Toward understanding the endocrine regulation of diverse facultative migration strategies

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Abstract

Migration is an important event in the annual cycle of many animals that facilitates the use of resources that vary across space and time. It can occur with regular and predictable timing, as in obligate migration, or with much greater flexibility, as in facultative migration. Most research aimed at understanding the endocrine mechanisms regulating the transition to a migratory stage has focused on obligate migration, whereas less is known about facultative forms of migration. One challenge for research into the endocrine regulation of facultative migration is that facultative migrations encompass a diverse array of migratory movements. Here, we present a framework to describe and conceptualize variation in facultative migrations that focuses on conditions at departure. Within the context of this framework, we review potential endocrine mechanisms involved in the initiation of facultative migrations in vertebrates. We first focus on glucocorticoids, which have been the subject of most research on the topic. We then examine other potential hormones and neurohormones that have received less attention, but are exciting candidates to consider. We conclude by highlighting areas where future research is particularly needed.

Keywords: movement, nomad, escape, fugitive, hormone, cues, glucocorticoid

1. Introduction

Migration facilitates the use of resources that vary across space and time and is an important event in the annual cycle of many animals. Mobile animals can use migration to avoid unfavorable conditions (e.g., high predation risk, severe weather, low food availability, parasites) or exploit favorable conditions (e.g., abundant or high-quality food resources, mating aggregations, thermal refugia) (Shaw, 2016). In many cases, migrations occur predictably in space and time with animals moving each year between the same locations at approximately the same time; we refer to these as obligate migrations (also termed to-and-fro or calendar migrations; see Box 1 for more on terminology). However, migrations can also occur with much greater flexibility with respect to their timing and destination (see Box 1). For example, individuals may be flexible in whether they undertake migration from one year to the next (e.g., facultative partial migration; Terrill and Able, 1988). Migrations may occur aseasonally, in response to either adverse or advantageous conditions (e.g., irruptive migration and nomadic migration; Dingle, 2014; Teitelbaum and Mueller, 2019). Alternatively, migrations may be irregular with respect to their destination, with individuals moving between varying locations (e.g., nomadic migration; Teitelbaum and Mueller, 2019). Collectively, we refer to these more flexible movement patterns as facultative migrations (following Newton, 2012; Ramenofsky et al., 2012; Watts et al., 2018).

The endocrine system plays a central role in coordinating changes in morphology, physiology, and behavior as animals transition between different stages in their annual cycle, including migration (Jacobs and Wingfield, 2000). At present, much of our understanding of the role of the endocrine system in regulating the transition to a migratory stage comes from studies of obligate migration – and predominately avian obligate migration – with much less known about facultative migrations. Yet facultative migrations occur in a wide array of taxa (Holland et al., 2006; Newton, 2006a; Plotkin, 2010; Teitelbaum and Mueller, 2019), including among species or individuals that also exhibit obligate migrations or are otherwise generally non-migratory (Hahn et al., 2004; Jakes et al., 2018; Teitelbaum et al., 2023; Terrill and Ohmart, 1984). Moreover, growing data on animal movements, facilitated in part by recent advances in tracking technologies, suggest that facultative migrations may be more common than previously recognized (Streby et al., 2015; Teitelbaum et al., 2023). These observations suggest that the study of facultative migrations, including across a diverse array of species, is central to a broad understanding of the endocrine mechanisms involved in mediating migratory transitions.

The diverse array of migratory movements presents a remarkable challenge to understanding the mechanisms that regulate facultative migration. Facultative migrations include nomadic wandering to locate rich but ephemeral food sources (Eby et al., 2014; Fryxell et al., 2004; Pedler et al., 2014; Roshier et al., 2008) as well as more localized to-and-fro movements to temporarily escape inhospitable conditions (e.g., snow storms: Hahn et al., 2004; O'Neill and Parker, 1978; or tropical storms: Udyawer et al., 2013). They are unified by a high degree of variability in spatial or temporal patterning in response to relatively unpredictable biotic or abiotic conditions. Yet, these movements are likely quite heterogenous with respect to the cues that trigger them and the physiological mechanisms that coordinate the response. But an overarching framework to describe and conceptualize this variation has been lacking. Indeed, this challenge is particularly apparent when one considers that varied forms of facultative migration may be routinely exhibited even within a single population or across the lifetime of a single individual (Bennetts and Kitchens, 2000; Newton, 2006a; Newton, 2006b). We propose that a consideration of the conditions at departure provides a unifying framework to describe variation in facultative migrations. This framework can be used to generate hypotheses about cues used to make departure decisions and the physiological mechanisms involved. Further, it can serve as a foundation for understanding variation within and across species in the use of particular cues and mechanisms. Here we give an overview of our framework and then review potential endocrine mechanisms involved in facultative migration in the context of this framework.

2. A framework for describing variation in facultative migrations

We describe variation in facultative migration along a continuum based on conditions at departure (Figure 1); this approach shares similarities with that used by Bennetts and Kitchens (2000) to explain movements by snail kites (*Rostrhamus sociabilis*). We first divide the continuum between exploitative and evasive movements. We define exploitative movements as those that occur while environmental conditions (e.g., foraging conditions) at departure are such that animals can adequately meet energetic or nutritional demands. Migration under these conditions can facilitate locating areas with higher quality resources that allow for increased reproductive output or resources that will be needed or available later in the year, but movements are not necessary for short-term adult survival. One example of this type of migration occurs in animals that move relatively predictably in time to locate spatially unpredictable seasonal resources – such as red crossbills (*Loxia curvirostra*) moving to locate newly developing cone crops in the early summer (Cornelius et al., 2021; Newton, 2006b). Another example is animals that move opportunistically to exploit unpredictable peaks in resources – such as many waterbirds, including banded stilts (*Cladorhynchus leucocephalus*) in Australia and red-billed queleas (*Quelea quelea*) in Africa, that move in association with rainfall (Dallimer and Jones, 2002; Pedler et al., 2014; Roshier et al., 2008; Ward, 1971). Such exploitative migrations can allow animals to utilize rich but unpredictable resources. Species that facultatively migrate to find rich but ephemeral resources have been called Rich Patch Exploiters or Rich Patch Fugitives (Cornelius et al., 2013b; Ford et al., 1993), and we draw from this terminology here. Exploitative movements need not only exploit food patches. For example, killer whales and some sharks move to warmer waters to facilitate skin molt and gestation, respectively, at variable times of the year (Nosal et al., 2021; Pitman et al., 2020).

