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Does Migration Constrain Glucocorticoid Phenotypes? Testing Corticosterone Levels during Breeding in Migratory Versus Resident Birds

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Synopsis Corticosterone, the main glucocorticoid in birds, is a major mediator of the incredible physiological feat of migration. Corticosterone plays important roles in migration, from preparation to in-flight energy mobilization to refueling, and corticosterone levels often show distinct elevations or depressions during certain stages of the migratory process. Here, we ask whether corticosterone's role in migration shapes its modulation during other life-history stages, as is the case with some other phenotypically flexible traits involved in migration. Specifically, we use a global dataset of corticosterone measures to test whether birds' migratory status (migrant versus resident) predicts corticosterone levels during breeding. Our results indicate that migratory status predicts neither baseline nor stress-induced corticosterone levels in breeding birds; despite corticosterone's role in migration, we find no evidence that migratory corticosterone phenotypes carry over to breeding. We encourage future studies to continue to explore corticosterone in migrants versus residents across the annual cycle. Additionally, future efforts should aim to disentangle the possible effects of environmental conditions and migratory status on corticosterone phenotypes; potentially fruitful avenues include focusing on regions where migrants and residents overlap during breeding. Overall, insights from work in this area could demonstrate whether migration shapes traits during other important life stages, identify tradeoffs or limitations associated with the migratory lifestyle, and ultimately shed light on the evolution of flexible traits and migration.

Introduction

Migration is a major physiological undertaking, and the phenotypes of migrants reflect the need for endurance (Weber 2009). In birds, which have been particularly well studied, migrants demonstrate a suite of flexible physiological phenotypes that help them to accomplish the difficult tasks involved in migration, such as fueling and then fasting during long flights and surviving in highly different environments (Piersma et al. 2005). Traits such as gut size, hematocrit, muscle size, and hormone levels (Piersma and Gill 1998; Piersma et al. 1999, 2000; Landys-Ciannelli et al. 2002; Krause et al. 2016; Eikenaar et al. 2020) are flexibly adjusted during different stages of migration. Migrants often demonstrate extreme elevations or depressions of certain trait values; for example, bar-tailed godwits (*Limosa lapponica*) migrating from Alaska to Oceania flew for 9 days straight with metabolic rates estimated to be 8–10 times above basal metabolic rate (Gill et al. 2009).

Most studies of the phenotypic traits that facilitate migration have concentrated on measuring traits immediately prior to and during migration; therefore, we have less of an understanding of when and how the phenotypes of migratory and non-migratory birds differ outside of migration season. The need to migrate could shape trait values during other important life stages: for example, traits elevated or depressed during migration could remain so into the breeding season, or could start

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to change at the end of breeding in preparation for migration.

The few studies that have explored flexible traits important to migration outside of the migratory season have typically found differences between migrants and residents. Migratory birds have been shown to differ from residents in fat storage patterns (Cornelius et al. 2021; but see Bergstrom et al. 2019), hematocrit levels (Krause et al. 2016), heart mass (Vágási et al. 2016), and metabolic rate (Wikelski et al. 2003; Jetz et al. 2008; Versteegh et al. 2012; however, this may be better explained by differences in the temperatures experienced by populations rather than migratory propensity, as noted in Wikelski et al. 2003; Jetz et al. 2008). Testosterone levels during breeding may also be at least partially explained by migratory status (Garamszegi et al. 2008).

Here, we explore whether glucocorticoids, hormones important for migration, show differences between migratory and resident populations during non-migratory times of year. Of the many hormones associated with migration (Ramenofsky 2011), glucocorticoids (predominantly corticosterone in birds) appear to play a particularly central role by promoting increased activity (Landys et al. 2006) and foraging, feeding, fattening, and energy use (reviewed in DeSimone et al. 2020; Bauer and Watts 2021). These latter roles are particularly important as birds undergo the alternating cycles of fuel accumulation prior to migratory departure and during stopover and energy mobilization during flight (DeSimone et al. 2020; Bauer and Watts 2021).

