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Primary productivity explains size variation across the Pallid bat's western geographic range

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Abstract

1. Body size is associated with many aspects of the life history, ecology and physiology of animals. Within a species, body size can vary substantially across space and time, and the mechanisms generating these patterns have been the focus of evolutionary and ecology research.
2. Bergmann's rule predicts a negative relationship between body size and temperature across the geographic range of endothermic animals; larger animals have a lower surface to volume ratio, which would allow for greater heat conservation. Despite the broad support for this pattern, its underlying mechanisms are heavily debated. Numerous alternative explanations have been proposed to explain why larger animals are found in colder climates and vice versa, including heat dissipation, environmental seasonality and resource availability.
3. We used the Pallid bat, *Antrozous pallidus*, as a model to evaluate Bergmannian size patterns and the relative support for major explanatory hypotheses of geographic body size variation. We tested the hypothesis that geographic size variation is predicted by productivity, as opposed to seasonality, heat conservation or dissipation, or some combination of these processes. Additionally, we investigated the potential ecomorphological consequences of size variation in Pallid bats by determining if skull shape (an indicator of bite performance) varies with size.
4. Whereas we did find that Pallid bat populations in northern latitudes are composed of larger individuals, our results suggest that net primary productivity and, to a lesser extent heat conservation, best explain size variation throughout the western range of this species. We also found that skull shape in Pallid bats changes in tandem with skull size, with larger bats having cranial traits associated with greater bite force production.
5. The results of our study indicate that variation in resource availability may be a key factor underlying spatial patterns in size, morphology and, possibly, feeding performance within wide-ranging bat species.

KEYWORDS
Bergmann's rule, Chiroptera, geometric morphometrics, productivity, spatial autoregressive model, Vespertilionidae

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1 | INTRODUCTION

Body size is tightly associated with the life history, ecology and physiology of animals (Isaac, 2005; Lindstedt & Boyce, 1985; Porter & Kearney, 2009). Within a species, adult body sizes can vary substantially across space and time, and the mechanisms generating these patterns have been the focus of evolutionary and ecology research for centuries (Ashton, 2002a; Bergmann, 1848; Mayr, 1956; Scholander, 1955). Of the most debated ecogeographic "rules," Bergmann's rule (1847, translation in James 1970) predicts a negative relationship between body size and temperature in endothermic animals. In its original formulation, Bergmann proposed that among these animals, a larger body size is selected for in colder environments due to its lower surface to volume ratio, which minimizes heat loss (Mayr, 1956). Whereas thermoregulation was the original mechanism proposed, latitude is frequently used as a proxy when testing for conformity to Bergmann's rule (reviewed in Ashton, Tracy, & Queiroz, 2000).

Bergmann's rule is broadly supported in endothermic vertebrates (i.e. individuals are larger at higher latitudes and/or in habitats with lower temperatures; e.g. Ashton, 2002a; Blackburn & Hawkins, 2004; Meiri & Dayan, 2003) and has also been invoked to explain latitudinal size gradients for various ectothermic vertebrates (Ashton, 2002b; Ashton & Feldman, 2003; Lindsey, 1966; Rypel, 2014), and arthropods (Arnett & Gotelli, 1999; Blanckenhorn & Demont, 2004; Parsons & Joern, 2014; Shelomi, 2012; Stillwell, Morse, & Fox, 2007). However, there are many taxa that do not exhibit these size clines (for reviews, see Ashton et al., 2000; Meiri & Dayan, 2003), as well as little support for the hypothesis that thermoregulation underlies clinal variation in body size (McNab, 2010; Scholander, 1955). Additionally, many ectotherms are characterized by reverse Bergmannian clines (Ashton & Feldman, 2003), which seem to be the product of season length limiting growth (e.g. Blanckenhorn & Demont, 2004).

Several alternative processes have been proposed to explain the pattern predicted by Bergmann's rule, including heat dissipation, and coping with environmental seasonality or changes in resource availability. James (1970) reformulated Bergmann's hypothesis and suggested that pressures for more efficient heat dissipation drive body size variation. Under this scenario, selection would favour a smaller body size in warm and humid environments (Correll, Prowse, & Prideaux, 2015). Conversely, Rosenzweig (1968) argued that primary productivity, and thus resource availability, influences body size. In this case, decreased food availability in environments with low primary productivity is predicted to limit body size. However, Boyce (1978) suggested that environmental seasonality explains patterns of body size variation; larger individuals are more resilient to the periods of food shortages that are associated with more seasonal environments.