At the other end of the continuum are reactive evasive movements that are initiated when conditions at an individual's current location are poor. For example, reactive evasive movements away from severe winter or snow conditions are described in birds, mammals, and sharks (Hahn et al., 2004; Jakes et al., 2018; Kaczensky et al., 2011; Matich and Heithaus, 2012; O'Neill and Parker, 1978), and potentially move fish away from parasite outbreaks (Birkeland, 1996). Reactive evasive movements, which likely reflect part of an emergency life history stage, may be triggered by negative energy balance (type 1 allostatic overload) which could result from declining resources or conditions that disallow foraging in the current home range (Wingfield, 2005; Wingfield et al., 1998). As such, reactive evasive movements generally facilitate escape from an immediate threat to survival. These movements have been distinguished from fight-or-flight flight responses mediated by the sympathetic nervous system (Jansen et al., 1995), such as in response to a predatory attack, in that reactive evasive movements reflect responses that occur over longer time scales (Wingfield et al., 1998). Such movements have also been called fugitive or escape migrations (Box 1) and likely occur in very different environmental and physiological contexts than do exploitative facultative movements.

Between these two extremes exist intermediate conditions whereby an animal is still meeting current demand but can anticipate being challenged to meet its daily energy needs or nutritional requirements in the near future. We refer to these movements as predictive evasive, as we expect that in this scenario animals are monitoring conditions and making movements before conditions severely deteriorate to avoid substantial declines in body condition. These types of migrations could occur as ephemeral food sources become depleted, such as in birds or mammals that feed on seeds, berries or rodents that exhibit boom-bust cycles (Newton, 2006a; Páez et al., 2018) or in response to drought (Dean et al., 2009). They can also occur in fish when available energy in the environment becomes lower than energetic demand, such as in brown trout (*Salmo trutta*; Forseth et al., 1999; Olsson et al., 2006). Facultative migration in response to tropical or tornadic storms (Streby et al., 2015; Udyawer et al., 2013) and wildfires (Sanderfoot et al., 2021) may also reflect predictive evasive movements given that many individuals move before conditions severely deteriorate. For instance, blacktip sharks (*Carcharhinus limbatus*) have been found to depart coastal areas in advance of a tropical storm (Heupel et al., 2003; Udyawer et al., 2013).

Although we have described three points along the continuum – exploitative, predictive evasive, and reactive evasive – we expect movements to fall between those points as well. For instance, the nomadic movements of some gazelles (Mueller et al., 2011) may fall between exploitative and predictive evasive, as changes in daily energy intake may be important in movement decisions that facilitate maintenance of high energy intake (Fryxell et al., 2004). Moreover, the migratory behavior of a population, or even an individual, is not necessarily fixed along this continuum. For instance, populations or individuals that typically make exploitative facultative migrations or seasonal obligate migrations, may also make reactive evasive movements under unfavorable conditions (Hahn et al., 2004; Terrill and Ohmart, 1984).

We hypothesize that the proximate cues used to evaluate conditions and make departure decisions vary across the departure continuum. Conditions could be evaluated using both internal and external cues, both of which could be transduced via endocrine signals. Internal cues could include indicators of metabolic or nutritional state (Cornelius et al., 2013a; Jachowski and Singh, 2015). Candidates for such indicators would be catabolic hormone levels (e.g., glucagon or corticosterone), metabolite indicators of anabolism versus catabolism (e.g., triglyceride versus free fatty acids), energy stores (e.g., adipocyte size), or levels of key nutrients (e.g., protein or salt). External cues about local conditions could include direct assessments of food availability, weather, daylength, or social information (Ramenofsky et al., 2012; Watts et al., 2018). We note that many environmental conditions can generate both external and internal cues that could be used to inform animal decision-making (e.g., food availability could be assessed visually or via an indicator of nutritional state; Hau et al., 2000), though our understanding of these processes in the context of migration is currently limited. Further, individuals likely integrate both internal and external cues to make departure decisions, as occurs in obligate migrants (Bauer et al., 2011; Newton, 2008). However, we hypothesize that the extent to which different cues are used or weighted varies along the departure continuum (Figure 1). That is, animals departing under good conditions are expected to rely more heavily on predictive cues that are indicators of environmental conditions in the future or at distant locations (e.g., photoperiod or indicators of distant rainfall), whereas animals departing in response to poor environmental conditions are likely responding to immediate, local cues indicative of the poor conditions (e.g., metabolic state, food availability, social information). Intermediate between these, we expect a more balanced use or a combination of immediate and predictive cues, including predictive cues that may function on a shorter time scale (e.g., changing barometric pressure or declining foraging efficiency). Though we note that even in cases where animals depart under good conditions, indicators of internal state may be important in fine-tuning the timing of departure, particularly in cases where physiological preparations precede departure.

