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Review

Understanding variation in migratory movements: A mechanistic approach

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ABSTRACT

Spatial and temporal fluctuations in resource availability have led to the evolution of varied migration patterns. In order to appropriately time movements in relation to resources, environmental cues are used to provide proximate information for timing and the endocrine system serves to integrate these external cues and behavioral and physiological responses. Yet, the regulatory mechanisms underlying migratory timing have rarely been compared across a broad range of migratory patterns. First, we offer an updated nomenclature of migration using a mechanistic perspective to clarify terminology describing migratory types in relation to ecology, behavior and endocrinology. We divide migratory patterns into three types: obligate, nomadic, and fugitive. Obligate migration is characterized by regular and directed annual movements between locations, most commonly for breeding and overwintering, where resources are predictable and sufficient. Nomadic migrations occur less predictably than do obligate migrations as animals make use of potentially rich but ephemeral resources that occur unpredictably in space or time. Fugitive migrations move animals away from an area in response to severe disruption of environmental conditions and occur as part of an emergency life history stage. We also consider partially migratory populations, which include a mix of sedentary and migratory individuals; the movement patterns of partial migrants are expected to fall into one of the three types above. For these various forms of migration, we review our understanding of the environmental cues and endocrine mechanisms that underlie the expression of a migratory state. Several common hormonal mechanisms exist across the varied migratory forms, but there are also important areas where further investigations are needed in order to gain broad insight into the origin of movements and the diversity of migratory patterns. We propose that taking a comparative approach across the migratory types that considers endocrine mechanisms will advance a new understanding of migration biology.

1. Introduction

Many animals cope with variations in resource availability by moving (migrating) to more productive locations. Geographic and temporal variations in resource availability create unique selective pressures on the behavioral and physiological traits that underlie how, when and where animals move. To support breeding and survival, individuals must successfully locate environments that offer the necessary resources (Boyle, 2017; Dingle, 2014; Swingland and Greenwood, 1983). Differing patterns of resource availability have led to the evolution of movement patterns that range from sedentary (or resident) to highly mobile and that can vary considerably in consistency. Temporal and spatial variations of predictable resources favor temporally and spatially predictable movements; whereas, unpredictability of resources favors more facultative patterns of movement in space, time or both. In shaping movement patterns, selection may also have acted upon the regulatory mechanisms underpinning different types of migration such that these mechanisms reflect variation in the predictability of resources. Thus, when varied movement types are expressed within a given taxonomic group, there are likely to be common mechanisms that can shed light on the origin of movement and the diversity of patterns.

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Across birds, there are a wide range of movement patterns that are expressed, and migratory behavior is a common means by which individuals are able to make use of environments where resource availability varies. Here we present examples representing the diverse patterns of migration across birds and review the associated environmental cues and endocrine mechanisms. We acknowledge that there are many examples of each migration type, but only a modicum of information is available on the underlying endocrine mechanisms. We begin by updating the categories of migration presented earlier (e.g., Terrill and Able, 1988) recognizing that controversy exists in terms of the nomenclature of animal migration. Thus, we offer a mechanistic approach to consolidate and reduce confusion over the terms of migration types in relation to ecology, behavior and endocrinology. Throughout, we focus particularly on types of migration that have generally received the least attention, and point readers to relevant reviews for the better-studied obligate migration. By considering both migratory patterns and underlying mechanisms, our goal is to gain a more complete understanding of the biological basis of bird migration. Furthermore, we hope that the general framework put forth here can be applied to other taxonomic groups, particularly other vertebrates.

2. Migration types

At the broadest level, populations can generally be categorized as resident (also termed sedentary) or migrant. **Resident** populations are composed of individuals that do not migrate but remain within a home range throughout their lives, except for dispersal – a permanent movement to a new home range – and the occasional fugitive migration (see Section 2.3). For residents, resources are predictably available within the home range to support development, breeding and survival throughout the annual cycle. **Migrant** populations include individuals that do not remain in one area but move from one location to another to meet their needs throughout the annual cycle. Migratory movements are characterized by being more persistent, generally directed in orientation, and of greater scale and duration than those occurring during the course of regular daily routines; such movements serve to transport animals between distinct habitats or home ranges (Dingle and Drake, 2007; Newton, 2008). Patterns of migratory movements fall into three general forms (Table 1): obligate migrations (described below in Section 2.1), nomadic migrations (Section 2.2), and fugitive migrations (Section 2.3). Both nomadic and fugitive migrations are types of facultative migrations – migrations that occur in response to fluctuations in resource availability that occur unpredictably in space and/or time. It is important to recognize that the designations of obligate, nomadic, and fugitive migration are not mutually exclusive as an individual may exhibit more than one type of movement pattern in a given year or across years. For example, some north temperate obligate migrants show fugitive movements during the autumn stage by continuing south beyond the recognized wintering range in the face of inclement weather, competition and/or increased potential of mortality (e.g., yellow-rump warblers, *Setophaga coronata*, Harris Sparrows, *Zonotrichia querula*, dark-eyed juncos, *Junco hyemalis*; Niles et al., 1969; Rohwer, 1978; Terrill and Ohmart, 1984). In fact, all populations can become fugitives under certain environmental conditions regardless of whether they are resident or migrant. Additionally, some populations include a mixture of migrant and resident individuals such that a portion of individuals remain sedentary each year while others migrate; the movement patterns of those individuals that migrate may be obligate or facultative. These populations are referred to as partially migratory (described in Section 2.4).

Table 1
Definitions and key features of migratory types.

