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# Environmental and Geographic Conditions on the Breeding Grounds Drive Bergmannian Clines in Nightjars

Aaron A. Skinner[1,2] | Alicia M. Korpach[3,4,5] | Susanne Åkesson[6] | Marja H. Bakermans[7] | Erin M. Bayne[8] | Thomas J. Benson[9] | Giovanni Boano[10] | R. Mark Brigham[3] | Simon S. Christiansen[11] | Greg J. Conway[12] | Christina M. Davy[13] | Ruben Evens[14,15] | Kevin C. Fraser[2] | Autumn-Lynn Harrison[16] | Anders Hedenström[4] | Ian G. Henderson[12] | Juha Honkala[17] | Lars B. Jacobsen[18] | Michiel Lathouwers[19,20] | Peter P. Marra[21] | Janet W. Ng[22] | Gabriel Norevik[23] | Amy L. Scarpignato[24] | Kasper Thorup[25] | Christopher M. Tonra[2] | Steven L. Van Wilgenburg[26] | Andrew C. Vitz[27] | Michael Ward[28] | Elly Knight[29]

**Correspondence:** Aaron A. Skinner (skinnerayayron93@gmail.com)

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**Keywords:** annual cycle | Bergmann's rule | body size | Caprimulgidae | GPS tracking | mechanism | nightjars | productivity | seasonality | temperature regulation

## ABSTRACT

**Aim:** To evaluate (1) whether three migratory nightjar species (Family Caprimulgidae) adhere to Bergmann's rule, (2) whether environmental factors on the breeding or wintering grounds determine body size, and (3) which mechanistic hypotheses best explain Bergmannian patterns in body size.

**Location:** North and South America; Europe and Africa.

**Taxon:** Eastern whip-poor-will (*Antrostomus vociferus*), Common nighthawk (*Chordeiles minor*) and European nightjar (*Caprimulgus europaeus*).

**Methods:** We used GPS tracking and morphometric data to assess competing hypotheses explaining variation in body size for each species, based on their breeding ($n = 3388$) and wintering ($n = 189$) locations.

**Results:** All three species exhibited Bergmannian patterns in body size, providing the first evidence that nightjars conform to Bergmann's rule despite adaptations to severe environmental conditions. Environmental and geographic variables at breeding sites were stronger predictors of body size than wintering-site variables. Although we found partial support for Bergmann's temperature regulation hypothesis, geographic variables, rather than specific environmental factors, emerged as the strongest predictors of body size variation.

**Main Conclusions:** Latitude and longitude correlated strongly with environmental variables and migratory distance; thus, these geographical variables likely encompass many factors that influence body size in nightjars. The present study is among the first to use tracking data from individual birds to understand how environmental pressures across the annual cycle are related to body size. Our findings highlight the critical role of geographic breeding-ground factors in shaping Bergmannian patterns, offering robust evidence to support nearly two centuries of research since Bergmann's rule was first described in 1847.

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First, second, and last authors are ordered by their contribution; Authors 3-28 are listed alphabetically.

For affiliations refer to page 13.

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## RESUMEN

**Objetivo:** Evaluar (1) si la regla de Bergmann se observa en tres especies de Caprimúlgidos (Familia Caprimulgidae) migratorios, (2) si los factores ambientales en las áreas de reproducción o invernada influyen más en el tamaño corporal, y (3) qué hipótesis mecanísticas explican mejor los patrones de tamaño corporal asociados a la regla de Bergmann.

**Ubicación:** América del Norte y del Sur; Europa y África.

**Taxón:** *Antrostomus vociferus*, *Chordeiles minor* y *Caprimulgus europaeus.*

**Métodos:** Utilizamos datos GPS para evaluar hipótesis que expliquen las variaciones en el tamaño corporal de cada especie, considerando su ubicación de reproducción e invernada.

**Resultados:** Las tres especies mostraron patrones Bergmannianos, siendo esta la primera evidencia de la regla Bergman en los Caprimúlgidos, a pesar de sus adaptaciones fisiológicas a condiciones extremas. Los factores ambientales en las áreas de reproducción fueron mejores predictores del tamaño corporal que los de las áreas de invernada. Aunque encontramos cierta base para la hipótesis de regulación térmica de Bergmann, las variables geográficas, más que los factores ambientales específicos, resultaron ser los principales predictores de la variación en el tamaño corporal.

**Conclusiones Principales:** La latitud y la longitud mostraron una fuerte correlación con las variables ambientales y la distancia migratoria, lo que sugiere que estas variables geográficas probablemente integran múltiples factores que influyen en el tamaño corporal de los Caprimúlgidos. Este estudio es el primero en utilizar datos de seguimiento de individuos de aves para comprender cómo las presiones ambientales a lo largo del ciclo anual moldean el tamaño corporal. Nuestros hallazgos destacan el papel fundamental de los factores geográficos en las áreas de reproducción para dar forma a los patrones Bergmannianos, proporcionando evidencia sólida que respalda casi dos siglos de investigación desde que la regla de Bergmann fue descrita por primera vez en 1847.

## 1 | Introduction

Bergmann's Rule describes a pattern wherein "body size varies inversely with ambient temperature, so that body size increases with latitude" (translated from the original German by Watt et al. 2010), a rule broadly supported in endotherms at both intraspecific (Ashton 2002; Henry et al. 2023; Meiri and Dayan 2003) and interspecific levels (Fröhlich et al. 2023; He et al. 2023). While thermoregulatory pressures have historically been considered the most likely mechanism driving Bergmann's Rule, other environmental clines (e.g., productivity, seasonality) that are correlated with latitude could also drive clines in body size (Meiri 2011). Despite strong support for Bergmann's Rule, the primary mechanisms causing widespread latitudinal clines in body size remain uncertain. Identifying these mechanisms is critical for predicting the impact of climate change on body size (Teplitsky and Millien 2014).

Several hypotheses have emerged to explain Bergmannian clines (Figure 1; Blackburn et al. 1999; Jones et al. 2005). Hypothesis 1 is phenomenological, because demonstrating a phenomenon (i.e., adherence to Bergmann's Rule) is a prerequisite to testing the mechanism behind the pattern (Meiri 2011). The remaining hypotheses explore mechanisms underlying potential geographic patterns in body size:

1. The geographic pattern hypothesis predicts body size variation with an organism's geographic position on Earth (latitude, longitude or elevation). Latitude and elevation influence temperature, and longitude is related to other potentially important environmental gradients (e.g., precipitation).
2. The temperature regulation hypothesis, originally invoked by Bergmann, suggests that homeothermic organisms closer to the poles experience selective pressure for efficient heat retention and thus have larger bodies to reduce the ratio of body surface area to volume (Salewski and Watt 2017; Watt et al. 2010). This hypothesis has been expanded to include more efficient heat dissipation in hotter climates (Blackburn et al. 1999).
3. The productivity hypothesis suggests that food availability is the most important determinant of body size, as juvenile growth can be limited by nutrition (Huston and Wolverton 2011; McNab 2010; Rosenzweig 1968). Compelling evidence exists for this hypothesis, particularly where food availability and latitude are negatively related, and organismal body size increases with food availability (i.e., larger at more southerly latitudes; Katti and Price 2003; Meiri et al. 2007).
4. The seasonality hypothesis (or the fasting endurance hypothesis; Ashton 2002; Blackburn et al. 1999) suggests that larger individuals have relatively lower metabolic rates compared to their smaller-bodied conspecifics, making them more resilient to periods of limited resources found in more seasonal environments (Lindstedt and Boyce 1985).
5. The migratory distance hypothesis is not related to environmental clines, but instead suggests that body size variation is determined by selective pressures related to long-distance migration (Alerstam et al. 2003; Vágási et al. 2016).

