a greater extent on local or immediate cues than more global seasonal factors. Consequently, the movements of facultative migrants show greater flexibility in timing and duration than those of calendar species. Phenotypic flexibility refers to cases in which an individual may express variable phenotypes throughout the year by altering their behavior, physiology and morphology to match changing demands of the environment. In other species (mainly insects), one genotype may produce a variety of phenotypes that may match the variability of environmental conditions; this is called phenotypic plasticity. An additional form of variation is phase-dependent polyphenism, in which alternate phenotypes can be induced within an individual by specific environmental conditions during both ontogenetic and adult stages (Harano *et al.*, 2012; Tanaka and Nishide, 2013). This process allows for a phenotype to more precisely match their behavioral and physiological state to current conditions.

## Taking a Life Cycle Approach to Studies of Migration

Across the general categories of obligate and facultative migrants, the life cycles are variable and complex. To draw relevant comparison across the varied life histories of exemplar insects and vertebrates, a life cycle approach is taken that includes both ontogenetic and adult stages where known (**Fig. 1**). The ontogenetic stages include all functions of growth, differentiation, and sex determination from the gamete to the adult. Progress through this process is forward and does not cycle. Adult life history stages include growth, differentiation and sexual maturity throughout the adult stage. For species that breed more than once in their life – iteroparous – the substages will show repeated cycles during adulthood before senescence. For those that breed only once in a life time – semelparous – the adult stages do not repeat but progress forward to senescence. Each division of the life cycle is composed of sequential stages that an individual will express. Each stage presents unique morphological, physiological and behavioral traits that best suit the current environmental conditions, allowing an organism to function successfully under varying conditions throughout its life cycle. Upon closer inspection, each stage is composed of three phases – development, mature capability and termination – that involve changes at the levels of cells, tissues and organs, resulting in specific behaviors, morphologies and physiological capabilities (**Fig. 2**). Environmental and endogenous factors regulate the onset, progression and termination of each stage but in most cases these factors are not well understood.

The following are examples of the life histories of 5 migratory species illustrating the diversity of adaptations to a variety of environments. Although the nature, timing and duration of the movements differ, as does the depth of our knowledge of any one

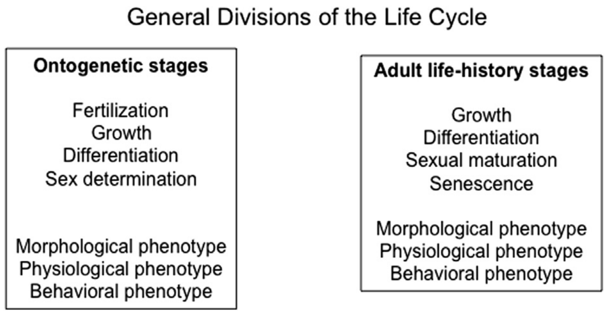


**Fig. 1** The two divisions of a life cycle: The ontogenetic stage starts with gametes and fertilization following through to completion of the juvenile stage. Progress is forward and does not reverse or cycle. This is followed by the adult life history stage that includes both reproductive and nonreproductive states. Some of the substages may cycle or reiterate before completion with aging and senescence.

