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Migratory shorebird adheres to Bergmann's Rule by responding to environmental conditions through the annual lifecycle

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Research

Migratory shorebird adheres to Bergmann's Rule by responding to environmental conditions through the annual lifecycle

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The inverse relationship between body size and environmental temperature is a widespread ecogeographic pattern. However, the underlying forces that produce this pattern are unclear in many taxa. Expectations are particularly unclear for migratory species, as individuals may escape environmental extremes and reorient themselves along the environmental gradient. In addition, some aspects of body size are largely fixed while others are environmentally flexible and may vary seasonally. Here, we used a long-term dataset that tracked multiple populations of the migratory piping plover *Charadrius melodus* across their breeding and non-breeding ranges to investigate ecogeographic patterns of phenotypically flexible (body mass) and fixed (wing length) size traits in relation to latitude (Bergmann's Rule), environmental temperature (heat conservation hypothesis), and migratory distance. We found that body mass was correlated with both latitude and temperature across the breeding and non-breeding ranges, which is consistent with predictions of Bergmann's Rule and heat conservation. However, wing length was correlated with latitude and temperature only on the breeding range. This discrepancy resulted from low migratory connectivity across seasons and the tendency for individuals with longer wings to migrate farther than those with shorter wings. Ultimately, these results suggest that wing length may be driven more by conditions experienced during the breeding season or tradeoffs related to migration, whereas body mass is modified by environmental conditions experienced throughout the annual lifecycle.

Keywords: Bergmann's Rule, body size, heat conservation, migration distance, migratory connectivity, phenotypic flexibility, piping plover



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Introduction

Where similar geographic patterns of phenotypic variation are found across divergent taxa, ecogeographic ‘rules’ may explain convergent responses to environmental conditions and selection pressures. One of the most widely known and contested ecogeographic rules is Bergmann’s Rule (Bergmann 1847), or James’ Rule at the intraspecific level (James 1970, Gaston et al. 2008), which describes a positive relationship between latitude and adult body size in endotherms (Watt et al. 2010). The primary mechanism proposed for Bergmann’s Rule is heat conservation in cold climates via lower ratio of body surface area to volume (Mayr 1956), and while the heat conservation hypothesis has only been experimentally validated in a few taxa (Brown and Lee 1969), it remains the default explanation for this pattern. Despite decades of research in numerous taxa, the patterns in endotherm body size and environmental mechanisms driving those patterns across latitudes and environments remains poorly understood (Scholander 1955, McNab 1971).

The uncertainty in adherence to Bergmann’s Rule is amplified in highly mobile species like migratory birds. Migration allows individuals to avoid harsh winter conditions in their breeding ranges, potentially allowing them to escape the selective pressure to adapt body size for heat conservation. Indeed, adherence to Bergmann’s Rule may be weaker in migratory species than in resident species (Ashton 2002, Meiri and Dayan 2003, Ramirez et al. 2007), but the evolutionary drivers of these differences are unclear (James 1970, de Queiroz and Ashton 2004). Patterns of body size are further complicated because some measurements of size may be phenotypically flexible, showing reversible within-individual variation throughout the year due to forces such as differential selection pressures or fluctuations in food availability (Piersma and Drent 2003, Husby et al. 2011). Such seasonal trait flexibility affecting adherence to Bergmann’s Rule is possible in non-migratory species; however, migration adds additional complexity by potentially changing the spatial arrangement of individuals between seasons. Bergmann’s Rule may therefore be observed in either or both relatively flexible (e.g. mass) or fixed (e.g. skeleton) aspects of body size, and either across seasons in a species’ annual life cycle or during only one season (e.g. breeding or non-breeding range) due to trait flexibility or spatial rearrangement.

The stress of migration itself may also affect body size through multiple and potentially opposing selection pressures, such as selection for smaller size to reduce wing loading (mass per unit wing surface area) or larger size via fat stores or wing musculature necessary for sustained flight (Blem 1975). Energetic constraints in particular may result in correlation of larger body size in individuals or populations with longer migratory distances, regardless of the causative direction of this relationship (i.e. whether larger body size allows for longer migration or longer migration selects for larger size; Marchetti et al. 1995, Alerstam et al. 2003). For example, Salomonsen (1955) and Hamilton (1961) found that variation in migratory behavior affected ecogeographic

body size patterns in common ringed plovers *Charadrius hiaticula*: those that bred at higher latitudes had longer wings and migrated farther south than those that bred at southern latitudes. Thus, this species showed an inverse relationship between latitude and wing length consistent with Bergmann’s Rule, but by a potentially different mechanism that may be unrelated to the usual heat conservation hypothesis.

Building from these insights, we propose that body size patterns in a migratory species under selection for body size according to Bergmann’s Rule is influenced by three factors: 1) whether the size metric considered is seasonally flexible, 2) size-related variation in migratory distance, and 3) consistency in selection pressure across seasons. As we are interested here in what the patterns of body size in migratory species look like in the presence of selection on body size resulting in a pattern adhering to Bergmann’s Rule, we assume point 3. The remaining points lead to four fundamental possibilities affecting whether Bergmann’s Rule is followed across the annual life cycle (Fig. 1a–d). For instance, if a species adheres to Bergmann’s Rule in a fixed size trait in one season (e.g. breeding), but low migratory connectivity results in the mixing of individuals from different populations in the other season (e.g. non-breeding), then adherence to Bergmann’s Rule in the latter season is not necessarily expected (Fig. 1a). However, a flexible size trait provides a mechanism to adhere

