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RESEARCH ARTICLE

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Decoupling pioneering traits from latitudinal patterns in a north American bird experiencing a southward range shift

Lynn Siefferman¹ | Alexandra B. Bentz^{2,3} | Kimberly A. Rosvall²

¹Department of Biology, Appalachian State University, Boone, North Carolina, USA

²Department of Biology, Indiana University, Bloomington, Indiana, USA

³Department of Biology, University of Oklahoma, Norman, Oklahoma, USA

Correspondence

Lynn Siefferman Email: sieffermanlm@appstate.edu

Kimberly Rosvall Email: krosvall@indiana.edu

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Abstract

- 1. Ecogeographic rules describe spatial patterns in biological trait variation and shed light on the drivers of such variation. In animals, a consensus is emerging that 'pioneering' traits may facilitate range shifts via a set of bold, aggressive and stress-resilient traits. Many of these same traits are associated with more northern latitudes, and most range shifts in the northern hemisphere indicate northward movement. As a consequence, it is unclear whether pioneering traits are simply corollaries of existing latitudinal variation, or whether they override other well-trodden latitudinal patterning as a unique ecogeographic rule of phenotypic variation.
- 2. The tree swallow Tachycineta bicolor is a songbird undergoing a southward range shift in the eastern United States, in direct opposition of the poleward movement seen in most other native species' range shifts. Because this organic range shift countervails the typical direction of movement, this case study provides for unique ecological insights on organisms and their ability to thrive in our changing world.
- 3. We sampled female birds across seven populations, quantifying behavioural, physiological and morphological traits. We also used GIS and field data to quantify a core set of ecological factors with strong ties to these traits as well as female performance.
- 4. Females at more southern expansion sites displayed higher maternal aggression, higher baseline corticosterone and more pronounced elevation of corticosterone following a standardized stressor, contrary to otherwise largely conserved latitudinal patterning in these traits. Microhabitat variation explained some quantitative phenotypic variation, but the expansion and historic ranges did not differ in openness, distance to water or breeding density.
- 5. This countervailing range shift therefore suggests that pioneering traits are not simply corollaries of existing latitudinal variation, but rather, they may override other well-trodden latitudinal patterning as a unique ecogeographic rule of phenotypic variation.

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KEYWORDS

body size, ecogeographic rule, glucocorticoid, maternal aggression, range expansion, range shift

1 | INTRODUCTION

Ecology and evolutionary biology have close ties to ecogeographic rules, which describe spatial patterns in biological trait variation and shed light on the drivers of such variation (Gaston et al., 2008). The last decade or so has seen a surge of new biological 'rules' related to global change (Gardner et al., 2011; Ryding et al., 2021; Zimova et al., 2021), including widespread shifts in species distributions (Chen et al., 2011; Parmesan & Yohe, 2003). In animals, a consensus is emerging around the hypothesis that particular 'pioneering' phenotypes may drive these range dynamics. Expansion populations often show improved cold tolerance, higher resting metabolic rates, heightened immune defences, more boldness and greater territorial aggression (Butin et al., 2005; Duckworth & Badyaev, 2007; Groen et al., 2012; Liebl & Martin, 2012; Martin et al., 2014, 2015; Michelangeli et al., 2017; Myles-Gonzalez et al., 2015). They also may exhibit improved movement performance (Llewelyn et al., 2010; Lombaert et al., 2014) and have larger bodies (Bowler & Benton, 2005; Chuang & Peterson, 2016; Clobert et al., 2009). Many of these same traits are associated with latitudinal diversification in life-history strategies, including lower survival towards the poles (Scholer et al., 2020), which often co-occurs with higher maternal investment (Ricklefs & Wikelski, 2002), higher glucocorticoid secretion (Jessop et al., 2013; Vitousek et al., 2019), larger body size (Ashton, 2002) and a faster pace of life (Gaston et al., 2009) at higher latitudes (see Figure 1). Notably, in 75%-80% of range shifts, organisms are moving to higher latitudes or altitudes (Chen et al., 2011; Parmesan & Yohe, 2003), leaving uncertainty as to whether pioneering phenotypes are simply corollaries of existing latitudinal variation, or whether they override other well-trodden latitudinal patterning as a unique ecogeographic rule of phenotypic variation.



towards the *south*, away from the poles?

FIGURE 1 Conceptual overview of this project, highlighting the typical spatial concordance of latitude and range expansion in the northern hemisphere. Southerly range expansions can decouple these ecogeographic processes.

