Ecogeographical patterns of body size differ among North American paper wasp species

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Abstract
Species with widespread distributions frequently show clines in body size across broad geographic areas. These clines may be the result of “ecogeographical rules” that describe spatial patterns of phenotypic differences driven by environmental variation. Intraspecific variation in body size, and the mechanisms causing this variation, have been poorly described in social wasps. This study examined ecogeographical patterns of body size for 12 native species and one non-native species of North American paper wasps (genus: Polistes) using body size measurements from > 14,000 pinned museum specimens. Intraspecific body size was correlated with latitude, elevation, and broadscale climate variation. However, the direction of this relationship was idiosyncratic across species, with Bergmann’s clines and converse Bergmann’s clines equally represented. There was no evidence of a phylogenetic signal in the direction of the cline between body size and the environment. Within species, the worker caste and the reproductive caste showed the same direction of response between body size and latitude, although for most species the reproductive caste was larger than the worker caste. Intraspecific variation in body size appears to be driven by differences in the response among species to similar environmental variables but the mechanisms causing this variation remain unknown.

Keywords Bergmann’s rule · Temperature size rule · James’ rule · Social wasps

Introduction
A fundamental challenge for biologists is to understand the processes driving variation in phenotypic traits within and among species (Thompson 2013). Body size is a particularly attractive trait to study because variation in body size is common and directly tied to fitness, physiology, and most life-history traits (Chown et al. 2002; Chown and Gaston 2010). Furthermore, species with widespread distributions often show clines in body size across broad geographic areas, which may be the result of “ecogeographical rules” that relate spatial patterns of phenotypic variation to environmental variation (Gaston et al. 2008; Kingsolver and Huey 2008). Social insects are an interesting group to test ecogeographical rules because their complex life cycles involve reproductive and worker castes, which may experience divergent selection pressures. However, broadscale patterns of body size variation and the mechanisms driving this variation have been poorly described in social insects.

Here we use museum specimens to examine variation in body size in the North American members of the widespread paper wasp genus Polistes (Hymenoptera: Vespidae).

A common ecogeographical pattern is Bergmann’s rule, which predicts that organisms will be larger in size at higher latitudes or colder climates because larger individuals have a smaller surface area to volume ratio thereby reducing the rate of heat loss (Bergmann 1847). Bergmann’s rule was initially proposed to explain size variation among species of homeothermic vertebrates, and studies of birds and mammals have largely supported this pattern (Meiri and Dayan 2003). Subsequently, Bergmann’s rule was expanded to consider intraspecific variation in size (James 1970) yielding mixed results when tested more broadly in endothermic organisms (Mousseau 1997). The relationship between body size and latitude is highly unpredictable across insect species, with a meta-analysis of insect body size across latitudinal and altitudinal clines finding that 29% of datasets reported Bergmann clines (body size increases with latitude), 30% of datasets...
Variation in body size may be driven by a diversity of mechanisms across divergent species, therefore looking at ecogeographical patterns across species with similar physiology and behavior may be instructive for identifying the underlying causes of these patterns (Angilletta and Dunham 2003).

This study examined the relationship between body size and the environment for twelve native and one introduced species of Polistes paper wasps distributed throughout North America. Polistes are an interesting group to examine ecogeographical patterns in body size for several reasons. All Polistes species are generalist predators of caterpillars (Richter 2000), and have similar life histories (Eberhard 1969; Reeve et al. 1991). Furthermore, many of the North American species are closely related (Santos et al. 2015), therefore we expect all species to have similar growth rates unless selection has specifically favored different growth trajectories among species. Most of these species have large geographic ranges spanning multiple degrees of latitude (Carpenter 1996; Miller et al. 2018), allowing for comparisons of body size across different climates. Lastly, pinned specimens of Polistes are well represented in museum collections. Body size is preserved in pinned specimens making it possible to rapidly measure the relationship between body size and the environment across the distribution of each species.