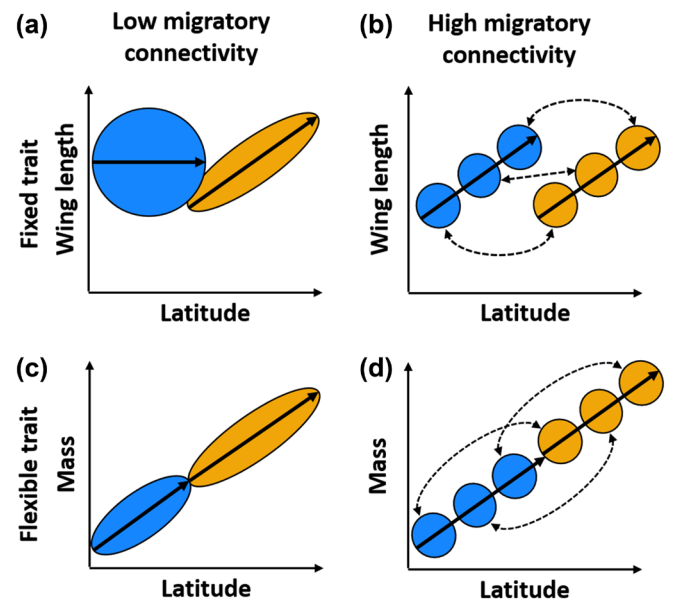


Figure 1. Potential scenarios of body size patterns across seasons in a migratory species based on trait flexibility and migratory patterns. Cross-seasonal adherence to Bergmann’s Rule depends on whether the metric of size is a fixed (a, b) or flexible (c, d) trait, whether there is low (a, c) or high (b, d) migratory connectivity, and where the individual is measured (breeding grounds: yellow; non-breeding grounds: blue). Ovals represent distinct migratory populations that remain connected throughout their annual lifecycle. Dashed lines represent hypothetical potential migratory pathways or constraints. Solid lines represent the direction of seasonal patterns in body size related to an environmental gradient.

to Bergmann's Rule throughout the full annual lifecycle despite mixing of different populations during migration (Fig. 1c). In contrast, high migratory connectivity would constrain the mixture of individuals across populations and seasons, driving adherence to Bergmann's Rule in a fixed size trait across seasons even if the selective pressure is experienced predominantly or even solely in the other season, and thus in an entirely different location (Fig. 1b). Adherence to Bergmann's Rule in a flexible size trait could occur regardless of degree of migratory connectivity; however, high connectivity could be distinguished by distinct spatial structure seen as groups of individuals that persist across seasons (Fig. 1d).

Few study systems can support tests of such scenarios, which require data on movements and measurements from multiple populations throughout the annual life cycle. Here, we offer one of these rare opportunities in a 16-year banding dataset on piping plovers *Charadrius melodus*, collected across 28 degrees of latitude. This species breeds throughout the Great Plains, Great Lakes, and the northern Atlantic coast of North America, and predominantly overwinters on coastal habitats in the Gulf of Mexico, southern Atlantic coast, and throughout the Caribbean (Haig and Oring 1985). Non-breeding populations are thought to be a mixture of distinct breeding populations and less distinct sub-populations (Gratto-Trevor et al. 2012). Piping plovers exhibit high site fidelity on both the breeding (Catlin et al. 2015) and non-breeding grounds (Gibson et al. 2018), and movements of individuals among breeding populations are rare. We addressed these questions using data from both the Atlantic and Central flyways of North America (Fig. 2), providing natural replication within this study.

Using mass and wing length measurements collected from individuals on breeding and non-breeding grounds throughout the annual life cycle, we investigated the effects

of trait type (flexible or fixed) and migratory distance on ecogeographic patterns of body size in piping plovers. Our central question was whether body size in this species was consistent with Bergmann's Rule across seasons, predicted as a positive relationship with latitude, and specifically the heat conservation hypothesis, predicted as an inverse relationship with climatic temperature. To differentiate between the four alternative scenarios (Fig. 1), we modeled the relationships between mass and wing length, respectively, with latitude, temperature, and individual level migratory distance presumed to be a function of migratory ability (i.e. wing loading, body condition). We also assessed migratory distance at the population level, which we interpreted as migratory connectivity (i.e. the degree to which individuals remain spatially associated across both breeding and non-breeding populations). Migratory distance thus stands both as a potential covariate for understanding the effect of migration on body size patterns in this species, and as an alternative hypothesis (hereafter, the migration distance hypothesis) that body size patterns are best explained by the energetic constraints of migration, predicted as positive relationships between both wing length and body size with migration distance rather than latitude or temperature.

Methods

Data collection

Piping plover body size data were collected as part of multiple independent research projects throughout the species' range (Cohen and Gratto-Trevor 2011, Catlin et al. 2015, Gibson et al. 2017, 2018, DeRose-Wilson et al. 2018, Stantial et al. 2018) from 2002 to 2018. For many birds,

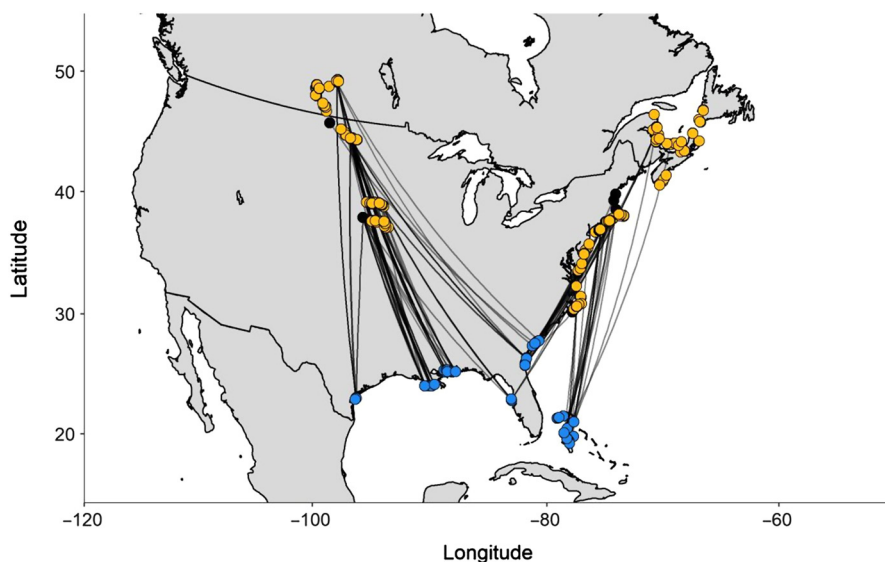


Figure 2. Locations of all piping plovers captured from 2002 to 2018 throughout Canada, United States, and the Bahamas. Individual migratory movements (black lines) were inferred from captures of individuals on both the breeding range (yellow circles) and non-breeding range (blue circles). Black circles represent observations of piping plovers without body size measurements.