Migratory type	Definition	Associated pattern of resource distribution
Obligate	Also known as calendar migrants. Stereotypical migrants, all individuals within the population undertake regular annual journeys between wintering and breeding grounds that may include stopovers to rest and refuel and/or to molt.	Seasonally predictable in distinct locations
Nomadic	Populations that undergo “wandering” movements often in relation to necessary resources. Movements may have a seasonal component, but direction of movement, routes, and destinations vary year to year. Often highly variable in timing, orientation and expression.	Seasonally unpredictable and ephemeral
Fugitive	Can be displayed by any species including sedentary species and any of the classes of migrant. Characterized by the Emergency Life History Stage resulting in movement out of areas and away from an unexpected extreme threat to survival (e.g., storms, fires, etc)	Can be associated with any pattern of resource distribution, but is expressed in response to a labile perturbation
Partial	Individuals within a population display a mix of migratory and resident strategies. Migratory/sedentary status may change across the lifespan of the individual in relation to body size, environmental conditions and social dominance (flexible partial migration). In other cases migratory/sedentary status is fixed for individuals across their lifespan (rigid partial migration)	Stable year round, seasonally predictable in distinct locations conditions, seasonally unpredictable

2.1. Obligate migration

Obligate migration, also called calendar migration, shows the greatest consistency in timing, distance and direction of movement and has therefore been studied most extensively. Here birds travel on a regular basis between consistent locations that provide seasonally predictable resources to support reproduction, self-maintenance, and survival. These locations are typically a breeding site and a nonbreeding or overwintering site, but refuge locations (*sensu* Dingle, 2014) may also be used. For example, some birds travel to a separate location to molt, in what is termed a molt migration. In preparation for movement between localities, obligate migrants anticipate and prepare for travel prior to departure. Although far from an exhaustive list, some examples of obligate migrants that have been well-studied from a mechanistic perspective include: Gambel’s white-crowned sparrows (*Zonotrichia leucophrys gambelii*), American redstarts (*Setophaga ruticilla*), white-throated sparrows (*Zonotrichia albicollis*), dark-eyed juncos, black-headed buntings (*Emberiza melanocephala*), red-headed buntings (*Emberiza bruniceps*) red knots, (*Calidris canutus*), bar-tailed godwits (*Limosa lapponica*), red-eyed vireos (*Vireo olivaceous*), northern wheatears (*Oenanthe oenanthe*), garden warblers (*Sylvia borin*), and European blackcaps (*Sylvia atricapilla*). Though highly regular in timing of migrations, obligate migrants are known to express fugitive movements under adverse circumstances, highlighting the complicated nature of movements in wild birds.

2.2. Nomadic migration

Nomadic migration, also termed "wandering" (Ford, 1978; Roshier et al., 2006), refers to seasonal and aseasonal movements that occur unpredictably in space or time in response to fluctuations in resource availability. Nomadic migration is typically observed in species that use resources that occur abundantly, but also unpredictably or ephemerally within a given geographic area (Newton, 2006). Thus, nomadic migration is most commonly seen in birds that feed on rodents (e.g., Tengmalm's owls, *Aegolius funereus*, and short-eared owls, *Asio flammeus*) or conifer seeds (e.g., red crossbills – called common crossbills in Eurasia, *Loxia curvirostra*, pine siskins *Spinus pinus*, and Eurasian siskins, *Spinus spinus*), and in desert species (e.g., banded stilts, *Cladorhynchus leucocephalus*, Pacific black ducks, *Anas superciliosa*, and gray teals, *Anas gracilis*). In some nomadic species, such as red crossbills, pine siskins, and common redpolls, movements have a seasonal component, with a temporally predictable window or windows when movements are most likely to occur, and which may be preceded by physiological and behavioral preparation for movement (Cornelius and Hahn, 2012; Pohl and West, 1976; Watts et al., 2017). Yet, even species showing such seasonal nomadic movements typically exhibit great variation in migratory timing and movement (e.g., distance and direction) compared to obligate migrants (Newton, 2012). Although other nomadic migrants are thought not to show regular seasonal components to their movements, recent studies of the Pacific black duck, gray teal, and banded stilt of Australia, as well as the snail kite (*Rostrhamus sociabilis)* of North America, suggest that movements are related to ephemeral sources of water associated with La Niña and other atmospheric conditions (Bennetts and Kitchens, 2000; Pedler et al., 2014; Roshier et al., 2008). A common theme among many nomadic species is that migrations allow animals to exploit "rich patches" (Cornelius et al., 2013b; Stojanovic et al., 2015).

2.3. Fugitive migration

Fugitive migration is movement away from an immediate area in response to perturbations in the environment. All forms – resident and migrants types – can become fugitives under conditions that threaten survival in the locality such as a disruption of food or resource availability, drought, deluge, increased predation and/or disease. A well-studied example of fugitive migration is the altitudinal migration of mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*), who escape late-spring storms on their high-altitude breeding grounds by moving to lower elevation refugia (Breuner and Hahn, 2003; Cornelius et al., 2013a; Hahn et al., 2004). When conditions are poor over relatively expansive geographic areas, large numbers of fugitives may be seen traveling outside their typical range or habitat. In the literature, such movements are called irruptions or irruptive migrations. Among the species that are recognized as frequent irruptive migrants are pine and Eurasian siskins, red crossbills, white-winged crossbills (called two-barred crossbills in Eurasia, *Loxia leucoptera*), waxwings (*Bombycilla* species), snowy owls (*Bubo scandiacus*), and long-tailed tits (*Aegithalos caudatus*; Newton, 2006; Svärdson, 1957). For example, white-winged and red crossbills experience wide-scale seed crop failure in North America and Europe several times per decade and as a result appear in great numbers in regions where they are not often found, sometimes persisting on non-conifer resources (Bock and Lepthien, 1976; Koenig and Knops, 2001). If birds are able to locate habitable sites via fugitive migration, they may remain to overwinter or breed, but generally birds will eventually return to their typical range (Newton, 2006; Romero and Wingfield, 2015; Wingfield and Kitaysky, 2002; Wingfield and Ramenofsky, 1997). Fugitive migrations may be one source of what are described as vagrants or vagrancy – birds making unusual appearances at distant sites from where they are typically found at a given time of year (Newton, 2008). The means by which a vagrant arrives at a particular location is often unknown, but some likely arise as a response to disruptive conditions within the home range.