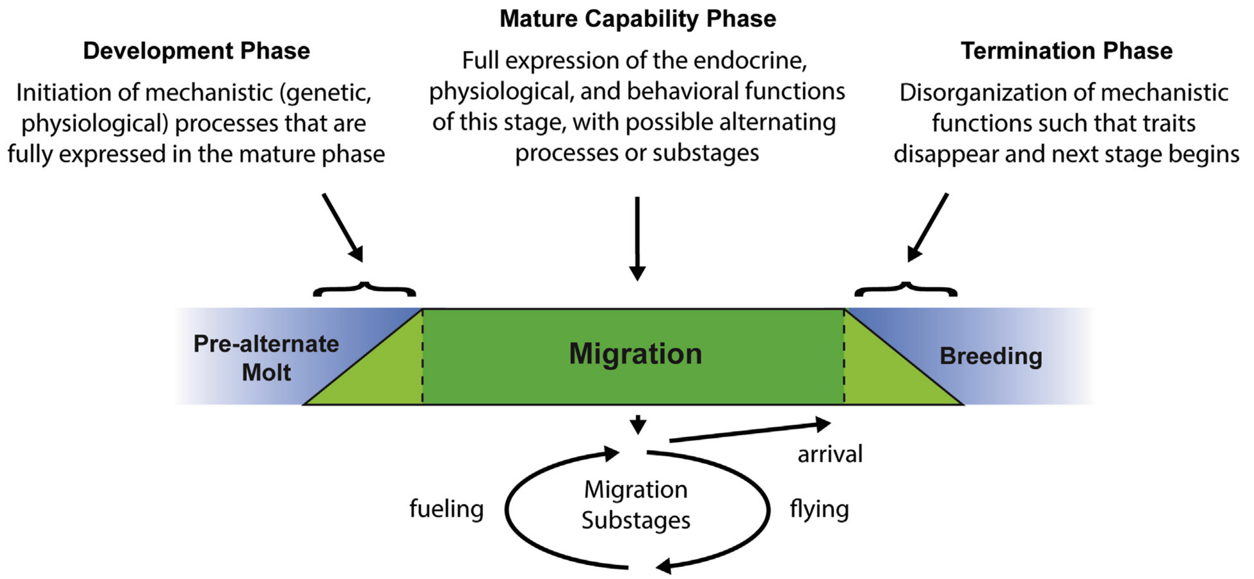


**Fig. 2** Each life history stage of the life cycle is further divided into 3 phases that include the development of the stage starting with building blocks of genomic activation and molecular synthesis of processes that will be poised to be fully expressed at onset of the next phase – Mature capability. Here all physiological behavioral and morphological functions are expressed. The substages of this phase may repeat as exemplified during migration; i.e., fueling and flying cycles continue until the destination is reach and concludes with the termination phase during which all the molecular and genomic apparatus developed for the stage subside allowing for progression to the subsequent stage. Figure designed and drawn by T. P. Hahn and J. L. Coombs-Hahn.

species, this comparative approach may help direct further studies of migratory patterns and potentially uncover commonalities of the underlying endocrine mechanisms regulating life cycles and movements.

## One-Way Migrations: Desert Locusts

In contrast to other species, the migratory routes of most insects are not round-trip but one-way excursions and probably represent an ancestral form of movement. The adults do not necessarily return to locations where they were hatched as seen in other migratory forms. A possible explanation for this is that migratory insects are "hedging their bets" by depositing offspring widely that may prove productive for the next generation and taking advantage of crop production in diverse locations. Another explanation is that if food availability is unpredictable in space and time then a strategy of nomadism occurs relying on local predictive cues informing individuals of resource richness in novel localities. A prime example of this is the desert locust, *Schistocerca gregaria*, a migratory desert species of Africa, the Middle East and Asia. The ontogenetic stages involve seasonal progressions from egg through multiple nymphal stages (instars) each physically resembling the adult form but differing in size and lacking wings and genitalia. As nymphs, individuals express either the gregarious or solitary behavior depending upon rearing conditions (Harano *et al.*, 2012; Tanaka and Nishide, 2013). Exposure to high density during the final instar induces the gregarious adult phenotype while low-density exposure produces the solitary form – a process described as phase-dependent polyphenism (**Fig. 3**). Population density is enhanced by periodic rainfall that portends a prolonged agricultural season that can extend the breeding period for the desert

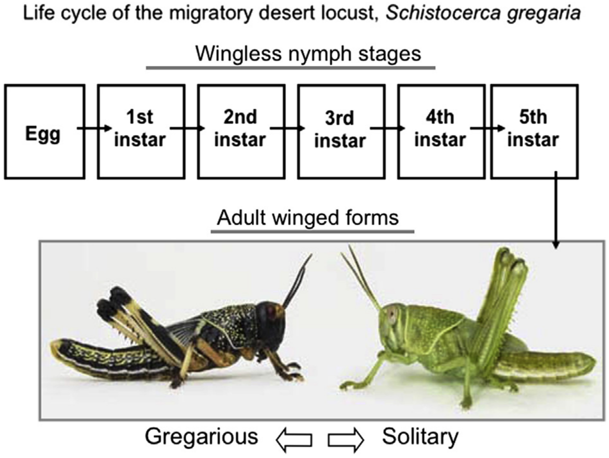


**Fig. 3** Life cycle of the desert locust (*Schistocerca gregaria*). Ontogenetic stages extend from the fertilized egg through 4 successive instars each of increasing size and development. All are wingless and terrestrial. The final instar molts into the adult stage that is one of two fully winged phenotypes depending upon the environmental conditions. In low densities, the solitary form appears and is rarely observed. Yet, under crowded conditions the gregarious phenotype develops and forms huge swarms and migrates great distances. Photograph by Tom Fayle.

locust. Under these conditions, the gregarious individuals join large aggregations forming massive swarms that migrate and land in agricultural areas where they deplete crops with devastating speed. The adults may breed multiple times and at various locations throughout the broad geographical range before succumbing. By contrast, the low-density solitary phenotype breeds but rarely forms groups or migrates and is not considered an agricultural pest.

Recent studies have identified endocrine regulation for the instar molts as well as the trigger for phase-dependent polyphenism. Throughout development, instars molt the cuticle (outer shell) allowing for growth. A successful molt is dependent upon juvenile hormone or JH that determines which instar will be produced and the ecdysteroid, ecdysis triggering hormone (ETH) synthesized in the Inka Cells of the trachea along with its receptor SchgrETHR synthesized in the various sites including the brain and peripheral tissues. Together these increase Ca+ and cAMP in the cuticle promoting the molt (Lenaerts *et al.*, 2017). Polyphenism of the adults is regulated by the neuropeptide serotonin (5-hydroxytryptamine, 5-HT) synthesized in the thoracic ganglia. Exposure to crowded conditions results in elevated levels of serotonin in solitary adults and transformation to gregariousness and migration (Anstey *et al.*, 2009). A highly conserved indolamine, 5-HT has been associated with neuronal plasticity in vertebrates and invertebrates but the effect on large-scale changes of population dynamics and onset of swarming migrations is novel.