More recently, McNab (2010) proposed a generalized "resource rule" in which the combined effect of prey size, food abundance and availability drive patterns of intraspecific body size variation across space and time. In the context of global climate change, the productivity hypothesis has gained increased support for explaining recent temporal changes in body size among mammals (Eastman, Morelli, Rowe, Conroy, & Moritz, 2012; Tomassini, Colangelo, Agnelli, Jones, & Russo, 2014; Yom-Tov, 2003) and birds (Cooch, Lank, Rockwell, & Cooke, 1991; Leafloor, Ankney, & Rusch, 1998). Additionally, precipitation frequently emerges as a key predictor of geographical size variation, leading to the conclusion that productivity or resource availability is major drivers of this pattern (Blois, Feranec, & Hadly, 2008; Bodganowicz, 1980; Cardini, Jansson, & Elton, 2007; O'Keefe, Meachen, Fet, & Brannick, 2013). However, given that environmental variables are frequently intercorrelated, understanding the mechanism generating "Bergmannian" size gradients requires contrasting multiple hypotheses simultaneously to gauge the relative contribution of different ecological or physiological processes (Ashton et al., 2000).

In this study, we use the Pallid bat, *Antrozous pallidus* (Le Conte 1856), as a model to evaluate the hypothesis that differences in primary productivity explain geographic variability in body size. The Pallid bat is a geographically widespread species in the Family Vespertilionidae, occurring throughout Western North America (Martin & Schmidly, 1982). Despite its extensive size variability across its range, previous studies have failed to identify clear geographic patterns, or associations between body size and environmental factors in this species (Martin & Schmidly, 1982). The Pallid bat is heterothermic and uses torpor on a daily basis to minimize thermoregulatory costs (Vaughan & Shea, 1976). Although little information exists in their winter hibernation phenology (Orr, 1954), torpor depth and duration are strongly influenced by ambient temperature conditions throughout their range (O'Shea & Vaughan, 1977; Rambaldini & Brigham, 2008a). The Pallid bat is generally considered a gleaning insectivore, relying on auditory cues to find large ground-dwelling arthropods (e.g. crickets, beetles, scorpions, centipedes; O'Shea & Vaughan 1977), but its' diet and foraging habits are highly variable throughout its range (Frick, Shipley, Kelly, Heady, & Kay, 2014; Herrera, Fleming, & Findley, 1993; Johnston & Fenton, 2001). In addition to arthropods, Pallid bats have been documented to consume small vertebrates (Lenhart, Mata-silva, & Johnson, 1894; O'Shea & Vaughan, 1977) and are unique among vespertillionids by being the only species known to exhibit facultative nectarivory and frugivory (Aliperti, Kelt, Heady, & Frick, 2017; Frick, Heady, & Hayes, 2009; Frick, Price, Heady, & Kay, 2013; Howell, 1980). The exploitation of cardon cacti (*Pachycereus pringlei*) has been observed exclusively in populations from Baja California, Mexico; thus, it remains unclear whether or not this foraging strategy is widespread across areas where the Pallid bat co-occurs with other columnar cacti. Given the Pallid bat's broad geographic distribution across a wide latitudinal range and diverse habitats, thermal ecology, varied diet and foraging behaviour, and extensive size variation, this species is an ideal model to assess whether resource availability is associated with size variation across their range.

Here, we first assessed whether Pallid bats conform to Bergmann's rule, characterized by larger individuals at northern portions of its range. We then tested the hypothesis that geographic size variation is driven by differences in primary productivity (and thus resource availability), as opposed to seasonality or temperature, or some combination of these factors. Consistent with findings in other endothermic vertebrates (Correll et al., 2015; Goodall & Crespo, 2013; Gür & Kart Gür, 2012; Morales-castilla, Rodríguez, & Hawkins, 2012; Wolverton, Huston, Kennedy, Cagle, & Cornelius, 2009) and ectothermic species (invertebrates; Pearson & Knisley, 1985; Arnett & Gotelli, 1999), we predicted that larger bats would be found in areas with higher annual net primary productivity (NPP). We also evaluated the potential ecomorphological influence of size variation in Pallid bats, in particular as it pertains to diet. Both size and cranial shape directly influence bite performance in mammals (e.g. bite force; Anderson, Mcbrayer, & Herrel, 2008; Freeman & Lemen, 2010; Santana, Grosse, & Dumont, 2012; Santana & Miller, 2016), and thus the spectrum of prey available for consumption (Aguirre et al., 2003; Marroig & Cheverud, 2005; Santana, Dumont, & Davis, 2010). In several mammal groups, cranial morphology is known to change in tandem with changes in skull size within and among species, and such isometric or allometric patterns can lead to differences in feeding performance and diet (e.g. Christiansen & Adolfssen, 2005; Marroig & Cheverud, 2005; Santana & Cheung, 2016). We tested the hypothesis that Pallid bats exhibit variation in skull shape that is associated with skull size. We predicted that larger individuals would exhibit skull features that enhance bite force, which would in turn enable them to have more generalized diets in areas of high productivity, where a wider range of prey types are expected to be available. Although we focus on a single predator species, our results have broader implications for understanding the mechanisms that drive body size variation among animals.