Latitude-body size relationships are more complex in migratory species (Mainwaring and Street 2021; Meiri and Dayan 2003), although they tend to exhibit Bergmannian clines as well (Ashton 2002; He et al. 2023). Long-distance migratory birds are morphologically adapted for lengthy migratory flights (Hein et al. 2012; Phillips et al. 2018), although selective pressures on traits often come into conflict. For example, being light-weight facilitates energy-efficient long-distance flight, yet large wings, muscle hypertrophy and energy stores provide the power and fuel for a costly journey (Alerstam et al. 2003). Wing size is also under strong selection from competing pressures including migration strategy (e.g., energy- or time-efficient strategies), overall distance

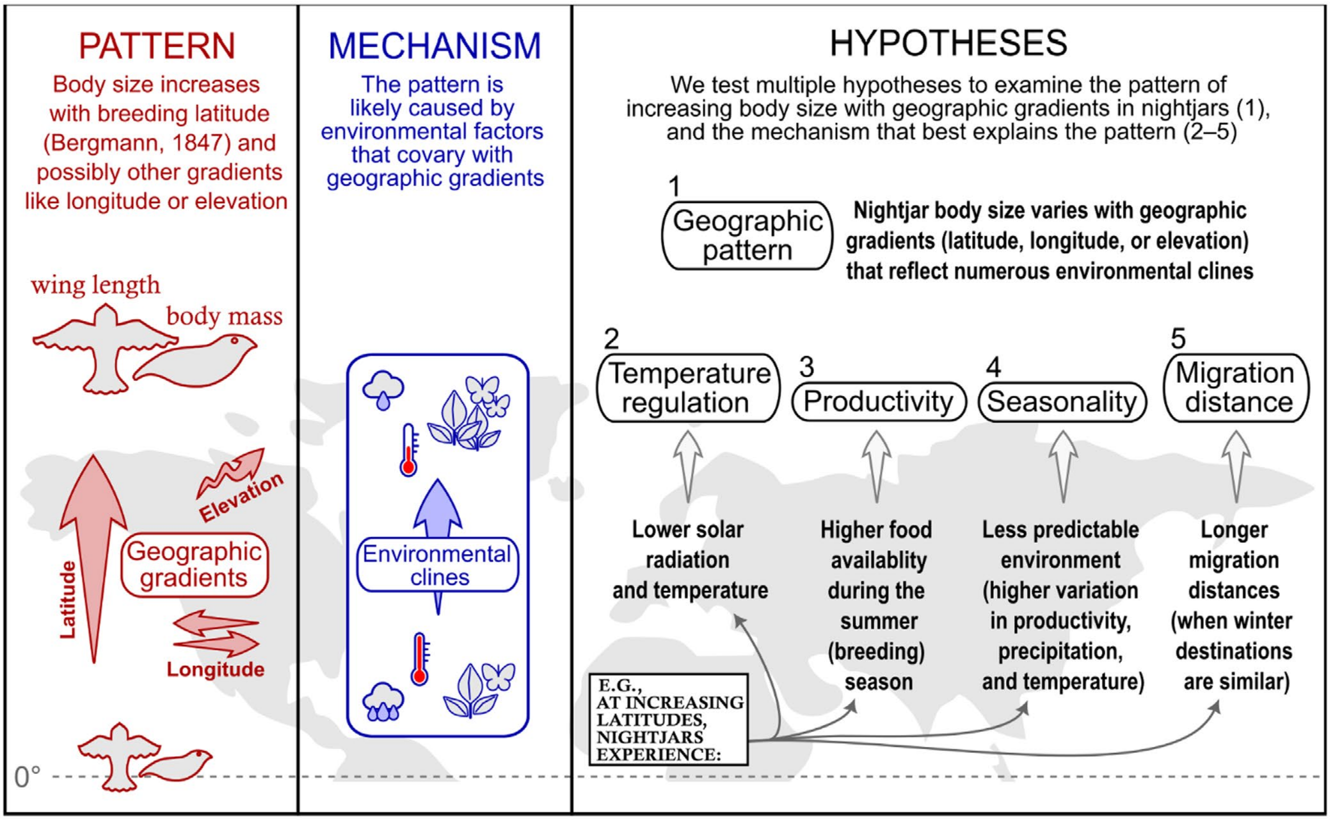

**FIGURE 1** | Body size within a species often varies with latitude or other geographic variables (e.g., elevation and longitude), presumably as a function of underlying environmental gradients. Establishing the existence of a pattern (1) is a prerequisite for testing potential mechanisms (Hypotheses 2–5). Each hypothesis except 5 (migration distance) can be tested in Caprimulgids using environmental data from breeding or winter locations.

and route, foraging behaviour (Marchetti et al. 1995) and habitat associations across the annual cycle (Hedenström 2008; Leisler and Winkler 2003; Rayner 1988; Saino et al. 2017). In species that minimise migration time (Hedenström 2008; Hedenström and Hedh 2024), selection is expected to favour individuals with longer wings and lower body mass at greater migration distances, due to the advantages these traits confer for higher flight speeds, aerodynamic efficiency, and faster energy accumulation at stopovers (Alerstam and Hedenström 1998). Because migration imoses diverse physiological and ecological challenges (Piersma et al. 2005), it is important to consider the migration distance hypothesis (distinct from the "migration ability hypothesis" summarised in Blackburn et al. 1999), where body size evolves in response to the demands of long-distance migration (Gibson et al. 2019).

Uncovering the mechanisms driving Bergmann's Rule is complicated in migratory birds, many of which spend more than half of the year on the wintering grounds (La Sorte et al. 2017), and thus are influenced by varying environmental conditions across the annual cycle. Indeed, some studies have found wintering grounds conditions to be important in determining body size (Bosco et al. 2023; Gibson et al. 2019; Weeks et al. 2020). When this is the case, the distribution of body sizes observed across the breeding range will be influenced by a species' migratory connectivity, or the degree to which individuals that breed in close proximity to each other also overwinter in close proximity (Webster and Marra 2005). Species with weak migratory connectivity may have varied morphology within breeding populations if diverse conditions (e.g., environmental, geographic) exist throughout the wintering grounds.

Adherence to Bergmann's Rule in migratory birds also depends on how body size is measured (Bailey et al. 2020; Teplitsky and Millien 2014). Most studies examining latitudinal clines in body size in birds use wing chord (i.e., the distance from the bend of the wing to the tip of the longest primary feather) to reflect overall body size (Ashton 2002). However, there is no single best metric of body size, particularly for migratory birds. For example, several studies argue that body mass is the best indicator of size (Blackburn et al. 1999; Freeman and Jackson 1990). However, body mass is flexible over time (Gibson et al. 2019), varying with body condition, reproductivestatus, and migratory phase (e.g., fattening prior to departure), and can fluctuate within and between seasons (Guglielmo 2018; Scott et al. 1994; Gosler et al. 1998). Wing chord, on the other hand, is relatively 'fixed' in species that moult flight feathers once a year (feather wear throughout the annual cycle negligibly influences wing length in most species; e.g., Fernández and Lank 2007). Wing chord, therefore, is the most repeatable single measure of body size in birds (Goodenough et al. 2010; Subasinghe et al. 2021; Gosler et al. 1998); however, it can be confounded with selective pressures from migration, such as migration speed (Bennett et al. 2019), distance (Vágási et al. 2016) or strategy (Vincze et al. 2019). Thus, it is important to consider multiple measures of body size as traits may respond differently to selective pressures (Bailey et al. 2020), resulting in 'shape shifting' (i.e., changes in body proportions) as well as changes in body size (Ryding et al. 2021).

