

Short communication

Corticosterone regulation in house sparrows invading Senegal

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ABSTRACT

What traits help organisms expand their ranges? Several behavioral and life history traits have been identified, but physiological and especially endocrinological factors have been minimally considered. Here, we asked whether steroid hormonal responses to stressors might be important. Previously, we found that corticosterone (CORT) responses to a standard restraint stressor were stronger at a range edge than at the core of the recent house sparrow (*Passer domesticus*) invasion of Kenya. In related work in the same system, we found that various behaviors (exploratory activity, responses to novelty, etc.) that are affected by CORT in other systems varied among sparrow populations in a manner that would suggest that CORT regulation directly influenced colonization success; birds at the range edge were less averse to novelty and more exploratory than birds from the core. Here, we asked whether the pattern in CORT regulation we observed in Kenya was also detectable in the more recent (~1970) and independent invasion of Senegal. We found, as in Kenya, that Senegalese range-edge birds mounted stronger CORT responses to restraint than core birds. We also found lower baseline CORT in range-edge than core Senegalese birds, but little evidence for effects of individual sex, body mass or body size on CORT. Follow-up work will be necessary to resolve whether CORT regulation in Senegal (and Kenya) actively facilitated colonization success, but our work implicates glucocorticoids as a mediator of range expansion success, making stress responses potentially useful biomarkers of invasion risk.

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1. Introduction

Many traits facilitate the expansion of the ranges of species (Jeschke and Strayer, 2006; Sol et al., 2012). At the level of individuals, though, and especially in terms of physiology (Martin et al., 2016), factors that directly impact success remain obscure (Brown et al., 2015; Duckworth and Badyaev, 2007). In part, this is because most work on range shifts so far has involved dispersal and natural range expansions (Chapple et al., 2012; Martin and Fitzgerald, 2005). Non-native and introduced species provide a natural experiment in how organisms expand their range in novel environments. Insight into factors facilitating invasion is important because invasive species cause billions of dollars annually in damage to native communities (Simberloff et al., 2013), and are a growing threat as human commerce continues to increase globally (Dukes and Mooney, 1999). One trait that might be influential to range expansions, natural or anthropogenically-aided, is the regulation of glucocorticoid hormones (Addis et al., 2011; Atwell et al., 2014, 2012; Graham et al., 2012; Liebl and Martin, 2012). Glucocorticoids, such as corticosterone (CORT, the dominant avian glu-

cocorticoid), affect how individuals i) behaviorally respond to novelty, ii) explore environments, iii) learn from experience, and iv) respond to natural enemies (Clinchy et al., 2013; Korte et al., 2005; Martin, 2009) among other traits. 'Baseline' (BL) CORT (i.e., levels circulating in the absence of stressors) mediates many of these effects, but CORT responses to acute stressors are oftentimes the drivers of organismal performance (Lailvaux and Husak, 2014).

Recently, CORT responses to short-term restraint were found to be related to the distribution of the house sparrow (*Passer domesticus*) in Kenya (Liebl and Martin, 2012; Martin and Liebl, 2014). House sparrows arrived to Mombasa, Kenya, around 1950 and have since spread northwestward towards Uganda (Lewis and Pomeroy, 1989). We found that birds captured at the Kenyan range-edge released more CORT to restraint than birds from the core (Liebl and Martin, 2012). Given the spatial scale of that work (>800 km separating populations) and the lack of strong influences of other factors on CORT (i.e., climate, elevation, etc.) in that study, we proposed that CORT regulation actively facilitated the range expansion of the species in Kenya by mediating particular behaviors in different sites (Canestrelli et al., 2016). In other work in that system, we found that range-edge sparrows were more exploratory (of a novel habitat) and less averse to novel foods (but not different in their responses to novel objects) (Liebl and Martin, 2012, 2014b). In

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other animal species, CORT also mediates such behavioral variation (Carere et al., 2010), but as yet, it remains unknown whether behaviors and CORT are causally related in house sparrows. Moreover, in Kenya, the species has been unable to colonize the entire country, tending to occupy only those regions with high human population density. Subsequently, in Kenya, we were unable to identify independent, replicate invasions (Schrey et al., 2014), which would have allowed us to determine whether CORT is central to range expansion success. To determine the generality of CORT as a mediator of range expansions, we investigated CORT regulation in a distinct yet also ongoing range expansion.