body mass is variable throughout an individual's annual life-cycle and is related to physiological responses to migration (Piersma et al. 1999, Kvist and Lindström 2001), weather conditions (Dugan et al. 1981), and variation in food quality (Lima 1986). Individual wing length also varies within the annual life-cycle as the tips of the primary feathers become more rounded and shorter due to friction, and eventually molt and new feather growth; however, the difference in length between newly molted and worn feathers in adult shorebirds is small and often not detectable (Fernández and Lank 2007). More importantly, this source of variation in wing length likely is not particularly responsive to environmental temperature and may be driven solely by the innate annual life-cycle of the species (Piersma and Drent 2003). Given the difference in potential for within-individual variability between body mass and wing length, we describe mass as an environmentally flexible size trait and wing length as an environmentally fixed trait. Although research interests and data collection protocols among research projects were variable, most records in our data set included measurements of mass (99.3%) and wing length (94.7%). Across projects, mass was measured with digital (± 0.1 g) or Pesola (± 1 g) scales and wing length was measured with a wing ruler (± 1 mm). Here, wing length represented the distance between the wrist and leading edge of the wingtip measured on an extended (i.e. not relaxed) wing. On capture, individuals were classified to age class (hatch year, after hatch year or unknown) from patterns in feather growth and coloration (Gratto-Trevor 2010). Sex cannot be reliably assigned by physical features throughout the annual life cycle; however, body size (i.e. mass, wing and bill length) is not sexually dimorphic in piping plovers (Catlin et al. 2014). Data collection was administered by multiple independent research groups, and we acknowledge that project-related variation in measurements may exist; however, we have no evidence that this was a substantial source of bias.

Covariate development

We used 1) latitude of capture (Mayr 1963); and 2) average (1970–2000) seasonal (i.e. breeding season (April–July) and non-breeding season (November–February)) dry-bulb ($^{\circ}$ C) temperature (Jones et al. 2005) as explanatory variables to assess similar hypotheses regarding the spatial variation in piping plover mass and wing length. Seasonal temperature surfaces were extracted from WorldClim ver. 2.0 (Fick and Hijmans 2017) for the entire study system at 30 arc-second resolution. We assigned each individual the mean seasonal temperature within a 10-km radius buffer surrounding the spatial coordinates associated with that individual. We assigned individuals captured on the breeding grounds the mean value associated with the breeding season and individuals captured on the non-breeding grounds the mean value associated with the non-breeding season. We used a 10-km radius scale as it was large enough to compensate for the resolution of the spatial data available and known error in the capture locations of individuals, yet small enough to avoid

substantial overlap of individuals among breeding or non-breeding populations.

For individuals observed on both the breeding and non-breeding grounds, we used the minimum distance between these locations (Fig. 2) to determine whether variation in the distance individuals migrated was associated with body size after accounting for variation in body size associated with latitude. For this analysis, we only considered individuals captured, weighed, and measured during breeding that were subsequently observed on the non-breeding grounds ($n = 584$), or individuals captured, weighed, and measured on the non-breeding grounds that were later observed breeding ($n = 131$).

Next, we measured the strength of migratory connectivity by comparing population-specific transition probabilities from each breeding cluster to each non-breeding cluster with the distances among these, and relative abundances within each population clusters. Migratory connectivity is often expressed as the correlation between the breeding and non-breeding observations of individuals within a single species (Webster et al. 2002), in which values near 0.0 indicate high levels of mixture of discrete breeding populations on the non-breeding grounds, and values near 1.0 indicate discrete breeding populations are associated with specific non-breeding grounds. Using methods described by Cohen et al. (2017) with R package MigConnectivity, we separated the breeding and non-breeding populations into spatial clusters (Cohen et al. 2017, Supplementary material Appendix 1 Table A1) based on natural breaks in the data and previous spatial delineations from range wide census efforts (Elliott-Smith et al. 2009). We generated transition probabilities by calculating the proportion of individuals associated with each breeding cluster ($n = 8$) that were observed in each non-breeding cluster ($n = 7$). We extracted relative abundances within each breeding cluster from an international piping plover census that occurred during the middle of data collection (Elliott-Smith et al. 2009).

First, we estimated migratory connectivity for all population clusters throughout the species breeding and non-breeding ranges. Secondarily, we separated these data into flyways (Atlantic and Central) to determine whether patterns in migratory connectivity were primarily related to patterns at the flyway-level. We regressed the observed migration distance against the original latitude of capture post hoc to assess spatial variation in individual's migration distance.

Model development

We used generalized linear mixed models (GLMM) to explore whether body mass or wing length were associated with each explanatory variable. We assigned individuals into groups ($n = 4$) based on the season-flyway combination in which they were captured and measured (i.e. Atlantic–breeding, Atlantic–non-breeding, Central–breeding, Central–non-breeding, Fig. 2), and each received an independent model intercept. For each hypothesis, we developed two models with identical structures, with one

that used body mass as the dependent variable and the other used wing length as the dependent variable. We allowed the influence of latitude or seasonal temperature on body size to be independent between seasons, but identical between the Atlantic and Central flyways. For the migration distance hypothesis, we constrained the association between body size and minimum distance travelled to be constant between seasons. We accounted for sources of temporal and individual variation in body size not directly associated with an individual's spatial location (Marchetti et al. 1995) through a random effect of year of capture ($n = 15$), and a fixed effect of age class at capture (hatch year [or second year], after hatch year [or after second year], and unknown). We also considered a season-specific, random effect of month of capture ($n = 13$, individuals were captured on both the breeding and non-breeding grounds in April) for each model, as we suspected individual body mass and wing length varied throughout the year in relation to various life history aspects (e.g. incubation, migration, molt).

Although most individuals within this dataset (80%, $n = 2570$) were captured and measured only once, we included individual as a random effect in each model to 1) account for repeated measures, and 2) infer patterns in individual repeatability (R), or the proportion of phenotypic variance attributed to among-individual, as opposed to within-individual, differences in body size (Falconer and Mackay 1996) that were not associated with individual age, and the timing (i.e. year or month) or latitude (or temperature) of capture. We measured R as the ratio between the residual among-individual variance (σ_{ind}) and the sum of the within-individual variance (σ_{ind}) and σ_{ind} (Dingemanse and Dochtermann 2012). As very few individuals in this data set were measured both on the breeding and non-breeding grounds ($n = 19$), R in this context only describes patterns in repeatable phenotypic variation within a life history stage (i.e. breeding or non-breeding), but not patterns in within-individual phenotypic variation between the breeding and non-breeding grounds.