2 | MATERIALS AND METHODS

2.1 | Specimens and geometric morphometric analysis

Our sample was composed of 175 adult Pallid bat crania (male = 82, female = 93) spanning a latitudinal gradient across the western part of their range (Figure 1, Table S1). Using a Canon Powershot SLR camera mounted on a copy stand, we obtained digital images (4,000 × 3,000 pixels) on lateral and ventral views of the cranium. We placed specimens on a custom platform to consistently align them for each view. We then digitized homologous and sliding semilandmarks for the lateral and ventral cranium (Figure 2, Table S2) using TPSDIG v 2.22 (Rohlf, 2006). To minimize measurement error resulting from landmark digitization, the same investigator carried out landmark placement for all specimens for the lateral and ventral cranium, respectively. We also selected a random subset of 10 specimens to perform landmark placement in triplicate on three separate occasions, from which we analysed the repeatability of landmark placement.

To obtain size and shape variables from the digitized landmarks configurations, we carried out a Generalized Procrustes Analysis using the package *"geomorph"* v. 3.0.0 (Adams & Otárola-Castillo, 2013) within R v. 3.1.2 (R Core Team, 2017). Generalized Procrustes Analysis removes the effects of rotation and scale from landmark data to obtain size and shape variables that are independent from one another (Rohlf & Slice, 1990). We used centroid size (i.e. the square root sum of the squared distances of each landmark from the centre of the landmark configuration) as a measure of cranium size and proxy for body size. Cranium centroid size is preferable to body mass as measure of body size because the latter varies substantially across nights and seasons in temperate bats (Coutts, Fenton, & Glen, 1973; Speakman & Rowland, 1999). We used the set of Procrustes coordinates as shape variables, and we also extracted the aligned Procrustes residuals to characterize skull shape in the context of allometry analyses. Due to the redundancy of landmarks given the symmetry in the ventral view of the cranium, we extracted the symmetrical shape component using the function *bilat.symmetry* in the *geomorph* package (Adams & Otárola-Castillo, 2013) for subsequent shape analyses.

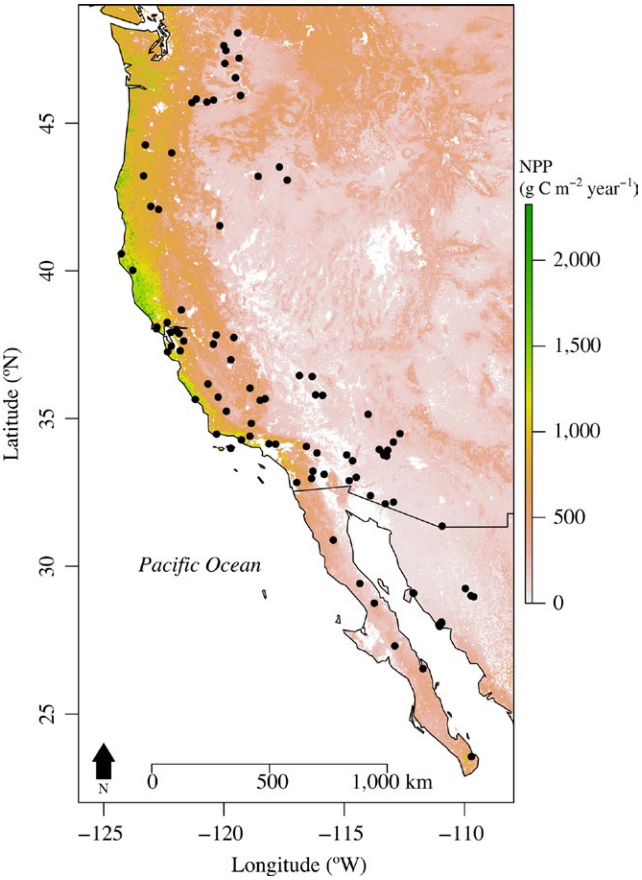

FIGURE 1 Collection localities for Pallid bat, *Antrozous pallidus*, specimens (black circles). Colours on the map represent mean annual net primary productivity (g C m^{-2} $year^{-1}$), obtained as gridded data from the Moderate Resolution Imaging Spectroradiometer MOD17 land product dataset (see Section 2)

2.2 | Environmental variables

We acquired spatially gridded environmental datasets to inform tests of the heat conservation and dissipation, seasonality and

FIGURE 2 Landmark configuration for the (a) lateral and (b) ventral views of the cranium of the Pallid bat. Black circles indicate homologous landmarks, and white circles indicate curve-sliding semilandmarks (placed equidistantly between homologous landmarks)

productivity hypotheses. Using the geographic coordinates of the collection site recorded for each individual, we extracted the corresponding environmental variables for all individuals. We first downloaded current climate data (World Clim 1.4) from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at 5 arc-minute resolution (*c*. 10 km grids). The current climate dataset is composed of temperature and precipitation raster layers, which were generated using data from weather station monthly averages between the years 1960–1990 (Hijmans et al., 2005).

To test the seasonality hypothesis, we extracted values representing both annual temperature and precipitation variation (the annual standard deviation of mean monthly temperature and precipitation, respectively). We then evaluated the explanatory power of temperature and precipitation seasonality, and used an information theory approach to select a single seasonality variable with the greatest explanatory power (Burnham & Anderson, 2002). We found that temperature seasonality provided a better fit to the size data ($\Delta AIC_c = 25$). Therefore, we used temperature seasonality in subsequent model comparisons.

