Received: 4 October 2019 | Accepted: 31 July 2020

DOI: 10.1111/1365-2656.13330

RESEARCH ARTICLE

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

Temperature drives caste-specific morphological clines in ants

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Funding information
Fonds de Recherche du Québec - Nature et Technologies, Grant/Award Number: 2016-NC-189273; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPIN-2015-06081

Handling Editor: Jonathan Zvi Shik

Abstract

1. The morphology of organisms relates to most aspects of their life history and autecology. As such, elucidating the drivers of morphological variation along environmental gradients might give insight into processes limiting species distributions. In eusocial organisms, the concept of morphology is more complex than in solitary organisms. Eusocial insects such as ants exhibit drastic morphological differences between reproductive and worker castes. How environmental selection operates on the morphology of each caste, and whether caste-specific selection has fitness consequences is largely unknown, but is potentially crucial to understand what limits ant species' distributions.
2. Here we aimed to examine whether ant shape and body size covaries with climate at the scale of an entire continent, and whether such relationship might be caste specific.
3. We used 26,472 georeferenced morphometric measurements from 2,206 individual ants belonging to 32 closely related North American species in the genus *Formica* to assess how ant morphology relates to geographic variation in the abiotic environment.
4. Although precipitation and seasonality explained some of the geographic variation in morphology, temperature was the best predictor. Specifically, geographic variation in body size was positively related to temperature, meaning that ants are smaller in cold than in warm environments. Moreover, the strength of the relationship between size and temperature was stronger for the reproductive castes (i.e. queens and males) than for the worker caste. The shape of workers and males also varied along these large-scale abiotic gradients. Specifically, the relative length of workers' legs, thoraxes and antennae positively related to temperature, meaning that they had shorter appendages in cold environments. In contrast, males had smaller heads, but larger thoraxes in more seasonal environments.
5. Overall, our results suggest that geographic variation in ambient temperature influences the morphology of ants, but that the strength of this effect is caste specific. In conclusion, whereas ant ecology has traditionally focused on workers, our study shows that considering the ecology of the reproductive castes is imperative to move forward in this field.

KEYWORDS

Bergmann's rule, climate, environmental gradients, Formicidae, functional traits, morphospace

1 | INTRODUCTION

An unresolved puzzle in biogeography is that species, even closely related ones, vary tremendously in the extent of their geographic distributions (Thuiller, Lavorel, Midgley, Lavergne, & Rebelo, 2004). We largely lack an explanation for such differences in species that share similar autecology and natural history. Perhaps a promising avenue is to examine which particular traits vary along environmental gradients across the range of a species and between closely related species. Functional traits are physical or chemical characteristics that relate to the ecological strategies and life histories of organisms and which, through interactions with the biotic and abiotic environments, should affect their fitness (McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007). Because morphology can influence the performance of an organism and dictate persistence in a given environment (Koehl, 1996), it often varies predictably along broad-scale environmental gradients (e.g. precipitation and temperature gradients; Pollock, Morris, & Vesk, 2012; Swenson & Weiser, 2010). Thus, identifying which morphological traits vary along environmental gradients and why they do might provide insights into mechanisms limiting the geographic distribution of species.

In animals, body size is possibly the most frequently studied trait, because it relates to virtually all aspects of their life history (Chown & Gaston, 2010). Body size in endotherms varies predictably along latitudinal gradients and such patterns are well studied (Meiri & Dayan, 2003). Endotherms often follow Bergmann's rule (Ashton, Tracy, & Queiroz, 2000; Olson et al., 2009), whereby body size increases as temperature decreases. A commonly proposed mechanism underlying this body size cline is that an endotherm's heat production relates to its volume, while heat loss negatively relates to its surface area (Salewski & Watt, 2017). Consequently, larger animals produce more heat and lose relatively less, providing an advantage in colder climates. In contrast, size clines are inconsistent for both vertebrate and invertebrate ectotherms (Shelomi, 2012). For instance, in insects, body size along environmental gradients either increases (Arnett & Gotelli, 1999; Heinze, Foitzik, & Fischer, 2003), decreases (Masaki, 1967; Schutze & Clarke, 2008) or does not vary (Adams & Church, 2008; Geraghty, Dunn, & Sanders, 2007). These opposite trends may result from several non-mutually exclusive processes.