## Expanding One-Way Migrations to Round Trip Movements: Monarch Butterfly

Multivoltine species such as the Monarch butterfly (*Danaus plexippus*) produce several generations per year that together complete annual round-trip migrations. This derived pattern is a response to the predictable and preferred food source for the larval stage caterpillars – milkweed (*Asclepiadaceae*) – that is abundant but seasonal across its extensive range. Monarchs show a variety of migratory paths throughout the Americas, Caribbean, Hawaiian and South Pacific Islands (Freedman *et al.*, 2018). In North America, Monarchs can be divided geographically into two regions. West coast populations are mainly altitudinal migrants wintering along coastal California and southern Arizona and northern Mexico (**Fig. 4**). In spring individuals migrate to higher elevations in the western mountain ranges of the US and Southern Canada. The eastern populations are largely latitudinal migrants that travel between northern and southern locations east and south of the continental divide of the Rocky Mountain Range (Reppert *et al.*, 2016; Urquhart, 1987). Throughout spring and summer, sequential populations migrate northward with the final brood of butterflies emerging as far north as the Great Lakes and northeastern US. In autumn with exposure to decreasing photoperiod and temperatures, this cohort initiates long-distance migration to overwinter in reproductive diapause for a period of 7 months in the cool sustained temperatures of the Oyamel fir forests (*Abies religiosa*) of the transvolcanic mountains of Central Mexico (Dingle, 2014; Reppert *et al.*, 2016) (**Fig. 5**). This period of quiescence/diapause persists until spring (February – March) when photoperiod and temperatures increase: butterflies arouse, feed, become reproductive, and migrate to more northern sites to mate and oviposit on maturing milkweed plants. Subsequently the second generation matures, migrates, mates and oviposits on emerging milkweeds at sites further north. This cycle continues multiple times and propagating Monarch populations throughout the geographic range to complete the annual migration at the most northern sites (**Fig. 6**). Unlike the autumn phenotype, lifespans of the summer phenotype are at most 4–6 weeks in duration, migratory distances are reduced and individuals show no reproductive diapause and thus illustrating phenotypic plasticity across the Monarch life cycle.

The phenotypic plasticity expressed is attributed to the endocrine system, notably through juvenile hormone (JH), an acyclic sesquiterpene produced by the corpora allata, a neuroendocrine gland within the pars intercerebralis, of the neurosecretory portion of the insect brain. During the ontogenetic stages, JH regulates development from the egg through pupation, hence its name. During the autumn and winter months, decreasing photoperiod and low environmental temperatures depress synthesis of the active forms