Here, we describe our efforts to determine whether CORT regulation might have influenced the range expansion of house sparrows in Senegal. The Senegal invasion is also recent and from South African stock (Anderson, 2006) with birds being introduced to Dakar around 1970 (Lever, 1989), probably from a ship. Records indicate subsequent spreading of the species northward along the coast to Saint Louis and then into the interior along the Senegal River, as far east as Podor (Summers-Smith, 2010), a city ~80 km east of Richard Toll (Fig. 1). One other published account (Sauvage and Rodwell, 1998) found that much of middle area of Senegal was unoccupied by house sparrows until at least 1994, again supporting one or few introductions to Dakar or points east and subsequent spread eastward across the country. The most recent avian field guide for Senegal (Borrow and Demey, 2013) partly corroborates this scenario, as birds now occupy most of coastal western Senegal but penetrate eastward only to the middle of the country (Fig. 1). Finally, perhaps the world's greatest

house sparrow enthusiast, Denis Summers-Smith, recounted in his book, *The Sparrows* (Summers-Smith, 1988), and his autobiography, *In Search of Sparrows* (Summers-Smith, 2010), the same pattern of introduction and range expansion to Senegal: introduction to Dakar followed by spread northeastward to Saint Louis, Richard Toll, Podor, and locales farther east. He and others also make no claims that sparrows were introduced elsewhere to Senegal than Dakar, nor is there evidence of overland invasions from Mauritania, Guinea-Biassau or Mali.

The first eBird reports of house sparrows in Saint Louis and Richard Toll were in 2007; eBird is a global repository of bird sightings made by the general public. Although eBird is questionable as a definitive resource to recreate the Senegal invasion history, it gave us a starting point for probing how corticosterone regulation might have influenced the expansion of house sparrows in Senegal. Altogether, we suspect that Saint Louis and Richard Toll are more recently invaded than Dakar; it is as yet unclear how much the first two differ in age although Saint Louis is probably older because it is nearer to Dakar and larger than Richard Toll (Table 1). This latter condition might have facilitated invasion because house sparrows routinely exploit human food resources, meaning that they are more likely to have been accidentally transported to Saint Louis on the back of large trucks transporting grains for human consumption. This mode of dispersal seems to have been important in the colonization of Kenya by house sparrows (Schrey et al., 2014).

As in Kenya, we expected that birds at the range-edge (Richard Toll and/or Saint Louis) would have stronger CORT responses to