For testing the heat dissipation and conservation hypotheses, we used the maximum temperature of the warmest month and minimum temperature of the coldest month, respectively, for each specimen. To account for potential coordinate errors in the specimen locality information, we applied a bilinear interpolation on these climatic variables. This method averages all values from the nearest four cells (10 km grids) of the specimen's locality.

The "resource rule" (McNab, 2010) predicts that body size is largely driven by the size, abundance, and availability of food resources. However, since detailed data on prey (e.g. arthropod) abundance are lacking for most bat species, indices, such as NPP, are frequently used as a proxy for resource availability (Gür & Kart Gür, 2012; Kaspari, Alonso, & O'Donnell, 2000; Wolverton et al., 2009; Zhao, Heinsch, Nemani, & Running, 2005). Therefore, to evaluate the productivity hypothesis, we obtained annual NPP (g C m^{-2} $year^{-1}$) gridded data, at a resolution of 30 arc seconds (*c*. 1 km grids), from the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD17A3 land product dataset (Zhao et al., 2005; http://www.ntsg.umt.edu). The MOD17 algorithm calculates gross primary productivity (GPP) using a combination of photosynthetically active radiation estimates from satellite data (MODIS), existing land cover classifications and local climate data, while accounting for daily respiration and maintenance costs.

TABLE 1 Summary of major hypotheses proposed to explain Bergmannian size patterns, the predicted trends and environmental variables used to test each hypothesis in this study

Hypotheses	Predictions	Environmental Variables	Descriptions
Heat conservation	Size increases as temperature decreases	*MinWinTemp*	Minimum temperature of the coldest month
Heat dissipation	Size decreases with humidity and environmental temperature	*MaxSumTemp*	Maximum temperature of the warmest month
Seasonality	Size increases with seasonality	*TempSeas*	Temperature seasonality
Productivity	Size increases with productivity and resource availability	*NPP*	Mean annual net primary productivity

The annual NPP estimate is the sum of daily GPP, after accounting for plant growth and maintenance, and closely corresponds to other, independently derived NPP estimates (Zhao et al., 2005). Therefore, as a proxy for local productivity to test the productivity hypothesis, we used the mean annual NPP averaged over all 13 years (2000–2013) for which the MOD17 estimates are available. For each specimen, we calculated average annual NPP within a 5.6 km radius, which was the mean coordinate uncertainty among specimens in our dataset and corresponds to estimated foraging ranges of Pallid bats (Baker et al., 2008). We extracted all environmental variables within R v. 3.1.2 (R Core Team, 2017), using the package "*raster*" v. 2.3 (Hijman, 2015).

2.3 | Data analyses

Prior to investigating geographic size variability, we tested for any evidence of sexual size dimorphism using Welch's two sample *t* test. Male and female Pallid bats did not differ in size (see Section 3), and therefore, we pooled males and females for subsequent analyses. To test for a latitudinal trend in skull size, we carried out ordinary least squares (OLS) linear regression, using centroid size as the response variable and latitude as the explanatory variable. To evaluate the relative support for each of the four hypotheses (Table 1) explaining size variability in the Pallid bat, we generated a candidate set of models including the main effects of each environmental variable and additive combinations of main effects using OLS linear regression. In addition to OLS linear models, which do not account for spatial autocorrelation, we fit spatial simultaneous autoregressive (SAR) models (Cressie, 1993) to account for spatial dependence in the data. Specifically, we used a spatial error model (SAR_{err}), which outperforms other SAR models in terms of parameter estimate precision, reduction in residual spatial autocorrelation and type I error control (Kissling & Carl, 2008). The SAR_{err} model is an extension of an OLS regression: $\mathbf{Y} = \boldsymbol{\beta} + \lambda W u + e$, with additional terms representing the spatial structure (λW) in the spatially dependent error term (u). In this equation, W is the spatial weight's matrix, and λ is the spatial autoregressive coefficient (Cliff & Ord, 1981; Kissling & Carl, 2008). We defined the weight's matrix (W) using row standardization, where we assigned equal weights to all neighbouring sites within a 100 km radius. We then fit SAR_{err} models using the *errorsarlm* function in the "spdep" package (Bivand, Pebesma, & Gómez-Rubio, 2013).

To enable comparison of effect sizes among predictor variables, we first centred each explanatory variable by their respective mean and then scaled these values by the standard deviation from the mean. Prior to fitting multiple regression models, we calculated Spearman's rank correlation coefficient (r) between all pairs of environmental variables. If two variables were highly correlated ($r > .7$), we did not include both variables in the same statistical model (Table S3). We used Akaike's information criterion corrected for small sample size (AIC_c) to select the top OLS and SAR_{err} models from the full candidate set of models explaining size variation in the Pallid bat. We considered the minimum AIC_c score, ΔAIC_c and relative Akaike weight (w) when ranking candidate models (Burnham & Anderson, 2002; Diniz-filho, Rangel, & Bini, 2008). Finally, to assess residual spatial autocorrelation, we calculated Moran's *I* for distance bands of 100 km from the residuals of each top ranking OLS and SAR_{err} model using the *correlog* function in the "pgirmess" package (Giraudoux, 2015). We considered significant spatial autocorrelation when the *p*-value of the Moran's *I* coefficient was below $\alpha = 0.05$ after Bonferroni correction (Bivand et al., 2013).