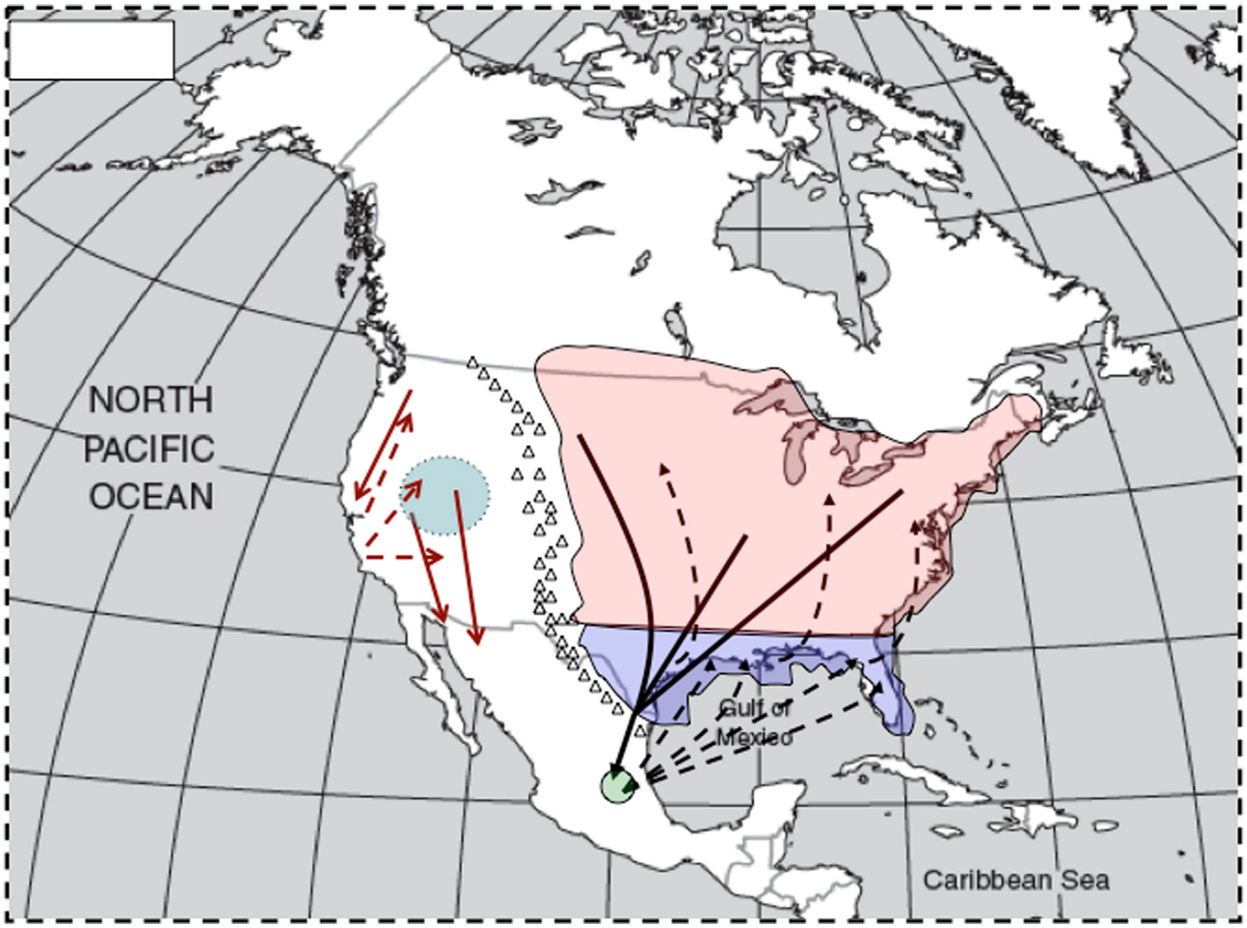


**Fig. 4** Round trip intergenerational routes of the Western and Eastern US populations of Monarch butterflies (*Danaus plexippus*). Routes of the western populations are indicated in red. The outbound routes are depicted by hatched arrows and return autumn routes by solid arrows. The site of the final summer breeding locations in the west is highlighted in the light blue circle but is uncertain. In the east, multiple generations of summer breeding adults move north and east to breed throughout the summer range (pink filled area). In autumn the most northern populations commence a southward migration to the overwintering site (green filled circle) in the Oyamel fir forests of the transverse neovolcanic belt of Mexico. Here adults congregate en masse in reproductive diapause in the fir trees. The dense forests and large number of individuals contribute to maintaining optimal temperatures for diapause. In March, the adults emerge from this state of repose and migrate to the gulf coast identified as the spring range (blue filled area) where they breed and oviposit on the southern milkweed plants (*Asclepias*) then succumb. Larvae hatch, feed on milkweed and soon metamorphose into the summer breeding adults to migrate into the breeding range. Successive generations gradually move north throughout the summer months relying on the phenology of the northern milkweed. In autumn, the last breeding population migrates south and west to the Oyamel forests. Portion of Rocky Mountain Range are indicated by small triangles. Figure adapted from Dingle, H., 2014. Migration, the Biology of Life on the Move. New York: Oxford University Press.

of Juvenile Hormones (JH I & II) in conjunction with down-regulation of insulin-signaling pathway. These endocrine conditions promote increased fat storage, migratory activity, longevity and reproductive diapause in the autumnal forms. In spring, increasing photoperiod and elevated temperatures release the inhibition of JH I & II and promote, migration, breeding and eventual death. Studies of gene expression have identified a suite of 40 genes with differential expression that appear to influence behavior and physiology of the Monarch. The results link key behavioral traits with gene expression profiles in the brain that differentiate the autumn and summer phenotypes, demonstrating that seasonal changes in genomic function influence expression of the migratory state.

## Round Trip Movements

### Ontogenetic Migrations: Pacific Salmon

Migratory movements are not restricted to the adult life history stage but may occur during ontogeny. Such migrations transpire only once and do not cycle on an annual basis. One example of this includes semelparous species that breed once and die, a common life history among diadromous fish that migrate between fresh and seawater. The most prominent organisms in this group are anadromous species namely two Agnathan genera of lamprey (*Petromyzon* and *Lampetra*), and such teleost fish as Pacific salmon (*Oncorhrynchus* sp) and southern populations of American shad (*Alosa sapidissima*). Another well-known example are the