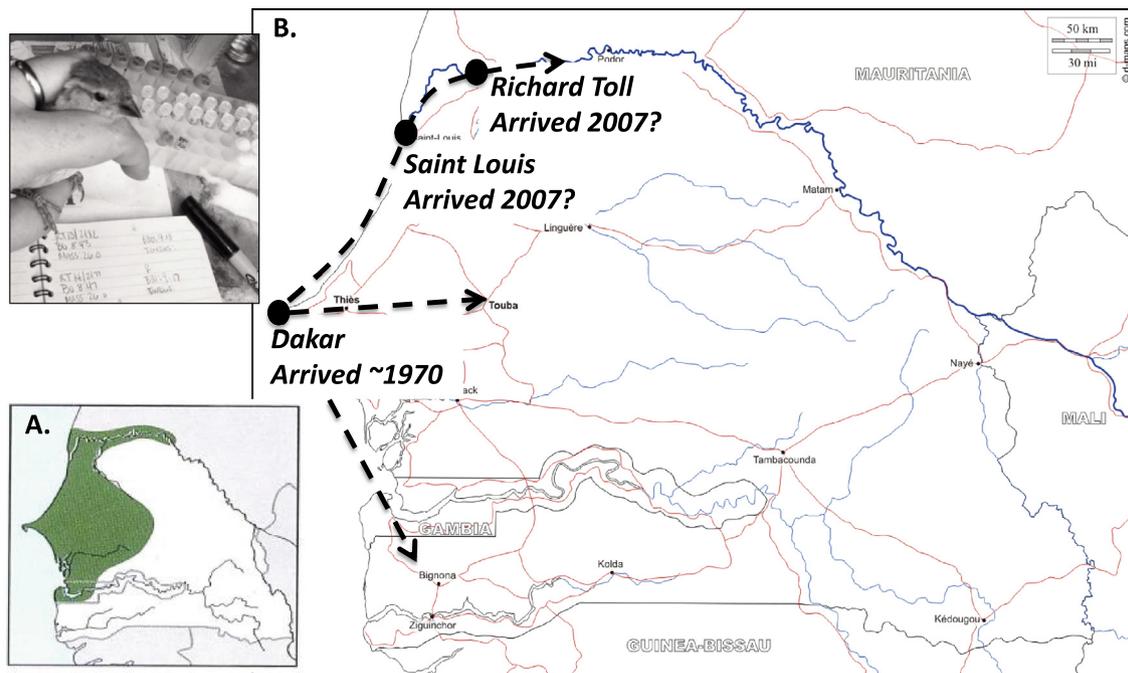


Table 1. Characteristics of capture sites in Senegal

	Date of first record	Distance from Dakar (km)	Altitude (m)	Annual mean temperature (°C)	Annual mean precipitation (mm)	Human population size (in 2005)
Dakar	1971	0	22	24.3	412.9	1,998,635
Saint Louis	??	179	2	26.0	261.3	130,750
Richard Toll	??	271	7	27.6	225.0	60,531

Fig. 1. Maps of Senegal and key details about cities from which house sparrows in this study were captured. A. Current house sparrow distribution in Senegal taken from Birds of Senegal and The Gambia, reprinted with permission. B. Physical map of Senegal denoting three capture cities (filled symbols) as well as roads (red lines) and rivers (blue lines). URL for map (http://d-maps.com/carte.php?num_car=r25265&lang=en). Table 1. Key information about cities from which sparrows were captured.

restraint than birds from the core population (Dakar). We had no predictions about baseline CORT, as we previously saw no pattern for baseline CORT in Kenya. As other studies have shown other factors to influence CORT regulation, we also assessed potential effects of sex and body mass, body size (i.e., tarsus length), and body condition (Romero and Wingfield, 2015) on CORT. Other traits, such as population density, climate, urbanization, and individual age and experience, and genetic factors were beyond the scope of this exploratory study, although we attempted to account for some of them by measuring CORT in adult birds captured from similar habitats in each city. We also provide key details about each city in Table 1 (Fig. 1), some of which plausibly also influence(d) CORT regulation.

2. Methods

2.1. Field work

We captured wild, adult (based on plumage and other morphological traits) birds ($n = 50$; Dakar = 21 (6 males (M), 15 females (F)), St. Louis = 13 (6 M, 7F), Richard Toll = 16 (6 M, 10F)) in December 2015 in the first few hours of the morning (0700–1030). Blood (25 μ L) was always collected from the brachial vein within 3 min of capture using a 26-gauge needle, at which time sex was also recorded for each individual. Birds were then held in cloth bags for 30 min before another blood sample (25 μ L) was taken (Liebl and Martin, 2012). We did not have the personnel to record exact bleeding times, monitor nets and extract birds, and collect blood samples from fresh capture and restrained birds; hence, data about individual bleed time were unavailable for incorporation in analysis. Blood was centrifuged immediately after collection, and plasma was removed and placed in liquid nitrogen until it was returned to the USA and stored at -40°C . After the first blood sample collection, body mass was measured with a spring-scale (to 0.1 g) and tarsus length was measured with calipers (to 1 mm); all measurements were made by the same individual to minimize measurement error. Sample export to the US was supported by USDA-APHIS permit #105345, and all procedures were approved in advance by the USF IACUC (#IS0000636) and the Senegalese Ministère de L'Environnement et du Développement Durable (#02541).