All covariates were z-standardized across groups, which allowed for direct comparisons of the effect sizes among groups for each explanatory variable, as well as among competing hypotheses. We specified each GLMM in a Bayesian framework within R (<www.r-project.org>) with the package 'jagsUI' (Kellner 2015) to call JAGS (Plummer 2003). For each model, we generated posterior distributions from four chains of 100 000 iterations ($\text{thin} = 2$) with additional adapt and burn-in periods of 25 000 iterations each. We considered models in which all parameters had Brooks–Gelman–Rubin criteria (\hat{R}) (Brooks and Gelman 1998) less than 1.1 to have converged.

Model support

The observed magnitude (i.e. effect size) to which within-species variation in body size is associated with spatial variation in an environmental condition is not considered to be a determinant of support of Bergmann's Rule. More importantly, relationships that were explanatory, but counter

to our a priori hypotheses (e.g. positive relationship between temperature and body size) would contribute to 'information explained' in deviance-based model selection frameworks (e.g. AIC, DIC), but would not necessarily be in support of a specific hypothesis. Thus, deviance-based model selection practices may not be an informative approach to decide which hypothesis 'best' fits the data, as highly variable or inconsistently supported relationships may explain more information than more consistent relationships with smaller effect sizes. Instead, we compared the direction of the effect sizes for each season to determine whether each metric of body size was likely influenced by a particular explanatory variable, as well as the extent to which the pattern varied across the species annual lifecycle. At each level of inference, we determined support when the 95% CI drawn from the posterior distribution were in congruence with each a priori hypothesis (i.e. not overlapping zero and in the hypothesized direction).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.97vq77g>> (Gibson et al. 2019).

Results

Support for Bergmann's Rule

Spatial variation in body mass followed Bergmann's Rule and the heat conservation hypothesis throughout the annual life cycle, but spatial variation in wing length showed similar relationships only on the breeding grounds. Body mass was positively associated with latitude of capture during both the breeding ($\beta_B = 1.87$; 95% CI: 1.56–2.18) and non-breeding seasons ($\beta_{NB} = 4.27$; 95% CI: 3.36–5.19; Fig. 3a, c), which resulted in individuals weighing approximately 0.32 and 0.73 g more for each ° latitude increase on the breeding and non-breeding grounds, respectively. Wing length was positively associated with capture latitude on the breeding grounds ($\beta_B = 3.75$; 95% CI: 3.47–4.03; Fig. 3b, d) but not on the non-breeding grounds ($\beta_{NB} = 0.49$; 95% CI: -0.37 to 1.34), which resulted in the average wing being approximately 0.65 mm longer per ° latitude increase on the breeding grounds. Body mass was negatively associated with temperature across both seasons ($\beta_B = -1.06$; 95% CI: -1.23 to -0.90; $\beta_{NB} = -1.30$; 95% CI: -1.58 to -1.03; Fig. 4a, c), which resulted in individuals weighing approximately 0.41 and 0.50 g less for each °C increase in mean environmental temperature on the breeding and non-breeding grounds, respectively. Wing length was negatively related to temperature on the breeding grounds ($\beta_B = -1.97$; 95% CI: -2.13 to -1.88) but not on the non-breeding grounds ($\beta_{NB} = -0.18$; 95% CI: -0.44 to 0.06; Fig. 4b, d), which resulted in the average wing being approximately 0.76 mm shorter per °C increase in environmental temperature on the breeding grounds.