Corticosterone's role during migration

The process of migration involves a series of stages: preparation, departure, flight, and stopover. Baseline corticosterone levels (measured immediately upon capture) and stress-induced corticosterone levels (measured after an animal's exposure to an acute stressor) (Wingfield et al. 1998) often change across these stages. Corticosterone is hypothesized to mediate migration through many mechanisms during these migratory phases. A number of reviews (Ramenofsky 2011; Cornelius et al. 2013; DeSimone et al. 2020; Bauer and Watts 2021) provide excellent, detailed summaries of what is known regarding corticosterone's levels and actions at each of these stages.

Baseline corticosterone

During migratory preparation, as birds put on fat to fuel flight, most birds show elevated baseline corticosterone levels (Holberton et al. 1996, 2008; Holberton 1999; Piersma et al. 2000). These increases in corticosterone likely promote hyperphagia and lipogenesis (Holberton et al. 1996, 2007; Landys et al. 2004a), key processes to fuel up for long flights.

Corticosterone typically rises in the weeks leading up to departure from wintering grounds (Piersma et al. 2000) and stopover sites (Landys-Ciannelli et al. 2002). Corticosterone levels also peak during the evening in migrants known to depart at nighttime (Landys et al. 2004b); and, in the hours just prior to stopover departure (Eikenaar et al. 2020). These elevations may occur because moderately elevated baseline corticosterone levels promote the mobilization of lipids (the primary fuel for migration; reviewed in Jenni and Jenni-Eiermann 1998; Cornelius et al. 2013) via the release of fatty acids (Landys et al. 2004a, 2005, 2006). These elevations may also prime birds to cope with the unpredictable environmental and social circumstances that could await them during migration and breeding (Piersma et al. 2000; Cornelius et al. 2013).

During migratory flight, corticosterone typically continues to remain elevated. Birds sampled during night migration show baseline corticosterone levels that are elevated above levels of resting and foraging birds (Falsone et al. 2009). Similarly, in migrating bar-tailed godwits (*Limosa lapponica*), individuals captured just short of a major stopover site show higher baseline corticosterone levels than individuals captured at the stopover site during their refueling period (Landys-Ciannelli et al. 2002). However, baseline corticosterone may not always be substantially elevated during migratory flight (Gwinner et al. 1992; Jenni-Eiermann et al. 2009). Moderate corticosterone elevations likely continue to promote the catabolism of lipids for energy, as noted above. More substantial corticosterone elevations may promote the catabolism of proteins such as flight muscles; this likely happens when a bird has exhausted most of its fat stores (Gwinner et al. 1992; Jenni et al. 2000).

Stress-induced corticosterone

During migration, the levels of corticosterone secreted in response to challenges likely represent a tradeoff between the benefits of responding appropriately to acute stressors and the costs of very high corticosterone levels, which might lead to catabolism of flight muscles (Holberton et al. 1996; Ramenofsky 2011) or impede essential behaviors like fueling or flying (Ramenofsky et al. 1995; Falsone et al. 2009). Stress-induced corticosterone levels during migration show less predictable patterns than baseline levels, perhaps representing the complexity of these tradeoffs.

During migratory preparation, some species show a reduced stress response (Holberton 1999). However, when held in captivity under conditions to stimulate migratory behavior, birds show normal, unsuppressed corticosterone stress responses (Landys et al. 2004b).

During migratory flight, some migrants show an increase in corticosterone in response to capture (Landys-Ciannelli et al. 2002; Falsone et al. 2009), while others show a decrease (Jenni-Eiermann et al. 2009). In birds caught within a few hours after landing from a long migratory flight, individuals with robust fat stores mount a stress response, whereas birds with more minimal fat show no corticosterone elevation in response to stress (Jenni et al. 2000). However, European robins (*Erithacus rubecula*) with lower fat scores secrete higher corticosterone levels in response to stress during migratory flight (Falsone et al. 2009).

The corticosterone stress response during migratory stopover also shows varying patterns; some migrants show the typical elevation of corticosterone in response to capture stress (Landys-Ciannelli et al. 2002), while others show no elevation (Ramenofsky et al. 1995; Holberton et al. 1996), and still others show their highest stress response of the annual cycle (O'Reilly and Wingfield 2003). Long and Holberton (2004) found that, during stopover, lean birds elevated corticosterone less in response to the stress of capture compared to fatter birds.