Comparing the relationship between environmental variables and body size across castes may also help to elucidate the causal mechanisms driving variation in body size in this group. Polistes are primitively eusocial species with females belonging to either the reproductive caste (foundresses/gynes) or the worker caste. The castes are morphologically indistinguishable (Eickwort 1969), although workers have been reported to be smaller or similar in size to the reproductive caste (Dani 1994; Haggard and Gamboa 1980; Tannure-Nascimento et al. 2005). In temperate latitudes, nests are started in the spring by one or more reproductive foundresses, members of the worker caste eclose and take over tasks related to foraging and rearing offspring in the early summer, and in the fall males and the next generation of female reproductive wasps emerge (Reeve et al. 1991; West 1967). Polistes nests are open to the environment, providing relatively little thermal buffering in comparison to other social insects (Höcherl et al. 2016), and because castes eclose at different times, reproductive and worker castes experience different temperature regimes during development and eclose during different stages of the nesting cycle. Lastly, reproductive females are the only caste to undergo diapause during the winter, therefore selection for overwinter survival may differentially affect this caste.

These proposed mechanisms for body size variation predict different patterns of inter- and intra-specific body size. Bergmann’s Rule, the temperature size rule, and the resistance hypothesis predict that inter- and intra-specific body size will increase with latitude. However, if larger size aids in cold tolerance or starvation and/or desiccation during the winter, this trend may be more pronounced in the reproductive caste. The seasonality hypothesis predicts the reverse trend, with body size decreasing with latitude. If body size is driven by other ecological factors that covary with latitude,
the direction of this trend is difficult to predict but regardless of the precise mechanism, we would expect a similar pattern of response across species. Moreover, if environmental variation is the sole driver of body size, then different species collected from the same location are predicted to be similar in size. Alternatively, intraspecific variation in body size in *Polistes* could result from differences in size between castes, and not environmental variation. If this is the case, we would predict workers to be smaller than the reproductive caste, but that mean body size within a caste would not vary with climate or latitude. Lastly, we also consider the null hypothesis that body size is unrelated to latitude or the environment, in which case we would expect no pattern between body size variation and environmental variation.

**Materials and methods**

**Measurement of body size**

We photographed pinned specimens of North American *Polistes* wasps from the collections at the American Museum of Natural History, the Cornell University Insect Collection, the Illinois Natural History Survey, the Smithsonian National Museum of Natural History, the Royal Ontario Museum, the University of Guelph Insect Collection, the University of Michigan Museum of Natural History, and the C.A. Triplehorn Insect Collection. Body size was measured for species with > 100 specimens across collections. This led to a dataset for twelve native species: *Polistes annularis* L., *P. apachus* (Saussure), *P. aurifer* (Saussure), *P. bahamensis* (Bequaert and Salt), *P. bellicosus* (Cresson), *P. carolina* L., *P. comanchus* (Saussure), *P. dorsalis* (Fabricius), *P. exclamans* (Viereck), *P. flavus* (Cresson), *P. fusatus* (Fabricius), and *P. metricus* (Say). We additionally photographed specimens of the invasive European paper wasp, *P. dominula* (Christ), collected in North America. *P. dominula* was first reported in Massachusetts in 1978 and has subsequently spread across the continental United States and into southern Canada (Liebert et al. 2006).

Using museum collections to evaluate variation in body size is advantageous because it allows for the rapid measurement of a large number of specimens from across a broad geographical range. A drawback of this approach is that specimens were collected haphazardly in regard to caste, location, and year. Specimens in our dataset were collected from 1879 to 2018, with collection year not provided for 1,415 specimens (10.9%). For many locales, specimens were collected only at a single time point, confounding the effect of location, year, and sometimes caste.

To compensate for variability in sampling regime, we maximized the number of samples in this study by developing a high-throughput approach to rapidly measure body size from pinned specimens. Boxes of pinned specimens were photographed inside a light tent with a 6D camera fitted with an EF 24–105 mm f/4L IS USM lens (Canon, New York). To reduce the effect of parallax, the camera was mounted to a copy stand to standardize the distance between the camera and the specimens, specimens were photographed in the center of the field of view, and photographs included a size standard at the average height of the pinned specimens (17 mm) (Zelditch et al. 2012).

Locality information was transcribed from specimen labels. For specimens without latitude and longitude coordinates, we approximated the longitude and latitude of each locality using GEOlocate (http://www.geo-locate.org) and google maps (http://maps.google.com). Specimens that could only be localized to a state (e.g. New York) were not included in the dataset. We also excluded a small number of specimens (*N* = 9) that were collected in locations that were outliers from the other occurrence records for that species as these likely represent misidentified specimens or casual species in these regions.