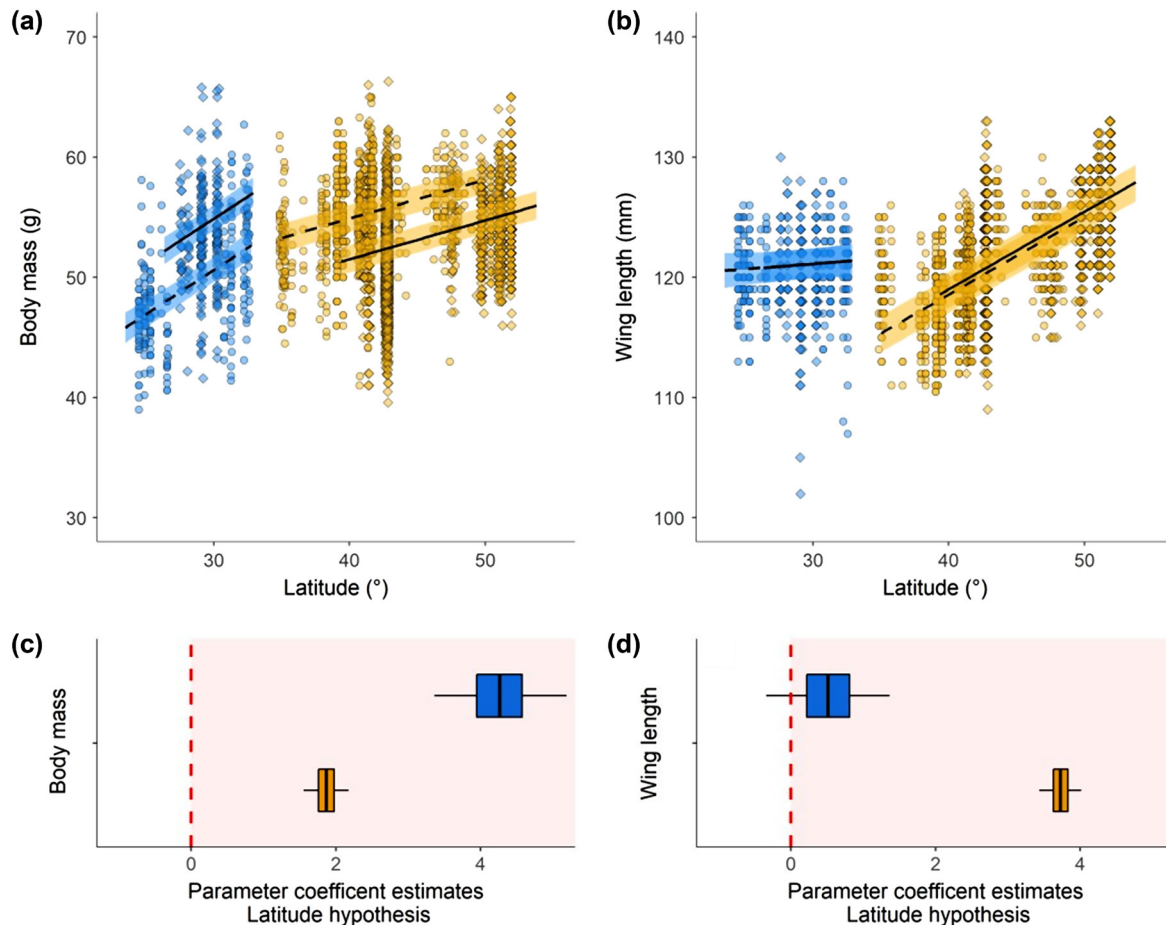


Figure 3. Piping plover body mass (a) and wing length (b) on the Atlantic (dashed lines, circles) and Central (solid lines, diamonds) flyways were positively associated with latitude during the breeding (yellow) season, but only body mass was correlated with latitude on the non-breeding grounds (blue). Scatter plots show the observed data, and regression lines represent the fitted model estimates with 95% Bayesian credible intervals around the median estimate. Parameter support for each of the body mass (c) and wing length (d) models was drawn from the amount of the posterior distribution for each parameter coefficient that was separate from zero (red dashed line) and in congruence with our a priori determination (shaded background), as opposed to counter to prior expectations. Whiskers of box plots represent the 95% CI drawn posterior for each parameter coefficient estimate with the median of the posterior distribution represented by the central line within each box plot.

Influence of migratory behavior on spatial variation in body size

After accounting for temporal and spatial variation in body size associated with the timing and latitude of capture, heavier individuals appeared to migrate longer distances ($\beta_{\text{Mass}} = 0.35$; 95% CI: 0.05–0.66; Fig. 5a, c) than lighter individuals. Likewise, individuals with longer wings tended to migrate farther than individuals with shorter wings ($\beta_{\text{Wing}} = 0.39$; 95% CI: 0.15–0.62; Fig. 5b, d). Regardless of an individual's capture latitude, larger individuals generally undertook longer migrations relative to smaller individuals. On average, individuals were approximately 1.08 g heavier or had wings 1.14 mm longer with each 1000 km increase in how far they successfully migrated.

Range-wide migratory connectivity was intermediate ($MC = 0.45$). However, within-flyway migratory connectivity

was absent ($MC_{\text{central}} = 0.08$; $MC_{\text{Atlantic}} = 0.08$), which indicated that migratory connectivity at the range-wide scale was primarily driven by individuals from the Central flyway overwintering on the Gulf Coast and individuals from the Atlantic flyway overwintering on the Atlantic coast. Thus, migration distance was highly variable among individuals and populations, and individuals from the same breeding areas were not geographically associated with each other on the non-breeding grounds. Additionally, individuals captured at more northern latitudes during the breeding season migrated farther than individuals associated with more southern breeding latitudes ($\beta_{\text{Dist}} = 80.40$ km; 95% CI: 61.70–99.61 km; Fig. 5e). However, this relationship was not supported on the non-breeding grounds, as individuals captured on more southern non-breeding sites did not migrate farther than individuals captured on more northern non-breeding sites ($\beta_{\text{Dist}} = -25.89$ km; 95% CI: -75.52 to 24.31 km; Fig. 5e).