3. Endocrine mechanisms of facultative migration

The endocrine system has been a focus of research aimed at understanding physiological mechanisms mediating facultative migration (Cornelius et al., 2013a; Ramenofsky et al., 2012; Watts et al., 2018). Here, we review potential endocrine mechanisms involved in facultative migration, using the departure continuum to consider variation in these mechanisms. We first focus on glucocorticoid signaling, which is arguably the best studied endocrine mechanism in the context of facultative migration. We then consider the potential role for other endocrine signaling molecules from fat, gut, thyroid and brain, which have thus far received less research attention. Although much existing research has focused on how changes in circulating hormone levels influence behavior, including migratory behavior, changes in other elements of endocrine signaling pathways (e.g., hormone receptors, enzymes involved in local synthesis or inactivation) may also be important (Balthazart et al., 2004; Rensel and Schlinger, 2016; Watts, 2020). In reviewing the literature on glucocorticoids, we consider several types of evidence for a role of a given endocrine signal in facultative migration (see Table 1). We consider the strongest evidence to include (i) changes in the circulating hormone and/or other elements of the signaling pathway (e.g., receptor expression) in association with the expression of facultative migration, in combination with (ii) hormone or receptor manipulation that changes expression of the behavior.

Either of these (i or ii) alone provide good, but more limited evidence. We also consider weaker evidence such as associations between cues known or likely to stimulate migration and changes in endocrine signaling pathways. We further distinguish between evidence from captive and free-living animals, since the ability to study the expression of migratory behavior in captivity is somewhat limited.

3.1 Glucocorticoids

In vertebrates, glucocorticoids are steroid hormones that coordinate whole body responses to real and anticipated energetic challenges (Landys et al., 2006) and are one of many hormones involved in regulating metabolism. Blood plasma concentrations of glucocorticoids are controlled by the hypothalamic-pituitary-adrenal/interrenal (HPA/I) axis. Glucocorticoids can be bound by both glucocorticoid receptors (GRs) and mineralocorticoid receptors (MRs) (Breuner and Orchinik, 2009; de Kloet et al., 1998), and their local availability in tissues can be altered via enzymatic deactivating or activating reactions by 11β-hydroxysteroid dehydrogenases (11β-HSDs; Sapolsky et al., 2000). The HPA/I axis is responsive to energy indicators in the blood plasma (e.g., blood glucose and free fatty acid levels) via reactive pathways as well as to anticipatory energy needs via processive pathways (e.g., fear processing in response to a perceived stressor) (de Kloet et al., 1998; Oh et al., 2012; Sapolsky et al., 2000). As energy demand increases and blood sugar or free fatty acid levels decline, glucocorticoids elevate to maintain energy substrates in the blood and induce energy storing cells to release more energy substrate to the blood (Kuo et al., 2015; Sapolsky et al., 2000). At high levels glucocorticoids are also thought to alter behavior in ways that favor adult survival in the context of the acute or anticipated stressor (Landys et al., 2006; Sapolsky et al., 2000). Sustained locomotor activity necessary for migration is energetically demanding (Schmidt-Nielsen, 1972; Weber, 2009). This energy demand may be anticipated in those individuals preparing to leave an area or experienced acutely if animals are forced to move in response to unanticipated conditions. Thus, glucocorticoids may play a role in both exploitative and reactive types of movements – but the physiological context is expected to be different (Ramenofsky et al., 2012).

Glucocorticoid signaling is frequently suggested to play an important role in stimulating reactive evasive migration, when departures occur under extremely poor conditions and food intake or body condition is in decline. As part of an emergency life history stage (Wingfield et al., 1998), these movements are thought to be promoted by increased glucocorticoid signaling (Landys et al., 2006; Wingfield et al., 1998; Wingfield and Ramenofsky, 1997). Severe weather conditions that physiologically challenge animals, including storms and extreme heat, can cause elevations in circulating glucocorticoid levels (Boyle et al., 2010; Dezetter et al., 2022; Huber et al., 2003; Jessop et al., 2013; Krause et al., 2018; Moagi et al., 2021; Rogers et al., 1993; Schwabl et al., 1985; Smith et al., 1994; Wingfield et al., 1992; Xie et al., 2017), as can fasting or declines in food availability (reviewed in de Bruijn and Romero, 2018). However, few field studies have linked such changes in glucocorticoid signaling, such as during severe weather, to migratory movements. Many of the studies linking changes in glucocorticoid signaling to severe weather have focused on cases in which animal appear to employ a strategy of attempting to ride out the adverse conditions rather than leaving (i.e., a “take-it" strategy rather than a “leave-it” strategy; Wingfield and Kitaysky, 2002). Other studies have suggested that animals may have been in the process of facultative movements when captured (Rogers et al., 1993; Smith et al., 1994), but movement data necessary to confirm this were not collected. A study of vagrant birds, likely displaced by winds during obligate migration, found that circulating glucocorticoids were not elevated compared to migrants that were not displaced, though it is not clear that vagrancy posed an immediate energetic challenge in these birds (Snell et al., 2022). While baseline corticosterone levels were extremely high in a single vagrant individual suffering very low body condition, they did not correlate with fat deposits across the multi-species dataset (Snell et al., 2022). Captive studies have found correlations between elevations in glucocorticoids and increases in locomotor activity in response to energetic challenges (Challet et al., 1995; Cornelius et al., 2010; DeSimone et al., 2021; Krause et al., 2017; Lynn et al., 2003; Spée et al., 2011) and exogenous glucocorticoids can stimulate increased locomotor activity in a variety of vertebrates in captivity (Astheimer et al., 1992; Breuner et al., 1998; Cash and Holberton, 1999; Challet et al., 1995; Øverli et al., 2002; Spée et al., 2011). Exogenous glucocorticoids can also alter movement patterns and performance in free-living animals (Breuner and Hahn, 2003; Jessop et al., 2018; O'Connor et al., 2010; but see, Algera et al., 2017). However, there is a lack of manipulative studies that directly link changes in glucocorticoid signaling to the expression of reactive evasive migrations in free-living animals.