In vertebrates, a number of studies suggest that glucocorticoid hormones, such as cortisol or corticosterone (Cort), may facilitate initial range expansion or persistence in new environments (Wingfield et al., 2015). This idea has intuitive appeal because glucocorticoid elevation can promote foraging, blood flow, tissue oxygenation, immune function or glucose metabolism (Sapolsky et al., 2000). Indeed, Cort is elevated in two separate range expansions for the invasive house sparrow Passer domesticus (Liebl & Martin, 2012; Martin et al., 2017), suggesting Cort may facilitate adaptation to novel environments. Glucocorticoid elevation also may promote adaptive responses to harsh or unpredictable environments, such as higher latitudes or altitudes, where snowstorms and unpredictable cold weather may favour higher glucocorticoids (Addis et al., 2011; Krause et al., 2016). The degree of Cort elevation is also moderately heritable (Pottinger & Carrick, 1999; Stedman et al., 2017) and associated with Darwinian fitness (Breuner & Berk, 2019; Schoenle et al., 2021). Glucocorticoid phenotypes are typically elevated towards the poles (Jessop et al., 2013; Vitousek et al., 2019, but see Thawley et al., 2019), suggesting that they may be ideal for teasing apart pioneering dynamics from latitudinal variation. To our knowledge, though, there have been no published studies on the traits that drive range expansion away from the poles, save for some analyses on invasive or introduced species that may not be representative of what occurs in native species (Westley, 2011). To understand the role of range expansion in shaping phenotypic variation, we need to evaluate a naturally occurring expansion that is not simply uncorrelated with latitude, but one that moves away from the poles.

The North American tree swallow *Tachycineta bicolor* is currently shifting in its breeding range southward and into the lower mid-west from the northeastern United States and Canada (Shutler et al., 2012; Winkler et al., 2020; Figure 2a). This shift is likely to expose birds to longer breeding seasons, shorter migration distances and/or less extreme spring weather, all of which differ from common selective pressures seen in other naturally occurring range shifts (Wingfield et al., 2015). For years, researchers have called for greater attention to these counter-predictive range shifts as an area of unmet need at the intersection of global change biology, ecology and evolution (Chen et al., 2011; Lenoir et al., 2010), particularly since these shifts may be more common than once thought (McCaslin & Heath, 2020).

We studied female tree swallows breeding at historical and expansion sites. Our focus on females is unique and important, considering that in birds, females are the dispersive sex and therefore drivers of range shifts. At each of seven populations, we quantified ecological parameters with strong ties to female reproductive success, including density of breeding conspecifics, distance to water and habitat openness. We also measured five distinct traits: maternal aggression, baseline Cort levels, Cort elevation in response to a stressor, body mass and tail length, the latter of which is a measure



FIGURE 2 (a) Map of study populations in the historic (blue) and expansion (orange) range. The current tree swallow breeding range is shown in grey (BirdLife International, 2016) and the dashed line marks the historic range estimated from the Birds of North America: A Guide to Field Identification (Robbins et al., 1966). (b) Breeding Bird Survey data show increases in tree swallow abundance in the expansion range, but not in the historic range. Lines indicate mean counts, with 95% CI showing variation among states or provinces. (c) Principal components (PCs) of habitat parameters also show 95% CI ellipses. Points are individuals and vectors indicate PC loadings. Higher PC1 values (eigenvalue = 1.89) indicate greater per cent openness, closer to water and lower conspecific density. Higher PC2 values indicate lower conspecific density and further from water (eigenvalue = 0.67).

of structural size (Shutler et al., 2006). Baseline and stress-induced Cort levels are regulated and can evolve separately (Pottinger & Carrick, 1999; Satterlee & Johnson, 1988; Vitousek et al., 2019), and so we treated them as separate traits. If the pioneering hypothesis transcends the direction of movement, then tree swallows in expansion populations should display behavioural, physiological and morphological traits that are associated with pioneering, despite their southward expansion: expansion birds should be larger, with higher baseline Cort, higher Cort elevation capabilities and more maternal aggression. If trait variation instead tracks more typical latitudinal patterning in thermal regimes, net primary productivity and a slower pace of life at lower latitudes, then expansion birds should be smaller, with lower baseline and stress-induced Cort and lower maternal aggression. Results that vary among traits may also begin to shed light on the processes driving any phenotypic patterns across this southward range shift.