2.4. Partial migration

Partial migration refers to populations with a mix of migratory and resident strategies (Chapman et al., 2011; Terrill and Able, 1988). This can occur when individuals breed sympatrically, but a subset of individuals in the population move away from the breeding grounds to over-winter in another location, while resident individuals within the population remain sedentary on the breeding grounds year-round with sufficient resources. Partial migration is observed throughout all temperate and tropical regions. Some of the most commonly studied species of partial migrants include European blackbirds (*Turdus merula*), European robins (*Erithacus rubecula*), and European blackcaps (*Sylvia atricapilla*). Notable species that have partially migratory populations in regions of North America include American robins (*Turdus migratorius*), white-crowned sparrows, and dark-eyed juncos. White-ruffed manakins (*Corapipo altera*) and tropical kingbirds (*Tyrannus melancholicus*) are tropical breeding species that have partially migratory populations. An alternative pattern of partial migration may occur when only a subset of the population migrates to the breeding grounds each year, with other individuals remaining on the wintering grounds and forgoing reproduction (skipped breeding partial migration, Chapman et al., 2011; Shaw and Levin, 2011). Long-lived sea birds are known to skip breeding in some years (Berman et al., 2009; Cam et al., 1998; Goutte et al., 2011), and in the case of red-footed boobies (*Sula sula*), non-breeding birds do not arrive to the breeding colony (Cubaynes et al., 2011). But cases of skipped breeding partial migration, in which non-breeding birds also fail to migrate, are not well documented. Finally, the case of heteropatry (Winker, 2010), in which a migratory population overwinters at the same location as a resident population, has also been considered a form of partial migration by some authors (Chapman et al., 2011; Dingle, 2014). However, given that this scenario reflects two breeding populations with much more limited gene flow compared to other forms of partial migration, it may be better described as two populations with different migratory patterns: one being residency and the other being obligate migration. Given this ambiguity, we do not discuss heteropatry further within the scope of this paper.

Among partial migrants, individuals may be rigid (obligate) or flexible (facultative) in their status as migrant or resident. European blackbirds and European blackcaps are examples of species that show rigid partial migration with the same individuals being resident or migratory each year (these examples are discussed further in later sections). On the other hand, skylarks, *Alauda arvensis*, and white-ruffed manakins show flexible partial migration with individuals switching between resident and migratory strategies across years. Previous authors have used the terms 'obligate' and 'facultative' to distinguish between these forms of partial migration (Terrill and Able, 1988; see also Dingle, 1996 for a discussion of how these might evolve as mixed evolutionarily stable strategies or conditional strategies); in this usage, these terms do not indicate the migratory pattern that is expressed in migratory individuals. Therefore, to avoid confusion, we use the terms 'rigid' and 'flexible'. This seems particularly appropriate given that among partial migrants, the degree to which the migratory pattern is rigid or flexible likely varies geographically within a species, with populations in more predictable regions resembling obligate migration and populations in less predictable regions resembling facultative migration.

3. Environmental cues and migratory systems

Across all migratory patterns, synchronizing the timing of movement with environmental conditions is critical to maximize fitness and survival. Therefore, migrants of all types must rely to varying degrees on environmental cues; however, this relationship is understood well for only some migratory types. The environmental cues relevant for this discussion can be grouped into three categories: initial predictive information, local predictive information, and labile perturbation factors (Wingfield, 2008). Initial predictive cues provide information about what environmental conditions are likely to be in the long-term future. Photoperiod is perhaps the best example of an initial predictive cue, as increasing day length signals the arrival of spring. Local predictive cues provide information about the immediate or near-future conditions including phenological progression of resources, current weather or other atmospheric conditions, community structure, and prey populations. Labile perturbation factors are severe conditions that occur unpredictably and generally have a negative impact on survival such as severe storms, droughts, infection/disease, depletion of available resources, increased competition, or other conditions that contribute to a loss of resources required to sustain life. It is by the use of these categories of environmental cues that migrations are timed.

3.1. Obligate migration

Initial predictive cues precipitate the development, expression and ultimately termination of annual life history stages, including migration (Hahn et al., 1997; Rowan, 1925; Wingfield and Farner, 1993). The vernal increase in day length in conjunction with endogenous cycles of time measurement provide both proximate and anticipatory information for initiating development and eventual expression of the spring life history stages, which for many migrants include prenuptial molt, migration and breeding (Kumar et al., 2010; Ramenofsky, 2011; Ramenofsky and Wingfield, 2007; Singh et al., 2015). For long distance migrants, this is important for scheduling both preparation for flight and departure from wintering grounds, as well as a timely arrival for the onset of breeding at a distant site. Initiation of development of the vernal migratory life history stage directs hyperphagia, body mass increase, fat deposition, alterations of flight muscle size and biochemistry, as well as expression of oriented and persistent flight (Dingle, 2014; Malik et al., 2006; Newton, 2011; Price et al., 2011; Velton et al., 2016). Once the developmental stage is underway, local predictive cues (i.e., weather conditions), can then affect the pace of progression either by speeding up or slowing down rate of progression throughout the stage (Bauer et al., 2008; Emmenegger et al., 2014; Follett et al., 1974; Hahn et al., 1997; Lofts and Murton, 1968; Ramenofsky, 2011; Rowan, 1925; Schwabl and Farner, 1989 b; Wingfield et al., 1990; Wolfson, 1942).