Glucocorticoids have also been hypothesized to play a role in predictive evasive migrations – those movements occurring in anticipation of impending metabolic challenge – particularly because elevations in circulating glucocorticoid levels are associated with cues that may stimulate these migrations. Increasing energy demand, particularly relative to what is available in the environment or in energy reserves, and social information about food availability can both alter glucocorticoid signaling in vertebrates (Cornelius et al., 2010; Cornelius et al., 2018; de Bruijn and Romero, 2018; Guinet et al., 2004; Jimeno et al., 2017). Indeed, experimental studies of captive finches – pine siskins (*Spinus pinus*) and red crossbills – that feed on conifer seeds and are known to make facultative, irruptive migrations in association with low or declining food availability (Bock and Lepthien, 1976; Koenig and Knops, 2001) have found that as food availability declines, circulating corticosterone and locomotor activity both increase (Astheimer et al., 1992; Cornelius et al., 2010; Cornelius et al., 2018; DeSimone et al., 2021; Robart et al., 2019; Robart and Watts, 2023). Interestingly, these studies found that circulating corticosterone was only modestly elevated (~2- to 4-fold increase above baseline levels compared to increases that can be 7- to 10-fold or greater in these species in response to more severe stressors; Astheimer et al., 1992; Cornelius et al., 2012; Cornelius et al., 2011; Knutie and Pereyra, 2012). This suggests that if corticosterone is involved in mediating the migratory transition under these conditions, it is at circulating levels that are much lower than maximal levels or the conditions experienced in these studies were not stimulatory of actual migratory departure. In contrast to findings from captive finches, studies of facultatively partial migrant brown trout have found that although reduced food availability is associated with adoption of a migratory phenotype (Wysujack et al., 2009), experimental elevation of cortisol does not directly stimulate migratory behavior (Midwood et al., 2016). Additionally, a recent observational study of free-living pine siskins found no relationship between circulating corticosterone and departure from the study area, though food availability may not have been low or in decline so it is unclear if the detected movement represented an exploitative or reactive migration (DeSimone et al., 2023).

For facultative migrations at the exploitative end of the continuum, a role for glucocorticoids is not clear. In seasonal obligate migration, glucocorticoids are hypothesized to elevate when migratory departure is imminent or during migration to support the metabolic demands of extended locomotion, though there is only limited evidence for this function (Bauer and Watts, 2021). Glucocorticoids could play a similar supportive role in exploitative migrations.

However, existing studies – which are unfortunately limited to a single species, the pine siskin, and have been performed primarily in a captive setting – have found no evidence for changes in circulating glucocorticoids (DeSimone et al., 2023; Robart et al., 2018) or changes in expression of genes that code for proteins involved in glucocorticoid signaling (e.g., MR, GR, 11β-HSD type 1 and type 2; Vernasco et al., 2021; Watts et al., 2019) in association with the seasonal expression of migratory behavior. The absence of evidence for changes in the expression of genes for receptors or enzymes involved in glucocorticoid signaling stands in contrast to results from an obligate avian migrant, Gambel’s white-crowned sparrow (*Zonotrichia leucophrys gambelii*), which found tissue-specific adjustments in glucocorticoid signaling genes in association with migratory preparations (Pradhan et al., 2019). Perhaps even more intriguingly, these findings contrast with existing evidence that is consistent with a role for glucocorticoids in predictive reactive movements by pine siskins (DeSimone et al., 2021; Robart et al., 2019; Robart and Watts, 2023) – thus highlighting the potential for endocrine mechanisms to vary across forms of facultative migration even within a species. But clearly data from a more diverse array of species are needed to properly evaluate the role of glucocorticoids in exploitative migrations more generally.

3.2. Other endocrine candidates

Beyond glucocorticoids, there are other, less studied, endocrine mechanisms that may be important in mediating facultative migratory transitions. We highlight candidates selected based on their roles in energy balance, locomotor activity, and/or their implication in obligate migration. The adipokines (i.e., signaling molecules released from fat) leptin and adiponectin, as well as the gastric hormone ghrelin may be signals of energetic state that could function across the departure spectrum. Our general expectation for these hormones is that in reactive movements indicators of a negative energy balance will promote departure and indicators of positive energy balance will suppress it. In exploitative movements we expect that indicators of positive energy balance should be permissive of movements, thus generating different patterns across the departure continuum (Figure 1).

There are also several candidates that are regulators of locomotor activity that we predict are more likely to play a role in just some forms of facultative migration (see below). We suggest that thyroid hormones and the neurohormone 7α-hydroxypregnenolone are likely candidates for roles in exploitative migrations, whereas the neurohormone corticotropin-releasing factor could play a role in reactive migrations. We describe candidate signaling molecules derived from brain or peripheral tissue individually below, but we note that many of these signals can interact with each other, with glucocorticoids, and with other neuropeptides involved in regulation of energy balance. Of particular note is the fact that, at least in mammals, neurons expressing neuropeptide Y (NPY) and Agouti-related protein (AgRP), as well as those expressing pro-opiomelanocortin (POMC), in the arcuate nucleus – neurons that are involved in regulating energy balance and food intake – express receptors for leptin, adiponectin, and ghrelin (Guillod-Maximin et al. 2009; Williams and Elmquist, 2012). NPY and AgRP have been proposed to be involved in regulating migratory fueling before flight in birds (Cornelius et al., 2013a). But NPY-AgRP and POMC neurons are also involved in regulating locomotor activity and evidence from rodents indicates that the effects of leptin and ghrelin on locomotor activity are mediated at least in part by their action on these neurons (Ceccarini et al., 2015; Huo et al., 2009; Méquinion et al., 2020). Thus, although our understanding of these systems outside of mammals is still quite limited, they highlight the potential for interactions between multiple endocrine signals and the neuropeptides in these systems to be important in migratory decision making. We review each candidate signal, starting with those released from tissues of the periphery, followed by those from the brain.