2 | MATERIALS AND METHODS

2.1 | Study sites and environmental data

Methods were approved by Appalachian State University IACUC #13–15 and US Master Banding Permit #23563. All animals were handled in such a way to reduce stress and avoid physical harm. All adults were released in their home territory. We conducted fieldwork during May–June 2015. Historical sites included Saukville, Wisconsin (43.382 N, 88.023 W), Long Point, Ontario (42.623 N, 80.465 W) and Wolfville, Nova Scotia (45.107 N, 64.378 W). Expansion sites included Bloomington, Indiana (39.142 N, 86.602 W); Ames, Iowa (42.073 N, 93.635 W); Davidson, North Carolina (35.438 N, 80.697 W); and Boone, North Carolina (36.196 N, 81.783 W). We recorded GPS coordinates at each nestbox (Garmin GPSmap 78s).

Sites were categorized as either historical or expansion based on prior publications (Lee, 1993; Shutler et al., 2012), bolstered by personal communications with local researchers and data from the Bird Breeding Survey (BBS; 1967-2017) (Sauer et al., 2017). Historical sites have abundant tree swallow breeding for >100 years (Winkler et al., 2020), whereas expansion sites have increased abundance since the 1960s. In the first 10 years of the BBS, Nova Scotia, Ontario and Wisconsin (historic sites) reported an annual average (\pm SE) of 458±87 breeding tree swallows, whereas Indiana, Iowa and North Carolina (expansion sites) reported only 2 ± 1 . In the most recent 10 years, breeding numbers have increased by 40-fold in expansion sites (Figure 2b; visualized at the state/province level in Figure S1a). Although BBS data surely underestimate abundance, these trends reflect site-specific data (Lee, 1993; Shutler et al., 2012). Notably, not all expansion sites are at the southernmost range edge (i.e. Tennessee, the Carolinas), and some expansion sites (Davidson and Boone, North Carolina) have more recent histories than others (Iowa, Indiana). All expansion sites are nonetheless beyond the historic core of the species distribution.

We quantified three key ecological factors at each site, using measurements in the field as well as satellite data. The purpose of these data was twofold: First, we sought to test whether the expansion and historic range differed in a core set of parameters with strong ties to tree swallow success. Second, we wanted to assess whether habitat variation might confound any range-related differences in traits. To achieve these goals, we characterized land use/land cover (LULC) using ArcGIS 10.2 (ESRI, Redlands, California). Analyses focused on a typical foraging range of 300m around each nestbox (McCarty & Winkler, 1999). LULC data were obtained from USGS National Land Cover Dataset (2011) or Gouvernement du Canada Land Use (2010), at 30×30m resolution. We selected LULC categories based on their relevance to tree swallows, which require open, wet habitat for aerial foraging of insect prey (Winkler et al., 2020). As such, we focused on the per cent of land with open habitat (pasture, open water or barren), and distance to water (streams, rivers, ponds, wetlands). In the field, we estimated conspecific density as the number of nestboxes within a 50m radius that were defended by other tree swallows; previous studies have linked density with aspects of aggressive behaviour (Bentz et al., 2013).

2.2 | Adult capture, morphology and blood sampling

Females were captured between 09:00 and 16:30h, during incubation or chick rearing (expansion: 44 incubating and 48 provisioning females; historic: 44 incubating and 36 provisioning). For provisioning females, average chick age was 6.3 days posthatch (95% CI 5.3-7.3 days). We started a timer as soon as we captured each bird and collected an initial blood sample (~40-80µL) from the wing vein. Samples that took >3 min were not used because Cort can elevate rapidly after handling (Schoech et al., 2013). We measured wing length, tail length and body mass, but excluded wing data due to inadvertent methodological differences among sites. Tail length is correlated with structural size (Bourret & Garant, 2017; Hainstock et al., 2010) and affects flying ability (Norberg, 1990), an important feature for aerial insectivores. We recorded age as 'second year of life' (SY, or yearling) or 'after second year of life' (ASY, or >1 year) using plumage coloration (Hussell, 1983). All birds were banded with an aluminium leg band, and we marked each female across the breast with a coloured marker to facilitate identification in during behavioural assays (Whittingham & Dunn, 2001). After processing, we placed each bird in an opaque paper bag until 30 min postcapture, a standardized restraint protocol to measure Cort elevation, or Δ Cort. We collected a second blood sample (~40-80µL) and released the bird shortly thereafter.