Differences in specimen preparation and preservation can result in a slight variation in the curvature of pinned specimens affecting measurements of overall body length. Portions of the specimen were occasionally obscured by other specimens in photographs and infrequently parts of specimens are damaged or missing. To account for these issues, we calculated a multivariate measurement of body size. For each specimen, we measured head width, thorax length, and forewing length in ImageJ (v1.49) (Schneider et al. 2012). Missing or obscured traits were given a value of “NA”. Of the 14,149 specimens in the dataset, 1,139 specimens had a missing value, resulting in a final dataset of 13,010 specimens with measurements of all three traits. Head, thorax, and forewing measurements were log transformed to homogenize variance and a principal component analysis (PCA) was performed with the R package “pcaMethods” (Stacklies et al. 2007) using the “svd” method, which uses the covariance matrix of the variables. The first principal component of body size (PC1) explained 88.5% of variation and was positively correlated with head width (Pearson’s R = 0.911, P < 0.0001, N = 13,008), thorax width (Pearson’s R = 0.926, P < 0.0001, N = 13,008), and forewing length (Pearson’s R = 0.960, P < 0.0001, N = 13,008). We tested the association between body size (PC1), and latitude, altitude and climate using linear regression analysis. All statistical analyses were conducted in R (R Core Development Team 2019).

**Altitude and environmental variables**

The altitude of each latitude and longitude was approximated by querying the geonames database (www.geonames.org) using the “rgbif” package (Chamberlain and Boettiger 2017). Altitude was determined using the “gtopo30” elevation
model which reports the average altitude across a sampling area of 1 km².

To examine broader climatic variables, we used the packages “raster” (Hijmans 2020) and “sp” (Pebesma and Bivand 2005) to download bioclimatic variables from the WorldClim database v2 at a resolution of 2.5 min (Fick and Hijmans 2017). These nineteen bioclimatic variables are related to monthly temperature and precipitation variables and are averaged across the years 1970–2000. We excluded specimens missing data for one or more bioclimatic variables from our analyses. As climate measures are frequently correlated with each other, we performed a PCA to generate a multivariate measurement of environmental variation with the function `prcomp`, using the correlation matrix because of scaling differences across variables. A description of each bioclimatic variable is given in Table S1.

**Caste designation**

Although *Polistes* castes are phenotypically indistinguishable, different castes vary in abundance temporally. Wasps collected from January to May (“Spring”, \(N = 2526\)) are primarily reproductive foundresses. Wasps collected from June to August (“Summer”, \(N = 5548\)) are primarily workers. We excluded female specimens collected in the fall from analyses based on castes as these specimens will be a mixture of workers and future reproductive wasps (\(N = 2044\)). Specimens that did not report a month when the specimen was collected were also excluded from analyses of castes (\(N = 1187\)).

Male wasps eclose in the fall. In most species, males can be easily distinguished from females because males lack a stinger and have entirely yellow faces (“Males”, \(N = 2844\)). However, in *P. annularis* both males and females have reddish-brown faces, and in *P. apachus* both sexes have entirely yellow faces. Males have an additional antennal segment compared to females, though it was generally not possible to confidently count antennal segments for specimens from our photographs. For *P. annularis* and *P. apachus* collected in the fall, when sex could not be determined readily from photographs, the specimen was excluded from analyses of caste. The relationship between size, latitude, and caste was tested using ANCOVAs with caste as a categorical variable.

**Phylogenetic comparative analyses**

More closely related species may have greater trait similarity than more distantly related species, therefore when comparing traits across related species it is necessary to account for phylogenetic distance (Felsenstein 1985). We tested if body size and/or the response of body size to latitude (e.g. Bergman’s cline or converse Bergman’s cline) showed a phylogenetic signal. Body size was determined using the average multivariate body size (PC1) for each species. To test for phylogenetic signal in the response of body size to latitude, we computed the slopes obtained from regressing intraspecific body size (PC1) on latitude and we also considered the direction of this response as a discrete trait, classifying species as Bergman’s cline or converse Bergmann’s cline.