3.2.1. Signals from the periphery: leptin, adiponectin, ghrelin, and thyroid hormones

Leptin is thought to be an adipostat, or marker of adiposity, in several vertebrate taxa (Evans et al., 2021). It is secreted by adipose tissue and could potentially signal internal energy stores to influence behavior (Choi et al., 2008; Nourbakhsh-Rey and Markham, 2021; Vivas et al., 2011), though maybe not in birds (Friedman-Einat and Seroussi, 2019). Indeed, leptin has been linked to the regulation of locomotor activity across a range of vertebrates, though with considerable interspecific variation in patterns and evidence of context specific effects within species (Choi et al., 2008; Henderson et al., 2018; Niewiarowski et al., 2000; Vivas et al., 2011; Wittert et al., 2005). There has been very little research into the role of leptin in any form of migration. Research thus far has focused on avian obligate migrants and has found little evidence for a role of leptin in regulation of migratory preparation or behavior (Cerasale et al., 2011; Churchman and MacDougall-Shackleton, 2022; Gogga et al., 2013; Rossi and Welch, 2023). Interpretation of these results must take into consideration evidence that leptin may function differently in birds than in other vertebrates and may not be an adipostat (Friedman-Einat and Seroussi, 2019). Thus, the potential role of leptin in any form of migration in other taxa remains an open question. If leptin does play a role as an adipokine in facultative migrations, this could occur across the departure continuum. We hypothesize that exploitative migrants might respond to high leptin as a signal that there are enough stores to attempt a movement. If this hypothesis is correct, then circulating leptin levels will be elevated in association with exploitative departures, and the expression of exploitative migratory behavior will be stimulated by the administration of exogenous leptin and suppressed by inhibiting the action of leptin. In the context of a reactive migration, on the other hand, high leptin should be associated with staying given that body condition is high and a movement need not be made, and low leptin should be associated with departure. This hypothesis predicts that circulating leptin levels will be low in association with reactive departures, and that the expression of reactive migratory behavior will be stimulated by blocking the action of leptin and suppressed by exogenous leptin.

Another adipokine that may play a role in mediating facultative migrations is adiponectin. Although adiponectin has been identified in fishes, birds and mammals, our understanding of adiponectin comes primarily from mammalian studies. Adiponectin generally circulates at levels that are positively associated with fasting or food deprivation, but expression of adiponectin and its receptors are influenced by a variety of nutritional signals (Hendricks et al., 2009; Sánchez-Gurmaches et al., 2012; Tang et al., 2021). Further, the relationship between circulating adiponectin and adiposity appears to be quite variable (Hendricks et al., 2009; Meier and Gressner, 2004; Stuber et al., 2013). Although adiponectin is perhaps better known for roles in regulating food intake, metabolism, inflammation, and reproductive physiology (Bernardi et al., 2021; Meier and Gressner, 2004; Tang et al., 2021), adiponectin may also play a role in regulating other behaviors – including locomotor – in association with energetic state (Burkhard et al., 2018; Vaanholt et al., 2007). In an avian obligate migrant, circadian patterns of circulating adiponectin differed between birds in migratory and non-migratory states, with adiponectin levels being elevated when locomotor activity is expressed (Stuber et al., 2013). Further, adiponectin levels were positively correlated with adiposity in migrants, leading to the hypothesis that adiponectin could function as a signal of energetic state to stimulate migratory behavior (Stuber et al., 2013). We hypothesize that adiponectin signaling could stimulate migration across the departure continuum, though the current understanding of adiponectin precludes strong assertions about its signaling function in relation to energy balance. The most likely scenario across most vertebrates is that increasing adiponectin signaling would stimulate reactive movements as an indicator of negative energy balance and inhibit exploitative movements, whereas low levels would facilitate exploitative movements. However, results from an avian obligate migrant suggest that it could stimulate exploitative migrations as a positive indicator of energetic state.

Ghrelin is a hormone produced by the gut that can regulate food intake, fat deposition, and in some cases locomotor activity, in mammals, birds, and fish (Jönsson, 2013; Kaiya et al., 2013; Kojima and Kangawa, 2005). Although increases in circulating ghrelin are generally associated with fasting, it can have both stimulatory and inhibitor effects on food intake and locomotor activity, with variation occurring within and across taxa (Jönsson, 2013; Kaiya et al., 2013; Lupi et al., 2022). Complicating our understanding of ghrelin is the fact that it occurs in two isoforms – acylated ghrelin and unacylated ghrelin – which may differ in their effects (Goymann et al., 2017), though this is not well understood. In birds, where there is evidence for a role of ghrelin in obligate migration, circulating ghrelin is elevated in association with greater fat deposits and can have a stimulatory effect (particularly in the case of unacylated ghrelin) on the expression of migratory behavior (Goymann et al., 2017; Lupi et al., 2022; Marasco et al., 2023), though these relationships are not ubiquitous (Eikenaar et al., 2018). It has been further suggested that in avian obligate migrants ghrelin may play a role in the mobilization of fat to fuel migration (Goymann et al., 2017; Marasco et al., 2023). In fish, it has been suggested that the stimulatory effects of ghrelin on locomotor activity may be specifically associated with motivation to forage (Jönsson, 2013) – this would be consistent with an effect of ghrelin on stimulating reactive movements. Thus, based on our current understanding, ghrelin could function in facultative migrations as a signal of either positive energy balance (promoting exploitative movements) or negative energy balance (promoting reactive movements). If ghrelin functions in either of these roles, then positive relationships between the expression of that form of migratory behavior and both circulating ghrelin levels and the administration of exogeneous ghrelin are predicted.

Thyroid hormones have been linked to more predictable migratory behavior. In songbirds, eels, and salamanders, thyroid hormones have a permissive or stimulatory effect on the expression of migratory behavior – though the relative importance of triiodothyronine (T3) and thyroxine (T4) remains unclear (Castonguay et al., 1990; Duvall and Norris, 1980; Imbert et al., 2008; Pant and Chandola-Saklani, 1993; Pérez et al., 2016). There are also indications that migratory versus residency strategies of avian subspecies are associated with differences in thyroid hormone signaling (Pérez et al., 2021), though the extent to which these differences are directly related to migratory behavior remains to be determined. Further, environmental cues of potential relevance to facultative migrations – temperature and food availability – have been found to alter thyroid hormone signaling (Boelen et al., 2008; Holloway et al., 1994; Nisembaum et al., 2020; Tomasi and Mitchell, 1996; Wada, 1993). We hypothesize that thyroid hormones may function in promoting (some) exploitative migrations. This hypothesis predicts that thyroid hormone signaling will be elevated in association with the expression of exploitative migratory behavior, that inhibition of thyroid hormone signaling will suppress the expression of this behavior, and that exogenous thyroid hormones will stimulate its expression.