**Fig. 5** Swarms of Monarch butterflies arriving at the overwintering site in the Oyamel fir forests of Central Mexico.

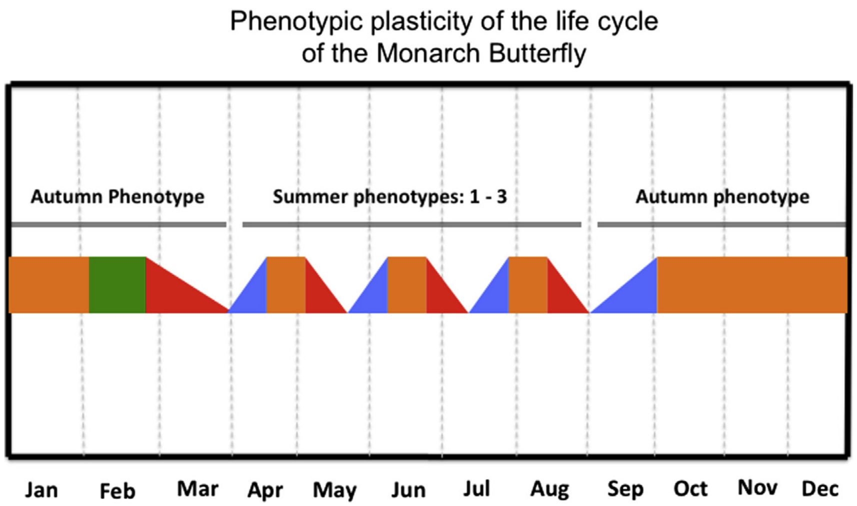


**Fig. 6** Phenotypic plasticity of the Monarch Butterfly. The annual cycle of the Monarch Butterfly is composed of two phenotypes each responsive to the seasonal demands of the environment. Each phenotype is depicted by a trapezoid figure containing the life history stages. *Autumn Phenotype*: Blue triangle represents the embryonic development from fertilized egg to volant adult, orange rectangle is the period of migration to southern overwintering site, to aggregate in large numbers and diapause, green rectangle is the period of arousal, refeeding, reproductive development and migration to more northern spring range, and red triangle represents the time of mating, ovipositing and succumbing. *Summer Phenotype*: Blue triangle represents the embryonic development from fertilized egg to volant adult, orange rectangle the period of migration to more northern breeding sites, red triangle is a period of reproductive development, mating, ovipositing and succumbing. The major distinctions between the Phenotypes are the greater duration of the autumn stage followed by reproductive diapause throughout the winter months that is then following by reproductive activity, and an additional migration followed by breeding. The Summer Phenotypes are shorter in duration and repeatedly expressed.

catadromous eels (*Aguilla* sp). Although great variation across these species exists, the general life cycle of the Pacific salmon provides the most well studied example in terms of behavioral endocrinology of migration. Seasonally, alevins hatch from eggs and emerge from the gravel of fresh water streams with an attached yolk sac (Fig. 7). This stage develops into fry followed by the parr stage that can be identified by vertical markings along the lateral line of the fish. Individuals exhibit rheotaxis with the stream-bed and maintain upstream position in flowing water where they feed and grow for variable periods of time. Lunar cycle and stream temperature are thought to induce metamorphosis from the parr to the smolt stage (called smoltification) involving dramatic changes in physiology and behavior to accommodate the impending saline conditions of the ocean (McCormick, 2013). Increased levels of thyroxine (T4) are associated with the onset of smoltification, including changes in body shape, silver coloration with guanine and hypoxanthine deposition in the scales and skin that serves to reduce water loss. Increased gill Na+/K+ ATPase activity promotes swimming efficiency and endurance for migration and osmoregulatory changes to prepare for hypersalinity environment once fish reach the ocean. Further changes in the endocrine milieu include increased plasma levels of growth hormone (GH), and insulin-like growth factor −1 (IGF-1). Plasma levels of cortisol increase during spring smoltification in some but not all species of Pacific salmon. After a period in fresh water, smolts enter seawater (sea run form) and travel throughout the

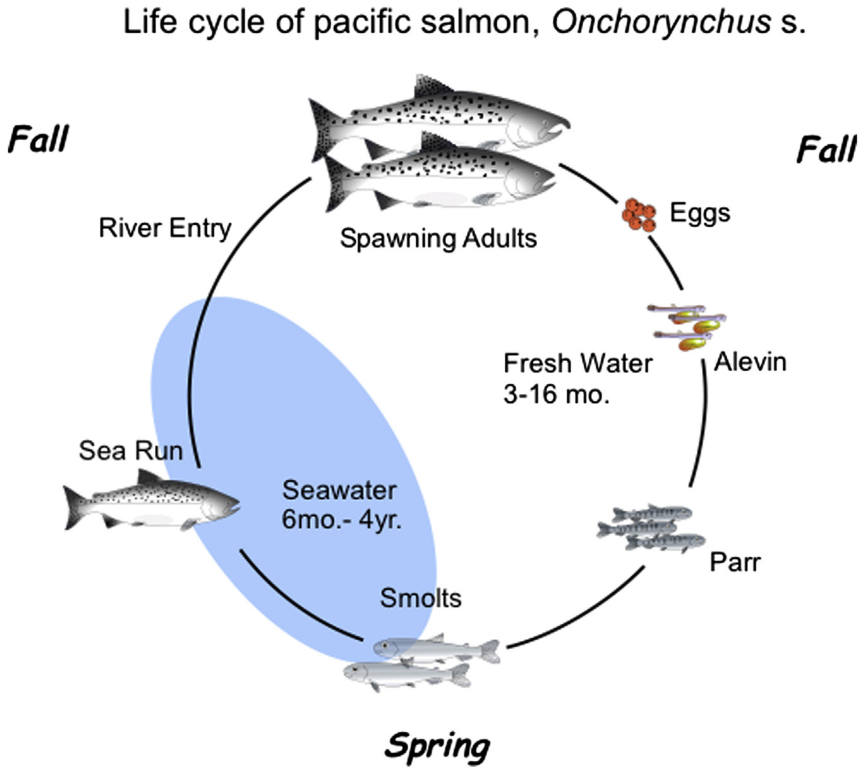


**Fig. 7** Life cycle of semelparous Pacific salmon (*Oncorhrynchus sp.*) occurring over a period of approximately 6–7 years encompassing the ontogenetic stages from fertilized egg to spawning adults. Figure adapted from figure by Kathleen Neely, NOAA, Seattle, Washington and.