2.3 | Assay of maternal aggression

Nest defence is a key component of adaptive maternal investment. We measured clutch and brood size and found no difference between expansion and historic sites (linear mixed model, LMM, with population as random effect, clutch: $\beta = 0.38 \pm 0.32$ SE, $F_{1,85} = 1.46$, p = 0.23; brood: $\beta = -0.09 \pm 0.43$ SE, $F_{1,77} = 0.05$, p = 0.84), and we therefore focused on a behavioural aspect of maternal investment. Specifically, we assayed maternal aggression against a simulated nest predator ~24 h after blood sampling, using an assay modified from (Winkler, 1992). Decoys were commercially manufactured models of the American crow *Corvus brachyrhynchos*, a widespread nest predator. We randomly rotated among six exemplars to limit psuedoreplication. Ahead of time, we affixed a decoy via wire, dangling from a ~0.7 m pole. Trials began by visually identifying the female and then deploying the decoy alongside crow calls from the Cornell Lab of Ornithology. The observer quickly slid the pole onto the existing nestbox and pole hardware, rapidly suspending the decoy above the box in a semi-natural flight position. The observer retreated to ~40m and began the behavioural assay. For 5 min, we measured the number of dives towards the model, within 1 m of the nestbox. In tree swallows, nest defence is a highly repeatable trait (Betini & Norris, 2012).

2.4 | Hormone assays

We quantified plasma Cort levels using an enzyme immunoassay kit that has high accuracy and assay parallelism (Cayman ELISA #500655, see Rosvall et al., 2012). Briefly, we added 10 µL plasma to 200μ L ultrapure H₂O, extracted 3× with ether, dried with N₂, and reconstituted with 600µL assay buffer. Each plate contained up to 33 samples in duplicate, an 8-point standard curve, blank, maximum binding, nonspecific binding and total activity controls, as well as three additional plasma pools used to calculate variability. Plates were balanced by site, breeding stage and time point (baseline or 30-min). We read absorbance at 412 nm and interpolated concentration using Gen5 software (v2.09: BioTek). Inter-plate variability was 10.2%, and intra-plate ranged from 3.7% to 12.4% (mean: 7.7%). We did not calculate extraction efficiency at a sample level; instead, we spiked a separate set of samples (n = 10) with 20uL H3-Cort (~2500 CPM), extracted 3x, and found average efficiencies to be 98.1%. Values may therefore underestimate true Cort concentrations, although our data are typical for this species (e.g. Zimmer et al., 2019), suggesting this effect is minimal.

2.5 | Data analyses

Statistical analyses were performed in R (v. 3.4.3, R Core Team, 2017). We report results as mean \pm 1 standard error, and α = 0.05. This study included data on 172 birds and the habitat surrounding each bird's nestbox; however, we did not collect all data from every bird, for example, because not all birds could be captured or identified during behavioural observations, some could not be bled quickly enough, some did not have full LULC data. Thus, sample sizes vary from 97 to 147 birds (Table 1).

To test whether ranges (expansion vs. historical) differed in habitat parameters, we used a permutational multivariate analysis of variance (PERMANOVA) using the *adonis2* function in VEGAN (Oksanen et al., 2016). We selected PERMANOVA because this TABLE 1 Summary of the top or most parsimonious model for each trait. Population was a random effect in each model. The test statistic was the t-value for all models except aggression in which it was the z-value. Marginal $R^2 (R_{marg}^2)$ is the variance explained by the fixed effects, and conditional $R^2 (R_{cond}^2)$ is the variance explained by the entire model (fixed and random effects). Asterisks denote significance (*p < 0.05; **p < 0.01).

Dependent variable	Fixed effects	Estimate (SE)	Test stat	p-value	R ² _{marg}	R ² _{cond}
Aggression ($n = 97$)	Range	1.64 (0.41)	3.97	<0.001**	0.33	0.33
	PC1	-0.44 (0.16)	-2.81	0.005**		
$\log(\text{baseline Cort}) (n = 117)$	Range	0.29 (0.13)	2.13	0.035*	0.09	0.09
	Stage	0.36 (0.13)	2.67	0.009**		
$\log(\Delta Cort)$ (n = 111)	Range	0.36 (0.12)	2.98	0.004**	0.07	0.07
Mass (n = 147)	Range	-0.20 (0.28)	-0.69	0.530	0.05	0.17
	Stage	-0.92 (0.22)	-4.10	<0.001**		
	PC1	0.37 (0.10)	3.80	0.023*		
	Age	0.79 (0.26)	3.04	0.003**		
	Time	0.001 (0.0003)	2.90	0.005**		
Tail (n = 140)	Range	1.11 (0.95)	1.17	0.294	0.12	0.24
	Stage	1.51 (0.58)	2.61	0.010*		
	Range×stage	-2.51 (0.98)	-2.56	0.012*		
	Age	1.29 (0.51)	2.54	0.012*		

nonparametric test is insensitive to multicollinearity, and we found moderate correlations among parameters (0.34 < |r| < 0.53). We visualized differences with a principal component analysis (PCA) using the *prcomp* function.