3.2.2. Signals from the brain: 7α-hydroxypregnenolone and corticotropin-releasing factor

7α-hydroxypregnenolone (7α-OH PREG) is a neurosteroid that regulates locomotor behavior in a range of vertebrates (Tsutsui et al., 2018). 7α-OH PREG generally has a stimulatory effect on locomotor activity (Haraguchi et al., 2011; Tsutsui et al., 2018), including in the context of obligate migrations by newts (Haraguchi et al., 2010) and salmon (Haraguchi et al., 2015). But initial studies of its role in avian obligate migration are less clear (Wingfield et al., 2018). Our understanding of the internal and external cues that influence 7α-OH PREG signaling is still developing, but melatonin and prolactin appear to be important in mediating daily and seasonal changes in 7α-OH PREG signaling (Tsutsui et al., 2018). We hypothesize that 7α-OH PREG could stimulate migratory movements across the departure continuum, though likely in response to different suites of cues. This hypothesis predicts that 7α-OH PREG signaling will be elevated in association with the expression of facultative migratory behavior and that exogenous 7α-OH PREG will stimulate its expression. Evidence of a potential pathway by which 7α-OH PREG might stimulate movement at the reactive end of the continuum is most clear, as elevations in circulating glucocorticoids have been found to stimulate 7α-OH PREG synthesis (Haraguchi et al., 2012). Thus, glucocorticoids and 7α-OH PREG may act in concert to stimulate reactive movements (Wingfield et al., 2018).

Finally, corticotropin-releasing factor (CRF) is a neuropeptide that is released as part of the vertebrate neuroendocrine stress response. In addition to its role in stimulating release of adrenocorticotropic hormone (ACTH) in the HPA/I axis, CRF can also act directly on the central nervous system to influence behavior (Koob and Heinrichs, 1999). Indeed, CRF appears to have a highly conserved stimulatory effect on locomotor activity, which can occur independently of downstream effects on glucocorticoids (Koob et al., 2007; Lowry and Moore, 2006). This behavioral effect has been shown in mammals, birds, amphibians, and fish (Lowry and Moore, 2006). Therefore, we hypothesize that CRF, acting in the brain, could be a stimulus of reactive movements. This hypothesis predicts that central administration of CRF will stimulate reactive movements in appropriate environmental contexts (see Lowry and Moore, 2006) and that CRF antagonists will inhibit reactive movements.

4. Outlook

Here, we have reviewed potential endocrine mechanisms involved in migration across a continuum of facultative migration types – ranging from exploitative movements initiated when conditions at departure are good to reactive movements in response to poor conditions. Whereas much research in this area has focused on the role of glucocorticoids in facultative movements (summarized in Table 1), more work remains to resolve their role across different forms of facultative migrations. Moreover, there are numerous other candidate endocrine mechanisms, beyond glucocorticoids, that warrant further research in the context of facultative migrations. Research that advances our understanding of the endocrine mechanisms involved in these flexible migratory behaviors may have the added benefit of providing insights that help clarify their roles in obligate movements as well. Although we have highlighted a number of promising candidates here for further research, the use of discovery-oriented approaches such as 'omics techniques (Garcia-Reyero et al., 2014) and mass spectrometry-based hormone profiling (e.g., Boggs et al., 2019; Jalabert et al., 2021) offer considerable promise. Incorporating these techniques into studies of facultative migrations will allow for examination of multiple potential mechanisms simultaneously and may reveal potential mechanisms that have yet to be considered.

Future research that elucidates the cues that stimulate facultative migrations, especially through experimental approaches (Birnie-Gauvin et al., 2020), will also be useful in generating new hypotheses about endocrine mechanisms. Notably, the cues driving many nomadic migrations remain particularly elusive (Teitelbaum and Mueller, 2019). Work to understand the cues and endocrine mechanisms involved in such exploitative movements, especially in species beyond those of current focus (i.e., red crossbills and pine siskins), would contribute to filling an important knowledge gap. We suggest that birds of the arid regions of Africa and Australia that make use of facultative migratory strategies on the exploitative end of the departure continuum (Dallimer and Jones, 2002; Kingsford et al., 2010; Pedler et al., 2014; Roshier et al., 2008; Ward, 1971) would be excellent subjects for this work.

In addition to expanding the breadth of endocrine mechanisms under study in the context of facultative migration, there is also a pressing need for research from a greater diversity of taxa. Most research to date has focused on a few species of birds and fishes highlighted here (but in invertebrates see also work on locusts, e.g., Anstey Michael et al., 2009; Guo et al., 2020). Mammalian systems where facultative migration is already relatively well-described (e.g., grey-headed Flying-foxes, *Pteropus poliocephalus* and Thomson's gazelles, *Gazella thomsoni*) would be good candidates for complementary studies on endocrine mechanisms. Among birds, there is tremendous potential to study a greater diversity of species including tropical birds that make altitudinal migrations in response to seasonal rain storms (Boyle et al., 2010), as well as birds of the arid regions of Africa and Australia noted above. Research on the endocrine mechanisms underlying migration in a diverse range of systems is necessary to make inferences about commonalities and sources of variation in these mechanisms and to understand strategies for coping with environmental variation more broadly.

Advances in tracking technology are also providing new opportunities for descriptive and experimental field studies of facultative migrants (DeSimone et al., 2023; Pedler et al., 2014;

Streby et al., 2015). Leveraging these tools to collect complementary behavioral and endocrine data, particularly in combination with endocrine manipulations (e.g., Angelier et al., 2007; Lupi et al., 2022; O'Connor et al., 2010) will be critical to advancing our understanding of the mechanisms underpinning facultative migrations. Field experiments, while logistically challenging in facultative migrants, will be especially informative given the difficulties in interpreting captive behavior and the need to better describe the movements and mechanisms in free-living birds.