Inconsistencies in size clines among insect groups and regions of the world may result from differences in developmental pathways and evolutionary adaptations to climate (Blanckenhorn, 2018; Kivelä, Välimäki, Carrasco, Mäenpää, & Oksanen, 2011). Lower temperatures slow ectotherms' growth rate linearly, but tend to increase their development time exponentially, which can explain positive size clines (Angilletta, Steury, & Sears, 2004; Atkinson & Sibly, 1997). In contrast, negative clines in body size could result from shorter growing seasons at higher latitudes. Specifically, shorter growing seasons can restrict time for development and lead to smaller body size (Blanckenhorn & Fairbairn, 1995; Chown & Klok, 2003). As such, the relative influence of these mechanisms, and their interactions, may dictate the relationship between body size and temperature.

Insects can overcome environmental constraints on body size through multiple means, possibly creating noise in the size cline, or eliminating it. As an example, they can evolve with faster growth rates and shorter developmental time to maintain an optimal size despite brief growing seasons (Blanckenhorn, 2018; Blanckenhorn & Demont, 2004). Adaptations may also include changes in the number of generations they complete within a year (i.e. voltinism) to palliate seasonal restrictions. Multivoltine species can diminish their number of generations per year, whereas semivoltine and partivoltine species can spread their development over two or more years respectively (Kivelä et al., 2011). Either of these mechanisms could lead to the absence of a size cline in insects.

Body size clines are relatively well studied in ants, yet, till date only one previous study compared size clines for a large number of closely related species (Economo et al., 2014). Assessing several closely related species is potentially a powerful approach as they tend to occur in similar regions and therefore share much evolutionary history. We might therefore expect mechanisms regulating size clines to be consistent among species and yield similar relationships to climate. Previous studies instead focused either on intraspecific clines for a small number of species, interspecific clines or community-wide clines. At the intraspecific level, previous work shows that ants increase in size with increasing latitude (Heinze et al., 2003) and elevations (Bernadou, Römermann, Gratiashvili, & Heinze, 2016; Purcell, Pirogan, Avril, Bouyarden, & Chapuisat, 2016; Shik, Arnan, Oms, Cerdá, & Boulay, 2019), consistent with the hypothesis that lower temperatures lead to larger body size. As for patterns among species, they are idiosyncratic. The sole study assessing ant body size at the interspecific level found no consistent trend with latitude (Geraghty et al., 2007). Average, community-wide, body size either increases with latitude (Cushman, Lawton, & Manly, 1993) or decreases with temperature (Bishop et al., 2016; Gibb et al., 2018; Kaspari, 2005) and precipitation (Gibb et al., 2018).

Most work asking how animal morphology varies geographically centres on body size, often neglecting to examine variation in body shape (here referring to allometry, or size-related changes of morphological traits, Klingenberg, 2016). This is also the case for myrmecology studies. Apart from a study showing that the dorsal spines of *Pheidole* workers evolved as a defence against predation (Sarnat, Friedman, Fischer, Lecroq-Bennet, & Economo, 2017), we could not find any that assessed ant shape across broad-scale gradients. This is problematic since not only size impacts performance. Indeed, the shape of an organism relates to life-history traits such as movement (Losos, 1990a, 1990b; Wootton, 1992), diet (Bernays, 1991; Nogueira, Peracchi, & Monteiro, 2009) and habitat preference (Herrel, Meyers, & Vanhooydonck, 2001; Schluter, 1993). Recent work on orthopteran assemblages even showed that morphological traits such as relative eye size, wing length and femur length vary systematically along an elevation gradient (Tiede et al., 2018). In ants, head shape relates to competition (Huang, 2010; Powell, 2008, 2009) and task partitioning (Powell & Franks, 2006). Relative thorax, mandible and postpetiole length relate to mating success in males (Abell, Cole, Reyes, & Wiernasz, 1999). Relative leg length relates to locomotion ability and habitat rugosity (Farji-Brener, Barrantes, & Ruggiero, 2004; Kaspari & Weiser, 1999), whereas

mandible shape (Ohkawara, Nakamura, Kadokura, & Terashita, 2017) and eye size (Weiser & Kaspari, 2006) relate to diet.