The preferred *Polistes* phylogeny from Santos et al. (2015) was captured with the “physketch” package (Revell 2017) and pruned to contain only the 12 native North American species. For continuous traits, we tested for phylogenetic signal by calculating Pagel’s \(\lambda\) (Pagel 1997) and Blomberg’s \(K\) (Blomberg et al. 2003) using the function `phylosig` in the “phytools” package (Revell 2012). Pagel’s \(\lambda\) ranges from 0 to 1, with \(\lambda = 0\) equivalent to a star phylogeny indicating no phylogenetic signal, and \(\lambda = 1\) corresponding to a model of Brownian motion. Values of \(K > 1\) indicate that species are more similar than expected under random drift, showing phylogenetic signal, whereas \(K < 1\) indicates that species are more divergent than expected. Model significance for Pagel’s \(\lambda\) is assessed with a likelihood ratio test, whereas the significance of \(K\) was determined by randomizing trait values 10,000 times to generate a null distribution. Both tests were performed within the `phylosig` function. Discrete traits were tested with the “caper” package (Orme et al. 2018) using the function `phylo.d` with 10,000 permutations to generate D (Fritz and Purvis 2010), a measure of phylogenetic signal for binary traits.

We tested if the slope of intraspecific body size (PC1) on latitude was correlated with mean body size, latitudinal range, or the intraspecific coefficient of variation for head width, thorax width, or forewing length using phylogenetic independent contrasts (PIC) (Felsenstein 1985). PICs were calculated with the function `pic` in the “ape” package (v5.4) (Paradis and Schliep 2019) and a regression analysis was done using a standard linear model with no intercept.

**Results**

The locations of the specimens used in this study are shown in Fig. 1. Four species, *P. apachus*, *P. aurifer*, *P. comanchus*, and *P. flavus*, occur only west of the Rocky Mountains. The eight remaining native species are primarily found east of the Rocky Mountains. The geographical distribution of specimens in our dataset covers nearly the entire range previously reported for each species (Buck 2008; Carpenter 1996). Regions from which specimens were not available were always at the range limits of each species, for example, Buck (Buck 2008) reported *P. carolina* in Ohio and Indiana, but our dataset did not include specimens from these states. The one exception is for the distribution of the invasive species, *P. dominula*. This species is now widespread across the United States and Canada (Liebert et al. 2006),
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Fig. 1 The distribution of the 14,149 specimens used in this study. Each point shows the location of a single specimen.
but specimens were only available from the northeastern United States and southeastern parts of Canada (Fig. 1).

*Polistes* species varied in average body size. The largest species was *P. annularis* and the smallest species was *P. dorsalis*. Across species, the mean head width ranged from 3.5 to 4.5 mm, thorax width ranged from 2.6 to 3.6 mm, and forewing length ranged from 11.2 to 20.5 mm (Table 1). Forewing lengths were consistent with previously reported values (Buck 2008).

There was a linear relationship between body size and latitude, but this relationship was idiosyncratic across species (Fig. 2). Body size increased with latitude in four species, consistent with Bergmann’s clines. Seven species had patterns consistent with converse Bergmann’s clines, showing a decrease in body size with increasing latitude, and two species had no relationship between body size and latitude. Altitude and body size had a similar relationship with five species displaying Bergmann’s clines, five species with converse Bergmann’s clines, and three species showing no relationship between altitude and body size (Figure S1). Notably, *P. flavus* showed a negative relationship between body size and altitude but a positive relationship between body size and altitude.

We also assessed the relationship between body size variation and environmental variation by generating a multivariate measurement of climate using a PCA of nineteen temperature and precipitation variables from the WorldClim database. The first principal component of environmental variation (ePC1) explained 38.5% of variation and the second principal component (ePC2) explained 27.1% of variation. Both ePC1 and ePC2 were significantly correlated with latitude (ePC1: Pearson’s *R* = −0.94, *P* < 0.0001, *N* = 14,031; ePC2: Pearson’s *R* = −0.04, *P* < 0.0001, *N* = 14,031) (Figure S2) and with longitude (ePC1: Pearson’s *R* = −0.32, *P* < 0.0001, *N* = 14,031; ePC2: Pearson’s *R* = 0.78, *P* < 0.0001, *N* = 14,031). We found a similar idiosyncratic relationship between body size (PC1) and climate variation (ePC1) as that previously shown between body size and latitude (Figure S3) suggesting that intraspecific variation in body size is correlated with environmental variation, but this response to the environment varies across species.

We next tested if the relationship between body size and latitude differed among castes. If body size is correlated with overwinter survival, we predicted that wasps collected in the spring would show a consistent relationship between body size and latitude, regardless of species. Contrary to this prediction, we observed differences in body size among species for spring wasps collected at the same latitude (Fig. 3). Spring, summer, and male specimens showed the same idiosyncratic relationship between body size and latitude as the full dataset for each species (Figures S4-5). The slope between body size and latitude trended in the same direction across castes, even if in some cases the relationship was no longer statistically significant, likely due to smaller sample sizes within each subgroup.