Human-induced environmental changes may pose a considerable threat to animal migrations across the globe (Bolger et al., 2008; Carey, 2009; Lennox et al., 2016) and may disrupt a wide range of physiological systems that are involved in orchestrating migratory transitions (Buchanan and Partecke, 2012; Helm et al., 2013; Lennox et al., 2016). Flexibility in migratory behavior may, however, represent an important means by which animals can cope with rapid and human-induced environmental change. An understanding of the mechanisms underlying facultative migratory decision-making may therefore be critical to predicting the capacity for animals to cope in the future (Wilcove and Wikelski, 2008). Moreover, the need to better understand facultative migrations specifically is all the more pressing because of the likelihood that facultative migrations may become more common with human-induced environmental changes such as increasing frequency of severe storms, extreme temperature events, droughts, and wildfires (IPCC 2021).

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Box 1. Terminology related to facultative migration

The terms **obligate** and **facultative** are applied to migration in two ways. First, they are used to distinguish between individuals that always migrate (obligate) versus individuals that only migrate under certain circumstances (facultative) (see Partial migration). Many obligate migrants are also highly consistent in their timing, distance and direction of migration. Consequently, the term **obligate migration** has been used to describe a broad suite of relatively predictable migratory behavior (also called to-and-fro, true, and calendar migrations). In contrast, the term **facultative migration** is applied to a variety of movements that are flexible in one or more aspects of timing and spatial patterning, thus encompassing more than partial migration (e.g., Newton, 2008).

Forms of facultative migration

Nomadic migration describes migrations that are irregular or variable with respect to direction and destination that occur repeatedly throughout an individual's life. Nomads exhibit low site fidelity and movements can be temporally irregular. For more see Dingle (2014); Dingle and Drake (2007); Teitelbaum and Mueller (2019).

Irruptive migration refers to temporally irregular movements that move animals away from unfavorable conditions (typically declining food availability). Irruption is often associated with large numbers of individuals moving outside of their typical range and can frequently occur in nomadic migrants if movements fail to locate resources within their typical range. This term is sometimes applied to facultative altitudinal and winter migrations, and escape migrations. For more see Newton (2012); Wingfield and Ramenofsky (1997).

Facultative altitudinal migration has been applied to movement to a new elevation in response to poor or deteriorating conditions at a given elevation (e.g., to lower elevation in response to rain or snow). Movements are often short in distance and may involve relocation for days to months. E.g., (Boyle et al., 2010; e.g., Hahn et al., 2004).

Facultative winter migration has been applied to movements in the winter away from poor or deteriorating conditions (e.g., caused by snow or cold), typically to lower latitudes. These have also been called facultative extension of fall migration. E.g., Jakes et al. (2018); Terrill and Ohmart (1984).

Escape or **fugitive migration** are general terms for movements away from poor or deteriorating conditions. They include facultative altitudinal and winter migrations. For more see Newton (2008); Péron et al. (2011); Watts et al. (2018).

Other related terminology

Partial migration refers to a population in which some individuals migrate and others do not, in a given year. Among partial migrants, individuals may be obligate migrants (i.e., an individual is always migratory or not) or facultative migrants (i.e., an individual may migrate in some years but not others). For more see Chapman et al. (2011); Terrill and Able (1988).

Differential migration refers to variation in migratory behavior (e.g., distance traveled, timing of movement) between different demographic classes of individuals within a population (e.g., age class or sex). Differential migration can occur among both obligate and facultative migrants. For more see Terrill and Able (1988)

Table 1. Summary of evidence for the role of glucocorticoid (GC) signaling in vertebrate facultative migration across movement types. Associations between changes in (1) GCs and/or (2) other elements of the HPA-axis in association with the environmental conditions expected to trigger migration are suggestive, but are considered to be relatively weak evidence. (3) Correlations between GC signaling and the expression of facultative migratory behavior and/or (4) hormone manipulations that change expression of facultative migratory behavior provide stronger evidence, particularly in combination. See main text for more detailed descriptions of findings. Note that in some cases evidence comes from very few studies or species.

	Exploitative	**Predictive evasive**	**Reactive evasive**
1) Circulating GCs elevated under conditions expected to trigger migration	No[a]	Yes, but only elevated to modest levels[d]	Yes, in many species, particularly if body condition is negatively impacted[h]
2) Other elements of GC signaling pathways altered under conditions expected to trigger migration	No[b]	Indirect - receptors change in response to social cues about food[e]	Lack of data
3) Correlation between elevated GCs (or other elements of GC signaling) and migratory behavior	No[c]	Yes, based on captive studies only[f]	Evidence for correlation with locomotor activity from captive studies[i], but lack of data on free-living animals
4) Changes in expression of behavior in response to hormonal manipulation	Lack of data	No, but data only from a single study (in different taxon from evidence for #1,2,3)[g]	Evidence of causal relationship with locomotor behavior from captive[j] and free-living animals[k], but lack of data on migratory movements in free-living animals

[a] Robart et al., 2018

[b] Vernasco et al., 2021; Watts et al., 2019

[c] DeSimone et al., 2023

[d] Cornelius et al., 2010; de Bruijn and Romero, 2018; Guinet et al., 2004; Jimeno et al., 2017

[e] Cornelius et al., 2018

[f] Astheimer et al., 1992; Cornelius et al., 2010; Cornelius et al., 2018; DeSimone et al., 2021; Robart et al., 2019; Robart and Watts, 2023

[g] Midwood et al., 2016

[h] E.g., de Bruijn and Romero, 2018; Huber et al., 2003; Jessop et al., 2013; Rogers et al., 1993; Schwabl et al., 1985; Xie et al., 2017; see main text for additional references