Corticosterone in migrants and residents outside of migration

In contrast to the many studies that have explored how corticosterone levels change during migration, only a handful have compared corticosterone levels in migrants and residents outside of migration, and the results are variable. The migrant subspecies of white-crowned sparrows (*Zonotrichia leucophrys gambelii*) has substantially higher baseline and stress-induced corticosterone levels than the resident subspecies (*Z. l. nuttalli*) during the breeding season (Krause et al. 2021), whereas residents have substantially higher baseline and stress-induced corticosterone levels than migrants during the winter (Krause et al. 2014, 2021). This pattern could be explained by when subspecies face their greatest environmental challenges: migrants during breeding (when they have a short window to breed) and residents during winter (Krause et al. 2021). In captivity, however, when these resident and migrant white-crowned sparrow subspecies are kept in photoperiod conditions reflecting the transition from winter to spring, they show no differences in baseline or stress-induced corticosterone levels, suggesting that the observed differences in wild birds result from environmental conditions (Ramenofsky et al. 2017). Migrant subspecies of white-crowned sparrows and rufous-collared sparrows (*Zonotrichia capensis*) have higher baseline and stress-induced corticosterone levels than resident subspecies during the breeding season (Gonzalez-Gomez et al. 2023). Finally, in partially migratory Cory's shearwaters (*Calonectris borealis)*, corticosterone levels in feathers grown during the winter are higher in males that migrated than males that stayed close to the breeding colony. It is unclear if these results reflect differing environmental conditions during the winter, the costs of migration, or something else (Pérez et al. 2016). Thus, evidence so far is mixed, and shows that corticosterone levels may or may not differ in migrants versus residents across the annual cycle. Studies to this point have only focused on one or a few species at a time, and we lack a broad understanding of corticosterone levels in migrants and residents across taxonomic groups.

Could migratory status constrain corticosterone phenotype?

Broad-scale comparisons of corticosterone levels between many species of migrants and residents could help us to understand the evolution of both migration and of glucocorticoids. Corticosterone clearly plays an important role in migration, but do migratory birds show consistently different corticosterone levels than resident birds outside of migration?

If migratory status does constrain corticosterone phenotype during other life-history stages, this could occur through maintenance of corticosterone levels from the migratory period into other stages—for example, migration levels of corticosterone continuing into the breeding season (i.e., McGlothlin and Ketterson 2008). It could also result from migrants and residents having different physiological needs in the breeding period. For example, baseline corticosterone levels could remain elevated to promote foraging behavior and mass gain (Holberton et al. 1996, 2007; Landys et al. 2004a, 2006), helping birds to recover from migration. Elevated baseline corticosterone levels could also prime birds to cope with the unpredictable conditions on their breeding grounds (Piersma et al. 2000), which, for long distance migrants, are unknown to them until they arrive. Similarly, the maintenance of a robust stress response could help recently arrived birds to respond appropriately to acute challenges in a new environment (Falsone et al. 2009).

There are potential costs to these corticosterone phenotypes, however. Elevated baseline corticosterone levels during early breeding can be associated with lower fitness (Bonier et al. 2009), and high levels of stress-induced glucocorticoids typically suppress reproductive investment (Wingfield and Sapolsky 2003). In sum, there may be complex cost and benefit tradeoffs involved in the modulation of corticosterone phenotypes in migrants during breeding.

In this study, we seek to understand whether corticosterone levels during breeding covary with migratory status (which we define as undergoing an annual migration) in birds. We tested this question using data from HormoneBase, which includes glucocorticoid measures from wild adult vertebrates where males and females were measured separately (Vitousek et al. 2018). We focus exclusively on birds because their migration is exceptionally well-studied compared to other taxonomic groups, and information about the migratory status of most birds is readily available from databases such as Birds of the World (Billerman et al. 2022).

As a first step in exploring the relationship between migratory status and corticosterone, we compared corticosterone levels in migratory versus resident species during the breeding season. Many birds differentially regulate corticosterone during the breeding and nonbreeding seasons (Casagrande et al. 2018), and the vast majority of available data in HormoneBase come from breeding birds. Therefore, we chose to restrict our analyses to the breeding season.