2.2. Corticosterone assay methods

We used an EIA kit (Arbor Assays, K014-H5) to measure total plasma CORT. Prior to measuring samples, we found adequate performance of this assay on house sparrow plasma when comparing other house sparrow plasma samples spiked with exogenous CORT to standard curves generate using kit reagents. Curves for spiked samples and standards were parallel across the measured range, and values obtained from this kit resembled values obtained from a similar EIA kit (Enzo Life Sciences, Ann Arbor, #900-097). Briefly, for the Arbor Assays kit, steroid displacement reagent (5 μ L) was added to 5 μ L of house sparrow plasma and allowed to incubate for 5 min. Then, 240 μ L of assay buffer was added to each sample, vortexed, and aliquoted in duplicate (100 μ L per well) to a plate. Standard curves (ranging from 200,000 to 32 pg) were also measured in duplicate on each plate, then samples and standards were incubated according to manufacturer's instructions with conjugated CORT and antibody while being shaken. Wells were then washed three times before substrate was added to all wells. Finally, plates were incubated again for 1 h at room temperature without shaking, and stop solution was eventually added to wells and plates read at 405 nm. Intra-assay variation was 4.2%; inter-assay variation was 15.0%. All samples were randomly assigned to and measured on one of 6 plates. Some assay conditions (i.e., sample

volumes and standard concentrations) differ from manufacturer's instructions because we found our conditions to be more appropriate for this study species.

2.3. Data analysis

Before analyses, all CORT data were \log_{10} transformed, which eliminated non-normality, then we tested the effects of several factors on CORT, considering sites to be of different age relative to their distance from Dakar (Liebl and Martin, 2012). Our approach was similar to our Kenyan study except that here we treated capture site as an ordinal variable because only three cities were available for comparison. We used a mixed-effects model with sex, city, and time (pre- and post-restraint) and two- and three-way interactions as predictors and body mass, tarsus length, and body condition as covariates (Dingemans and Dochtermann, 2012). We also included individual bird as a random effect (intercept) to account for repeated-measures (Martin and Liebl, 2014). We did not include random slopes for individuals in models, as we lacked the samples sizes necessary to do so (Martin et al., 2011). Given the similar arrival dates of birds to St. Louis and Richard Toll (Sullivan et al., 2009), we followed up this analysis with a second model that treated capture site as a binary predictor: core versus edge. We used SPSS v23 for all analyses and GraphPad Prism v6.0 for figures.

3. Results

3.1. Body morphometrics

Mean body mass of Senegalese sparrows was 23.7 g (males: 23.5 g \pm 1.9 (SD; $n = 17$); females (23.8 g \pm 1.7 (SD; $n = 31$)), but mass was not affected by capture site ($F_{1, 47} = 0.48$, $P = 0.49$) or sex ($F_{1, 47} = 0.32$, $P = 0.57$). Tarsus length averaged 21.1 mm (males: 20.9 mm \pm 1.3 (SD; $n = 17$); females (21.2 mm \pm 0.6 (SD; $n = 30$)), but it was also unaffected by capture site ($F_{1, 46} = 1.18$, $P = 0.28$) or sex ($F_{1, 46} = 1.5$, $P = 0.23$). Body condition differed among sites ($F_{1, 46} = 3.7$, $P = 0.03$) but not between sexes ($F_{1, 46} = 1.2$, $P = 0.19$), with birds from Dakar being in lower body condition than birds from the other two sites (means \pm SD, Dakar: -0.37 ± 1.05 ; Saint Louis: 0.22 ± 0.74 ; Richard Toll: 0.31 ± 0.95).

3.2. Corticosterone regulation

Only two factors predicted variation in CORT: restraint ($F_{1, 41} = 86.3$, $P < 0.001$) and the restraint \times capture site interaction ($F_{2, 39} = 3.9$, $P = 0.03$; Fig. 2A–C). Baseline CORT concentrations were typically lower than post-restraint values ($t_{41} = -8.5$, $P < 0.001$), and CORT responses differed among sites such that birds from Richard Toll had larger responses than both Saint Louis ($t_{41} = 2.6$, $P = 0.01$) and Dakar ($t_{41} = 4.4$, $P < 0.001$; Fig. 2D). Site ($F_{2, 39} = 1.7$, $P = 0.2$) and sex alone ($F_{1, 39} = 0.2$, $P = 0.70$) and the sex \times time ($F_{1, 41} = 1.3$, $P = 0.30$) and sex \times site ($F_{2, 39} = 0.9$, $P = 0.40$) interactions were not significant. The three-way interaction was marginally non-significant (site \times time \times sex: $F_{2, 41} = 3.0$, $P = 0.06$), but neither body mass ($F_{1, 39} = 0.0$, $P = 1.0$) nor tarsus length ($F_{1, 39} = 0.2$, $P = 0.65$) impacted CORT. Individual identity, treated as a random effect, was not a significant source of variance (Wald $z = 0.3$, $P = 0.76$). As body condition also differed among sites, we constructed another model replacing body mass and tarsus length with body condition as the sole covariate. This model revealed no effects of individual body condition on CORT ($F_{1, 40} = 0.002$, $P = 0.97$); otherwise, model results were consistent with the above model with body mass and tarsus length. We thus did not consider impacts of body condition further.