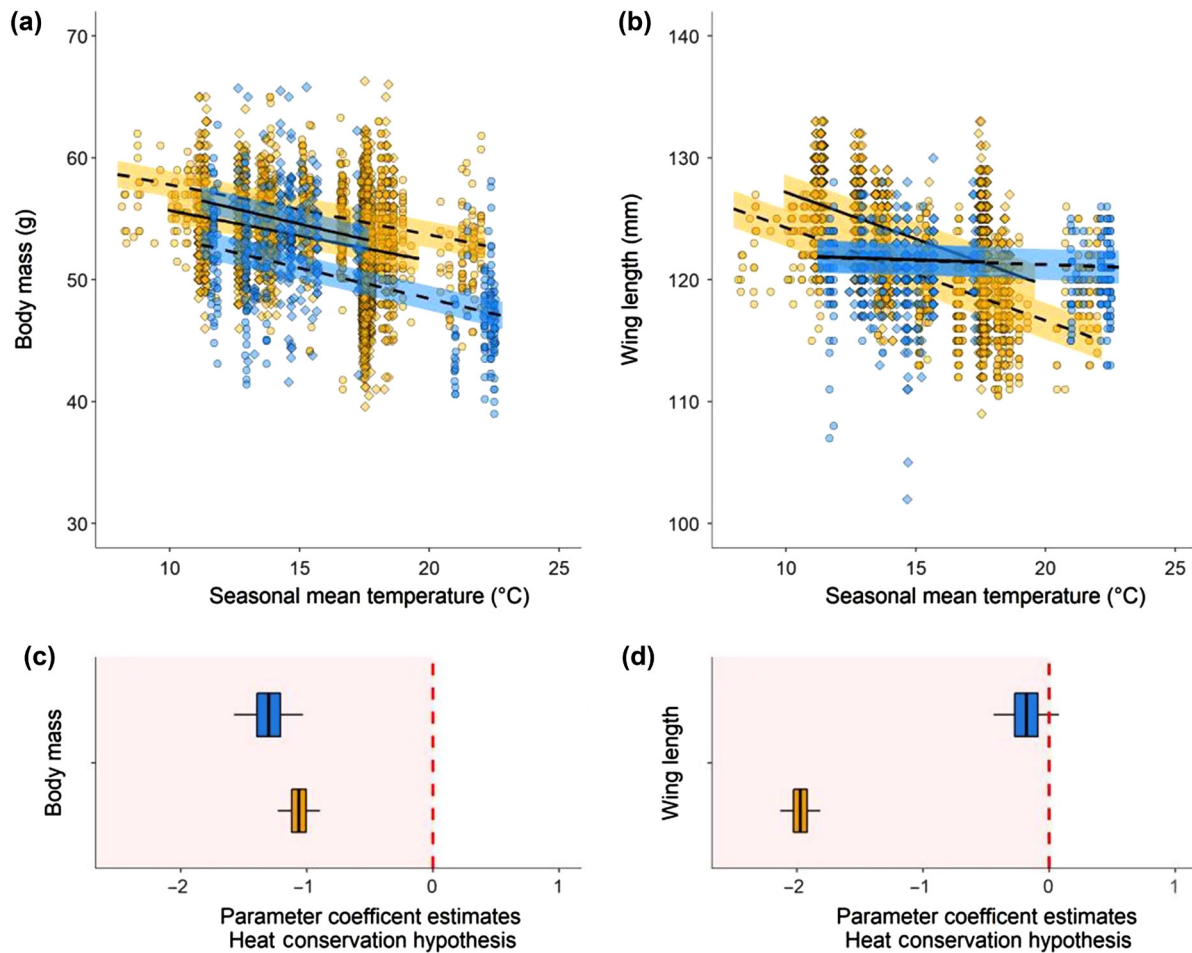


Figure 4. Piping plover body mass (a) and wing length (b) on the Atlantic (dashed lines, circles) and Central (solid lines, diamonds) flyways were negatively associated with environmental temperature during the breeding (yellow) season, but only body mass was correlated with temperature on the non-breeding grounds (blue). Scatter plots show the observed data, and regression lines represent the fitted model estimates with 95% Bayesian credible intervals around the median estimate. Parameter support for each of the body mass (c) and wing length (d) models was drawn from the amount of the posterior distribution for each parameter coefficient that was separate from zero (red dashed line) and in congruence with our a priori determination (shaded background), as opposed to counter to prior expectations. Whiskers of box plots represent the 95% CI drawn posterior for each parameter coefficient estimate with the median of the posterior distribution represented by the central line within each box plot.

Together, these results were in alignment with the results of the migration distance analysis, as they suggest that individuals that migrated greater distances were, on average larger or associated with more northern latitudes during the breeding. However, the variation in body size associated with migratory distance was substantially smaller than the variation best explained by latitude or temperature, therefore patterns in migration were not the primary mechanism driving geographic variation in body size for piping plovers.

Repeatability and seasonal effects

After accounting for known spatial and temporal variation in body size, body mass was estimated to be more repeatable ($R=0.57$; 95% CI: 0.53–0.62) than wing length ($R=0.43$; 95% CI: 0.40–0.48). This suggests that body mass was,

proportional to the among-individual variance in the data, less variable at the individual-level relative to wing length, potentially due to a large amount of variation in wing length associated with molting (Fig. 6b). From an absolute variance perspective, body mass ($\sigma_e=4.83$) was more variable within-individuals than wing length ($\sigma_e=4.09$). However, there was less residual among-individual variation in wing length ($\sigma_{ind}=4.97$) than body mass ($\sigma_{ind}=6.43$), which reduced the relative repeatability of wing length. Contrary to expectations, within-year variation in wing length was similar to that of body mass (Fig. 6a, b), which indicated that both traits exhibited similar patterns of growth during the non-breeding season. However, body mass was clearly more variable than wing length between the breeding and non-breeding seasons, indicative of a potential environmental response in that aspect of size.