Unlike the spring stage, the cues regulating autumn migration have been less vigorously investigated. The few captive studies have shown that the rate of increase of vernal photoperiod influences the timing of expression of the linked post breeding events including photorefractoriness, post nuptial molt and preparations for autumn migration in Gambel's white-crowned sparrows and common chaffinches (*Fringilla coeleb*; Dolnik, 1980; Gavrilovv and Dolnik, 1974; Moore et al., 1982, 1983). Studies of American tree sparrows (*Spizella arborea*) have shown that thyroidectomy prior to photostimulation prevents development of breeding, onset of photorefractoriness, and post-nuptial molt, while thyroidectomy conducted during the first week following photostimulation inhibits only photorefractoriness and molt (Wilson and Reinert, 1996, 1999). While autumn migration was not explicitly examined in these studies they provided strong evidence for the organization of a separate program for the autumnal events by photoperiodic cues occurring in the spring. Field studies, offer further understanding of this mechanism. Timing of the molt and preparations for autumn migration are less synchronous across individuals than in spring as schedules of each individual vary according to the investment and timing of reproduction and molt (Farner and Follett, 1979; Morton and Pereyra, 1994; Runfeldt and Wingfield, 1985). Thus, birds entering the final preparatory stages for autumn departure are on independent schedules. Nevertheless, once preparations for flight are complete, including achieving the appropriate body condition, the actual cue(s) for departure in autumn, as well as spring, are not well understood. The best information available come from correlative studies indicating that departure timing is largely related to supportive atmospheric conditions, temperature, internal clock, fuel load and social facilitation (Bauer et al., 2008; Danhardt and Lindstrom, 2001; Deppe et al., 2015; Duriez et al., 2009; Morton, 2002; Sjoberg et al., 2015).

3.2. Nomadic migration

Among species of nomadic migrants, initial predictive cues often do not convey accurate information about the condition of critical resources either locally or at distant locations, though this can vary across species and habitats. However, initial predictive cues may still be used to direct developmental of the preparatory stages of migration. For example, while the nomadic movements of red crossbills are spatially variable, they may be able to make use of initial predictive cues to time their movements in search of newly developing conifer seed crops – which consistently become available to crossbills in early summer (Fowells, 1965). But in general, direct assessment of local environmental cues such as rainfall, temperature, green growth, bud burst, etc., provides more credible information about phenological progression for nomadic migrants. Assessment of such cues locally or over long-distances (e.g., using low-frequency sound or olfactory cues; Pedler et al., 2014; Poiani, 2006) can induce nomadic migrants to either stay or depart in search of more productive sites.

A spring migratory stage develops in at least some nomadic migrants, though they are not as well characterized as for obligate species. Red crossbills, pine siskins, and common redpolls (*Acanthis flammea*) all show a response of fattening and/or migratory behavior coincident with increasing spring photoperiods (Cornelius and Hahn, 2012; Pohl and West, 1976; Watts et al., 2017). This suggests that at least some nomadic migrants use initial predictive cues to prepare for seasonal movement. But whether actual departure occurs and how far birds move, are likely more heavily influenced by local conditions (e.g., sufficient resources). Presumably, the use of a combination of predictable seasonal preparation, based on initial predictive cues, in concert with a high degree of flexibility in the expression of migratory behavior in response to local predictive cues, will evolve when patterns of resource availability are characterized by windows when resources are most likely to change or decline, but there is considerable degree of variation in how much those resources change (i.e., may or may not precipitate a movement). In this case, preparation for movement is seasonally consistent and actual movement is more facultative and related to local resource abundance. A programmed spring migratory period in nomadic migrants may also function to return birds to their typical range and habitat in years when birds had made fugitive migrations in the previous fall or winter.

There are several hypotheses for how preparation for and expression of a spring migration might work in a seasonal nomadic migrant. It is possible that departure is programmed and largely photoperiod-driven in nature, as in a obligate migrant, but settlement may be immediately possible such that no significant movement occurs if resources remain sufficient (Svärdson, 1957). Alternatively, preparation may be programmed and largely photoperiod-driven in nature but actual departure may be trigged by a decline in local resources such that movement only occurs if local conditions are unsuitable for breeding and, in the extreme, survival. If local conditions were extremely unfavourable then an emergency life history stage (ELHS, described in detail in Section 3.3) would be activated and fugitive migration would ensue (Wingfield, 2003). However, we suggest that for most nomadic migrants there exists a range of conditions, less severe than those that would induce an ELHS, but that can stimulate migratory departure as part of a nomadic migratory life history stage. Thus, while many nomadic migrations are most certainly responses to local and immediate environmental conditions, the movements may still be predictive of declining resources rather than occurring as part of an ELHS.

Nomadic migrants also show tendencies to migrate in the fall and winter, though migration at this time appears to be variable and flexible within and across species. While nomadic pine siskins routinely make autumn migrations, including irruptions, autumn migration is less common in the nomadic red crossbill though autumn irruptions of red crossbills do occur (Adkisson, 1996; Dawson, 2014). Moreover, within pine siskins, expression of migratory state appears to be more variable in the autumn than the spring (Watts et al., 2017).

In species on the extreme end of nomadic migrants, there is no apparent seasonal component to the expression of a migratory state (Roshier et al., 2008). This type of migration is best represented by species of Australian nomads that move in order to exploit highly unpredictable sources of water in an arid environment. An understanding of how environmental cues influence movements in these species remains elusive. The two hypotheses that have emerged are that (i) long-distance environmental cues provide important information about current conditions at distant locales, and (ii) birds may rely heavily on previously acquired information about temporal and spatial patterns of resource distribution (Pedler et al., 2014; Poiani, 2006; Roshier et al., 2008). Among nomads, exploratory forays may play an important role in collecting information about resource distribution that could be used to make decisions about nomadic migrations in the short or long-term (Bennetts and Kitchens, 2000; McEvoy et al., 2015). For example, snail kites (*Rostrhamus sociabilis*) make exploratory movements during periods of food abundance, which could provide information to be used in future migrations (Bennetts and Kitchens, 2000). Similarly, Pacific black ducks (*Anas superciliosa)* perform nocturnal exploratory forays prior to travelling long-distances to ephemeral bodies of water in the xeric interior of Australia to breed; these exploratory movements are triggered by local environmental conditions and long-distance movements appear to involve integration of diverse atmospheric cues on diverse temporal and spatial scales (McEvoy et al., 2015). The behavior of Pacific black ducks thus suggests that even highly nomadic species may be more responsive to local environmental cues than generally recognized. More broadly, the picture that is emerging of nomads is that the attribute of "wandering" may be overstated. Furthermore, the use of long-distance cues and previously acquired information about resource distribution may also be important to the directionality and spatial patterns of movements in the more seasonal nomads, though extremely little is currently known.