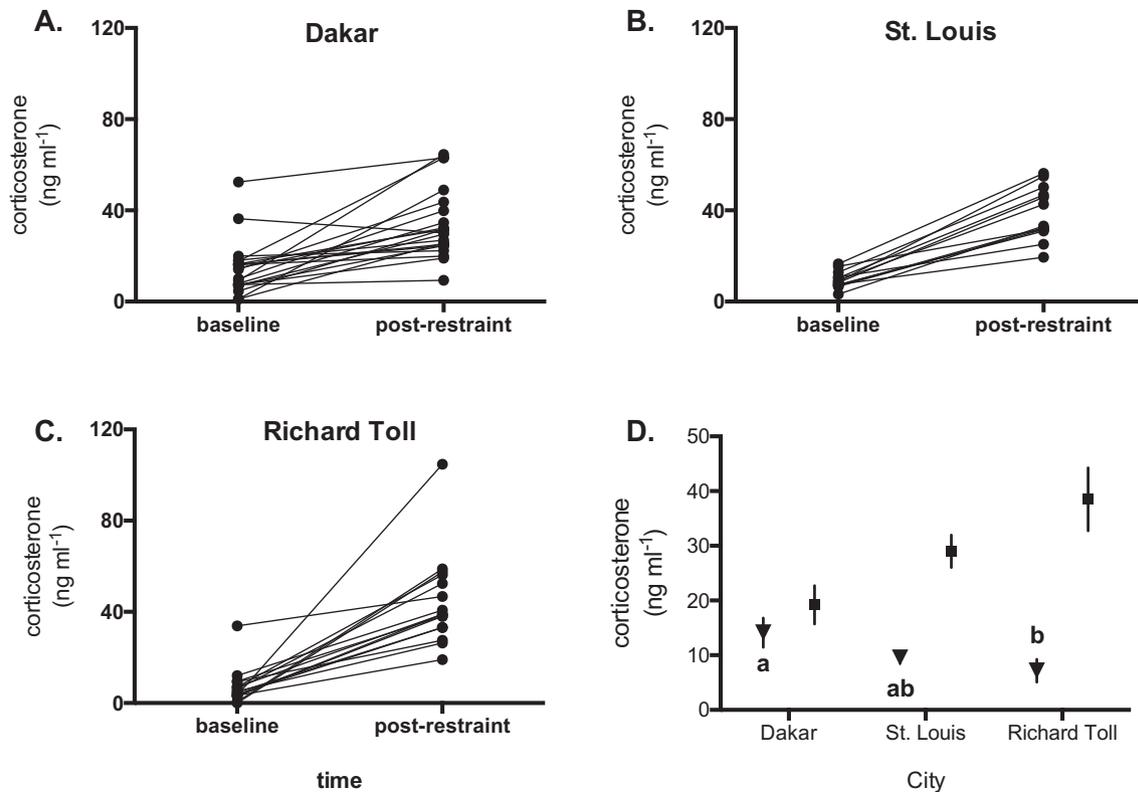


Fig. 2. Corticosterone concentrations in Senegalese house sparrows; lines represent values from individual birds. A. Dakar (colonized ~1970); B. Saint Louis (first sighting 2007); C. Richard Toll (first sighting 2007). D. Population means and variation ($\pm 1SE$); triangles denote baseline values and squares denote post-restraint (30 min) values, and letters denote group membership by Bonferroni comparisons.