[i] Challet et al., 1995; Cornelius et al., 2010; DeSimone et al., 2021; Krause et al., 2017; Lynn et al., 2003; Spée et al., 2011

[j] Astheimer et al., 1992; Breuner et al., 1998; Cash and Holberton, 1999; Challet et al., 1995; Øverli et al., 2002; Spée et al., 2011

[k] Breuner and Hahn, 2003; Jessop et al., 2018; O'Connor et al., 2010

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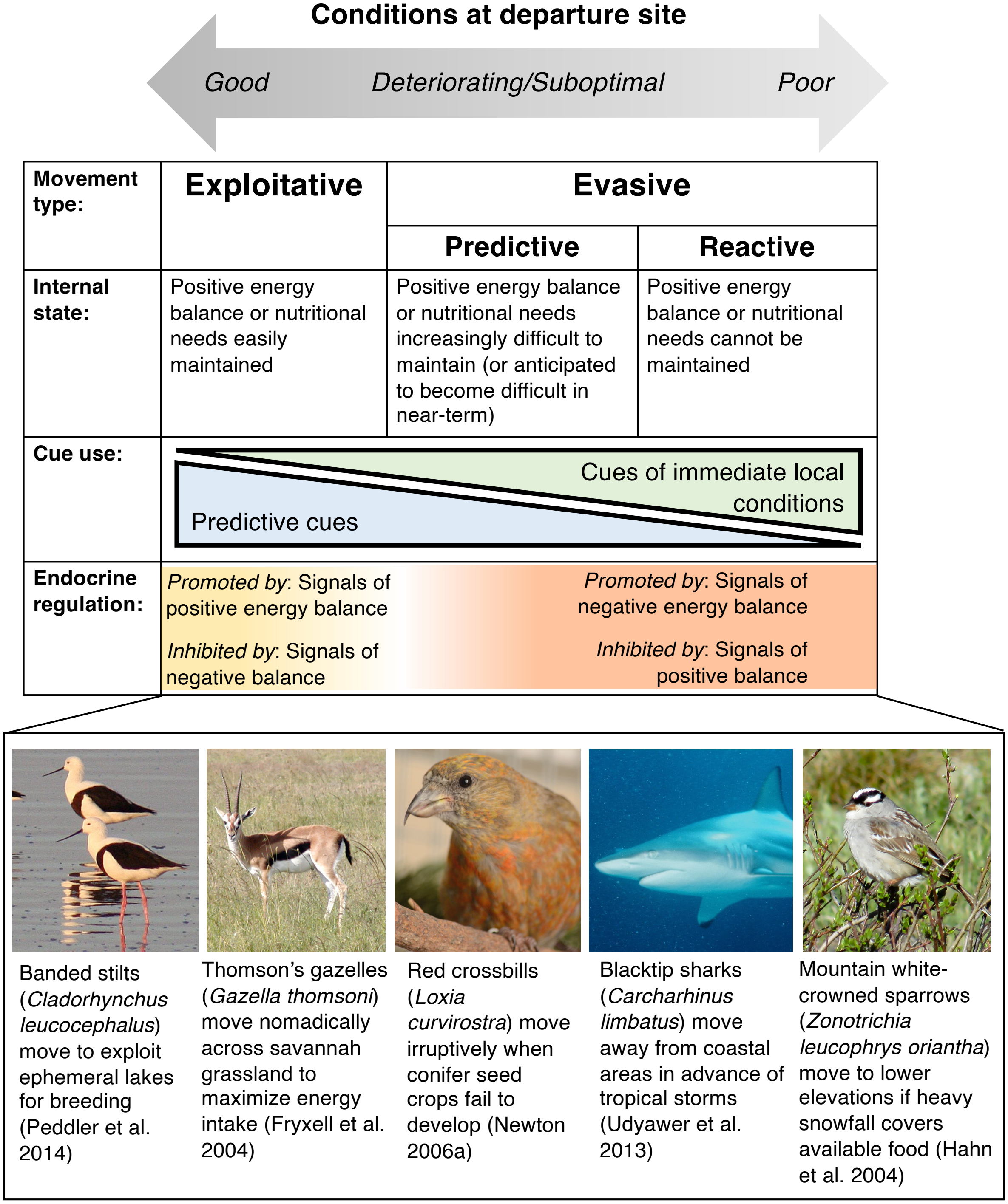
Figure 1. Conceptual framework describing variation in facultative migrations across a range of conditions at departure, with examples to illustrate movements across the continuum. Note that a given species may engage in more than one form of facultative migration (e.g., red crossbills make both exploitative and reactive movements). Hypothesized patterns of cue use and endocrine regulation across the movement types are also shown. Photo credits from left to right: Cas Liber, Heather Watts, Jamie Cornelius; Albert Kok, Tom Hahn.



Movement type:	**Exploitative**	**Evasive**	
		Predictive	**Reactive**
Internal state:	Positive energy balance or nutritional needs easily maintained	Positive energy balance or nutritional needs increasingly difficult to maintain (or anticipated to become difficult in near-term)	Positive energy balance or nutritional needs cannot be maintained
Cue use:	Predictive cues		Cues of immediate local conditions
Endocrine regulation:	*Promoted by*: Signals of positive energy balance *Inhibited by*: Signals of negative balance		*Promoted by*: Signals of negative energy balance *Inhibited by*: Signals of positive balance

Banded stilts (*Cladorhynchus leucocephalus*) move to exploit ephemeral lakes for breeding (Peddler et al. 2014)

Thomson's gazelles (*Gazella thomsoni*) move nomadically across savannah grassland to maximize energy intake (Fryxell et al. 2004)

Red crossbills (*Loxia curvirostra*) move irruptively when conifer seed crops fail to develop (Newton 2006a)

Blacktip sharks (*Carcharhinus limbatus*) move away from coastal areas in advance of tropical storms (Udyawer et al. 2013)

Mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) move to lower elevations if heavy snowfall covers available food (Hahn et al. 2004)