We next tested how five putatively pioneering traits differ between historic and expansion ranges. A random effect of populations was included in all models. We performed separate analyses for each trait. LMMs were used to analyse all traits, except for anti-predator aggression, which was over-dispersed count data better suited to a negative binomial generalized LMM. Models were run in LME4 (Bates et al., 2015), and we tested residuals for normality with a Shapiro-Wilk test. Two variables required logtransformation to meet model assumptions: baseline Cort and Δ Cort. There were seven individuals (n = 5 historic; n = 2 expansion) that showed negative $\Delta Cort$ values. We had no indication that they were disturbed by us or something else, but their responses are not the biological norm, and so we removed them from subsequent analyses under the assumption that they do not represent the typical stress-induced Cort elevation that we seek to understand. Two extreme outliers were detected for tail length (Grubb's test, p < 0.05), and these points were removed prior to model comparison.

For each trait, we ran a series of models, all of which contained range (historic vs. expansion) and all combinations of: stage (incubating vs. provisioning), a range×stage interaction, PC1 of the habitat parameters, age and capture time, in addition to the intercept only (null) model. Capture time was unrelated to anti-predator aggression and was not included in those models. We used Akaike information criterion corrected for small sample sizes (AICc) to find the most appropriate model (Burnham & Anderson, 2002). Models within two Δ AICc of the top model are equally fit, and, when this occurred, we present the most parsimonious model. Model selection was conducted with maximum likelihood estimation, but variable significance of the top model was done using restricted maximum likelihood. Both marginal (R^2_{marg} ; variance explained by fixed effects) and conditional (R^2_{cond} ; variance explained by fixed and random effects) R^2 are estimated using MuMIN (Bartoń, 2019). See Appendix S1 for greater detail on (a) how we accounted for spatial parameters, (b) how we evaluated range versus latitude as predictors of trait variation and (c) how we used a heterogeneity analysis to assess the degree of population specificity of any rangerelated trait differences.

3 | RESULTS

3.1 | Environmental parameters in historic versus expansion populations

The PERMANOVA showed that habitat parameters did not differ by range ($F_{1,156} = 2.25$, p = 0.141, $R^2 = 0.01$). This was visually inspected via a PCA plot, with overlap in 95% CI, in which the first two PCs explained 85.1% of the variance in habitat parameters (Figure 1c). Higher PC1 values indicate greater per cent openness (loading = 0.62), closer to water (loading = -0.57) and lower conspecific density (loading = -0.54); PC1 explained 62.9% of the variation (eigenvalue = 1.89). PC2 explained 22.2% of the variation (eigenvalue = 0.67), with higher values indicating habitats with lower conspecific density (loading = -0.78) further from water (loading = 0.62). Despite habitat similarities in the expansion and historic range, Placeholder Textthese parameters did differ by site (PERMANOVA: $F_{6.151} = 65.50$, p = 0.001, $R^2 = 0.72$, see Figure S1b),

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and so we included PC1 of habitat variance in model comparisons on phenotypic variation. We did not use PC2 because its eigenvalue <1.

3.2 | Phenotypic differences among birds in historic versus expansion populations

Birds sampled at expansion versus historic ranges differed in multiple components of the phenotype. We report only p-values and top models here, with test statistics in Table 1 and additional models within two Δ AlCc of the top model in Table S1.

First, females at expansion sites were more aggressive towards a simulated predator, compared to females in the historic range (p < 0.001; Table 1; Figure 3). Females breeding in areas with a smaller PC1 value (lower per cent openness, further from water and higher conspecific density) were also more aggressive (p = 0.005; Table 1). Model residuals showed no spatial autocorrelation (Moran's l = 0.05, p = 0.28).