3.3. Fugitive migration

Fugitive migrations occur in response to labile perturbation factors – unpredictable events causing unsuitable or severely deteriorating conditions in the environment. In response to such conditions, individuals experience an increase in allostatic load, which is defined as the energy required to maintain positive energy balance in the face of increasing costs of both predictable and unpredictable environmental conditions (Wingfield, 2005; Wingfield et al., 2017; Word, 2016). If allostatic load continues to rise with degrading unpredictable conditions then a neuroendocrine/endocrine response is mounted that manifests an ELHS (Wingfield et al., 2015). How fugitives perceive an increasing allostatic load or mounting negative energy balance is of great interest and may provide important clues for future research of migrants (Romero and Wingfield, 2015; Word, 2016). Moreover, it is not well known if fugitives are able to prepare metabolically and behaviourally for departure. If the perturbation is sudden it is not likely that preparation is possible and many individuals may succumb during flight. Interestingly, it is possible that in some cases birds may be able to use local predictive cues to anticipate impending perturbation. For example, evidence from several species indicates that birds can perceive declines in barometric pressure that precede storms (Breuner et al., 2013; Kreithen and Keeton, 1974; Metcalfe et al., 2013; Von Bartheld, 1994). However, the extent to which such cues are used for fugitive migration remains unclear. The direction and distances covered by fugitive migrants are highly variable as indicated by individuals showing up in uncommon locations (Newton, 2006), though other circumstances such as weather conditions that carry birds off their intended course may also contribute to such vagrancies. Thus, the general framework for understanding fugitive migration is that it is part of an ELHS, which disrupts the progression of the current life history stage by directing individuals to move away from deleterious conditions until these conditions ameliorate (Romero and Wingfield, 2015; Wingfield, 2003; Wingfield and Ramenofsky, 2011). However, more work is needed to develop a more comprehensive view of fugitive migration. In addition to the possibility that fugitive migrations may occur in response to local predictive cues, it is also possible that some birds may avert an ELHS and subsequent fugitive migration by decreasing allostatic load through behavioral alterations before conditions become extreme. In particular, nomadic migrants may respond to declining food availability and increasing allostatic load by making preemptive migrations before a more extreme fugitive migration becomes necessary. However, at present it is not clear whether these different types of movements can be neatly categorized into fugitive or nomadic migrations. For example, these movements may reflect a continuum rather than categories. We suggest that a deeper understanding of the mechanistic basis of fugitive migrations may help to clarify how they should be described and categorized.

3.4. Partial migration

The cues that stimulate partial migration remain poorly understood, but differ depending on whether migration within a given population reflects rigid or flexible partial migration. In rigid partially migratory populations, individual strategies are primarily influenced by endogenous differences and animals migrate annually regardless of social and environmental factors (Terrill and Able, 1988). Evidence for endogenous contributions to partially migratory behavior comes from captive crossbreeding experiments on songbirds (Berthold and Querner, 1982; Biebach, 1983; Pulido and Berthold, 2010; Pulido et al., 1996). These studies suggest that migratory behavior is at least to some extent inherited in some populations and have led to the use of a quantitative genetic threshold model to describe how partially migratory populations can become completely migratory or sedentary via selection on standing variation (Cobben and van Noordwijk, 2016). Although data are limited, we suggest that among rigid partial migrants, the migratory pattern expressed by migrating individuals is typically that of an obligate migrant, with similar use of environmental cues (described in Section 3.1). Consistency in mean population migration dates in fall and spring in European blackbirds indicates day length could act as an initial predictive cue for the onset of migration (Fudickar et al., 2013). Like other obligate migrants, migratory blackbirds in partially migratory populations also store fat prior to autumn migration.

In flexible partially migratory populations, individual migratory phenotypes are plastic and influenced by body size, social status, and environmental cues (Hegemann et al., 2015; Jahn et al., 2010; Terrill and Able, 1988). Most often, subdominant individuals and individuals in poorer condition are more likely to migrate (Chapman et al., 2011). The frequent observation that dominant age and sex classes are often over-represented in the sedentary fraction of flexible partially migratory populations suggests that in order to survive, subdominants are forced to migrate when food is limited following the breeding season and is suggestive of a fugitive condition, which the allostasis approach would predict (Adriaensen and Dhondt, 1990; Ketterson et al., 1991; Lundberg, 1985). It follows that with age, flexible migrants gain dominance and as a result increased access to food, which can result in a decrease in migratory tendency (Newton, 2008). Among flexible partial migrants, the migratory pattern that is typically reported for those birds undertaking migration resembles that of an obligate migratory pattern (Adriaensen and Dhondt, 1990; Ketterson et al., 1991; Lundberg, 1985). Correspondingly, we expect that similar environmental cues are used to time the onset and termination of migration, though again, data are limited (Silverin, 1997; Wingfield and Silverin, 2009).

4. Endocrine mechanisms of migration

Responsiveness to environmental cues to synchronize migratory movements requires multiple levels of regulation by the neuroendocrine and endocrine systems. This involves perception of the cue by the sensory nervous system, followed by transduction of the neuronal signal into neuroendocrine pathways, and endocrine secretion in the peripheral circulation affecting physiological and behavioral actions (Ramenofsky and Wingfield, 2007; Wingfield, 2008, 2015). Given that the three levels of environmental cues (initial predictive, local predictive, labile perturbation factors), provide different types of information and elicit differential response, we suggest that neuronal, neuroendocrine and endocrine pathways involved in perception, integration and responses across the cues are likely to differ. Broadly speaking, the responses to initial and local predictive information are involved in timing and progression through the migration and breeding stages to varying degrees across all migratory types and mainly include hypothalamic–pituitary–gonad and -thyroid axes (HPG and HPT) along with associated neuropeptides, peptides and steroids (Cornelius et al., 2013a; Holberton et al., 2008; Ramenofsky, 2011; Wingfield and Farner, 1978). In contrast, responses to labile perturbation factors and the initiation of an ELHS primarily involve the hypothalamic-pituitaryadrenal axis (HPA) influencing fugitive escape/irruptive behavior and affect all migratory types (Wingfield, 2003; Wingfield et al., 2017).