As a general rule, workers collected in the summer developed at cooler temperatures in the spring than reproductive individuals who developed in late summer. However, the temperature-size rule was only moderately supported by our data. Female wasps collected in the summer were on average smaller than wasps collected in the spring, although this pattern was not consistent across species (Fig. 4, Table 2). Similar results were observed when considering head width, thorax width and forewing length independently (Table S2). Additionally, males were typically smaller than female wasps collected in the spring or summer (Figure S6, Table S3-S4), suggesting that body size variation was not solely driven by environmental temperature during development. Due to the large temporal range of samples in this study, for *P. fuscatus*, the species with the largest sample size, we examined the effect of year on these relationships (Table S5) and found that our original model was a better fit for the data than a more complex model including year (ΔAIC = 322).

The presence of nearly equal species with Bergmann’s clines and converse Bergmann’s clines could be driven by an evolutionary transition, therefore we tested for phylogenetic signal in our multivariate measurement of mean body size (PC1) and in the direction of the cline between body size and latitude. Mean body size showed some evidence of phylogenetic signal. Pagel’s λ for mean body size was 0.99 (*P* = 0.12), consistent with a model of Brownian motion, although this value was not statistically significant likely due to the small number of species in this comparison (Fig. 5). Blomberg’s K was 0.79 (*P* = 0.02), suggesting that species were more divergent in body size than expected under random drift. Results were similar when considering head width, thorax width, and forewing length independently, and for comparisons within each caste. In contrast, the direction of the response of body size with environment showed no evidence of phylogenetic signal. Treating the slope of the regression of body size (PC1) on latitude as a continuous trait, we found λ = 0.00007 (*P* = 1) and *K* = 0.62 (*P* = 0.08) (Figure S7). Similarly, classifying the relationship between body size and latitude as a discrete trait (Bergmann’s cline or converse Bergmann’s cline) showed that the direction of the cline was randomly distributed across the phylogeny (*D* = 1.045; probability of resulting from no structure: *P* = 0.46; probability of resulting from Brownian structure: *P* = 0.19) (Fig. 5). Species with a positive association between size and latitude (Bergmann’s cline or converse Bergmann’s cline) tended to be smaller, have larger ranges, and slightly greater intraspecific coefficients of variation, but none of these variables were statistically significant (Body size: *R*² = 0.20, *P* = 0.08; latitudinal range: *R*² = 0.08, *P* = 0.19; head width CV: *R*² = 0.11, *P* = 0.15; thorax width CV: *R*² = 0.24, *P* = 0.06; forewing length CV: *R*² = 0.20, *P* = 0.08).
Table 1  Mean size ± SE of head width, thorax width, forewing length, and a multivariate measure of body size (PC1) for each species