We hypothesized that there would be no difference in baseline corticosterone or stress-induced corticosterone levels between migrants and residents during breeding (i.e., Ramenofsky et al. 2017). This might be the case given the flexibility of glucocorticoid levels across life-history stages (Romero 2002) and in response to challenges (Wingfield et al. 1998), and given the immense phenotypic flexibility of physiological traits in migrants. Despite seasonal elevations in baseline corticosterone and declines or increases in stress-induced corticosterone associated with migration, during breeding, these birds could return to levels akin to those of residents.

Alternatively, we hypothesized that migratory birds would have higher baseline corticosterone and higher stress-induced corticosterone than resident birds during breeding, matching some patterns observed during migration and reflecting findings in subspecies of white-crowned sparrows and rufous-collared sparrows (Krause et al. 2021; Gonzalez-Gomez et al. 2023). This might be the case if the corticosterone phenotypes of birds during migration carry over to the breeding period, or if migrants and residents have differing physiological needs.

Methods

Corticosterone and migration data

We downloaded data from HormoneBase, a database of vertebrate steroid hormone levels (Vitousek et al. 2018) that includes both baseline and stress-induced glucocorticoid measurements from adult individuals of known sex, to explore the relationship between birds' migratory status and their corticosterone levels. We filtered the dataset to just include populations that had corticosterone measurements during breeding (Breeding_Cycle = "Breeding").

We then researched each population in the resulting dataset to determine whether it migrated, choosing from the following options: migratory, resident, or unknown. Migration can be defined in many ways. Here we defined migration as seasonal movements to and from different geographic locations (Winkler et al. 2016). We did not consider dispersal or one-time movements to be migration. Additionally, we did not consider altitudinal migration to be true migration because all the clear instances of altitudinal migration in this dataset were shorter movements. For example, the i'iwi (*Drepanis coccinea*) is a known altitudinal migrant, however, even its longer measured movements are less than 20 km (Guillaumet et al. 2017), so we listed this species as resident. The one exception was a single population of dark-eyed juncos (*Junco hyemalis*), which made more substantial seasonal altitudinal migrations of about 72 km (Atwell et al. 2012). Because this population had some individuals that underwent this longer seasonal movement and others that did not, we classified this population as "unknown." Finally, if a bird population underwent irruptive or erratic movements, or if the species was listed as a partial migrant and there was no indication of what the specific population under study did, we listed its migratory status as "unknown."

To determine each population's migratory status, we started by consulting the Cornell Lab of Ornithology's Birds of the World database (Billerman et al. 2022). If we needed further information, we consulted the Cornell Lab of Ornithology's All About Birds database (www.allaboutbirds.org) for birds found in North America. We also consulted the original paper that reported the corticosterone values; often, the authors would identify whether the population was migratory. Finally, if necessary, we performed a literature review to find more information about the population. Any additional sources used beyond Birds of the World and the original paper are noted in the column "Additional_Sources_Migration" in the dataset.

Though some of the species in the dataset were clearly all migratory or all resident, in other species, populations differed in their migratory status. If we could not determine whether the specific population studied was migratory or resident, we classified it as "unknown." Likewise, if we could not find any information about whether a species migrated, we listed its status as "unknown."

Table 1 Sample sizes for each model.

Model	Number of species	Number of populations	Number of mean corticosterone measurements
Baseline corticosterone	119	202 112 migratory/90 resident	817 484 migrants/333 residents
Stress-induced corticosterone	86	136 80 migratory/56 resident	346 234 migrants/112 residents

Phylogenetic tree

We used a species-level phylogenetic tree that was constructed for the species included in HormoneBase, as previously described (Johnson et al. 2018; Vitousek et al. 2019). For birds, taxonomy was matched between the species in HormoneBase and Jetz et al. (2012). For each of our two analyses (baseline and stress-induced corticosterone), we created a final tree by dropping tips from that tree to match the species in the respective analysis.