Assuming that biotic interactions intensify at lower elevations and latitudes (Jeanne, 1979; Roslin et al., 2017; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), then we might expect a shift in the shape of workers relating to defence ability or competitive performance that covaries with latitude. For example, since workers with larger heads can use them to block nest entrances and fight enemy ants (Huang, 2010; Powell, 2008), the relative head size of workers may increase towards lower latitudes. Simultaneously, productivity (Gillman et al., 2015) and the diversity of prey species (Brown, 2014; Price, Diniz, Morais, & Marques, 1995) increase towards the tropics, which might produce a shift in shape relating to resource acquisition. Therefore, we might expect that traits relating to diet, such as head shape (Ohkawara et al., 2017; Weiser & Kaspari, 2006), will vary along environmental gradients. For instance, if ants become increasingly predatory when more prey species are available, they would potentially have longer heads, because they allow faster mandible strikes (Paul, 2001). As for males and queens, they may show different responses to environmental gradients. For instance, if harsher climates do promote a switch from independent to dependent colony founding (Heinze & Rueppell, 2014), then queens may invest less energy in unnecessarily large wing muscles. Simultaneously, males may need to invest more energy in becoming better flyers and female seekers.

Another limitation of the current body of research on ant morphology along climatic gradients is that they focus almost exclusively on the worker caste. Yet, in ants the combined performance of all individuals explains colony fitness (Hölldobler & Wilson, 2009; Oster & Wilson, 1978). As such, traits of the reproducing castes should play important roles in colony founding, growth and fitness. Moreover, because each caste has unique life-history traits, they might be under different selection pressures. As such, we should expect morphological clines to differ between ant castes.

Here we used morphometric measurements taken on 2,206 ant specimens of workers, males and queens belonging to 32 Nearctic species in the genus *Formica* (group *fusca*). We used this comprehensive dataset to test the hypothesis that ant size negatively relates to temperature, which is expected if they follow Bergmann's rule. Moreover, we tested this hypothesis within and between species and castes, with the expectation that size clines would be consistent throughout. We then explored how ant shape varies along large-scale abiotic gradients. However, we did not have specific a priori predictions regarding variation in ant shape along such gradients.

2 | MATERIALS AND METHODS

2.1 | Morphological data

To characterize the size and shape of ants, we used data previously compiled for a taxonomic revision of the Nearctic *Formica* species (Francoeur, 1973) within the *fusca* group (Creighton, 1950). It consists of morphological measurements taken on 3,280 mounted specimens, which came from several museum collections (listed in Francoeur, 1973). Of these, we used 337 queens, 211 males and 1,658 workers, for a total of 2,206 specimens (Table S1). We had measurements on workers for all 32 species, on queens for 27 species, and on males for 20 species. We used the 12 measurements taken on the greatest number of specimens (Figure S1), for a total of 26,472 measurements. These traits are appropriate because they are associated with ecological functions (Table S2).

2.2 | Geographic location

The specimens within our dataset were labelled with a locality name (e.g. Montréal, QC), thereby we obtained coordinates for the centroid of the provided locality using GeoHack and GoogleMaps. To diminish the effect of geographic inaccuracy, we removed specimens solely labelled with a province or state name; counties were the lowest resolution used. The maximum average distance from a border to the centroid of a county is approximately 44 km (calculated by excluding island states and by assuming counties were square-shaped), which roughly represents a resolution of 0.5° in North America; an acceptable resolution in biogeography studies (Pinkert, Brandl, & Zeuss, 2017). With these coordinates, we mapped the specimens' locations using QGIS (QGIS Development Team, 2015; Figure 1).

2.3 | Environmental data

The use of microclimatic data for our study would have been ideal, since microhabitat temperature dynamics are important for small ectotherms such as insects (Kaspari, Clay, Lucas, Yanoviak, & Kay, 2015; Sunday et al., 2014). However, the nature of our data, which was taken on museum specimens collected across a range of years, prevented us from doing so. Instead, we used global climate layers. We modelled morphological traits against the following variables; mean annual temperature (MAT), mean annual precipitation (MAP) and temperature seasonality (TS; i.e. difference between the annual maximum and minimum temperatures, hereafter referred as seasonality; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We avoided using all environmental variables available on WORLDCLIM to avoid autocorrelation issues and instead selected annual means to encompass the environmental variation experienced by ant species throughout the year. We used seasonality, temperature and precipitation specifically (see Table S3 for their autocorrelations), because they drive patterns of morphological variation across insect taxa (Blanckenhorn & Demont, 2004; Stillwell, Morse, & Fox, 2007).