| Species  | Head  | Thorax | Wing  | PC1  | Head  | Thorax | Wing  | PC1  | Head  | Thorax | Wing  | PC1  | Head  | Thorax | Wing  | PC1  | Head  | Thorax | Wing  | PC1  |
|----------|-------|--------|-------|------|-------|--------|-------|------|-------|--------|-------|------|-------|--------|-------|------|-------|--------|-------|------|
| annularis| 4.5±0.01 | 3.6±0.01 | 20.5±0.09 | 0.441±0.01 | 4.6±0.02 | 3.7±0.02 | 20.9±0.17 | 0.471±0.01 | 4.6±0.02 | 3.7±0.02 | 20.9±0.14 | 0.469±0.01 | 4.0±0.06 | 3.3±0.05 | 18.4±0.61 | 0.250±0.04 |
| apachus   | 4.3±0.02 | 3.4±0.02 | 16.3±0.14 | 0.215±0.01 | 4.3±0.05 | 3.5±0.05 | 16.1±0.38 | 0.219±0.03 | 4.3±0.03 | 3.4±0.04 | 16.3±0.22 | 0.214±0.02 | 4.2±0.07 | 3.3±0.06 | 16.3±0.40 | 0.172±0.04 |
| aurifer   | 3.9±0.01 | 3.0±0.01 | 14.2±0.04 | 0.003±0.004 | 3.9±0.02 | 3.0±0.02 | 14.3±0.11 | 0.015±0.01 | 3.9±0.01 | 3.0±0.01 | 14.1±0.06 | -0.007±0.01 | 3.9±0.02 | 2.9±0.02 | 14.0±0.08 | -0.021±0.01 |
| bahamensis| 3.4±0.01 | 2.6±0.01 | 12.4±0.09 | -0.233±0.01 | 3.4±0.02 | 2.6±0.02 | 12.2±0.13 | -0.236±0.01 | 3.4±0.02 | 2.5±0.03 | 11.7±0.23 | -0.306±0.02 | 3.4±0.05 | 2.5±0.05 | 11.9±0.37 | -0.270±0.03 |
| bellicosus| 4.0±0.01 | 3.0±0.01 | 14.5±0.08 | 0.035±0.01 | 4.0±0.02 | 3.0±0.02 | 14.2±0.15 | 0.020±0.01 | 4.0±0.02 | 3.0±0.02 | 14.5±0.14 | 0.029±0.01 | 4.0±0.03 | 3.0±0.03 | 14.6±0.20 | 0.033±0.02 |
| carolina  | 4.3±0.02 | 3.4±0.01 | 17.3±0.10 | 0.253±0.01 | 4.4±0.03 | 3.5±0.02 | 17.8±0.18 | 0.300±0.01 | 4.4±0.03 | 3.4±0.02 | 17.8±0.18 | 0.293±0.01 | 4.0±0.03 | 3.2±0.02 | 15.9±0.18 | 0.130±0.01 |
| comansius | 4.5±0.01 | 3.6±0.01 | 19.2±0.08 | 0.378±0.01 | 4.5±0.03 | 3.6±0.03 | 19.1±0.24 | 0.378±0.02 | 4.4±0.01 | 3.4±0.01 | 18.5±0.11 | 0.320±0.01 | 4.4±0.07 | 3.6±0.10 | 19.9±0.58 | 0.400±0.04 |
| dominula  | 3.5±0.01 | 2.7±0.02 | 11.2±0.13 | -0.279±0.01 | 3.7±0.06 | 3.0±0.06 | 13.0±0.38 | -0.086±0.04 | 3.4±0.02 | 2.7±0.03 | 11.0±0.17 | -0.296±0.02 | 3.5±0.05 | 2.7±0.05 | 10.8±0.30 | -0.321±0.03 |
| dorsalis  | 3.5±0.01 | 2.4±0.01 | 11.6±0.04 | -0.306±0.01 | 3.4±0.01 | 2.4±0.01 | 11.2±0.08 | -0.352±0.01 | 3.5±0.01 | 2.4±0.01 | 11.7±0.07 | -0.288±0.01 | 3.5±0.02 | 2.4±0.02 | 11.5±0.09 | -0.317±0.02 |
| exclamationis| 3.6±0.01 | 2.6±0.01 | 13.9±0.06 | -0.109±0.01 | 3.7±0.02 | 2.8±0.02 | 14.3±0.14 | -0.050±0.01 | 3.5±0.02 | 2.6±0.02 | 13.4±0.10 | -0.153±0.01 | 3.7±0.03 | 2.6±0.03 | 13.7±0.18 | -0.122±0.02 |
| flavus    | 4.3±0.02 | 3.5±0.03 | 16.5±0.14 | 0.240±0.01 | 4.2±0.08 | 3.4±0.08 | 16.1±0.45 | 0.189±0.04 | 4.3±0.03 | 3.5±0.03 | 16.4±0.20 | 0.224±0.02 | 4.4±0.1 | 3.6±0.10 | 16.5±0.42 | 0.272±0.04 |
| fuscatus  | 3.7±0.01 | 2.9±0.003 | 13.5±0.02 | -0.078±0.002 | 3.8±0.01 | 2.9±0.01 | 14.0±0.06 | -0.024±0.01 | 3.7±0.01 | 2.8±0.01 | 13.2±0.03 | -0.100±0.01 | 3.7±0.01 | 2.8±0.01 | 13.5±0.04 | -0.079±0.004 |
| metricus | 4.1±0.01 | 3.4±0.01 | 15.9±0.07 | 0.178±0.01 | 4.2±0.02 | 3.4±0.02 | 16.1±0.11 | 0.200±0.01 | 4.1±0.02 | 3.4±0.02 | 15.7±0.16 | 0.161±0.01 | 4.2±0.03 | 3.4±0.03 | 15.8±0.17 | 0.181±0.01 |

The full dataset shows the mean for all specimens. Spring and Summer categories show female wasps separated by caste, with wasps collected in the spring predominately from the reproductive caste and wasps collected in the summer predominately from the worker caste. Male is the mean value for male specimens.
Discussion

*Polistes* in North America had a linear relationship between intraspecific body size and latitude, altitude, and environmental variation, strongly suggesting a role of the environment in generating these patterns. The direction of this relationship was idiosyncratic across species, with Bergmann’s clines and converse Bergmann’s clines.
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Almost equally well represented in our dataset. There was no phylogenetic signal for the direction of the cline, ruling out the possibility that this pattern is caused by a single evolutionary transition. As a result, the exact mechanism driving interspecific and intraspecific body size variation in paper wasps remains unclear.