To test for correlated changes in skull shape with skull size, we conducted Procrustes ANOVAs, with a randomized residual permutation procedure (10,000 permutations) for significance testing, using the *proc.D.allometry* function in the "*geomorph*" package (Adams & Otárola-Castillo, 2013; Collyer, Sekora, & Adams, 2015). We first performed a Procrustes ANOVA to test for differences size–shape relationship between males and females. As these were NS (see Section 3), we pooled data from males and females to estimate the amount of variation in shape that is explained by covariation with size.

3 | RESULTS

We found no evidence of sexual size dimorphism when we used centroid size of the lateral or ventral views of cranium as proxies for *A. pallidus* body size, (lateral cranium: $t = -0.57$, $df = 173$, $p = .57$, ventral cranium: $t = -0.27$, $df = 173$, $p = .78$). Our analysis of replicate error in landmark digitization suggested that repeatability of landmark placement was higher for the ventral cranium (92%) than the lateral cranium (84%). Therefore, here we present the results of size analyses for the ventral cranium (results were nearly identical for the lateral cranium; however, *results not shown*). When we evaluated the hypotheses proposed to explain geographic size variation in the pallid bat, spatial ($\mathrm{SAR_{err}}$) models always outperformed equivalent aspatial models (OLS) on the basis of $\mathrm{AIC_c}$ and model fit (R^2) (Tables 2 and S4). We focus on the results from spatial models below, although patterns were generally consistent whether or not we accounted for spatial dependency in the data (Figures 3 and 4).

Consistent with Bergmann's rule, we found that Pallid bats tend to be larger in the northern part of their range (Table 2). Among our full set of candidate models, the top ranking spatial model included environmental variables associated with three of the hypotheses: productivity, seasonality and heat conservation (w = 0.46, Table 2, Figures 3 and 4). However, a second model representing the productivity and heat conservation hypotheses also received considerable support ($\Delta\mathrm{AIC_c}$ = 0.16, w = 0.43, Table 2). The top ranking aspatial model included the same environmental predictors (Table S4); however, the equivalent spatial model had a higher R^2, a lower $\mathrm{AIC_c}$, and no significant spatial autocorrelation pattern in its residuals (Figure S1). The standardized coefficients for models testing the productivity (NPP) and heat conservation (*MinWinTemp*) hypotheses suggest that productivity has the largest effect on size variation in the Pallid bat (Figure 3). Although seasonality was included in the top ranking model, the 95% confidence intervals of the coefficient value included zero and were NS ($\beta = -0.41 \pm 0.25$, p = .10, Table 3, Figure 4).

The best-supported spatial model was consistent with the productivity hypothesis; larger bats are found in areas of higher

TABLE 2 Spatial ($\mathrm{SAR_{err}}$) model selection results for variables predicting cranium centroid size in the Pallid bat. The top model is indicated in bold. See Table 1 and methods for details about model variables

SAR models	R^2	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w	λ
NPP + MinWinTemp + TempSeas	**.56**	**618.2**	**0**	**0.46**	**0.42**
NPP + MinWinTemp	.55	618.3	0.16	0.43	0.48
NPP (Productivity)	.54	621.7	3.53	0.08	0.43
NPP + TempSeas	.54	623.7	5.49	0.03	0.44
TempSeas + MaxSumTemp + MinWinTemp	.53	630.7	12.57	0	0.64
Latitude	.51	633.7	15.56	0	0.66
TempSeas + MinWinTemp	.51	634.5	16.24	0	0.55
MaxSumTemp (Heat dissipation)	.48	642.2	24.04	0	0.59
TempSeas + MaxSumTemp	.48	643.4	25.24	0	0.56
MaxSumTemp + MinWinTemp	.48	644	25.85	0	0.61
TempSeas (Seasonality)	.47	647.2	29.08	0	0.62
MinWinTemp (Heat conservation)	.46	647.9	29.74	0	0.69