Nightjars (Family Caprimulgidae, hereafter 'Caprimulgids') are a widespread group of cryptic, nocturnal, aerial insectivores that are notoriously difficult to study (Holyoak 2001). Temperate-breeding Caprimulgids are migratory with high site fidelity (Bakermans et al. 2022; Ng et al. 2018; Norevik et al. 2025), making them ideal candidates for understanding how evolutionary pressures across the annual cycle influence body size. Furthermore, Caprimulgids have evolved behavioural and physiological adaptations to help withstand severe environmental conditions, which otherwise could strongly select for locally-adapted body sizes. For example, Caprimulgids can experience significant heat stress while roosting or nesting (Newberry et al. 2021; O'Connor et al. 2017), and food intake may be restricted during certain times of the month when low moonlight levels inhibit aerial foraging (Evens et al. 2020; Norevik et al. 2019; Souza-Cole 2021). To withstand these temperature extremes and periods of fasting, Caprimulgids leverage low metabolic rates (Lane et al. 2004), torpor (Brigham et al. 2006; Smit et al. 2011), gular fluttering and efficient evaporative heat dissipation. These adaptations help tolerate severe environmental conditions, which could reduce adherence to Bergmann's rule (He et al. 2023; Ryding et al. 2021). This is consistent with the only available study examining Bergmann's rule in Caprimulgids, which found that the Common nighthawk (*Chordeiles minor*) did not exhibit a Bergmannian cline on the breeding grounds (James 1970).

We used temperate-breeding migratory Caprimulgids as a focal group to explore intraspecifically how multiple factors drive patterns in body size across the annual cycle. We used cross-continental breeding and winter locations from three species: the Neotropical-Nearctic Eastern whip-poor-will (*Antrostomus vociferus*) and Common nighthawk, and the palaearctic-Afrotropical European nightjar (*Caprimulgus europaeus*). We had the following objectives: (1) determine whether migratory species from the Caprimulgid family adhere to the pattern of Bergmann's Rule; (2) evaluate whether environmental conditions at the breeding or wintering grounds have a stronger influence on body size; and (3) test various mechanistic hypotheses for any observed geographic variation in body size (Figure 1).

## 2 | Methods

### 2.1 | Capture, Tag Deployment and Measurement

In total, 7318 Caprimulgids were captured using mist nets and conspecific playback across North America and Europe (Figure 2). We ringed birds using uniquely numbered bands, aged and sexed individuals, and measured wing chord using a wing ruler (precision = 1 mm) and mass using a digital scale (precision = 0.1 g), or a Pesola scale in rare cases (precision = 1.0 g; Pyle 1997). For individuals that were captured multiple times, we averaged wing chord and mass measurements across all captures where the individual was the same age, prioritising morphometrics from adults (each individual was included only once to avoid pseudoreplication). We examined error in wing chord measurements but found negligible differences with individuals recaptured within the same season (Figure S1).

A subset of 215 Caprimulgids were tagged with GPS loggers that tracked their geographic location during migration and on the wintering grounds (Figure 2). Whip-poor-wills and European nightjars were tagged with archival GPS loggers $\leq 3.6\%$ of the bird's mass, and nighthawks were tagged with Argos-GPS satellite loggers $\leq 5.0\%$ of the bird's mass. Tags took GPS fixes (accuracy 10 m) during migration and the over-winter period, with fix frequency ranging from every few hours to every 10 days. We recaptured whip-poor-wills and European nightjars the following summer using the same methodology. See the following references for additional details on field methods for each species (Knight et al. 2021 for nighthawks; Bakermans et al. 2022; Korpach et al. 2022; Skinner et al. 2022 for whip-poor-wills; Lathouwers et al. 2022; Norevik et al. 2019 for European nightjars). Given that only a small subset of individuals had wintering data, we divided our data into two datasets: one with all breeding locations of individuals that passed filtering (hereafter, 'breeding dataset'; see *dataset manipulation* section in the Supporting Information), and one with just individuals with wintering data (hereafter, 'annual cycle dataset').

### 2.2 | Body Size Measures

We used wing chord and body mass as separate measures of body size. We assumed that, while mass is a dynamic trait that fluctuates within and across seasons, that mass on the breeding grounds is correlated with mass on the wintering grounds. We find that this is true when examining the mass of Kirtland's Warbler (*Setophaga kirtlandii*) individuals measured first on the wintering grounds, and then measured on the breeding grounds a few months later ($\beta_{\text{scaled}} = 0.78$, $p = 2.84 \times 10^{-6}$; data from Nathan Cooper, Figure S2). We believe this is a reasonable assumption for our focal species as well for two additional reasons. First, body mass is largely a function of structural size outside of periods of migratory fattening and egg-carrying (Freeman and Jackson 1990). Nightjars in our study had little fat within the stationary breeding season (62.5% of fat scores were 0), and migratory fattening appeared minimal in Whip-poor-will and Nighthawk (Figure S3). Thus, there is evidence that these two species do not deposit extensive fat reserves, so we believe their mass may be less variable compared with other species of migratory birds (also see Hidalgo-Rodríguez et al. 2021). European nightjars did increase in fat as migration approached, so we subset our data to remove individuals captured during periods of migratory fattening (Figure S3). Second, of repeat captures in our dataset, > 50% of the variation in mass *across years* is attributed to measurements coming from the same individual (Figure S3). The most parsimonious explanation for this finding is that body mass is correlated across the annual cycle.

We also examined the intraspecific allometric scaling relationship between mass and wing chord in our focal species (Santoro and Calzada 2022). Generally, wing chord increases proportionally with body mass to the one-third power (i.e., under isometric scaling), but this is species-specific and can vary substantially depending on a species' life history. We used