Many of the proposed mechanisms for explaining ecogeographical patterns in body size predict the same direction of response in closely related species with similar physiology and behavior, making these mechanisms unlikely explanations for the divergent patterns in our data. For example, we did not see a consistent increase in body size with latitude.
or temperature as would be predicted for decreasing the rate of heat loss (Bergman’s Rule) or resisting the effects of starvation or desiccation (Resistance Hypothesis) (Chown and Gaston 2010; Cushman et al. 1993; Shelomi 2012). Moreover, we found that species collected at the same latitude differed in body size, thus we can reject models based solely on biophysical constraints during development. For species with narrow distributions, lower sample sizes, or uneven sampling regimes, we had lower power to detect ecological trends, particularly non-linear patterns. Therefore, increased sampling of body size across the entire range of each species may reveal a more precise or nuanced relationship between body size and environment but is unlikely to change the overall trends we observed.

In the recently introduced species, *P. dominula*, we detected a converse Bergman’s cline. *P. dominula* was first observed in the United States in 1978 and recorded in Ontario Canada by 1997 (Hoebeke and Wheeler 2005). Specimens of *P. dominula* used in the study were collected from 1984 to 2011 and represent < 30 generations since introduction, intraspecific variation in body size of *P. dominula* is most likely the result of phenotypic plasticity, suggesting that *Polistes* body size can vary plastically in response to environmental variation. However, the rapid evolution of ecogeographic clines has been observed in other introduced species. For example, introduced populations of the seven-spotted lady beetle (*Coccinella septempunctata* L.) have reversed the direction of a cline of melanistic coloration within 60 years (O’Neill et al. 2017). The relationship between body size and latitude has not been measured within the native range of *P. dominula* or in other introduced populations of this species in South Africa (Eardley et al. 2009). Therefore, future studies comparing climate variables and size across the range of *P. dominula* will be informative for identifying the causal mechanisms driving these patterns in this species.

Intraspecific body size variation was correlated with variation in climate, but the effect of environmental variation on body size differed among species. Together these results suggest that different species are differentially responding to similar environmental conditions. These findings match a prior study which found differential variation in cooperative nesting behavior in responses to environmental variables for four *Polistes* species (Sheehan et al. 2015). Below we explore several possible explanations for this pattern.

Seasonality has been predicted to favor converse Bergmann’s clines due to the reduced time for development at higher latitudes (Blanckenhorn and Demont 2004). *Polistes* have a bivoltine life cycle (Hunt and Amdam 2005) and we did not observe a saw-tooth pattern in the distribution of body size, which is characteristic of a change in the number of generations (Chown et al. 2002). The effects of seasonality might be more pronounced for larger-bodied species, or species with more northerly distributions. Accordingly, we found a non-significant trend towards larger species showing converse Bergmann’s clines, matching a wider pattern across arthropods of converse Bergmann’s clines in larger species and Bergmann’s clines in smaller species (Blanckenhorn and Demont 2004). Seasonality may also favor a non-linear relationship between body size and latitude, with species changing growth trajectories across their range, although the heterogeneous nature of our dataset made it difficult to test this prediction.