Statistical analyses

We used the MCMCglmm package (Hadfield 2010) in R version 4.3.1 (R Core Team 2023) to build models investigating the relationship between migratory status and corticosterone levels. All models used a Gaussian distribution and specified relatively uninformative inverse gamma priors ($v = 1$, nu $= 0.002$). We ran models for 2,000,000 iterations with a burn-in of 50,000 and a thinning of 200.

We ran two separate models with baseline or stress-induced corticosterone as response variables. All corticosterone measures were natural log-transformed. In both models, migratory status and sex were fixed effects, and species, population identity, and lab identity were random effects, following Vitousek et al. (2019). Species (the matrix of phylogenetic relatedness) was included to account for the shared evolutionary history among species in the analyses. Population identity was used as a random effect to account for multiple records from the same populations. Finally, lab identity was used as a random effect to account for variation in corticosterone levels that occur based on the laboratory where assays were performed (Fanson et al. 2017).

We visually inspected all trace plots to confirm that the chains had converged. We also checked autocorrelation values, which were all < 0.05. To confirm stability of results, we ran each model three times. We also reran each model with highly informative priors ($v = 1$, nu $= 1$) to confirm that prior specification did not affect results.

Results

After filtering just to data from breeding birds, our dataset contained 149 species, with 756 measures of mean corticosterone levels in bird populations. Of these, 373 were from migrant populations, 266 from residents, and 117 from populations of unknown migratory status. For all further analyses, we removed populations classified as unknown, which left 120 species total in the dataset. Table 1 shows the specific sample sizes for the two models run, including breakdowns of migratory versus resident sample sizes. Populations in this study were distributed around the globe, with sampling on every continent (Fig. 1).

Migratory status did not predict baseline corticosterone or stress-induced corticosterone during the breeding season (Table 2). Sex predicted both baseline and stress-induced corticosterone, with males having higher baseline and stress-induced corticosterone levels than females (Table 2). All models showed evidence of a strong phylogenetic signature (Pagel's λ: baseline corticosterone $= 0.779$, stress-induced corticosterone $= 0.806$).

Discussion

We found no evidence that migratory and resident birds differ in baseline or stress-induced corticosterone levels during the breeding season. This aligns with the findings of Ramenofsky et al. (2017) in captive white-crowned sparrows. It also matches one of our sets of hypotheses that baseline and stress-induced corticosterone would not differ between migrants and residents. Both baseline and stress-induced corticosterone are highly flexible traits that are modulated in response to predictable changes in life-history stage or season (Romero 2002; Romero et al. 2017) and to within-season changes in context (Breuner and Hahn 2003; Lendvai et al. 2007). Our results suggest that, on a broad scale, migration likely does not constrain flexible modulation of corticosterone during breeding. Instead, breeding season corticosterone values are likely driven by breeding season conditions alone.

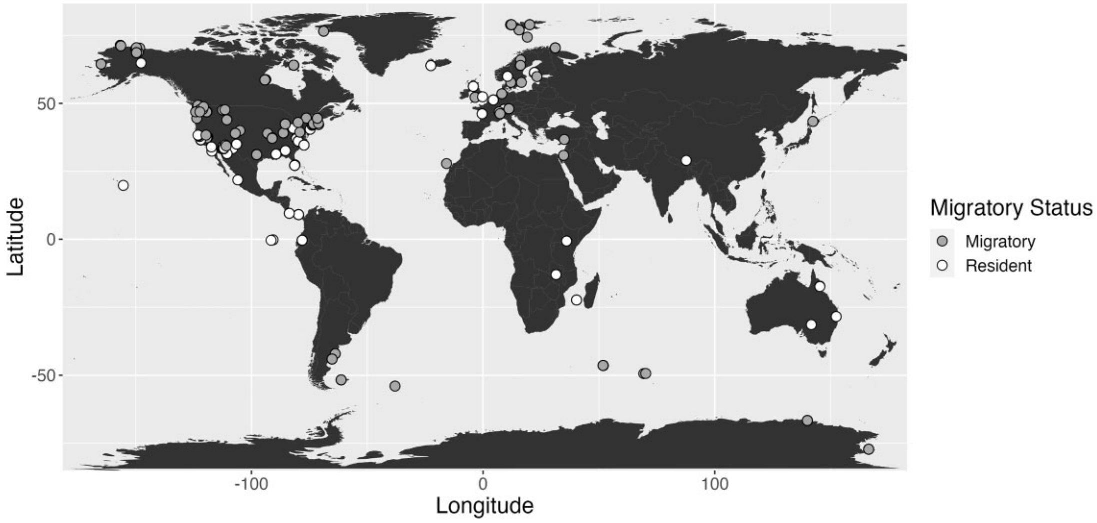

Fig. 1 Sampling locations around the globe. Each point represents one population of birds that was sampled.