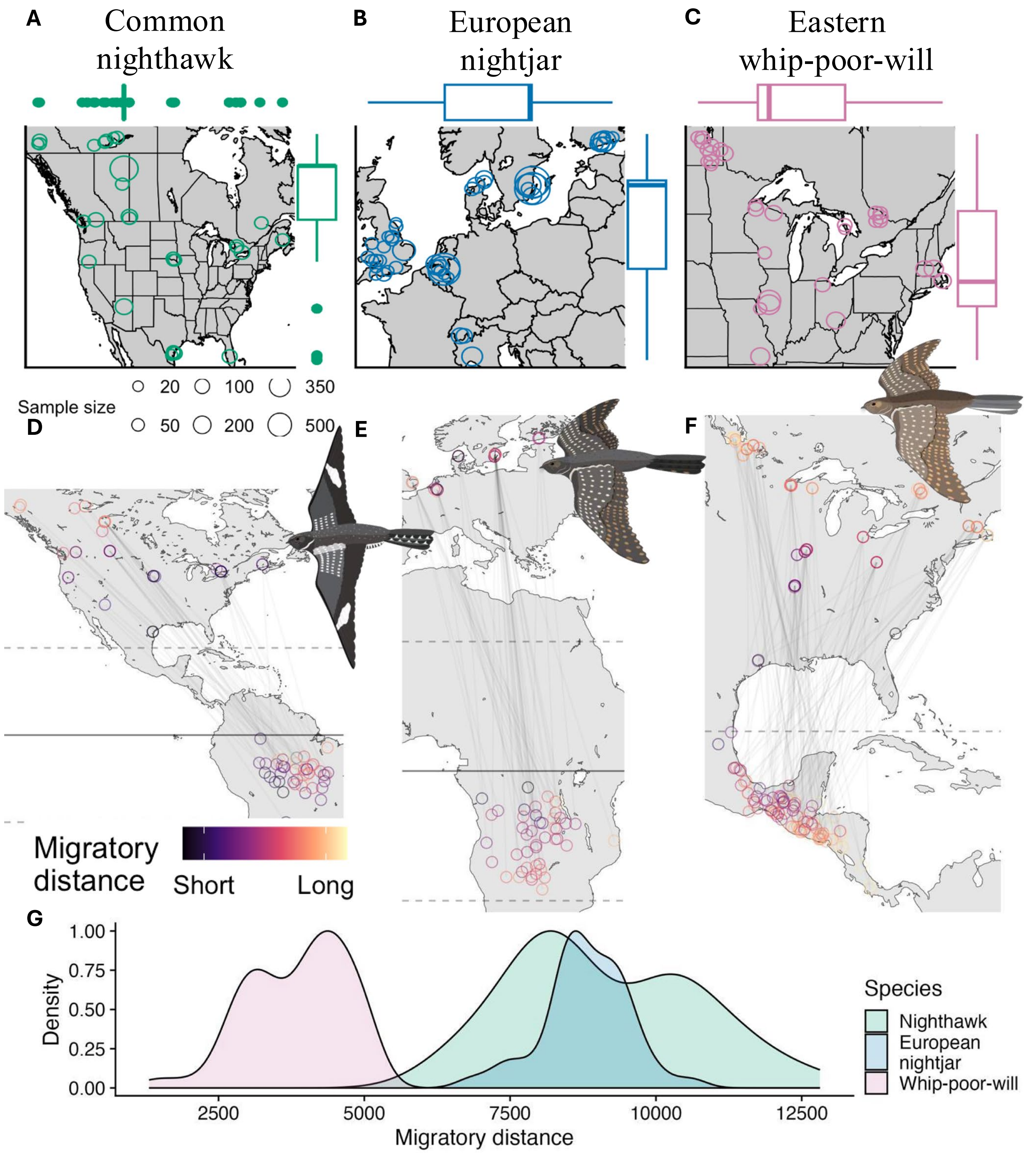

**FIGURE 2** | Panels (A–C) depict breeding locations for 3,388 Caprimulgids captured on the breeding grounds in North America and Europe. Each circle depicts the number of individuals captured in a quarter degree grid cell, and sample sizes should be interpreted as 'less than' the number in question (e.g., the smallest circle is < 20 captures). Box and whisker plots show the distribution of latitudes and longitudes where outliers are depicted as points, the whiskers extend to 1.5 *the interquartile range, the hinges represent the 25th and 75th percentiles, and the central bar is the median. Panels (D–F) show breeding and wintering connections for 189 Caprimulgids tagged with archival GPS tags in North America and Europe. Lines represent the great-circle paths between the breeding and wintering locations (i.e., not the actual migratory paths). Panel G shows the distribution of migratory distances for each species.

standardised major axis regression in the 'smatr' package in R (Warton et al. 2012) to examine scaling of wing and mass in our three species. We found that allometric scaling in European nightjars is consistent with isometry, whereas scaling in nighthawks and whip-poor-wills is hyperallometric (Figure S4).

## 2.3 | Dataset Manipulation

We filtered both breeding and annual cycle datasets in several ways prior to analysis to minimise extraneous variation in body size due to age, sex, time of day, time of year and the potential influence of climate change (Table S1). Our final breeding and annual cycle datasets consisted of 3388 and 189 Caprimulgids, respectively (Section 'Dataset manipulation', Figures S3, S5, S6).

## 2.4 | Environmental Predictors

We extracted environmental data from the summer capture site on the breeding grounds and the first wintering location (determined via GPS data; Figure 2) using Google Earth Engine with the package 'rgee' (Aybar 2021) for each bird. We extracted climate variables from WorldClim 2.1 (historical monthly averages from 1970 to 2000; Fick and Hijmans 2017), and the Enhanced Vegetation Index (EVI) from Landsat 8 Collection Tier 1 8-Day EVI composites (Chander et al. 2009; Huete et al. 2002; see Table 1 for specific environmental variables). We extracted values within a circular buffer corresponding to the mean home range size for each species in each stationary season (whip-poor-will: breeding 500 m, winter 100 m | Bakermans et al. 2022; Skinner et al. 2023; Tonra et al. 2019; Wilson 2003; nighthawk: breeding 5000 m, winter 1000 m | Ng et al. 2018; European nightjar: breeding 500 m, winter 100 m | Mitchell et al. 2020; Sharps et al. 2015). We used migratory dates from tracked individuals and published literature to establish the relevant months that environmental variables influence individuals on both the breeding and wintering grounds (Table S2). We used mean monthly climatic values because (1) our hypotheses did not necessarily correspond to minimum or maximum values, (2) environments were relatively stable during the months in question and (3) the mean, maximum and minimum values were highly correlated. We then averaged climatic variables across months in examination of the temperature regulation and productivity hypotheses, whereas we calculated the coefficient of variation (standard deviation/mean) in examination of the seasonality hypothesis (Table 1).

## 2.5 | Migration Distance

Migration distance was calculated as the sum of the great-circle distances between each consecutive GPS fix between the breeding grounds and the first wintering location. We examined the impact of tag sampling resolution on our calculated migration distances and found that fix rate impacted migration distance only in whip-poor-wills. Thus, we rarefied Whip-poor-will migration data from Canada so that sampling resolution resembled that of other data collectors, after which there was no further relationship between sampling resolution and migration distance ($t = -1.51$; $p = 0.13$, df = 93; Supporting Information 'Rarefaction of GPS data' section).

## 2.6 | Statistical Analysis

We created 12 sets of models, one for each combination of body size measure (2), species (3) and dataset (2). For the breeding dataset, we used Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$) to examine how the confounding factors of age and sex influenced wing and mass, and how the quadratic variable 'time since sunset' (the difference between the capture time and local sunset) influenced just mass (Figures S7, S8), for each species × body size measure (Bartoń 2023). For the annual cycle dataset, we examined the importance of the quadratic variable 'time since sunset' as a confounding variable using a similar AICc framework ('*Confounding variables*' section). While we could not control

**TABLE 1** | Nine combinations of potential hypotheses for the pattern/mechanism that explains Bergmann's rule and the season of influence.

| Hypothesis | | Season | Global model |
|---|---|---|---|
| 1 | Geographic pattern | Breeding | Latitude (+), longitude (+/−), elevation (+) |
| 1 | Geographic pattern | Winter | Latitude (+), Longitude (+/−), Elevation (+) |
| 2 | Temperature regulation | Breeding | Solar radiation (−), Temperature (−) |
| 2 | Temperature regulation | Winter | Solar radiation (−), Temperature (−) |
| 3 | Productivity | Breeding | EVI (+), Precipitation (+) |
| 3 | Productivity | Winter | EVI (+), Precipitation (+) |
| 4 | Seasonality | Breeding | EVI CV (+), Precipitation CV (+), Temperature CV (+) |
| 4 | Seasonality | Winter | EVI CV (+), Precipitation CV (+), Temperature CV (+) |
| 5 | Migration distance | NA | Migratory distance (+/−) |

*Note:* Numbers for hypotheses (H) match those used in the text. We show the associated global model, and the predicted direction of effect (on the breeding grounds) for each variable: Positive (+), negative (−) or differing predictions (+/−) by species or dependent variable. For example, for the migration distance hypothesis we predict that wing length will increase, but body mass will decrease, with longer migratory journeys. Note the geographic pattern hypothesis is phenomenological (i.e., examining patterns in body size), where all other hypotheses test the underlying mechanisms.
Abbreviations: CV, coefficient of variation; and EVI, Enhanced Vegetation Index.

for age or sex in analyses using the annual cycle datasets due to small and uneven sample sizes, we conducted the analysis twice, once using all ages and sexes ($n = 189$) and once using only adult males ($n = 145$).