Second, related to physiology: The top model for baseline Cort indicated significant main effects of range and stage. Baseline Cort was higher in expansion females (p = 0.035) and females provisioning chicks (p = 0.009; Table 1; Figure 4a). The degree of Cort elevation also differed by range (p = 0.004; Table 1; Figure 4b); expansion females more strongly elevated Cort when presented with



FIGURE 3 Birds breeding in the expansion site displayed significantly more antipredator aggression. Aggression counts (# of dives) were square-root transformed to improve visual clarity. Box plots denote median and quartiles; violin plots reflect probability distributions.

a standardized stressor. Top model residuals showed no evidence of spatial autocorrelation for baseline Cort (Moran's l = 0.02, p = 0.58) or Δ Cort (Moran's l = 0.04, p = 0.32).

Finally, body mass did not differ by range, but as expected, females provisioning nestlings had significantly smaller body mass than incubating females (p < 0.001; Table 1). Mass was also larger for females captured later in the day (p = 0.005; Table 1) and for females breeding in an area with a larger PC1 (greater openness, closer to water and lower density; p = 0.023, Table 1). The top model for mass showed no residual spatial autocorrelation (Moran's I = -0.01, p = 0.91). For tail length, which represents a more fixed measure of structural size, the top model showed residual autocorrelation (Moran's l = 0.13, p < 0.001) and was re-fit using spatial autocorrelation structure. There was a significant interaction between range and stage (p = 0.012; Table 1; Figure 5), in which tails were longer for provisioning females but only in the historical range (least square means: -1.51 ± 0.58 , t = -2.61, p = 0.012). Thus, females who initiated breeding earlier were larger but only in the historic range. Older females also had a larger body mass (p = 0.003; Table 1) and longer tails compared to females in their first breeding season (p = 0.012; Table 1), supporting established age patterns in this species.

3.3 | Quantitative variation within and among populations

There was significant heterogeneity among populations in all traits, except for Δ Cort (see SI text and Figure S2). However, when populations were grouped by range, heterogeneity (l^2 ; the proportion of variation in traits due to between-population heterogeneity) declined from an average l^2 of 74.90% (\pm 8.99SE) to an average l^2 of 71.95% (\pm 10.48SE) in historical and 56.46% (\pm 15.30SE) in expansion sites (Figure S2), suggesting similarity in traits within each portion of the range, particularly within the expansion range.

When we directly contrasted range with latitude as a predictor of trait variation, range consistently outperformed latitude. For all traits, the top or most parsimonious model contained range, not latitude (Table S2). In addition, the categorical effect of range was an overall better predictor of trait variation than quantitative variation in latitude (Figure S3; average variable importance for latitude = 0.38 ± 0.06 SE, for range = 0.61 ± 0.06 SE).

4 | DISCUSSION

Like many organisms, tree swallows are shifting their breeding range, but this species is going against the grain, moving southward and into the lower Midwest, from their historic range in Canada and the northern US (Shutler et al., 2012). Sampling across seven sites, we found phenotypic differences that oppose otherwise common latitudinal trait variation. Specifically, females at expansion sites defended young more aggressively from a simulated predator, they had higher baseline Cort secretion, and they displayed a greater capacity



FIGURE 4 (a) Baseline Cort levels at the time of capture were significantly higher for females breeding in expansion range (orange) compared to the historical range (blue) and for females sampled while provisioning. (b) The degree of Cort elevation (ΔCort) after a 30-min standardized stressor was significantly higher for females breeding in the expansion range. Box plots denote median and quartiles; violin plots reflect probability distributions.



FIGURE 5 Tail length was significantly larger for females sampled while provisioning nestlings, but only for females in the historical range, denoted with asterisk. Box plots denote median and quartiles; violin plots reflect probability distributions.

to elevate Cort in response to a standardized stressor. Although we found no difference in morphology due to range alone, these remaining phenotypic differences match predictions of the pioneering hypothesis, which has not been previously tested in a range expansion that directly countervails movement to higher latitudes seen in most contemporary range shifts. We also showed that habitat quality covaried with individual differences in some traits (i.e. aggression, body mass), but the historic and expansion range do not differ in distance to water, habitat openness, conspecific density, clutch size or brood size. In essence, range-related phenotypic differences appear to override within-population microhabitat variability that has strong ties to success in this system. Because this range shift countervails the typical latitudinal direction of movement, this case study follows the path forged by other 'exceptions' that probe biological patterns in new ways (e.g. sex role reversal; Trivers, 1972). In doing so, we suggest that pioneering phenotypes represent a unique ecogeographic rule of range expansion, one that is not simply a corollary of existing latitudinally driven phenotypic variation.