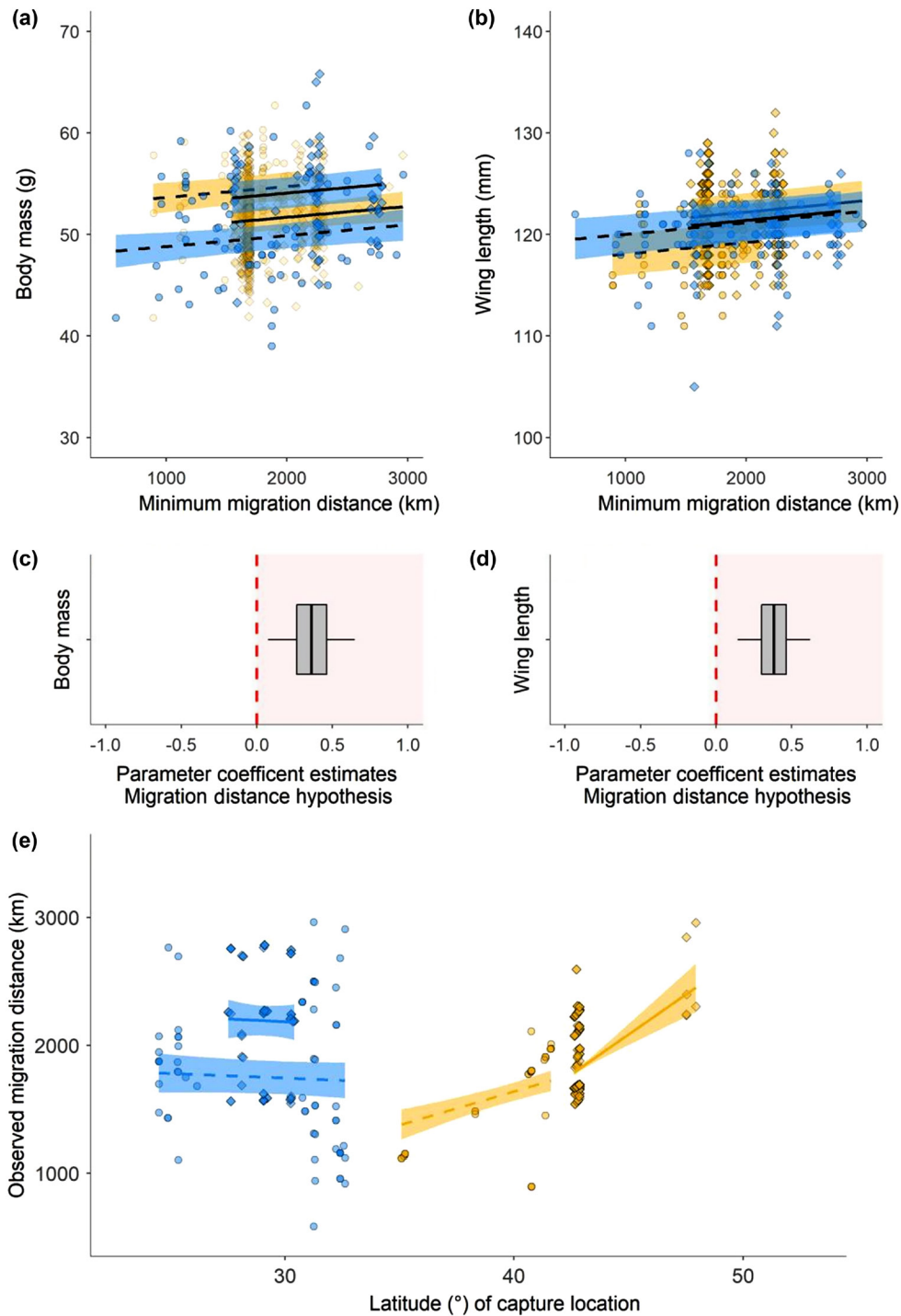


Figure 5. The association between the minimum distance between an individual's breeding (yellow) and non-breeding (blue) territories (migration distance) and an individual's body mass (a) and wing length (b) for piping plovers associated with the Atlantic Coast (dashed lines, circles) or Central (solid lines, diamonds) flyways. Scatter plots show the observed data, and regression lines represent the fitted model estimates with 95% Bayesian credible intervals around the median estimate. Parameter support for each of the body mass (c) and wing length (d) models was drawn from the amount of the posterior distribution for each parameter coefficient was separate from zero (red dashed line) and in congruence with our a priori determination (shaded background), as opposed to counter to prior expectations. Whiskers of box plots represent the 95% CI drawn posterior for each parameter coefficient estimate with the median of the posterior distribution represented by the central line within each box plot. (e) The seasonal (breeding: green; non-breeding: blue) associations between latitude of capture and observed migration distance for piping plovers associated with the Atlantic Coast (dashed lines, circles) or Central (solid lines, diamonds) flyways. Scatter plot represents the observed data, and regression lines represent the fitted model estimates. Error bands represent 95% Bayesian credible intervals.

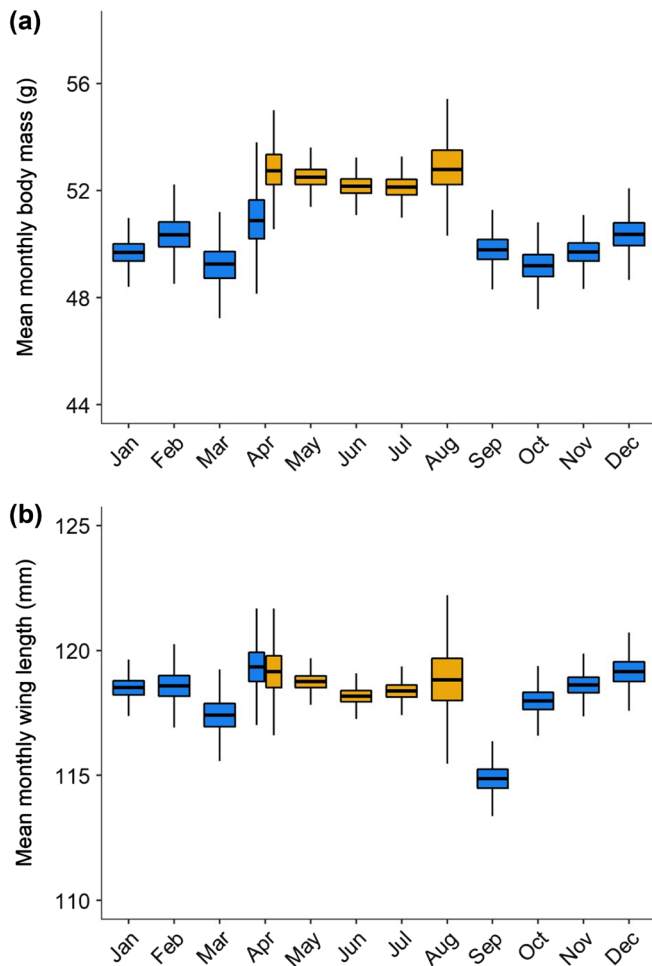


Figure 6. Estimated monthly mean body mass (a) and wing length (b) for individuals associated with the seasonal mean latitude. Blue indicates captures occurred on the non-breeding grounds, and yellow indicates captures occurred on the breeding grounds. Records from April were split into two classifications as they included individuals captured on both the breeding and non-breeding grounds.

Discussion

Piping plover body size generally varied with latitude as predicted under Bergmann's Rule and with temperature as predicted under the heat conservation hypothesis, but with different patterns and inferences depending on the metric of size employed and the season considered. Across both body mass and wing length, larger individuals were on average found at higher latitudes and colder temperatures than smaller individuals. The associations with body mass, a flexible trait, were found on both the breeding and non-breeding grounds despite low migratory connectivity between these seasons. This result suggests that individuals were able to modify their body size via shifts in soft tissue in response to environmental conditions experienced at their current latitude in each season. In contrast, wing length was only correlated positively with latitude, and inversely with temperature, during the breeding season.

Although we found evidence of within-individual variation in wing length, we suspect it was primarily related to the seasonal variation related to normal wear, molt, and growth during the annual life cycle (Piersma and Drent 2003), as opposed to being flexible to local environmental conditions. We attribute the absence of an association between environmental temperature and wing length on the non-breeding grounds to not only wing length being a relatively fixed trait at the individual level, but also that longer-winged individuals migrated longer distances relative to shorter-winged individuals with relatively low levels of migratory connectivity among individuals moving between breeding and non-breeding grounds. These factors resulted in mixing of individuals, and thus wing-size phenotypes, from across breeding latitudes at similar non-breeding latitudes, with no mechanism to change this aspect of size.

Qualitatively, the use latitude or seasonal temperature as predictor variables resulted in similar support for ecogeographic patterns in body size. However, quantitatively, the magnitude of the absolute effect of latitude on either wing length or body mass was approximately twice as large as the effect of seasonal temperature on wing length or body mass. Given that latitude is usually thought to be a proxy for the true driver of ecogeographical pattern in body size, it is counterintuitive for the proxy to be more explanatory than our mechanistic variable, seasonal temperature. However, the seasonal temperature variable is less precise due to being a spatially extrapolated temporal average, which may have reduced its ability to accurately describe the environmental conditions experienced by a specific individual. Latitude of capture, on the other hand, is extremely precise at the individual level, and although it may not adequately explain the functional relationship between body size and environmental conditions, it may often fit the data better.

Patterns and mechanisms of Bergmann's Rule

We found support for Bergmann's Rule and the heat conservation hypothesis as a mechanistic explanation of this pattern in piping plovers, as body size was negatively associated with environmental temperature across seasons. Similar to Ramirez et al. (2007), the relationship between temperature and body mass was more apparent on the non-breeding grounds. Despite these similar patterns, our interpretation is in contrast to Ramirez et al. (2007) based on our understanding from both body mass and wing length together. Ramirez et al. (2007) found that the relationship between temperature and body mass was stronger on the non-breeding grounds, inferred that conditions on the non-breeding grounds were therefore the mechanistic driver of Bergmann's Rule, and that migratory behavior weakened this relationship to a residual association observed on the breeding grounds. Although we agree that the relationship between latitude and body size is likely driven by multiple selective pressures, we found that, in addition to the pattern of body mass across seasons, wing length was only associated with temperature on the breeding grounds. Because structural

size is not flexible, we conclude that the patterns of body size during the breeding season were not simply residual based on selective pressure during the non-breeding season, and in fact structural size was driven by conditions on the breeding grounds. Given that the association between temperature and body mass was stronger on the non-breeding grounds, we may have inferred the same as Ramirez et al. (2007) if body mass was the only trait considered. We further speculate that the stronger association they found between temperature and body mass in the non-breeding season may have been due to flexibility of this trait, and particularly the 1) release from tradeoffs in optimal body size with reproductive costs, as may occur in the breeding season (Kitaysky et al. 2002); and 2) increased variation in body mass related to seasonal hypertrophy (Liknes and Swanson 2011).