For each of the 12 model sets, we organised the potential predictors of body size into unique and mutually exclusive hypotheses (Table 1) and generated a global model for each hypothesis. Thus, model sets consisted of a global model and all subsets of the global model for each hypothesis, as well as a null model to help determine the explanatory ability of the other models. This approach provides a framework for nested model construction from a theoretically justified global model, rather than arbitrary combinations of predictors. For the annual cycle dataset we generated two global models for each hypothesis, one for the breeding grounds and one for the wintering grounds. This allowed for direct competition of breeding versus wintering models (in line with objective 2), and kept the number of models reasonable for each species × body size measure (Burnham et al. 2011). The number of models differed in each species × body size measure × dataset combination due to collinearity between predictor variables (Figure S9). There were 116 models from the breeding dataset (between 17 and 21 models per species × body size measure) and 226 models from the annual cycle dataset (between 34 and 42 models per species × body size measure). We scaled and centered all predictor and response variables to allow for the comparison of parameter estimates across species. We modelled the relationship between body size and our predictors using linear regression, and considered models within $\Delta AIC_c \leq 4$ from the top model to be 'important' for addressing our three objectives, only if the null model was not within $\Delta AIC_c \leq 4$ (Burnham et al. 2011; Burnham and Anderson 2004). We then conducted model averaging on parameters from 'important' models to understand the strength and direction of the effects (Bartoń 2023). Inclusion of models $2 < \Delta AICc < 4$ in model averaging is a more conservative approach than using a cutoff of $\Delta AICc < 2$, as it incorporates additional uncertainty in our parameter estimates (Burnham et al. 2011; Richards et al. 2011). See 'Model validation' section in the Supporting Information for details on the inspection of residuals, multicollinearity and spatial autocorrelation (Figures S10–S11).

## 2.7 | Evaluation of Objectives

To test whether Caprimulgids adhere to Bergmann's rule (Objective 1), we examined model selection results along with model averaged parameter estimates. A species followed Bergmann's rule if: (1) breeding latitude was in at least one 'important' model, (2) birds were larger at higher breeding latitudes and (3) the 85% unconditional confidence interval did not overlap zero.

To test the relative influence of breeding vs. wintering grounds on body size (Objective 2), we examined the number of models from the breeding vs. wintering grounds within $\Delta AIC_c \leq 4$ of the top model. The number of models with breeding vs. wintering data was roughly equivalent in each annual cycle model set, although across all species × body size measures there were 8 more models with wintering data due to reduced collinearity in predictor variables on the wintering grounds.

To evaluate which hypothesis best explains variation in body size (Objective 3), we compared the strength and direction of parameter coefficient estimates for each species × body size measure using the dataset we determined most important in Objective 2. For example, if the breeding grounds are determined more important than the wintering grounds in the annual cycle analysis, we will assess support for the varying hypotheses using the breeding dataset.

# 3 | Results

## 3.1 | Confounding Variables

In the breeding dataset, the most supported model controlling for confounding variation in both mass and wing included age and sex for all species (except age for nighthawks; see Supporting Information "Confounding variables" section), and the quadratic variable time since sunset in controlling for mass (Table S3). In the annual cycle dataset, the top model included the time since sunset in mass models for European nightjars and whip-poor-wills (Table S4).

## 3.2 | Objective 1—Adherence to Bergmann's Rule

Breeding latitude appeared in 'important' models for all species × body size measures (Table 2). Parameter estimates were always positive and 85% unconditional confidence intervals did not overlap zero (Figure 4).

## 3.3 | Objective 2—Importance of Breeding vs. Wintering Grounds

Using the annual cycle dataset, models from the breeding season received the highest likelihood in four of six species × body size measure combinations, while the null model appeared within $\Delta AIC_c \leq 4$ for the other two species × body size measures (Nighthawk and European nightjar mass; Table S5). We found qualitatively similar patterns whether we ran the analysis with all individuals or only adult males (Figures S12–S13). Thus, we examine Objective 3 using the breeding dataset.

## 3.4 | Objective 3—Testing Hypotheses

When using the breeding dataset, we observed support for the geographic pattern hypothesis in all species × body size measures (Figure 3), and support for the temperature regulation hypotheses in the whip-poor-will x mass model set (Table 2). Latitude was a particularly strong predictor of body size (six of the seven largest parameter estimates; Figure 4 and Table S6), and was positively correlated with both mass and wing chord for all three species. Longitude had a relatively weaker effect on size but still appeared in 'important' models in whip-poor-will and nighthawk mass, as well as whip-poor-will wing, and was positive in these three cases. Elevation was also found in 'important' models for all species × body size measures, although the direction of effect was opposite to that predicted by Bergmann's rule for whip-poor-will wing chord, and the 85% confidence intervals

**TABLE 2** | 'Important' ($\Delta \mathrm{AIC}_c \leq 4$) models plus the top model from each hypothesis constructed using the breeding data for six species × body size measures. $K$ is the number of model parameters (the intercept and residual variance parameters are both estimated as well), *wt* is the model weight, and $R^2$ is the coefficient of determination.

**Nighthawk mass—fixed variables: time since sunset$^2$ + sex**

| **Model** | ***K*** | **ΔAICc** | **wt** | **−2 Log-likelihood** | **Hypothesis** | **$R^2$** |
|---|---|---|---|---|---|---|
| Elevation + Latitude + Longitude | 8 | 0.00 | 0.79 | −371.49 | Geographic pattern | 0.39 |
| Latitude + Longitude | 7 | 2.72 | 0.20 | −373.90 | Geographic pattern | 0.38 |
| Temperature | 6 | 17.98 | 0.00 | −382.58 | Temperature Regulation | 0.34 |
| EVI CV + Temperature CV | 7 | 28.09 | 0.00 | −386.59 | Seasonality | 0.33 |
| Precipitation | 6 | 41.85 | 0.00 | −394.51 | Productivity | 0.29 |
| Null | 5 | 45.87 | 0.00 | −397.57 | NA | 0.28 |

AICc value of best model = 759.46.

**Nighthawk wing—fixed variables: sex**

| **Model** | ***K*** | **ΔAICc** | **wt** | **−2 Log-likelihood** | **Hypothesis** | **$R^2$** |
|---|---|---|---|---|---|---|
| Latitude | 4 | 0.00 | 0.36 | −431.70 | Geographic pattern | 0.18 |
| Elevation + Latitude | 5 | 0.26 | 0.32 | −430.80 | Geographic pattern | 0.19 |
| Latitude + Longitude | 5 | 1.76 | 0.15 | −431.55 | Geographic pattern | 0.18 |
| Elevation + Latitude + Longitude | 6 | 2.29 | 0.11 | −430.78 | Geographic pattern | 0.19 |
| Temperature | 4 | 4.33 | 0.04 | −433.86 | Temperature Regulation | 0.17 |
| Precipitation | 4 | 21.90 | 0.00 | −442.65 | Productivity | 0.13 |
| Temperature CV | 4 | 25.07 | 0.00 | −444.24 | Seasonality | 0.12 |
| Null | 3 | 35.77 | 0.00 | −450.61 | NA | 0.08 |

AICc value of best model = 871.52.

**European nightjar mass – fixed variables: age + time since sunset$^2$ + sex**

| **Model** | ***K*** | **ΔAICc** | **wt** | **−2 Log-likelihood** | **Hypothesis** | **$R^2$** |
|---|---|---|---|---|---|---|
| Latitude | 7 | 0.00 | 0.71 | −1546.88 | Geographic pattern | 0.50 |
| Elevation + Latitude | 8 | 1.78 | 0.29 | −1546.76 | Geographic pattern | 0.50 |
| Solar radiation + Temperature | 8 | 12.93 | 0.00 | −1552.33 | Temperature Regulation | 0.49 |
| Temperature CV | 7 | 92.70 | 0.00 | −1593.23 | Seasonality | 0.46 |
| Precipitation | 7 | 116.26 | 0.00 | −1605.01 | Productivity | 0.45 |

(Continues)

**TABLE 2** | (Continued)

**European nightjar mass – fixed variables: age + time since sunset$^2$ + sex**

| **Model** | ***K*** | **ΔAICc** | **wt** | **−2 Log-likelihood** | **Hypothesis** | ***R*²** |
|---|---|---|---|---|---|---|
| Null | 6 | 177.32 | 0.00 | −1636.55 | NA | 0.43 |

AICc value of best model = 3107.83.