2.4 | Statistical analyses

2.4.1 | Assessing differences in the morphology of species and castes

For our analyses, we used specimens for which all 12 traits of interest were measured. Although this reduced the number of

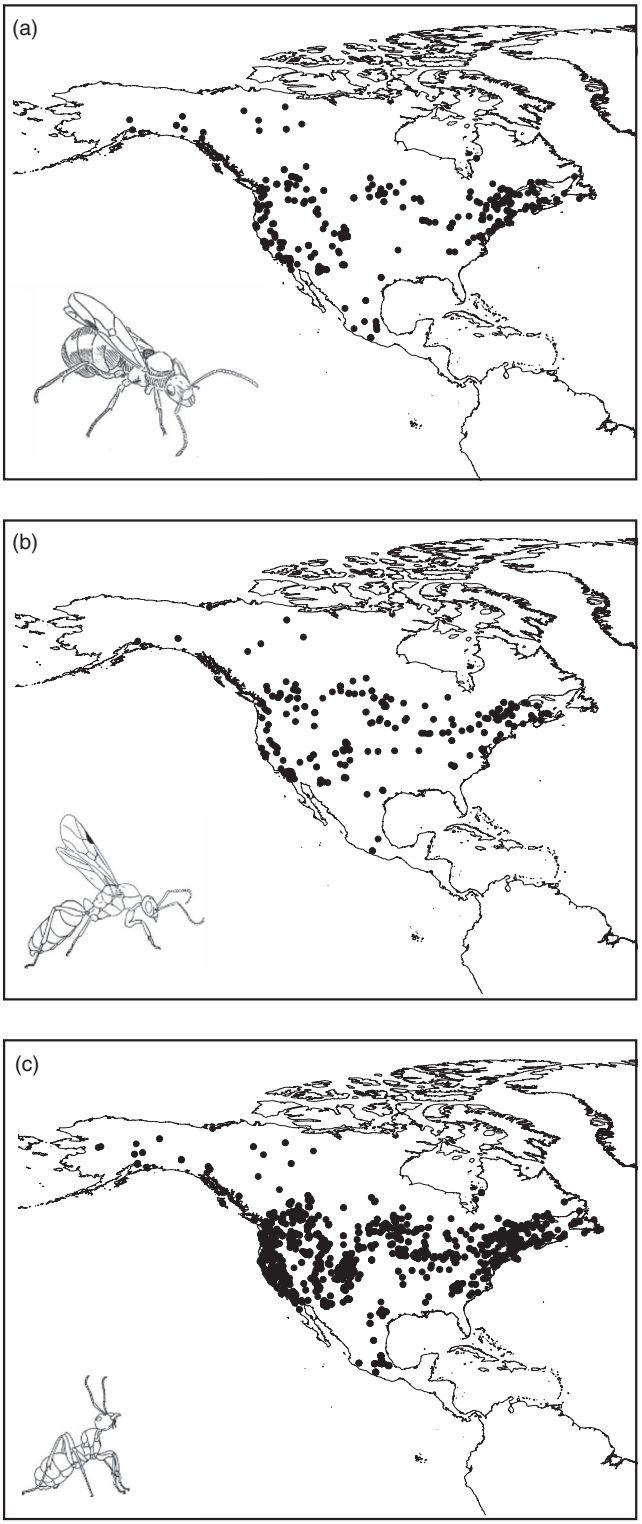

FIGURE 1 Distribution map of the *Formica* (a) queens, (b) males and (c) workers of the Francoeur dataset (Francoeur, 1973)

specimens in subsequent analyses, it allowed us to produce size and shape proxies incorporating variation embedded within more traits.

We transformed morphological measurements using the Aitchison transformation (Aitchison, 1986). This transformation ensures that all traits included are on the same scale, and therefore no particular trait exerts a stronger influence on the ordination. Moreover, this transformation extracts the size and shape components of morphometric traits (Peres-Neto & Magnan, 2004). Since we used 12 traits, the Aitchison transformation produced 12 size-free shape variables and one shape-free size variable. We used the shape-free size variable (hereafter referred as size) as a size proxy. The 12 size-free shape variables represent the scaling of each morphometric measurement in relation to the overall size, meaning that the shape of a morphological structure represents its relative length compared to the size of the individual. We ran a PCA using size and all 12 shape variables to assess the extent of morphological differentiation among castes. Then, we used the 12 shape variables to run PCAs on each ant caste. We then extracted the first and second principal components (i.e. PC1 and PC2) to create two univariate shape variables, hereafter referred as shape PC1 and shape PC2 (see Table S4 and Figure S2 for correlations between PC1 and PC2 axes and traits for each caste), which we used in linear models (Gotelli & Ellison, 2004). Moreover, we took an alternate approach to explore how morphology varies with environmental variation by using a distance-based redundancy analysis (db-RDA; Legendre & Andersson, 1999), using environmental variables as predictors and morphological traits (i.e. size and the 12 size-free shape variables) as response variables (see Figure S3). However, since these showed similar correlations between traits and environmental variation, especially temperature, we elected to do our main analyses using our first approach.