In terms of secondary mechanisms affecting biogeographical patterns in body size, we propose that adherence to Bergmann's Rule may be tempered by the ecological costs of being large at lower latitudes (Witter and Cuthill 1993, Gosler et al. 1995). Although primarily informed by interspecific patterns in body size, the association between body size and temperature generally weakens at lower latitudes (Blackburn and Hawkins 2004, Rodríguez et al. 2008). Given that we observed the opposite pattern at lower latitudes, we propose that the risks associated with exposure to predators during resource acquisition may outweigh potential thermoregulatory challenges, selecting for lower masses during the winter to decrease wing loading and aid in predator avoidance (Katti and Price 1999). In this scenario, selection pressure for small body size in warm areas would contribute to the adherence to Bergmann's Rule observed here, but for reasons secondarily related to heat conservation. Indeed, there likely are numerous factors affecting body size beyond what we could address in this work, such as the such as the availability of food resources, or the ability to access these resources (Yom-Tov et al. 2002, Huston and Wolverton 2011). In considering the consistency in selection pressure across seasons, these forces can be further classified into those that are mechanistically consistent or simply consistent in the direction of selection pressure. However, the consistent relationship we found between body mass and temperature across seasons strongly suggests that this trait reacts flexibly to environmental temperature in a way consistent with the heat conservation interpretation of Bergmann's Rule.

Effects of migration on adherence to Bergmann's Rule

Though the migration distance hypothesis did not offer the best explanation for patterns in body size variation, our results support the idea that migratory behavior can influence whether a species adheres to Bergmann's Rule throughout its annual life cycle. Salomonsen (1955) and Hamilton (1961) found that wing length of migratory individuals on the non-breeding grounds did not necessarily follow, and often was counter to, Bergmann's Rule. They attributed this observation to the influence of more northern, and thus larger,

migrants travelling farther south than individuals from more southern, smaller-bodied populations. Similarly, we found that while both mass and wing-size are spatially structured on the breeding grounds, wing-size phenotypes are mixed on the non-breeding grounds.

Wing size can affect migration, particularly in relation to body mass and thus wing loading. There are potential tradeoffs between migratory flight efficiency (Norberg 1995) and an individual's wing load and escape velocity, and therefore, its ability to avoid predators (Burns and Ydenberg 2002) as well as store fat (Witter and Cuthill 1993). Thus, the selective pressures on body size may be more stabilizing than directional (Burns and Ydenberg 2002), such as a tradeoff between positive selection for both musculature and structural size to improve escape velocity and wing shape for migratory potential and negative selection for non-essential aspects of body mass. This may promote phenotypic flexibility, including the muscle and organ hypertrophy often seen prior to seasonal migrations (Piersma 1998).

As piping plover mass is heritable (Catlin et al. 2014), maintaining adherence to Bergmann's Rule in that trait presupposes geographic variation in body size on the breeding grounds but not necessarily on the non-breeding grounds; high natal philopatry (Catlin et al. 2015) therefore reinforces Bergmann's Rule patterns on the breeding grounds. Adherence could be achieved on the non-breeding grounds through either high migratory connectivity or phenotypic flexibility, with evidence here for the latter. Our finding of low connectivity is consistent with what is known of piping plover migratory behavior, as adult plovers tend to migrate independently from their mates and offspring (Weithman et al. 2017), young-of-year plovers generally are not found overwintering with either parent, and this species shows both high breeding (Catlin et al. 2015) and non-breeding site fidelity (Gibson et al. 2018) but without geographic consistency in the arrangement of individuals across seasons. We thus infer that variation in body size, and ultimately size-related migratory distance, leads to this low migratory connectivity based on the physical migratory potential of each individual.

Conclusion

Moving forward, this study revealed two important points in relation to body size adaptation in a migratory species. First, patterns of body size variation and inferences of adherence to Bergmann's Rule are related to which size metric was employed (body mass or wing length) should not be understated. Future research should at least be cognizant of the potential for such mismatch and frame questions accordingly, and at best should employ more than one metric to better describe phenotypic patterns and potential selective tradeoffs therein. In addition, choosing an aspect of size that is under selection along a secondary gradient or cline (e.g. bill length related to probing depth; Nebel et al. 2002; wing length related to migratory constraints, this study) may bias inference, so careful consideration of expectations and extent

of the relationship between size and the explanatory variables of interest should be made prior to analysis.

Second, variation in the distances that individuals migrate affects patterns of latitudinal body size variation. These migratory patterns affect the extent to which the species can adhere to Bergmann's Rule throughout its annual lifecycle. By returning to their natal habitat for the breeding season, piping plovers effectively mate assortatively according to both metrics of body size, which are heritable (Catlin et al. 2014) and thus perpetuate the geographic patterns in size. This intraspecific variation in size can have microevolutionary consequences. As individuals exhibiting a range of size phenotypes associated with discrete breeding populations converge onto common non-breeding grounds (Gratto-Trevor et al. 2012), shifts in the environmental conditions governing these size-related selective pressures (e.g. climate change; Teplitsky et al. 2008, Salewski et al. 2009) may disproportionately impact individuals from certain breeding latitudes, or vice versa, as a function of reduced fitness associated with previously adaptive reaction norms (Reed et al. 2010). Thus, without sufficient individual flexibility, these potential mismatches between phenotype and environment may manifest at the population level as lower local population persistence and ultimately shifts in the species distribution. This highlights the need to consider threats throughout migratory species' complete annual life cycles to fully address conservation concerns and objectives (Marra et al. 2015).

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Supplementary material (available online as Appendix ecog-04325 at <www.ecography.org/appendix/ecog.04325>). Appendix 1.