**European nightjar wing – fixed variables: age + sex**

| **Model** | ***K*** | **ΔAICc** | **wt** | **−2 Log-likelihood** | **Hypothesis** | ***R*²** |
|---|---|---|---|---|---|---|
| Elevation + Latitude | 6 | 0.00 | 0.52 | −2405.48 | Geographic pattern | 0.35 |
| Latitude | 5 | 0.16 | 0.48 | −2406.57 | Geographic pattern | 0.34 |
| EVI CV + Temperature CV | 6 | 250.31 | 0.00 | −2530.64 | Seasonality | 0.26 |
| Precipitation | 5 | 377.20 | 0.00 | −2595.09 | Productivity | 0.21 |
| Solar radiation + Temperature | 6 | 550.31 | 0.00 | −2680.63 | Temperature Regulation | 0.14 |
| Null | 4 | 769.07 | 0.00 | −2792.03 | NA | 0.03 |

AICc value of best model = 4823.

**Whip-poor-will mass – fixed variables: age + time since sunset$^2$ + sex**

| **Model** | ***K*** | **ΔAICc** | **wt** | **−2 Log-likelihood** | **Hypothesis** | ***R*²** |
|---|---|---|---|---|---|---|
| Temperature | 7 | 0.00 | 0.42 | −611.32 | Temperature Regulation | 0.35 |
| Latitude + Longitude | 8 | 0.26 | 0.37 | −610.42 | Geographic pattern | 0.35 |
| Elevation + Latitude + Longitude | 9 | 1.78 | 0.17 | −610.14 | Geographic pattern | 0.35 |
| Precipitation CV + EVI CV + Temperature CV | 9 | 12.90 | 0.00 | −615.70 | Seasonality | 0.34 |
| Precipitation | 7 | 19.84 | 0.00 | −621.24 | Productivity | 0.32 |
| Null | 6 | 121.33 | 0.00 | −673.02 | NA | 0.17 |

AICc value of best model = 1236.87.

**Whip-poor-will wing – fixed variables: age + sex**

| **Model** | ***K*** | **ΔAICc** | **wt** | **−2 Log-likelihood** | **Hypothesis** | ***R*²** |
|---|---|---|---|---|---|---|
| Latitude + Longitude | 6 | 0.00 | 0.45 | −589.66 | Geographic pattern | 0.42 |
| Elevation + Latitude + Longitude | 7 | 0.22 | 0.40 | −588.74 | Geographic pattern | 0.42 |

(Continues)

**TABLE 2** | (Continued)

**Whip-poor-will wing – fixed variables: age + sex**

| Model | *K* | ΔAICc | wt | −2 Log-likelihood | Hypothesis | $R^2$ |
|---|---|---|---|---|---|---|
| Elevation + Latitude | 6 | 3.17 | 0.09 | −591.24 | Geographic pattern | 0.42 |
| Precipitation CV + Temperature CV | 6 | 6.44 | 0.02 | −592.88 | Seasonality | 0.41 |
| EVI + Precipitation | 6 | 13.73 | 0.00 | −596.53 | Productivity | 0.41 |
| Temperature | 5 | 14.89 | 0.00 | −598.13 | Temperature Regulation | 0.40 |
| Null | 4 | 144.14 | 0.00 | −663.77 | NA | 0.23 |

AICc value of best model = 1191.48.

overlapped zero half of the time (Figure 4). Finally, the univariate model with temperature was the top model for predicting whip-poor-will mass (Table 2), and had a large effect size in the direction consistent with Bergmann's rule (Figure 4). Table S6 shows parameter estimates and unconditional confidence intervals from 'important' models and Table S7 shows full model selection results.

## 4 | Discussion

Bergmann's rule is perhaps the oldest biogeographical rule, yet not all warm-blooded vertebrates follow this rule (Åkesson et al. 2020; Ashton et al. 2000; Blackburn and Gaston 1996; Meiri and Dayan 2003; Watt et al. 2010), and a consensus regarding the underlying mechanisms has evaded scientists. The present work is among the first to leverage tracking technology to understand how selective pressures from across the annual cycle are related to body size in migratory birds (but see Shipley et al. 2022). We found that the three Caprimulgid species we examined (Common nighthawk, Eastern whip-poor-will, and European nightjar) adhere to Bergmann's rule. We also found that explanatory variables associated with the breeding grounds, particularly related to a bird's geographical location on Earth, were the best predictors of body size. We did not find conclusive evidence for any single mechanistic hypothesis and suggest that geographic variables likely rose to the top in model selection because they combine information across many important environmental gradients. Our results demonstrate that despite being migratory, nocturnal and having adaptations to mitigate severe environmental conditions, Caprimulgids exhibit similar patterns in body size variation as other groups of birds, reinforcing the generalizability of Bergmann's rule.

### 4.1 | Influence of Winter vs. Breeding Grounds on Body Size

Variables measured at breeding locations were better predictors of body size than variables at wintering locations in all three species, particularly when wing chord was used as the size metric. The breeding grounds may be more important than wintering grounds in determining body size for three primary reasons. First, thermoregulation in the nestling period, before birds have grown feathers, may be particularly impactful on stress levels, survival and ultimately in determining body size at the population level (Newberry and Swanson 2018). This is likely exacerbated in Caprimulgids, which build scrape nests in open habitats like the forest floor or bare ground, and are more exposed to environmental conditions relative to species that build insulated nests in closed habitats (e.g., trees or bushes; Mainwaring and Street 2021). Experimental and observational evidence suggests that high temperatures during development lead to smaller nestlings, and that these size differences persist as adults (Andrew et al. 2017; Youtz et al. 2020; but also see Nord and Nilsson 2011). While there is strong evidence for the importance of heat dissipation during hot breeding months (Andrew et al. 2018; Speakman and Król 2010), thermoregulatory pressures from a warming climate may shape body size in complex ways, potentially

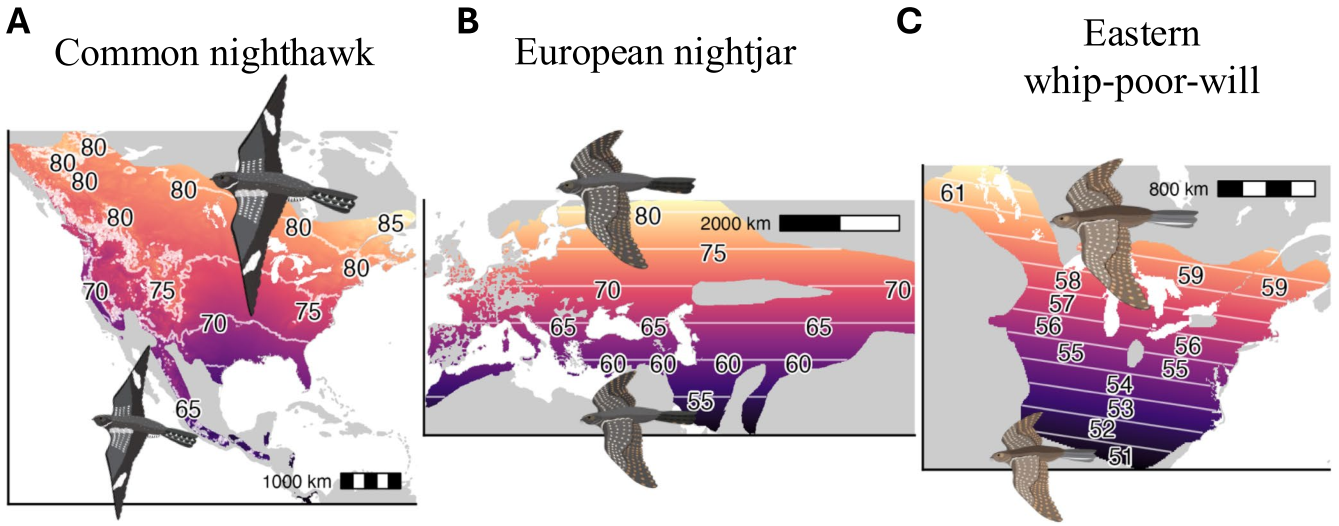

**FIGURE 3** | Isoclines of body mass based off of the top geographic model for three Caprimulgid species (Nighthawk: Latitude + longitude + elevation; European nightjar: Latitude; Whip-poor-will: Latitude + longitude). Mass was predicted for adult males and while holding the time since sunset at the mean for each species. Spatial predictions for wing chord were qualitatively similar.

exerting different selective pressures at different life stages (e.g., nestling vs. adult). Thus, additional research is needed to understand how selection acts across life stages and whether body size trade-offs exist between early-life constraints (e.g., chick survival) and adult thermoregulatory demands (Shipley et al. 2022).