4.1. Obligate migration

The endocrine mechanisms regulating migration have best been studied in the development of the spring migratory stage in obligate migrants, though these mechanisms are probably are acting in varying ways in the other migratory types. Since this topic has received attention in several reviews and recent publications (Cornelius et al., 2013a; Kumar et al., 2010; Ramenofsky, 2011; Ramenofsky et al., 2012; Ramenofsky and Nemeth, 2014; Schwabl and Farner, 1989a; Tonra et al., 2011; Wingfield et al., 1990), we provide only a brief summary and highlight some new findings since those reviews. Synchronization of environmental conditions and endocrine mechanisms regulating development of the spring migratory, breeding and post breeding stages are linked by the initial predictive factor of photoperiod. Increasing day lengths in spring activate secretion of androgen and affect neural thyroid hormone signaling, both of which play prominent roles (Deviche, 1995; Pérez et al., 2016; Ramenofsky and Nemeth, 2014; Weise, 1967; Wingfield et al., 1990). The mechanisms by which, together or independently, androgen and thyroid hormones influence development and expression of the migratory phenotype (pre-alternate molt, hyperphagia, mass increase, fat deposition, flight muscle hypertrophy and biochemical alterations and migratory restlessness/*Zugunruhe*) are not fully understood. However, it seems likely that for complete expression of these migratory traits, both hormones are necessary in conjunction with photostimulation (Gupta and Kumar, 2013; Ramenofsky and Nemeth, 2014; Rani et al., 2005).

The processes by which photoperiod induces development of the spring stages involves photoreception, circadian oscillators and hypothalamic gene regulation (Follett et al., 1974; Majumdar et al., 2015; Surbhi, 2015). Recently Wang et al. (2013) identified separate mechanisms of photoperiodic time measurement regulating vernal migration and breeding in Gambel's white-crowned sparrow. Using spring photoperiods of low penetration green light (wavelength at 510λ), birds developed migratory traits but without gonadal recrudescence. This photic manipulation effectively severed the development and expression of the migratory and breeding stages suggesting separate pathways for each creating a temporal dissociation of the two stages such that the progression of the migratory life history precedes that of breeding.

At the level of the brain, the *yin and yang* of migratory traits - fueling and flight - though not fully understood are thought to be under endocrine control. Photoinduced hyperphagia or enhanced food intake in preparation for migration leads to an increase in body mass and fattening exceeding that of the previous wintering stage (Boswell and Dunn, 2015). This dramatic change in the body set point, called rheostasis, sets in motion deposition of fuels required for endurance flight (Jenni and Jenni-Eiermann, 1998; Mrosovsky, 1990; Ramenofsky, 1990). The new seasonal level is maintained by homeostatic mechanisms that intervene when mass and fat levels oscillate between the fueling and flight cycles during migration. A central control site for homeostatic regulation of food intake and body condition in birds is the arcuate nucleus of the hypothalamus (Boswell, 2005; Boswell and Dunn, 2015). Here reside opposing sets of neurons of the central melanocortin system. The stimulatory set, which synthesizes neuropeptide Y (NPY) and agouti-related protein (AGRP), acts to enhance feeding and protein mass gain. Contrasting these actions are the interconnected neurons that express pro-opiomelanocortin (POMC) and cocaine-and amphetamine regulated transcript (CART) genes, neurons that act to reduce feeding and promote mass loss. Part of the regulatory control of the arcuate nucleus in birds is thought to come from peripheral sources as these neurons are positioned in the basal hypothalamus adjacent to the third ventricle and median eminence. In this location, the neurons are exposed to circulating levels of proteins, metabolites, and hormones that may serve as indicators of metabolic state to the central nervous system (Boswell and Dunn, 2015). The arcuate nucleus expresses receptors for circulating cholecystokinin (CCK), ghrelin, glucocorticoids, insulin, and leptin that are proposed to regulate food intake. Recently, studies conducted at a spring stopover site in the Mediterranean Sea found plasma ghrelin concentrations to be negatively correlated with fat score in arriving garden warblers, *Silvia borin* (Goymann et al., 2017). Late afternoon injections of the unacylated form of ghrelin decreased food intake but increased migratory restlessness in captive birds held overnight. Such results suggest a strong association between body condition, ghrelin, and the switch from states of fueling to flight during migration. Central injections of NPY increase feeding in Gambel's White-crowned sparrows (Richardson et al., 1995). However, studies supporting evidence for the other regulators of energy balance in obligate migrants are very limited (Stuber et al., 2013). Glucocorticoids, namely corticosterone, in birds have long been associated with hyperphagia in migrants but results across studies have not revealed a consistent pattern (Landys et al., 2006; Ramenofsky, 2011). Glucocorticoid influences on feeding are best explained by their permissive roles on energy balance affecting insulin, insulin-like growth factor-1, fatty acid synthase, adipose tissue lipoprotein lipase, low-density lipoprotein, and NPY action (Dallman et al., 1993; Landys et al., 2006; Ramenofsky et al., 1999; Savard et al., 1991; Yuan et al., 2008). The protein leptin is known to be a strong regulator of energy balance in mammals. However, its history in birds has been mired in controversy owing to the lack of identification of the avian leptin gene (Friedman-Einat et al., 1999). Only recently has the avian leptin gene been identified (Friedman-Einat et al., 2014; Prokop et al., 2014) offering promise for future studies extending to migration. Nevertheless, a study on white-throated sparrows found that injection of heterologous leptin depressed food intake, foraging and fat mass in wintering birds but without effect during migratory period. Furthermore, the long-form leptin receptor (LepR) was expressed in tissues including the hypothalamus but no change in expression was noted with migratory condition (Cerasale et al., 2011). A few other studies working with obligate migrants in this context report mixed results (Kochan et al., 2006; Yosefi et al., 2010). Thus, the relationship of peripheral signals of steroid, thyroid hormones or metabolites affecting fueling awaits further developments in obligate migrants, as well as in other migratory types where many of these same mechanisms may be acting but have rarely been studied.