Pacific Gyre where they mature into nonreproductive adults. Duration of this stage is variable and likely influenced by available food resources. This effect of an individual's achieved body condition on the time spent in the ocean represents flexibility within the life history stage. The endocrinology of the sea run stage is not completely established but at its termination, sexual maturation is initiated (Hayashida *et al.*, 2013). Salmonid gonadotropin releasing hormone, GnRH (sGnRH) synthesis increases in the preoptic area of the hypothalamus and upon release into the median eminence induces teleost gonadotropins (GTH) synthesis in the anterior pituitary. These glycoproteins stimulate gonadal growth and development, gametogenesis and steroidogenesis in the gonads resulting in elevations of plasma estradiol 17ß, testosterone, 11-keto-testosterone and the progesterone metabolite $-17\alpha$,20β-dihydroxy-4-pregnen-3-one (DHP). The degree to which environmental or endogenous cues regulate the initiation of the spawning migration is not known but definitely the hypothalamic-pituitary-gonad axis (HPG) is activated as fish prepare for entry into fresh water, navigating back into natal rivers and streams to spawn. Navigation of natal waters has been attributed to imprinting of the chemical composition of the natal streams experienced by smolts during the outward migration and guided by the accumulated memories of olfactory cues. Molecular mechanisms of imprinting have identified transcription of the olfactory receptor gene (SORB) and two vomeronasal receptors (SVRA and SVRC) that increase expression during the parr-smolt transition. At this time, prolactin and cortisol are thought to regulate osmoregulatory changes as fish enter fresh water. Navigation up the natal streams is influenced by cortisol, which may prime or activate regions in the hippocampus of the teleost brain and olfactory neurons to recall memory and help guide the fish for the return trip. Also during this period, plasma levels of sex steroids increase with gonadal maturation resulting in morphological and behavioral changes supporting territoriality and reproductive behavior. At the same time, plasma levels of the pituitary protein, somatolactin (SL), are elevated promoting $Ca+$ metabolism and swimming endurance. Experimental studies have demonstrated that castration will prolong life, but only for a few months, suggesting that death post-spawning is programmed and not necessarily driven by steroid levels. What is of interest is the prolonged high levels of cortisol in conjunction with gonadal steroids that together may contribute to programmed cell death. The connection in semelparous vertebrates is reminiscent of the life histories of a number of insects, suggesting a fruitful avenue for further comparative investigations (Wingfield and Sapolsky, 2003).

Evolutionary explanations for Salmonid semelparity characteristic of the Pacific Salmonids revolve around a combination of factors that include age and topography of the Pacific coastlines, distances from marine to fresh water sites and arduousness of the return trip that render adults spent after the production of a multitude of gametes. Also, streams in which the young hatch are largely nutrient-poor and decaying carcasses of moribund adults can deliver dissolved elements including nitrogen and phosphorous that serve to enrich the nursery conditions for the young fish (Quinn, 2005).

## A Seasonal Obligate Migrant: White-Crowned Sparrow

The behavioral endocrinology of the migratory life history is best known from studies of songbirds that have been the focus of scientific investigations for well over 150 years. The descriptions that follow are based on the literature with a particular emphasis drawn from a long distance migratory subspecies of the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) (Fig. 8). Most seasonal migrants express phenotypic flexibility throughout 6 stages of the 12-month annual cycle (Fig. 9). The wintering stage occurs over the longest period and is followed by the prealternate molt that involves replacement of crown and body feathers. The cue for initiation of the molt is not well known though spring photoperiod is a likely candidate. Development of the vernal migratory stage for most north temperate species is the seasonal increase in day length in conjunction with endogenous rhythms. This stimulus activates gene expression, protein biosynthesis and cellular activation that will affect both the migratory and breeding stages. Duration of the developmental phase is at least a month, following which the mature capability phase sets in. Here testosterone and thyroid hormones contribute to hyperphagia, muscle and liver hypertrophy and physiological changes directing synthesis and deposition of fuel for flight, namely lipid and increased protein for enhance contractile forces for endurance flight and aerobic capacity for lipid utilization once migration begins (Pérez *et al.*, 2016; Ramenofsky and Nemeth, 2014). Oxygen carrying capacity of the blood rises with increased synthesis of red blood cells (erythropoiesis) as measured by hematocrit (Krause *et al.*, 2015). Synthesis of erythropoietin, a growth factor produced by the liver and kidney, is thought to be regulated by gonadal androgen and thyroid hormones. In a number of migrants, plasma corticosterone increases prior to departure and presumably contributes to the preparation for and transition to endurance flight. Timing of actual departure appears to be facultative and correlated with conducive weather conditions namely favorable tail winds and clear skies. After flight ensues, the levels of corticosterone remain elevated that in conjunction with other mediators of lipid and protein catabolism, all of which serve to meet the energetic demands of flight. Most migrants will undergo cycles of fueling and flight throughout the migratory period (Fig. 2). At stopovers,