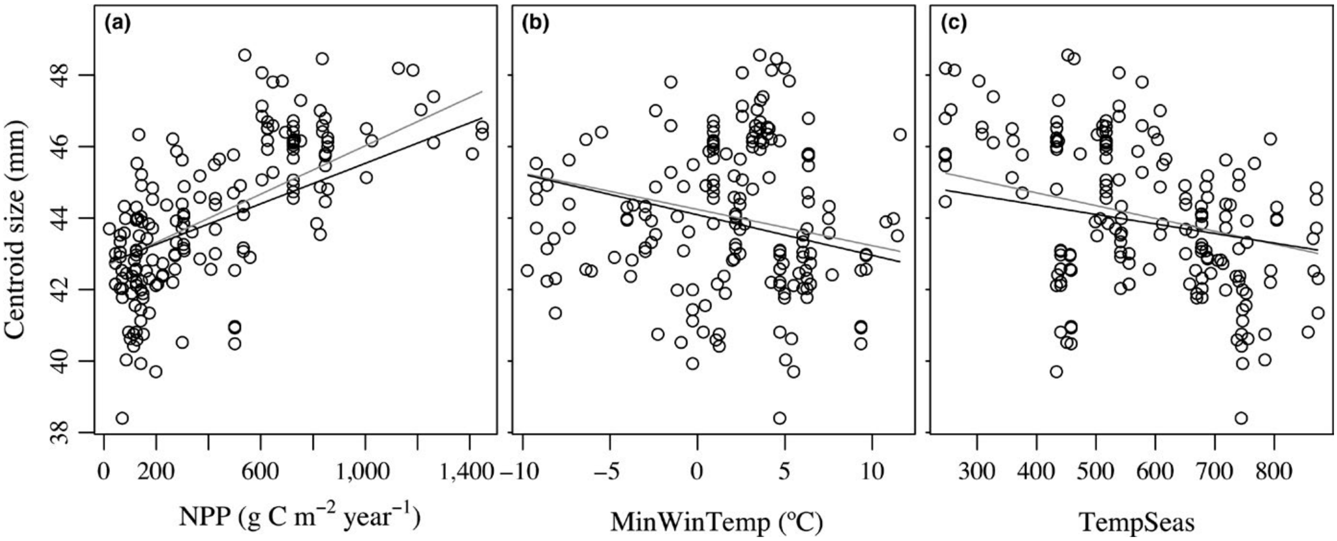

FIGURE 3 Fitted relationships between centroid size of the Pallid bat cranium and environmental variables from the top $\mathrm{AIC_c}$ ranked aspatial (grey lines) and spatial (black lines) models explaining size variation in the Pallid bat: (a) Net primary productivity (productivity hypothesis), (b) Minimum temperature of the coldest month (heat conservation hypothesis) and (c) Temperature seasonality (seasonality hypothesis)

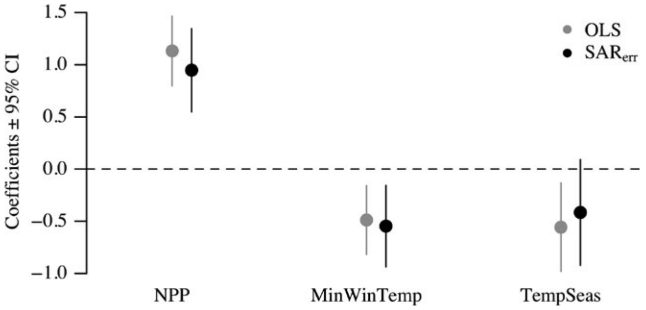

FIGURE 4 Coefficient estimates ± 95% confidence intervals for the environmental variables in the top AIC$_c$ ranked ordinary least squares and SAR$_{err}$ models explaining size variability in the Pallid bat. To allow comparisons among effect sizes, variables were first scaled and centred prior to statistical model fitting

TABLE 3 Coefficient estimates for variables included in the top ranked spatial (SAR$_{err}$) model predicting variation in cranium centroid size in the Pallid bat

Variables	β	*SE*	*p*
NPP	0.95	0.20	<.001
MinWinTemp	−0.55	0.20	<.01
TempSeas	−0.41	0.25	.1

NPP, net primary productivity.

productivity (NPP) (β = 0.95 ± 0.20, $p < .001$, Table 3, Figure 3a). Net primary productivity was the only univariate model that received any relative Akaike weight ($w = 0.08$) among the full set of candidate spatial models (Table 2). Our best-supported spatial model was also consistent with the heat conservation hypothesis (*MinWinTemp*), although the standardized effect was less than NPP (β = −0.55 ± 0.20, $p < .01$, Table 3, Figure 4). Interestingly, we found that minimum winter temperature alone had no significant effect on size in the Pallid bat (β = −0.31 ± 0.17, $p = .07$), but that it was influential only after accounting for the effects of NPP and temperature seasonality (Table 2). We also found that size decreased with increasing maximum summer temperature (*MaxSumTemp*; Table 2), which is consistent with the heat dissipation hypothesis. However, among the full set of candidate models explaining size variation in the Pallid bat, maximum summer temperature received little AIC$_c$ support (Table 2).

We also found a significant association between variation in the size and shape of the cranium. In the lateral view, we found that larger bats generally had a more pronounced sagittal crest and a more posteriorly projected intraparietal region (SS = 0.01, MS = 0.01, $df = 1$, $R^2 = .06$, $p < .001$, Figure 5a). In the ventral view, larger bats tended to have broader zygomatic arches, shorter rostrum and broader braincase (SS = 0.003, MS = 0.003, $df = 1$, $R^2 = .05$, $p < .001$, Figure 5b). There were no difference in these size–shape relationships between males and females in the lateral (Procrustes ANOVA $p = .79$) or ventral (Procrustes ANOVA $p = .13$) views of the cranium.