4.1 | Expansion females have higher maternal aggression

Territorial aggression (in defence of territories) and maternal aggression (in defence of young) are widespread and adaptive behaviours in females (Rosvall, 2011; Stockley & Bro-Jørgensen, 2011). Here we report elevated maternal aggression in newer populations versus those at the historic core in the expansion range. Female aggression may be particularly relevant in birds because females are the dispersive sex and therefore front-line responders to breeding in new locations.

The environmental factors that drive this behavioural variation may have some connection to habitat quality: less aggressive females bred in putatively higher quality habitats (more open and closer to water) with more conspecifics breeding nearby, and yet expansion and historic ranges did not differ in any of these ecological parameters. This suggests to us that range-related differences in maternal aggression are unlikely to stem from simple land use differences that alter predation regimes per se (Rendell & Robertson, 1990). We also did not find range differences in body mass that would indicate expansion females are in poorer condition, or excluded into suboptimal habitat; rather, expansion females are more aggressive than birds in the historic range, despite similar overall habitat quality between the ranges. Higher maternal aggression in the more southerly expansion range may also come about from correlated evolution with other types of aggression (Cain et al., 2011) or from a variety of experiential processes that promote proactive behavioural traits during the establishment phase of a range shift (Bowler & Benton, 2005; Chuang & Peterson, 2016; Clobert et al., 2009). Regardless of its root cause, this behavioural pattern is striking because expansion populations 'should' display lower maternal aggression, based on latitudinally varying life-history trade-offs between survival and reproduction (Ricklefs & Wikelski, 2002; Scholer et al., 2020), but their high maternal aggression is instead more similar to what is seen in other range expansions that move towards the poles or to higher altitudes

4.2 | Expansion females have elevated corticosterone, contrary to larger latitudinal patterns

Individuals in the expansion range also showed higher baseline Cort and more pronounced abilities to elevate Cort following a standardized stressor. Latitude and net primary production are often correlated with Cort reactivity, with higher stress-induced Cort towards the poles (Jessop et al., 2013). Similarly, baseline Cort is typically higher in lower temperatures and higher altitudes (Bokony et al., 2009; Jessop et al., 2013, 2016; Vitousek et al., 2019), including one study reporting higher baseline Cort secretion in tree swallows breeding in Alaska versus Tennessee (Zimmer et al., 2020). Our results reverse this pattern with more sampling in populations at the southern end of the tree swallow range. Similar patterns have been reported in edge populations in invasions and more natural range expansions (Addis et al., 2011; Dunlap & Wingfield, 1995; Krause et al., 2016; Liebl & Martin, 2012; Martin et al., 2017), although none of these previous cases involve an organic range expansion that directly opposes the typical latitudinal pattern of movement seen in response to climate change. These observations therefore support the hypothesis that elevated Cort is a generalized adaptation to diverse environmental challenges, not simply driven by colder, more unpredictable, polar environments as summarized above in past work. Furthermore, novel challenges may reverse otherwise ubiguitous latitudinal patterns (Thawley et al., 2019), potentially creating U- or inverted-U-shaped relationships with traits that are enhanced at the northern and southern ends of the range, based on different ecological pressures.

Cort secretion also has strong connections with fitness (Bonier et al., 2009; Breuner & Berk, 2019; Cox et al., 2016; Schoenle et al., 2021), and the patterns identified here may stem from some combination of plasticity and evolutionary change. Because our top

model of baseline Cort does not show a relationship with habitat quality and because the expansion and historic ranges did not differ in habitat quality, we do not find it parsimonious that spatial filtering of certain phenotypes shunted birds into suboptimal habitat in the expansion range. Likewise, average baseline Cort levels were typical for their breeding stage (Zimmer et al., 2019). Baseline Cort is more situationally plastic (Romero et al., 2009; Taff et al., 2018) and has far lower heritability than the ability to elevate Cort, that is, 0.14 versus 0.38 respectively (Stedman et al., 2017). Range-related differences in baseline Cort are therefore likely to relate to plasticity, as evidenced by the main effect of breeding stage. Our analyses did not identify the environmental factor driving these trait differences, although there may not be a single unified factor. Indeed, diverse challenges, such as cold weather and heightened competition, can be integrated into baseline Cort levels and passed via egg-based maternal effects (Potticary & Duckworth, 2020). Our cross-sectional analysis would not capture any site-specific environmental drivers of phenotypic variation, although we can nevertheless provide a potential mechanism for hormones to shape phenotypic divergence along new trajectories related to global change and its ensuing shifts in breeding range.