Table 2 Model outputs for baseline corticosterone and stress-induced corticosterone models. All models included species, population identity, and lab identity as random effects.

Model	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	*p* MCMC
Baseline corticosterone					
Intercept	2.174	1.332	2.980	9750	< 0.0001
Migratory status (Resident)	-0.066	-0.348	0.212	9408	0.645
Sex (Male)	**0.092**	**0.014**	**0.176**	**9418**	**0.027**
Stress-induced corticosterone					
Intercept	3.690	3.048	4.368	9750	< 0.0001
Migratory status (Resident)	0.032	-0.206	0.273	9750	0.789
Sex (Male)	**0.135**	**0.047**	**0.222**	**8832**	**0.002**

Fixed effects are bolded if the 95% confidence interval (CI) of the mean does not cross zero.

Previous studies in white-crowned sparrows and rufous-collared sparrows (Krause et al. 2021; Gonzalez-Gomez et al. 2023) have found that baseline and stress-induced corticosterone levels are higher in migrants than in residents during breeding. However, these differences may result from environmental conditions at breeding sites rather than migratory status (as has been suggested to explain differences in metabolic rate between migrants and residents; see Wikelski et al. 2003; Jetz et al. 2008). Another possible explanation is that migrant sparrows could show strong carry over of migratory corticosterone phenotypes into the breeding season, or could have different physiological needs during breeding, while most other species do not.

Of the studies that have compared flexible traits other than corticosterone between migrants and residents outside of the migration season, most have found differences between migrants and residents (Wikelski et al. 2003; Garamszegi et al. 2008; Jetz et al. 2008; Versteegh et al. 2012; Krause et al. 2016; Vágási et al. 2016; Cornelius et al. 2021; but see Bergstrom et al. 2019); however, note that some of these differences may be better explained by differences in temperatures between populations rather than by migratory propensity (Wikelski et al. 2003; Jetz et al. 2008). Ours is one of the rare studies to find no differences between the phenotypes of migrants and residents during breeding. However, it is also possible that these types of explorations suffer from positive publication bias (Smart 1964; Thornton and Lee 2000; Fanelli 2012). Furthermore, many of these studies are limited to comparisons between individuals of the same species, or a few closely related species (but see Garamszegi et al. 2008; Jetz et al. 2008; Vágási et al. 2016). Thus, though there are sometimes differences between migrants and residents when comparing subspecies or a few species, our results show that there are no consistent patterns detectable across many species.

Despite the clear negative results in our analyses, it is still possible that further explorations that focus on specific stages of breeding, or that focus on the entire annual cycle, could uncover consistent relationships between migratory status and corticosterone. In this study, we chose to use corticosterone measurements from the entire span of the breeding period, as opposed to limiting our analyses to measurements taken during specific stages of breeding such as courtship, nest building, incubation, and provisioning. We chose to lump all breeding measures together to keep our sample size large enough for meaningful analyses; however, corticosterone levels can vary within the breeding season (Landys et al. 2010; DuRant et al. 2013). If a relationship does exist between migratory status and corticosterone during the breeding season, it is possible that it was obscured by variation in corticosterone levels during different stages of breeding. Future studies could focus on early breeding, just after the completion of migration; this stage likely has the highest probability of demonstrating "carry over" migratory phenotypes.

Additionally, our study focused on just a single part of the annual cycle. HormoneBase did not have enough measurements from both migratory and resident birds during different parts of their annual cycle to explore corticosterone levels at other times of the year beyond breeding. However, breeding is just one snapshot of what birds experience, and what corticosterone levels they display, over a year. Future studies should compare corticosterone levels in both migrants and residents across the annual cycle.