Similarly, the endocrine mechanisms regulating onset of migratory flight are not clearly resolved. Tracking migrants as they initiate flight under natural conditions is understandably difficult. Nevertheless a few field studies have observed elevated plasma corticosterone in bar-tailed godwits and northern wheatears prior to departure from stopover sites during spring and autumn migration, respectively, and associated with conditions of migratory preparedness in red-eyed vireos in autumn (Eikenaar et al., 2017; Landys-Ciannelli et al., 2002; Lohmus et al., 2003; Ramenofsky et al., 1995). These presumptive increases in corticosterone at the time of departure may represent preparation for behavioral and metabolic adjustments for uncertain conditions *en route* and thus may have less to do with an actual stimulus for flight (Landys-Ciannelli et al., 2002; Ramenofsky et al., 2008). In captive studies, onset of migratory restlessness is expressed at the beginning of the dark phase and is associated with increased plasma corticosterone in Gambel's white-crowned sparrows (Landys et al., 2004). However, these elevations fall below the diel peak recorded measured at the end of the dark phase, indicating more of a response to increased locomotor activity rather than a stimulus for the activity (Breuner et al., 1999; Ramenofsky et al., 2008; Ramenofsky and Wingfield, 2017). Extending the period of migratory restlessness for 48 h with continuous exposure to nighttime conditions revealed elevated levels of corticosterone overriding the natural diel pattern of corticosterone secretion. In field studies, circulating corticosterone levels were found to be elevated in birds caught both during and at the conclusion of migratory flight (Falsone et al., 2009; Landys-Ciannelli et al., 2002). In a related context, plasma levels of corticosterone sampled in experienced racing pigeons (*Columbia livia*) after flights of varying distances were highest in birds who traveled the farthest (Haase et al., 1986). Together these results suggest that corticosterone acts as a metabolic hormone supporting the energetic demands of endurance flight. However, a few other studies found no elevation of corticosterone either during or following flight in the field or a wind tunnel, suggesting possible species or experimental differences (Gwinner et al., 1992; Hasselquist et al., 2007; Jenni-Eiermann et al., 2009). Thus, more work is needed to resolve the roles of corticosterone in migration in general and flight activity specifically. Another potential candidate that may serve to support migratory-type movements is the neurosteroid 7-hydroxypregnenolone that has been associated with diurnal locomotor activity in Japanese quail (*Coturnix japonica*) (Tsutsui et al., 2012, 2008). Thus, working with these clues, further studies are warranted to fully assess the role of the endocrine system in migratory flight.

4.2. Nomadic migration

Nomadic migrations appear to encompass a range of movements that vary in their degree of predictability, thus it seems likely that there are multiple endocrine mechanisms involved in stimulating development and expression of a migratory state in these species. Literature surrounding endocrine mechanisms of nomadic migration is extremely sparse. It is probable that some of the same mechanisms that have evolved to support obligate migrations are involved in nomadic movements that are seasonally predictable. Some data published in the context of breeding describe seasonal patterns of thyroid hormones and testosterone in nomadic finches, providing limited insight. Patterns of T3/T4 in free-living pine siskins (Van't Hof, 1992) and testosterone in captive red crossbills (Hahn, 1995) and free-living pine siskins (Van't Hof, 1992) suggest that these hormones may have a similar permissive or stimulatory role in seasonal nomadic movements as in obligate migrants, but no studies have addressed these hormones specifically in the context of migratory behavior or physiology. Given the more facultative nature of nomadic migration, it seems likely that the HPA axis is also involved and may be a mechanism for integrating information about local conditions and energy balance to stimulate or prolong nomadic movements throughout the year. Though entirely speculative, an interesting hypothesis to pursue in regards to nomadic migration is that a stronger role of the HPA allows for a more facultative migration. More generally, this hypothesis would predict that the relative roles of typical seasonal regulators like the HPG and HPT axes versus facultative regulators like the HPA axis – may underlie the flexibility inherent to different migratory strategies. Regardless, it is clear that endocrine regulation of nomadic migration is a prime candidate for future research.

4.3. Fugitive migration

Activation of the ELHS in response to unpredictable severe and deteriorating conditions is what sets fugitive migration apart from the other forms of migration. Activation of the HPA axis occurs when environmental conditions degrade to such a point that allostatic load surpasses the amount of available energy (Wingfield, 2003). The neuroendocrine cascade that follows entails release of hypothalamic corticotrophic releasing factor (CRF) from the median eminence stimulating pituitary adrenocorticotropic hormone (ACTH) that acts on the synthesis and release of corticosterone from the adrenal cortex. In addition, release of arginine vasotocin (AVT) and mesotocin (MT) from the nerve terminals of the median eminence affect cleavage of peptides from pro-opiomelanocortin (POMC) including β-endorphin and α-melanocyte stimulating hormone (α-MSH) (Romero and Wingfield, 2015). The actions of these pituitary peptides in relation to migratory systems are not well known. However, plasma corticosterone is hypothesized to circulate and function at three levels (Landys et al., 2006). Basal or absolute baseline secretion (Level A) maintains essential functions of energy and salt balance. Level B includes diel and seasonal cycles of hormone secretion (i.e., increasing with predictable energy demands). At the highest level (Level C), hormone secretions spike in response to unmitigated, very high allostatic load – directing behavioral and physiological responses of the ELHS away from the current circumstances. At this level, corticosterone molecules saturate the low affinity glucocorticoid receptors that stimulate behavioral responses directing movement away from the local environment and allowing the fugitive to cope and recover (Wingfield et al., 2011).

A number of captive studies have demonstrated enhanced locomotor activity, perhaps reflecting an escape response, in relation to hormonal components of the ELHS. In Gambel's white-crowned sparrow an elevation in plasma corticosterone, induced either by food restriction or administration of corticosterone-laced mealworms resulted in enhanced locomotor activity (Astheimer et al., 1992; Breuner et al., 1998). Additionally, intraventricular injections of CRF have been found to increased locomotor activity in chickens (*Gallus domesticus*) (Lowry and Moore, 2006). The nomadic and irruptive red crossbill also shows increased activity and plasma corticosterone in response to food reduction in captivity – and the hormonal response is further enhanced by social information from similarly food-reduced neighbors (Cornelius et al., 2010). These studies are consistent with the hypothesis that the HPA axis underlies fugitive movements and that the mechanism may be common across migratory types, though we acknowledge that much more work is required to define the spatial and temporal patterns of fugitive migrations, the physiological mechanisms underlying them and, importantly, potential interactions between the two.