In light of the significant restraint \times site interaction, we queried whether a GLM with only site as a factor could predict BL CORT. BL CORT differed among sites ($F_{2,49} = 4.3$, $P = 0.02$), and simultaneous Bonferroni post hoc tests revealed that differences between the oldest site Dakar and the site farthest from Dakar, Richard Toll, drove this effect; the intermediate site Saint Louis was indistinguishable from the other sites (Fig. 2D). Also, as it is unclear whether Richard Toll and Saint Louis are different ages (Sullivan et al., 2009), we conducted a second mixed model analysis with capture site as a binary variable (Dakar vs. the two younger cities); the model structure was otherwise similar to the initial one. Results of this simpler model were similar to the one above for three cities: only restraint ($F_{1,41} = 69.4$, $P < 0.001$) and the site \times sex \times restraint interaction ($F_{1,41} = 4.1$, $P = 0.05$) were significant predictors of CORT; the site \times restraint was marginally non-significant ($F_{1,41} = 3.2$, $P = 0.08$). Birds from the range-edge tended to release more CORT in response to restraint than birds from the core, but this pattern was stronger for females than males. Neither restraint \times sex ($F_{1,41} = 0.42$, $P = 0.52$) or site \times sex ($F_{1,39} = 1.9$, $P = 0.17$) interactions were significant. Likewise, main effects of sex ($F_{1,39} = 0.15$, $P = 0.70$) and site ($F_{1,39} = 0.10$, $P = 0.76$) and body mass ($F_{1,39} = 0.22$, $P = 0.64$) and tarsus length ($F_{1,39} = 0.37$, $P = 0.55$) as covariates were not significant predictors of CORT. Individual identity was also not a significant predictor of CORT variation (Wald $z = 0.16$, $P = 0.87$).

4. Discussion

We found additional support that variation in CORT regulation is directly related to range expansion in house sparrows. As before in Kenya (Liebl and Martin, 2012), individual house sparrows at the presumed Senegal range-edge tended to release more CORT during

a restraint stressor than birds from the core of the range. Due to the comparative nature of this project and the few sites studied, we cannot claim that CORT caused success of individuals in new areas. Indeed, the marginally non-significant three-way interaction involving sex raises the possibility of sex-specific effects of CORT on the success of house sparrow range expansions. There was little evidence for sex-specific roles of CORT in the Kenya invasion though, which is why we did not attempt to account for sex of birds more rigorously during our capture sessions. So, even though more work is needed about the possible role of sex-specific effects of CORT in sparrow invasions, it is compelling to have observed a similar pattern in CORT regulation in Senegal and Kenya given their independence (Anderson, 2006). Our longer term work in Kenya suggests that CORT regulatory variation is at least partly related to differences in the value of particular behaviors, specifically exploratory disposition (Liebl and Martin, 2012) and response to novelty (Liebl and Martin, 2014a), among old and new sites. Other work suggests that CORT regulation might also affect how sparrows interact with parasites too (Coon et al., 2014; Coon and Martin, 2014; Martin et al., 2014, 2015). The next step (in both invasions) is to link CORT and other aspects of individual phenotypes directly, and determine whether such integration (and its concomitant effects on fitness (Bonier et al., 2009; Breuner et al., 2008) explains the geographic patterns across the two range expansions (Wada, 2008).

One of the most intriguing issues we hope to resolve in the future is whether the particular stress responses observed in Senegal (and Kenya) are induced (i.e., arise via phenotypic plasticity) or naturally-selected based on factors unique to familiar and unknown areas. The type and density of natural predators, availability of nutritious and readily-available food, shelter resources, commonness of inter- and intra-specific competitors, and the

threat of infection might differ among sites, and any one of these factors could affect CORT regulation (Liebl et al., 2013; Schrey et al., 2014). Indeed, two factors, none of which have anything to do with population age, differ among the three cities: aridity and urbanization. Both aridity (Deviche et al., 2016; Sorensen et al., 2016) and urbanization (Bonier, 2012; Fokidis et al., 2009) influence CORT regulation in passerines, and although only one (urbanization, assuming human population density is a good surrogate; Table 1) differs substantially among sites, both warrant future consideration. In regards to plasticity versus selection though, we expect that plasticity in response to one or more of the above factors underlies the patterns we have observed. In Kenya, we found that core birds could converge on a similar CORT regulatory profile as range-edge birds if kept under standard conditions for a week (Martin and Liebl, 2014). Follow-up work on such plasticity (flexibility) is thus also warranted in Senegal (Baugh et al., 2014; Hau and Goymann, 2015; Taff and Vitousek, 2016).