Second, it is possible that the responsibilities associated with chick-rearing (particularly feeding and thermoregulation) during the breeding period may prevent Caprimulgids from using evolved behavioural or physiological mechanisms for thermal tolerance (e.g., torpor), or strongly select for birds that can withstand periods of prolonged fasting (e.g., allowing for continued thermoregulation of chicks). Thus, Caprimulgids may rely more on behavioural approaches to maintain thermoregulatory and metabolic equilibrium in the non-breeding season, while relying on optimal surface-area-to-volume ratios during the breeding season.

Third, all three Caprimulgids studied here had low migratory connectivity, such that birds from across large breeding ranges converge on core wintering areas (Knight et al. 2021; Korpach et al. 2022; Norevik et al. 2020; Skinner et al. 2022). We expect winter environmental conditions to be fairly uniform in species with low migratory connectivity, reducing the amount of environmental heterogeneity experienced on the wintering grounds in our study populations (Gibson et al. 2019; Jones et al. 2005). That being said, the distribution of breeding and wintering latitudes were similar in all three species, and birds could select wintering locations at smaller spatial scales to provide more favourable environmental conditions for their given body size (especially when wintering in mountainous areas). Thus, we conclude that the distribution of breeding and wintering latitudes were comparable, and instead the relative stability and benign conditions experienced on the tropical wintering grounds likely result in weaker selective pressures than the breeding grounds (e.g., winter environments may be entirely in species' thermoneutral zones; Ryding et al. 2021).

Finally, it is important to recognise the limitations of our annual cycle dataset, and the inconclusive results from this analysis when mass was the dependent variable. Indeed, the null model was the most supported in nighthawk and European nightjar mass in the annual cycle dataset. Given that nighthawk and European nightjars exhibited strong geographic gradients in body mass when we used the full breeding dataset, there was likely not enough of a latitudinal gradient on the breeding grounds (particularly in European nightjars), or statistical power to detect an effect in the annual cycle dataset in these two species × body size measures. Furthermore, we recognise that mass was only measured on the breeding grounds, and mass may change significantly throughout the annual cycle (perhaps even adaptively in response to the winter environment; Gibson et al. 2019). Future work measuring mass during wintering months would greatly improve our understanding of how environmental pressures from across the annual cycle influence body size.

## 4.2 | Mechanisms Underlying Bergmann's Rule

We were unable to identify a single mechanism that clearly explained the Bergmannian pattern for all three Caprimulgid species. Combinations of geographic variables (latitude, longitude and elevation) were almost always better predictors of body size than environmental variables (as in Gibson et al. 2019), suggesting that multiple environmental variables that covary with geographic clines are responsible for determining body size within Caprimulgid species, and that geographic variables may reflect a composite of mechanisms. In migratory organisms, Bergmann's rule has often been assessed with the most easily accessible data—geographic information from the breeding grounds (Ashton 2002). Our research suggests that these readily available data may indeed represent the most important variables influencing body size, and thus, past conclusions on Bergmann's rule in migratory birds are likely robust. Despite the difficulties in determining mechanisms in highly

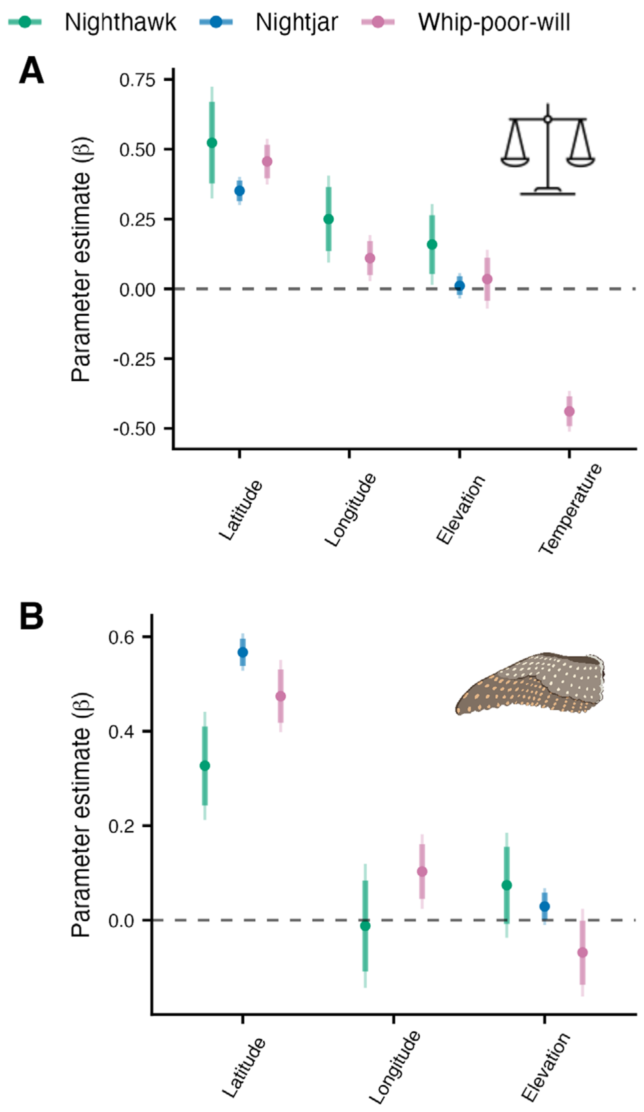

**FIGURE 4** | Parameter estimates (circles) 85% (thick error bars) and 95% (thin error bars) unconditional confidence intervals of all variables from 'important' models (those within 4 ΔAICc points of the top model), estimated using breeding season data from 3388 Caprimulgids. We included the 85% confidence intervals because they align with an AIC model selection framework and acknowledge the explicit link between AIC scores and *p*-values (Sutherland et al. 2023). We also include 95% confidence intervals to facilitate comparison with related work. Both predictor and response variables were scaled and centered to facilitate direct comparison between species.

collinear systems (Wigginton and Dobson 1999; Yom-Tov and Geffen 2011), examining model selection results, strength and direction of parameter estimates, and correlations between geographic and environmental variables can still provide insights into the mechanisms at play.

Latitude was the strongest predictor of body size in nearly all species × body size measures, with larger-bodied individuals occurring at higher latitudes. Generally, at more northerly latitudes conditions were cooler (and with less solar radiation), drier, less productive and more seasonal. Temperature regulation likely has a dominant role in determining body size in these Caprimulgid species (especially whip-poor-wills), given that it was often the mechanistic model with the most support (as in Fan et al. 2019; Henry et al. 2023; Romano et al. 2021). Seasonality models often received some support as well, and parameter estimates tended to be positive and did not overlap zero (as predicted by Bergmann's rule). Low nighttime temperatures early in the breeding season may limit flying insect activity (Taylor 1963), particularly at the northern extremes of breeding ranges. Thus, larger-bodied individuals would be better-equipped to withstand such variations in prey availability (Ashton 2002; Blackburn et al. 1999; Lindstedt and Boyce 1985). Migration distances were also substantially longer for individuals breeding at more northerly latitudes in whip-poor-wills and nighthawks, consistent with the migration distance hypothesis for wing but not mass. Finally, we conclude that productivity is unlikely to be the driving force behind Bergmannian clines in Caprimulgids, given that more northerly sites were less productive than more southerly sites. Note that this is in direct contrast to previous studies that show body size tracking environmental gradients irrespective of latitude (Katti and Price 2003; Meiri et al. 2007; Nwaogu et al. 2018). Importantly, our data exhibited a negative productivity cline in 'ecologically and evolutionarily available' productivity as well (i.e., during the peak breeding season; unpublished data), which may be more relevant in determining body size in some species (Huston and Wolverton 2011).