Differences in ecogeographical patterns in body size could also occur if *Polistes* species cope with environmental

### Table 2

| Species | df | F    | P     | df | F    | P     | df | F    | P     |
|---------|----|------|-------|----|------|-------|----|------|-------|
| annularis | 1  | 53.25 | <0.0001 | 1  | 3.43  | 0.06  | 1  | 17.80 | <0.0001 |
| apachus   | 1  | 22.50 | <0.0001 | 1  | 0.01  | 0.92  | 1  | 0.84  | 0.36  |
| aurifer   | 1  | 0.69  | 0.41   | 1  | 3.25  | 0.07  | 1  | 0.29  | 0.59  |
| bahamensis | 1 | 10.55 | 0.001  | 1  | 7.27  | 0.007 | 1  | 0.01  | 0.91  |
| bellicosus | 1 | 12.31 | 0.0005 | 1  | 0.00  | 0.98  | 1  | 2.75  | 0.10  |
| carolina  | 1  | 0.02  | 0.89   | 1  | 0.04  | 0.84  | 1  | 1.73  | 0.19  |
| comanchus | 1  | 5.42  | 0.02   | 1  | 8.80  | 0.003 | 1  | 1.60  | 0.21  |
| dorsalis  | 1  | 53.84 | <0.0001 | 1  | 10.18 | 0.001 | 1  | 15.83 | <0.0001 |
| exclamans | 1  | 11.18 | 0.0009 | 1  | 57.35 | <0.0001 | 1  | 0.85  | 0.36  |
| flavus    | 1  | 10.04 | 0.002  | 1  | 0.52  | 0.47  | 1  | 6.56  | 0.01  |
| fuscatus  | 1  | 32.99 | <0.0001 | 1  | 105.8 | <0.0001 | 1  | 1.02  | 0.31  |
| metricus  | 1  | 15.18 | 0.0001 | 1  | 1.21  | 0.27  | 1  | 9.93  | 0.002 |
| dominula  | 1  | 17.73 | 0.0001 | 1  | 16.61 | 0.0001 | 1  | 0.06  | 0.8   |

The analysis considered only female specimens collected in the spring (reproductive caste) or the summer (worker caste). Significant effects are shown in bold.
Ecogeographical patterns of body size differ among North American paper wasp species

Fig. 5 Phylogenetic signal of body size and the cline between body size and latitude. The cladogram was adapted from Santos et al. (Santos et al. 2015) and shows the twelve native species in this study. The mean body size of each species is indicated by the width of the black circle. Species with Bergmann’s clines are shown with gray dots and converse Bergmann’s clines are shown with open circles.

variation through alternative mechanisms. For example, darker body coloration in Polistes has been broadly associated with cooler environments (Souza et al. 2020, 2017), likely because darker colored ectotherms warm more quickly than lighter colored individuals (Clusella Trullas et al. 2007). The species measured in this study vary in the extent of melanistic coloration (Buck 2008; Carpenter 1996), and therefore coloration differences among species could influence how body size responds to environmental variation.

Paper wasps are eusocial organisms, which complicates the interpretation of ecogeographical patterns. Polistes workers develop at cooler temperatures than the reproductive caste. Correspondingly, our intraspecific data showed moderate support for the temperature-size rule, with reproductive females being larger in size than workers for many species. However, size differences between castes could also result from several confounding factors. Workers and reproductive castes may follow different developmental rules, encapsulating at different sizes (Hunt et al. 2007). Body size in Polistes corresponds with food quantity during development (Karsai and Hunt 2002). Although an increase in the amount of food for a nest may lead to the production of more offspring rather than larger offspring (Tibbetts and Curtis 2007). Reproductive females typically receive more food and care than developing workers and a larger body size in the reproductive caste may aid in overwinter survival, winning dominance interactions when founding nests, and/or provide resources needed for laying eggs (Jandt et al. 2014; Strassmann et al. 1984; Turillazzi and Pardi 1977; Zanette and Field 2009).
Finally, variation in body size can result not only from the abiotic environment but also from biotic interactions. One mechanism by which this can occur is through interspecific competition as the availability and quality of resources can influence body size (Chown and Gaston 2010). We observed interspecific variation in body size among sympatric species. When species have overlapping distributions, they may utilize different resources or differ in foraging efficiency on resources to avoid competition (Schluter 2000).

Size variation may also result from tradeoffs in resource allocation within colonies. For example, larger species may have adopted a strategy of building a smaller nest with fewer larger individuals whereas smaller species may have adopted the opposite strategy. Distinguishing between these possibilities will require future studies of diet, growth, and developmental variation across species.

Differences in intraspecific body size can occur as a result of phenotypic plasticity or local adaptation. We found no evidence of a phylogenetic signal in the direction of the cline of phenotypic plasticity or local adaptation. We found no developmental variation across species.

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Author contributions SEM conceived the study and collected the data. The manuscript was written by SEM with input from MS.

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Data availability Data is available at https://doi.org/10.5061/dryad.0k6djh9zb.

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Compliance with ethical standards

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