4.3 | Individuals with larger structural size breed earlier in the historic but not expansion range

In the historic range, larger, heavier and older females breed earlier, with more success (Robertson & Rendell, 2001). We did not find any mass-related differences by range, but we found an interaction between breeding stage and range in tail length. Because we visited each population once, females tending chicks must have initiated breeding earlier than females tending eggs. Therefore, we speculate that breeding stage may be autocorrelated with unmeasured variation in individual quality, particularly since tail length is a measure of heritable structural size (Bourret & Garant, 2017; Hainstock et al., 2010), which does not change within a season. Rather, in the historic range, earlier breeding (putatively high-quality) females are larger bodied compared to later breeding females. We did *not* see this same result in the expansion range, hinting at the potential for divergent selection on morphology in expansion versus historic range.

Notably, tree swallows are not shifting towards the poles where cold weather events, such as an early spring blizzard, should favour a larger body size (i.e. Bergmann's rule), and tail length was uncorrelated with PC1 habitat quality, making dispersal filtering based on tail length a less likely explanation. This allows a unique test of the proposed 'third universal response' to climate change—a morphological change following a change in species distribution (Gardner et al., 2011). Current data suggest that all tree swallow populations migrate, although birds that breed further south have shorter migration distances (Gow, Burke, et al., 2019; Gow, Knight, et al., 2019; Knight et al., 2018), which should relax selection for larger morphologies. Ecogeographic patterning in body size has been widely

evaluated in the context of global change (Gardner et al., 2011; Youngflesh et al., 2022), and our results uniquely couple *less* movement (i.e. shorter migration distances) with range expansion towards the wintering grounds, not summering grounds. We therefore highlight the direction of movement as important to understanding how range dynamics interact with trajectories of phenotypic change.

5 | CONCLUSIONS

Understanding how animals respond to global change is an important issue at the interface of the biological sciences, and the tree swallow range shift is useful for probing emerging and established ecogeographic rules in new ways. Because we sampled older expansion areas (Iowa, Indiana) as well as newer ones (North Carolina), we know that phenotypic differences are not limited to the initial dispersers or the range edge (e.g. South Carolina, Alabama; Wright et al., 2019). This broad sampling also may account for our relatively small effect sizes $(R_{marg}^2 < 0.33)$, although even subtler effects can lead to pronounced divergence in a few decades (Gardner et al., 2014). Critically, range outperformed latitude as a predictor of quantitative variation for all traits, substantially so for maternal aggression and baseline Cort. This sort of discrete variation points to nonclinal variation in habitat ecotones, or population genetic processes that limit heterogeneity, particularly within the expansion range. Similarly, trait heterogeneity declined when populations were grouped by range, especially in the expansion range. Thus, even though the expansion range included more variation in latitude, birds breeding in the expansion range were phenotypically similar to one another.

More work is needed to understand the degree to which rangerelated differences in pioneering phenotypes are due to phenotypic plasticity or genetical evolution. We did not see a clear division between patterning of the putatively more plastic traits (i.e. mass, baseline Cort) versus more heritable traits (i.e. Δ Cort, aggression or tail length). We also do not know if these differences pre-date the moment of dispersal, or if they accumulate over time as individuals spent more time in southern environments. Longitudinal analyses in rangeexpanded populations are deeply needed to differentiate these alternatives, asking for instance, whether naïve, young birds at the range front already display pioneering traits, and whether pioneering traits are associated with improved performance within the expansion range. In all likelihood, the origin of adaptation is a duality, an inextricable duet between plasticity and evolution, which in this case has produced expansion phenotypes that appear to be thriving in the south (Monroe et al., 2008), even when a suite of well-established latitudinal rules on trait variation would have predicted the opposite.

AUTHOR CONTRIBUTIONS

Lynn Siefferman and members of her laboratory conceived of the study and collected data in the field. Kimberly A. Rosvall analysed the hormone data. Alexandra B. Bentz and Kimberly A. Rosvall performed statistical analyses. All authors contributed to writing and gave final approval for publication

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi. org/10.5061/dryad.2fqz612nq (Siefferman et al., 2023).

ORCID

Lynn Siefferman ^(D) https://orcid.org/0000-0002-9600-2902 Alexandra B. Bentz ^(D) https://orcid.org/0000-0003-2445-4886 Kimberly A. Rosvall ^(D) https://orcid.org/0000-0003-3766-9624

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Supplimental Methods and Results.

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