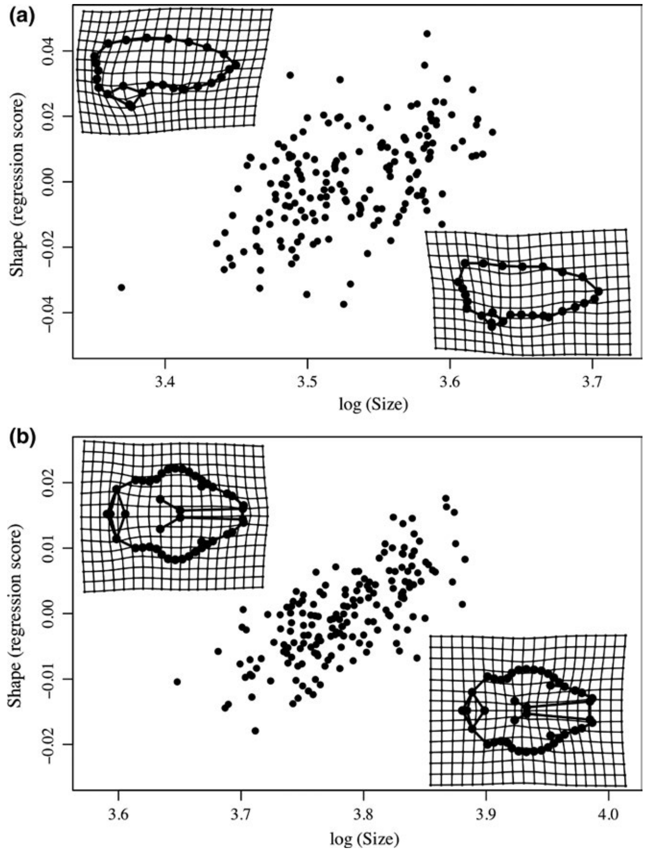

FIGURE 5 The relationship between size (log$_{10}$ centroid size) and shape in the (a) lateral and (b) ventral cranium views of the pallid bat. Deformation grids are shown to illustrate the shape of the smallest (left) and largest (right) specimens relative to the average shape

4 | DISCUSSION

The Pallid bat exhibits substantial geographic variation in body size and dietary ecology, and our objective was to identify the environmental factors that best explain this variation. We found that Pallid bats tend to be larger in the northern part of their range (Table 2). This pattern is consistent with latitudinal size clines observed in other mammals (Ashton et al., 2000; Meiri & Dayan, 2003), birds (Ashton, 2002a) and various ectothermic species, including reptiles (Ashton & Feldman, 2003), amphibians (Ashton, 2002b) and arthropods (Blanckenhorn & Demont, 2004). Although we did find that larger bats inhabit more northern latitudes, the latitudinal trend was weak relative to combined effects of productivity and minimum winter temperature. Whereas heat conservation was the original mechanism proposed to explain this trend (Bergmann, 1848; Mayr, 1956), our results do not support this rationale; minimum winter temperature alone failed to explain a significant amount of body size variation in Pallid bats (Table 2, Figure 3b). Instead, we found that the size cline in the Pallid bat is best explained by the combined effects of NPP and minimum winter temperature (Table 2). Our results strongly suggest that the latitudinal cline in Pallid bat size is related to variation in productivity, as opposed to temperature alone.

The productivity hypothesis has been invoked to explain both geographic and temporal size variations among mammals (Correll et al., 2015; Goodall & Crespo, 2013; Gür & Kart Gür, 2012; Meiri, Yom-Tov, & Geffen, 2007), birds (Leafloor et al., 1998; Morales-castilla et al., 2012) and arthropods (Arnett & Gotelli, 1999; Stillwell et al., 2007). As the sole predictor of cranium size, NPP explained 54% of the variation, with only an additional 2% explained by the top ranked spatial model (Table 2). Therefore, our study demonstrates that the relationship between productivity and body size may extend to Chiroptera as well.

We also evaluated the support for alternative hypotheses (Table 1), in addition to productivity, in explaining geographic size variation in the Pallid bats. When we considered the combined effect of productivity and heat conservation, these emerged as important predictors, but productivity was still clearly the most influential in terms of its standardized effect on body size (Table 3, Figure 4). In contrast, our results were not concordant with the seasonality hypotheses. Specifically, we found that Pallid bats tend to be smaller in more seasonal environments (Table 3, Figure 3c). These results contradict the prediction from the seasonality hypothesis, which proposes that, because larger individuals have proportionally larger fat stores, they have greater overwinter fasting endurance in more seasonal environments (Boyce, 1978; Lindstedt & Boyce, 1985). It is possible that differences in measurement error among climate variables could have obscured our ability to identify trends (Hijmans et al., 2005). Additionally, our use of a skeletal metric (cranium size) as a measure of body size could have obscured a size-seasonality relationship; for example, body mass but not skeletal size is correlated with seasonality among Swedish moose (Sand, Cederlund, & Danell, 1995). Nevertheless, skull size is a more appropriate metric for drawing generalizations about geographic size variability in temperate bats because their body mass can vary over 50% on a nightly basis (Coutts et al., 1973), and previous studies using linear measurements have found significant relationships between size and seasonality in mammals (Gür 2010) and insects (Stillwell et al., 2007).