We were unable to include latitude as a covariate in our analyses due to its tight relationship with migratory status in our dataset (Fig. 1). However, latitude may be an important piece of the puzzle in understanding the relationship between corticosterone levels and migratory status. Baseline corticosterone is lower in species with longer breeding seasons (Hau et al. 2010) and stress-induced corticosterone is higher in birds breeding at higher latitudes (Bókony et al. 2009; Jessop et al. 2013). Future work could compare corticosterone phenotypes in migrant and resident populations breeding at similar latitudes; this would eliminate the possible confounding effect of latitude on corticosterone and allow direct comparisons between migrant and resident individuals who experience comparable conditions during breeding.

In the future, targeted studies of closely phylogenetically related migrants versus residents during both their breeding seasons and wintering seasons, and during the spring and fall when migration occurs in some populations, could provide insight into how corticosterone levels change over the annual cycle, and whether the type and magnitude of changes differ by migratory status. Related to this, studies of partial migrants (species where some individuals migrate and others do not) over the annual cycle could prove especially incisive. In partial migrants, baseline corticosterone levels are often higher in migrant versus resident individuals when they are sampled just before or during migration (Nilsson and Sandell 2009; Fudickar et al. 2013; see Eikenaar et al. 2015, for differences between spring and fall migration). Further information about corticosterone levels across the annual cycle from migrant versus resident individuals within the same partially migratory species may illuminate patterns in corticosterone secretion that could affect behavior throughout the year.

We found that males had higher baseline and stress-induced corticosterone levels than females, a pattern has also been found in another study using HormoneBase bird data (Casagrande et al. 2018).

Corticosterone studies on non-breeding birds are uncommon. Of all the bird records in HormoneBase, 80% are from the breeding season and only 16% can be identified to the non-breeding season (the remaining records cannot be ascribed to a specific time in the annual cycle). With incomplete knowledge of how corticosterone varies over the annual cycle, our conclusions about whether migratory status covaries with corticosterone levels across life-history stages is limited, and future studies should focus on measuring corticosterone levels outside of just the breeding season.

Additionally, though our dataset had hundreds of entries and spanned all seven continents, certain taxonomic groups and regions were severely under-sampled compared to others. The vast majority of birds in our dataset are passerines, and more even sampling across all bird orders would allow us to draw more comprehensive conclusions about whether corticosterone varies between migrants and residents. Furthermore, as is often the case in ecological studies (Martin et al. 2012), North America and western Europe are very well represented in this dataset, while Asia, South America, Africa, and Australia have poor representation. More broadly, migration in the Southern Hemisphere ("austral migration") is greatly understudied compared to migration in the Northern Hemisphere (Dingle 2008; Winkler et al. 2016). Our dataset is too small to divide migrants into neotropical and palearctic (Northern Hemisphere) and austral migrants. In the future, comparisons of corticosterone levels in neotropical and palearctic versus austral migrants could explore whether there are physiological differences between these two types of migration, and whether physiological differences present throughout the annual cycle.

Flexible traits that enable the astounding physiological feat of migration have long been studied during the migratory time of birds' annual cycles. However, these traits are rarely studied during non-migratory times of year in a comparative framework that allows us to identify whether there are consistent differences in trait expression between migrants and residents. Studying these patterns can shed light on the tradeoffs and limitations associated with the migratory lifestyle. Future work should continue to tackle questions surrounding year-round expression of flexible traits associated with migration. Ultimately, this could lend exciting new insights into the evolution of both migration and the traits that enable migration, and illuminate whether migration affects the expression of flexible traits during other important life stages.

Author contributions

Conceptualization: J.J.U., E.R., and M.N.V. Data collection (identifying migratory status of birds in HormoneBase): J.J.U. and E.R. Data analyses and Fig.: J.J.U. Writing: J.J.U. Review/editing: J.J.U., E.R., and M.N.V.

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Conflict of interest

The authors have no conflicts of interest to declare.

Data availability

The HormoneBase dataset is publicly available at https://hormonebase.org/database/. All additional data, code, and files associated with this paper are publicly available at: https://github.com/juehling/HormoneBase_Migration_data_analyses.

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