4.4. Partial migration

The endocrine regulation of partial migration is not fully understood but important inroads have been made. Most work to date has focused on autumn rigid partial migration in European blackbirds and autumn flexible partial migration in willow tits (*Parus montanus*). One early hypothesis for the endocrine regulation of partial migration was that circulating testosterone levels regulated autumn migratory status, with sedentary birds maintaining higher testosterone levels that inhibited migration (Lack, 1954). However, data from both European blackbirds and willow tits are inconsistent with this hypothesis. Studies of captive and free-living European blackbirds have found that within age and sex classes migratory birds do not show lower levels of testosterone compared with sedentary birds, and in fact within some age and sex classes migratory birds show higher levels of gonadal steroids compared to sedentary conspecifics of the same class (Schwabl et al., 1984). Thus, although testosterone does not appear to inhibit migration in European blackbirds, a stimulatory role for gonadal steroids in autumn migration cannot be ruled out. In willow tits, migratory and non-migratory juveniles, the only age class to migrate, have similar levels of circulating testosterone (Silverin et al., 1989). Therefore, in willow tits testosterone seems to play neither an inhibitory nor a stimulatory role in autumn migration. Thus, in terms of Lack's hypothesis, elevated testosterone appears to have little effect on modulating migratory status. However, field data from European blackbirds indicate that among sedentary birds circulating testosterone levels are higher in males than females, and are elevated during harsh winter conditions when feeding competition is most intense, though these testosterone levels are very low in comparison to breeding levels (Schwabl et al., 1985). Thus, the current thinking for at least for some partial migrants, is that gonadal steroids may be involved with competition for limited food resources and that the competitive outcomes may influence migratory tendencies (either at a proximate level for flexible partial migrants or at an ultimate level for rigid partial migrants).

Work in European blackbirds and willow tits has also examined the role of corticosterone in autumn partial migration. In European blackbirds, Schwabl et al. (1984) found no consistent differences in corticosterone between migratory and sedentary birds. However, among sedentary birds experiencing severe winter conditions plasma levels of corticosterone were higher in adult females and first year birds than in adult males (Schwabl et al., 1985). Thus, elevated corticosterone in these birds may reflect low social status and intense feeding competition. Further, these differences among age and sex classes in the extent to which winter conditions are challenging may help explain observed age and sex differences in the propensity to migrate (Schwabl, 1983; Schwabl et al., 1985). However, more recent work suggests that patterns of partial migration in this species are better explained by sex differences in the fitness costs and benefits of migratory versus residency strategies (Fudickar et al., 2013). In the same study, Fudickar et al. (2013) found that there was a tendency for baseline corticosterone levels to elevate just prior to autumn migration in migratory blackbirds, suggesting a potential role for corticosterone. Migrants in this study had greater fat reserves prior to autumn migration indicating a potential role for corticosterone in energy acquisition and mobilization immediately prior to migration. Patterns of corticosterone secretion in willow tits also suggest a potential role for this steroid; migratory juveniles, those birds that did not successfully join flocks, had higher plasma corticosterone than non-migratory individuals (Silverin et al., 1989). Moreover, when administered corticosterone during the period of autumn migration, juveniles move away from the study area (Silverin, 1997). However, in contrast to the European blackbird study, migratory willow tits had poor body condition compared to non-migratory birds suggesting they may have experienced food restriction inducing fugitive movements for survival. Overall, more data are needed to more fully appreciate the regulation of migration in partial migrants particularly in comparisons with the other migratory forms.

5. Conclusions

The basic tenet for migration is that resource availability varies in time and space and thus serves as a strong selective agent for how, when and where animals move. To better understand the different forms of migration and the endocrine mechanisms mediating the specific responses to the environment, we start with definitions of the major types. Resident or sedentary populations are composed of individuals who remain solely within a single geographical or home range where resources that support all stages of the annual cycle are available. Migratory populations do not reside in a single home range but travel to distant sites exploiting seasonal resources at each location. We divide migratory patterns into three divisions: obligate, nomadic, and fugitive based on the parameters of movement, environmental influences, and endocrine mechanisms. Obligate migration is characterized by regular and directed annual movement between locations for breeding and overwintering where resources are predictable and sufficient. Such migrants show physiological preparations for migration, such as anabolic preparation for impending flight. Nomadic migrations occur less predictably than do obligate migrations as animals make use of potentially rich but ephemeral resources that occur unpredictably in space or time. Fugitive migrations may occur in any of these groups and represent an ELHS or escape response that moves an animal away from a severe disruption of environmental conditions. These movements are often described as irruptions when animals move in large numbers and to locations where they are not typically found. We also considered partial migration as a special case. Partially migratory populations include a mix of sedentary and migratory individuals, though the movement patterns of partial migrants are expected to fall into one of the three divisions above.

The endocrine system plays an integral role in mediating behavioral and physiological responses to environmental conditions, and influencing migratory patterns. Environmental cues are perceived by the sensory nervous system and transduced in the neuroendocrine system with peripheral responses affected by the endocrine functions. While the endocrine system is highly conserved across the vertebrates and specifically migratory types, the distinctions among migratory types likely arise from the specific environmental cues and how migrants perceive and respond to them. Thus, we suggest that a more comprehensive understanding of environmental cues and the endocrine responses across the migratory types will be essential to advance our understanding of migration biology. Specifically, we need to know the types of cues used, the degree of sensitivity to them, and the mechanisms by which these cues stimulate or inhibit the expression of migratory behavior and physiology. It is this approach that will help to advance our understanding of the evolution and plasticity of migratory systems.

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