**Fig. 8** White-crowned sparrow (*Zonotrichia leucophrys gambelii*). Photo by John C. Wingfield.

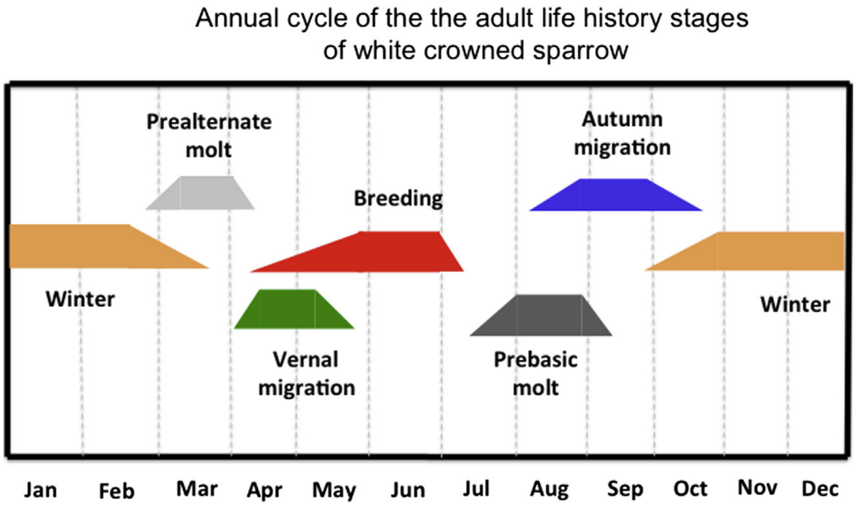


**Fig. 9** The annual cycle of the adult life history stages of the White-crowned Sparrow. Each of the 6 stages are represented by a trapezoid containing the 3 phases. For each trapezoid, the left triangle represents the developmental phase, followed by the central rectangle, the mature capability, and the right triangle, termination phase. Months indicated along the X-axis.

anabolic functions take over to replace the depleted stores of fuel experienced during flight. How quickly and effectively birds recover from flight, regain mass, fat and muscle lost en route are not known but such information along with the underlying endocrine mechanisms are vital for understanding the mechanisms regulating migratory patterns. Once birds arrive at the breeding destination and conditions allow initiation of breeding, migratory traits associated with movement cease, making way for the reproductive stage. The autumn stage of migration, though similar in terms of development, is distinct in terms of the environmental conditions and traits that typify it. Photoperiod is now declining, the reproductive system and gonadal steroids are basal, and corticosterone levels are lower and less dynamic that those of spring. The selective pressures on individuals to arrive on the wintering grounds are much reduced compared to those during spring. Once birds arrive on wintering grounds, migratory traits dissipate as the wintering stage ensues.

Taking a life cycle approach to the migratory life history provides information about the timing and duration. Each stage of the annual cycle in Fig. 9 represented by a trapezoid depicts the 3 phases: development (left triangle), mature capability (central rectangle) and termination (right triangle). What is obvious from the figure is that the stages appear distinct with relatively little contact or overlap as it is not energetically feasible to simultaneously express mature capability phases of two stages. For example, birds cannot migrate and breed simultaneously, but in some cases individuals may compromise by overlapping the development of one stage with the mature capability of the previous stage. This is evident with the vernal and breeding stages. For example, the environmental cue in spring initiates activation of the HPG for both migration and breeding stages. However, the expression of the mature capability phase of migration precedes that of breeding by at least 2 months. Given that preparation for breeding - gonadal development and gametogenesis – requires at least a month to complete, the development of the breeding axis must start during the migration stage. This is particularly critical for birds that breed at high latitude and altitude where windows of opportunity for breeding are shortened by the brevity of favorable conditions. With this kind of phenotypic flexibility, species can adjust the timing of development and expression of stages in response to demands of the environment. Other examples of overlap of phases of two stages across the annual cycle exist as well.

## A Nomadic Facultative Migrant: Red Crossbill

The nomadic Red Crossbill (*Loxia curvirostra*) (Fig. 10) relies primarily on conifer seeds that nourish both adults and young. Cones develop seasonally but where and for how long seeds will be available to birds is uncertain across the landscape (Fig. 11). To locate profitable cone sources, migration and breeding patterns of Red Crossbills rely on both seasonal and local environmental cues to detect current conditions, and to prepare for and execute nomadic movements. Field and laboratory studies identify seasonal fattening, elevations of luteinizing hormone (LH) and gonadal growth in May cued by photoperiod, similar to those observed in seasonal species (Hahn, 1998). If the cone crop at the current site is insufficient, birds will move in a seasonal nomadic migration searching widely and unpredictably distributed productive sites. This movement diverges from consistently oriented navigations of obligate migrants given the uncertainty of where cones with seeds will be located. If a good stand is located, crossbills will settle in for summer breeding, which then ceases for prebasic molt in late summer and early fall, a time of peak seed availability that supports feather replacement. Once molt is completed, if local seed supply remains ample a facultative winter/spring breeding may occur from late December to early April. If the supply is inadequate for breeding but sufficient for survival, birds may remain. However, if food supply declines too much as open cones shed seeds during fall and winter making them unavailable, birds may move facultatively to locate a productive seed source for survival (Adkisson, 1996).