Importantly, the thermal physiology of bats may also explain why body size can lack a significant relationship with seasonality; bats use torpor and hibernation to cope with periods of food shortage and/or seasonality (Ruf & Geiser, 2015). Temperate bats show extensive flexibility in their use of daily torpor and hibernation phenology depending on their energetic state (Boyles, Dunbar, Storm, & Brack, 2007; Matheson, Campbell, & Willis, 2010; Norquay & Willis, 2014; Rambaldini & Brigham, 2008b), and thus, behavioural and physiological responses may be more important than morphological or size adaptations for coping with highly seasonal environments. Among some insects, body size appears to be limited by the length of the growing season in seasonal environments (Blanckenhorn & Demont, 2004; Chown & Klok, 2003; Roff, 1980). Thus, changes in the length of the growing period, rather than overwintering starvation resistance, may be more influential in determining adult body size among heterothermic mammals, such as Pallid bats (Lindstedt & Boyce, 1985). Future studies comparing body size gradients among bat species that differ seasonal torpor patterns could help clarify whether the degree of heterothermy mediates the relative influences growing season length and fasting endurance on body size.

At a coarse scale, using proxies such as NPP to test the productivity hypothesis allowed us to distinguish between the two broad mechanisms proposed to explain geographic size variation in Pallid bats, thermoregulation (heat conservation and dissipation hypotheses) and food resource availability (seasonality and productivity hypotheses). The fact that productivity is most closely related to size variation in the Pallid bat (Figure 4) is consistent with growing evidence that resource availability drives both geographic (Correll et al., 2015; Goodall & Crespo, 2013; Wolverton et al., 2009) and temporal (Tomassini et al., 2014; Yom-Tov, 2003; Zalewski & Bartoszewicz, 2012) patterns of intraspecific size variation. The geographic trends were robust despite the fact that climate data and specimen age were not temporally matched. Our Pallid bat samples were originally collected between 1918 and 2010, but the climate and NPP data we acquired did not span this entire range, and we had to use averaged annual estimates (see Section 2). Although we cannot provide a causal link between body size and NPP, arthropod biomass is positively correlated with productivity (Kaspari et al., 2000; Sweet et al., 2015), and thus, increased body size in Pallid bats could be the result of higher prey availability. More detailed dietary information throughout the range of the Pallid bat is necessary to gain a thorough understanding of how food resource availability may be associated with changes in body size.

We also found that differences in cranial morphology are significantly associated with differences in size in Pallid bats (Figure 5). Larger bats exhibit cranial morphologies that may allow them to consume relatively larger and harder prey (Aguirre et al., 2003; Freeman, 1984; Freeman & Lemen, 2010; Santana & Cheung, 2016; Santana et al., 2010) (Figure 5). Broader zygomatic arches and a more pronounced sagittal crest can accommodate larger temporalis (jaw closing) muscles that can produce more forceful bites (Christiansen & Adolfssen, 2005; Santana et al., 2010; Senawi, Schmieder, Siemers, & Kingston, 2015). Similarly, a relatively shorter and wider rostrum allows for more forceful bites and a greater resistance to torsional forces when chewing hard prey (Dumont, Piccirillo, & Grosse, 2005; Freeman & Lemen, 2010; Santana et al., 2010). Qualitatively, these morphological trends could explain some of the geographic variations in Pallid bat diets that have been described by previous studies (Johnston & Fenton, 2001). Comparing the diet of Pallid bat populations from the California central coast and Death Valley, Johnston and Fenton (2001) found considerable diet variability between populations; bats in the coastal population (which experience high NPP; Figure 1) consume harder and larger prey and hard parts of the prey, which are culled by bats in the inland desert population (low NPP). The correlated changes in cranial size and shape described here indicate that Pallid bats from the coastal population can feed on relatively larger and more mechanically challenging prey not only because of their larger size, but also because of allometric cranial features that enhance bite force production.

Our study suggests that productivity, a proxy for food resource availability, is a key predictor of geographic body size variability in the

Pallid bat. This adds to the growing evidence that resource availability may be responsible for body size variation in space (Correll et al., 2015; Goodall & Crespo, 2013; Wolverton et al., 2009) and time (Arnett & Gotelli, 1999; Eastman et al., 2012; Tomassini et al., 2014; Yom-Tov, 2003). Importantly, our results underscore the importance of evaluating multiple environmental parameters, as opposed to just latitude or temperature, when attempting to explain patterns of geographic size variation (Ashton et al., 2000). Additionally, our research emphasizes the importance of size variation in generating morphological and ecological diversity within a species.

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

AUTHORS' CONTRIBUTIONS

R.M.K. and S.E.S. conceived the ideas and designed methodology. R.M.K. and R.F. collected the data. R.M.K. analysed the data. R.M.K. and S.E.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c5805 (Kelly, Friedman, & Santana, 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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