The correlation between longitude and body size in whip-poor-wills and nighthawks was counterintuitive. Whip-poor-wills and nighthawks tended to be larger farther east, where it is generally hotter, wetter, more productive and less seasonal, and it seems unlikely that these variables would exert selective pressures on body size differently than they do along latitudinal gradients. An examination of parameter estimates associated with productivity models and migration distance in nighthawks confirmed that these factors were not responsible for variation in size along longitudinal gradients. This suggests that there could be unexplored additive or interactive effects (or functional forms) of environmental variables that were not explored in this study, or alternative pressures influencing body size along longitudinal gradients (e.g., pesticide use; Martínez-Padilla et al. 2017). While longitude has not been included in many Bergmann's rule studies, we argue that it can be related to important environmental gradients, similar to latitude or elevation, and thus should be included in studies aiming to understand environment-morphology relationships (e.g., James 1970).

Elevation can also be an important predictor of body size in birds, where colder temperatures at higher elevations are thought to increase body size for thermoregulatory reasons (Blackburn and Ruggiero 2001; García et al. 2021; Romano et al. 2021). We observed this pattern in nighthawks and European nightjars but not in whip-poor-wills. In European nightjars and whip-poor-wills, effect sizes were relatively small, 85% confidence intervals largely overlapped zero, and elevational gradients were minimal (95% of individuals occupied a gradient < 500 m). Thus, we focus on nighthawk response to elevational gradients. In addition to cooler climates at higher elevations, nighthawks experienced increased solar radiation and more arid climates, which may favour larger individuals as water lost to the environment is reduced in larger birds (James 1970; Jirinec et al. 2021; Nwaogu et al. 2018; Yom-Tov and Geffen 2006). Future work should include models testing the impact of both fluid and temperature regulation in selecting for avian body size. Finally, through examining parameter coefficients we note there is marginal evidence of increased *relative* wing length at higher elevations in European nightjars (Gutiérrez-Pinto et al. 2014; Youngflesh et al. 2022). Future work should tie wing and mass measurements together at the level of the individual (e.g., allometric-informed indices of relative wing length; Youngflesh et al. 2022) to detect shapeshifting along geographical or environmental gradients.

### 4.3 | Conclusions for Conservation

Biological response to climate change can be split into three main categories: (1) range distribution shifts, (2) adaptation through phenotypical or phenological change or (3) local extinction (Millien et al. 2006). There is evidence that the northern limit of the nighthawk's breeding range is shifting northward (see eBird trend map) (LaSorte and Thompson III 2007), and climate change models predict that whip-poor-will ranges have the potential to expand at the north edge and contract at the south edge under a warming scenario (https://www.audubon.org/field-guide/bird/eastern-whip-poor-will). However, it is unclear whether Caprimulgid morphologies are also tracking environmental conditions through time, as seen by many species globally (Jirinec et al. 2021; Salewski et al. 2010; Weeks et al. 2020). Species that respond to spatial temperature gradients generally also respond to temperature increases through time (Youngflesh et al. 2022), suggesting that our focal species may be capable of altering morphology in response to increasing temperatures associated with climate change. However, given that Caprimulgids have high site fidelity (Bakermans et al. 2022; Ng et al. 2018; Norevik et al. 2025), long lifespans (> 10 years) and low diversity in migratory strategy (e.g., obligate migrants, small non-breeding ranges), they may be particularly susceptible to rapid changes in climate (Both et al. 2010; Gilroy et al. 2016). Our data show that European nightjars have increased in wing chord and decreased in body mass from 1990 to 2022, suggesting that they have increased in relative wing length in response to increasing temperatures (as in several other recent studies; Ryding et al. 2024; Weeks et al. 2020; Youngflesh et al. 2022). Long-term morphological datasets are needed for nighthawks and whip-poor-wills, and future research should work to better understand whether morphological changes (1) represent a genetic or plastic response to temperature gradients (Millien et al. 2006; Romano et al. 2025; Teplitsky and Millien 2014), and (2) if any observed changes are biologically significant for thermoregulation (Nord et al. 2024).

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### Affiliations

[1]Department of Zoology, The University of British Columbia, Vancouver, British Columbia, Canada | [2]School of Environment and Natural Resources, The Ohio State University, Columbus, Ohio, USA | [3]Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba, Canada | [4]Department of Biology, University of Regina, Regina, Saskatchewan, Canada | [5]University of Winnipeg, Winnipeg, Manitoba, Canada | [6]Department of Biology, Lund University, Lund, Sweden | [7]Department of Integrative and Global Studies, Worcester Polytechnic Institute, Worcester, Massachusetts, USA | [8]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada | [9]Illinois Natural History Survey, Prairie Research Institute, University of Illinois Urbana-Champaign, Champaign, Illinois, USA | [10]Museo Civico di Storia Naturale, Turin, Italy | [11]Skagen Bird Observatory, Birdlife Denmark, Skagen, Denmark | [12]British Trust for Ornithology, Norfolk, UK | [13]Department of Biology, Carleton University, Ottawa, Ontario, Canada | [14]Biodiversity Research Centre, Université Catholique de Louvain (UCL), Louvain-la-Neuve, Belgium | [15]Department of Biology, Behavioural Ecology and Ecophysiology Group, University of Antwerp, Wilrijk, Belgium | [16]Autumn-Lynn Harrison, Migratory Bird Center, Smithsonian's National Zoo and Conservation Biology Institute, Washington, District of Columbia, USA | [17]Zoology Unit, Finnish Museum of Natural History, Pb 17, 00014, University of Helsinki, Helsinki, Finland | [18]Center for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen, Denmark | [19]Research Group: Zoology, Biodiversity and Toxicology, Hasselt University, Centre for Environmental Sciences, Diepenbeek, Belgium | [20]University of Namur, Department of Geography, Institute of Life, Earth and Environment (ILEE), Namur, Belgium | [21]The Earth Commons Institute; Department of Biology, McCourt School of Public Policy, Georgetown University, Washington, District of Columbia, USA | [22]Environment & Climate Change Canada, Canadian Wildlife Service, Regina, Saskatchewan, Canada | [23]Department of Biology, Centre for Animal Movement Research, Lund University, Lund, Sweden | [24]Migratory Bird Ccenter, Smithsonian's National Zoo and Conservation Biology Institute, Washington, District of Columbia, USA | [25]Center for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen, Denmark | [26]Environment & Climate Change Canada, Canadian Wildlife Service, Saskatoon, Saskatchewan, Canada | [27]Massachusetts Division of Fisheries and Wildlife, Westborough, Massachusetts, USA | [28]Department of Natural Resources and Environmental Sciences, University of Illinois Urbana-Champaign, Urbana, Illinois, USA | [29]Migratory Bird Center, Smithsonian's National Zoo and Conservation Biology Institute, Washington, District of Columbia, USA

### Author Contributions

A.A.S. and E.K. conceptualized the article. A.A.S. led the analysis with assistance from E.K. and A.M.K. A.A.S. wrote the initial draft. All authors provided morphological and/or tracking data and contributed comments on manuscript drafts.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data and code needed to reproduce all analyses, figures, and tables in the main text of the manuscript are available on Dryad (https://datadryad.org/stash/share/3Ic-u0MVyd1TgknPDNcMOZBw2O4lBxdD_4np321u2Yw). The collation of this rich morphological dataset with information across the annual cycle is the most complete for Caprimulgids to date. We would be interested in future collaborations using these data.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.