Nomadic movements depend on perception of local conditions – the cone crop – and involve coordination of information across the flock. For example, if the local crop is poor or declines to an unsustainable level, birds will respond with facultative or irruptive movements searching for a more prolific cone crop. Captive studies have demonstrated that eliminating or reducing access to food is associated with elevations of plasma corticosterone and increased locomotor and vocal activity. These cues may be perceived by neighboring birds creating information flow or "public information" serving to coordinate irruptive movements

**Fig. 10** Red crossbill (*Loxia curvirostria*). Photograph by T.P Hahn.

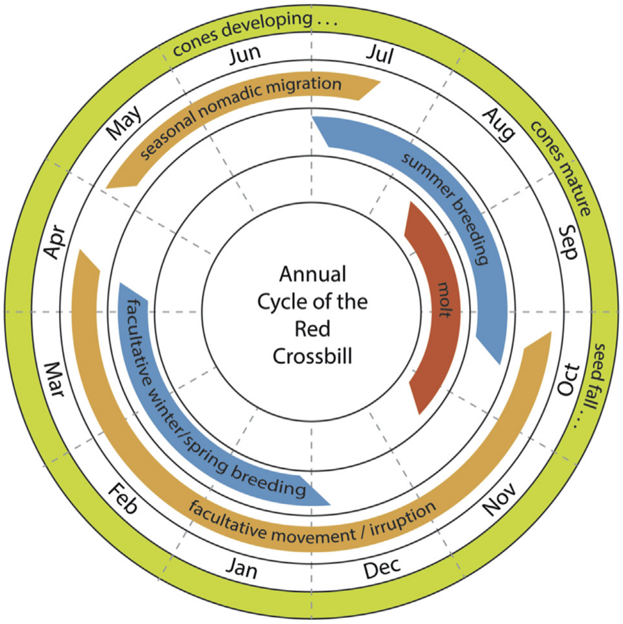


**Fig. 11** The annual cycle of the adult life history stages (migration/movement in orange, breeding in blue, plumage molt in red) of the Red Crossbill. The outer green circle represents the phenology of conifer cone crops, from when the cones start to develop in late spring and early summer through maturation, opening, and beginning to shed seeds in late summer and early autumn. Seeds may fall precipitously after cone opening, rendering them unavailable to foraging crossbills, or be retained for variable periods of time through winter and into the next spring. The "crossbill year" begins with a seasonal, nomadic migration in May and June, when the birds search for a large developing cone crop. They regularly settle in early-mid summer to breed, using the developing but still closed cones they have found, prying them open and extracting the immature seeds with their specially crossed mandibles. Summer breeding typically ceases, and gonads collapse, in September or early October, when the cones are opening, providing a rich resource for the seasonally regular annual pre-basic molt. If cones retain large number of seeds through the winter and into spring, facultative winter/spring breeding can occur prior to initiation of the seasonal nomadic migration the next May. Facultative movements (in the extreme, population-wide irruptions) in search of better seed crops can happen from late summer onward if the birds fail to find a good cone crop in summer, or if seed fall reduces seed availability too much. Figure designed and drawn by T. P. Hahn and J. L. Coombs-Hahn.

within a flock (Cornelius *et al.*, 2010). Such findings suggest connections between a local environmental cues, corticosterone and irruptive movements of a nomadic species.

## Conclusions

Considering migration in a life history/life cycle perspective provides a heuristic model for investigating regulatory mechanisms of behavior and physiology. Compartmentalizing the divisions across and within life history stages helps to visualize and compare across a variety of life histories and identify, where possible, environmental influences and behavioral and physiological responses. Migration is a solution to the problem of variation of resource availability in the environment. If the source is seasonal and reliable then the movement patterns will be regular in timing and duration as seen in calendar movements of the Monarch butterfly and White-crowned sparrow. But in cases where the resource availability is erratic and unevenly spread across the landscape, the periods of mobility lengthen and searches may expand over broad areas as seen in Pacific salmon and Red crossbills. Phase-dependent polyphenism of the desert locust provides an additional mode of flexibility during both the ontogenetic and adult stages under conditions of extreme resource unpredictability. The endocrine mechanisms where identified serve to transduce the relevant environmental information (i.e, photoperiod, resource availability, population density) into the behavior and physiological processes conducive to movement. Further studies identifying the life cycles of migratory organisms and the environmental conditions to which they are tied will be extremely valuable to more fully comprehend the roles of endocrine systems in migration.

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