A final intriguing observation to highlight is that the effects of population age on stressor-induced CORT are similar in Kenya and Senegal even though the Kenyan invasion is ~20 years older. The persistence of variation in both countries suggests that one or both range expansions are ongoing, which is plausible given that Kenyan house sparrows remain uncommon in Kisumu, the third largest city in Kenya (by human population). House sparrows, which are strong human commensals, should thus be common in Kisumu if they had enough time to establish. In Senegal, predominantly, we only had records from the eBird database to estimate population ages of individual cities (Sullivan et al., 2009). As eBird is comprised of data coming from motivated ornithologists, it is not ideal for determining population age; many sightings probably go unreported, and reports from large cities are probably more common than those from small cities simply because of the greater number of avian enthusiasts in the former. For these reasons (and for consistency with our approach in Kenya), we used distance from Dakar as a proxy for population age. However, even when we conservatively treat Dakar as core and the two other sites as range-edge, we see that CORT responses to stressors are larger in birds from the newer sites.

In the future, it will be important to elucidate directly whether and how CORT affects range expansions. Differences in the timing of life history stages among sites warrant particular consideration for this initiative (Romero, 2002). To account for any potential confounds of life history stage, we collected all blood samples in a narrow time frame, but we do not yet have breeding phenology data for Senegalese sparrows to know that populations were synchronous. Populations might schedule their lives differently in each city; near the equator, the timing of breeding is more mediated by rainfall (Nhlane, 2000) than photoperiod, which is the dominant driver at northern latitudes (Anderson, 1994). Rainfall timing and abundance can vary quite dramatically over small spatial scales, so at the levels of population, individuals, or both, vagaries in the timing of life events mediated by rainfall might further impact CORT regulation in Senegal and hence the effects of CORT on dispersal or success at new or core sites. In Kenya, we were able to detect a geographic pattern in CORT regulation only in the breeding season (Liebl and Martin, 2012); when birds were molting, population age was unrelated to CORT responses to restraint. CORT responses to stressors are often (Romero, 2002), but not always (Deviche et al., 2016), damped in birds during molt. In Senegal, local variation in life-history staging could thus affect how CORT is regulated and thus what it means for range expansions.

Another important line of future work is to determine whether other aspects of the hypothalamic-pituitary-adrenal axis differ among birds and sites. Indeed, we do not yet know whether hippocampal glucocorticoid receptor (GR) expression (a major site of

negative feedback on CORT release) or other aspects of CORT regulation (e.g., binding globulins, hepatic 11-beta hydroxysteroid dehydrogenase levels, etc.) vary among sites in Senegal. In Kenya, hippocampal GR expression, relative to mineralocorticoid receptor (MR) expression, was higher in younger populations (Liebl and Martin, 2013); this pattern might enable more rapid negative feedback in those range-edge birds, offsetting the damaging effects of persistently elevated CORT. In Senegal, we expect similar GR (and MR) patterns to Kenya, but we have yet to test this possibility. It will also be interesting to investigate more the differences in baseline CORT in Senegal sites we revealed. As we had no *a priori* expectations for this pattern, we are reticent to interpret it here. Nevertheless, it warrants future attention given the diverse roles of baseline glucocorticoids (Romero, 2004) and their impacts on individual fitness (Bonier et al., 2009; Ouyang et al., 2013). The regulation of other hormones, too, might be influential to range expansions, but little work has yet tested this possibility (Martin et al., 2016).

In sum, our work provides further support that CORT regulation influences the distribution of non-native birds and perhaps even other vertebrates (Martin et al., 2010; Taff and Vitousek, 2016). If CORT responses are generally predictive of invasion potential, they might be useful biomarkers to manage populations (McCormick and Romero, 2017), implicating individuals most apt to exploit climate or other anthropogenic changes or become pests should they escape the pet or livestock trade (Dantzer et al., 2014; Martin et al., 2010).

Acknowledgments

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