To test for differences in the size of castes and species, we used ANOVAs. We then tested for morphological differences among the different castes and species by running PERMANOVAs using the Mahalanobis distance in the package VEGAN (Oksanen et al., 2016). For subsequent pairwise comparisons we used ADONIS (Arbizu, 2017), using the false discovery rate (FDR) correction (Benjamini & Hochberg, 1995).

2.4.2 | Assessing the environmental determinants of ant morphology

To assess the effect of environmental variation on morphology, we built linear mixed effect models using the package LME4 (Bates, Maechler, Bolker, & Walker, 2014). To identify the best predictors for size we compared models with the Akaike information criterion (AIC) using the package AICCMODAVG (Mazerolle, 2015). Specifically, we compared linear mixed models with the size of a caste as the response variable and different combinations of environmental variables (MAT, MAP and TS) as fixed effects, and species as a random effect. We used species as a random effect since no phylogeny at the species level is currently available for Nearctic *Formica* species (but see Romiguier, Rolland, Morandin, & Keller, 2018 for a partial phylogeny of Palearctic *Formica* species).

Furthermore, we examined if the relationships between environmental variables and size found in our linear mixed models were caste specific. To do so, we used an ANCOVA, using size as

the response variable and, as fixed factors, we used caste, the main environmental variable driving size variation found in the previous analysis, and the interaction between caste and this environmental variable.

To examine intraspecific patterns in size variation within each caste, we used the same approach, but substituted caste with species in our models. If the interaction was significant, we then ran simple linear regressions for each species using the FDR correction (Benjamini & Hochberg, 1995), with size as the response variable and the main environmental variable previously found to drive interspecific patterns as the fixed effect. Within a caste, we only used species with at least 10 individuals (see Table S1).

Finally, to assess the influence of the environment on the shape of ants, we ran all the models described above using shape PC1 or shape PC2 as the response variable (except for ANCOVA analyses, because shape variables represent different morphological aspects in each caste).

We examined our models' residual plots visually to test for the normality and homoscedasticity assumptions, (Chatterjee & Hadi, 2006). Marginal R^2 and conditional R^2 values for mixed models were obtained using the package MuMIn (Bartoń, 2016). We performed all analyses using R (R Core Team, 2017).

3 | RESULTS

3.1 | Assessing differences in the morphology of species and castes

ANOVAs show that size varied significantly between both castes ($F_{2,\ 2,203} = 1612$, $p < 0.001$; Figure 2) and species ($F_{31,\ 2,174} = 7.91$, $p < 0.001$). Similarly, PERMANOVAs show that morphology varied significantly among both castes ($F_{2,\ 2,203} = 194.41$, $p = 0.001$) and species ($F_{31,\ 2,174} = 20.91$, $p = 0.001$). However, castes formed more distinct units within the morphospace (Figure 2).

3.2 | Assessing the environmental determinants of ant body size

Mean annual temperature was the environmental variable that best predicted geographic variation in ant body size across all castes (Table S5). Indeed, all castes increased in size with increasing temperatures (Table 1; Figure 3). There was a significant interaction between caste and temperature ($F_{2,\ 2,200} = 5.50$, $p < 0.01$), meaning that the rate at which size varied with temperature was caste-specific. However, temperature was not the sole driver of size variation. Indeed, in our best model, precipitation influenced size in workers and queens. Specifically, there was a positive interaction between temperature and precipitation, meaning that higher precipitations intensified the effect of temperature on the size of the female castes (Table 1). In contrast, ANCOVAs show that within a caste, variation in size was not species specific: there was no significant interaction between species and temperature for queens ($F_{20,\ 290} = 0.85$, $p = 0.65$), males ($F_{13,\ 177} = 1.22$, $p = 0.27$) and workers ($F_{27,\ 1598} = 1.16$, $p = 0.26$). Thus, within a caste, the effect of temperature on size is consistent among species.

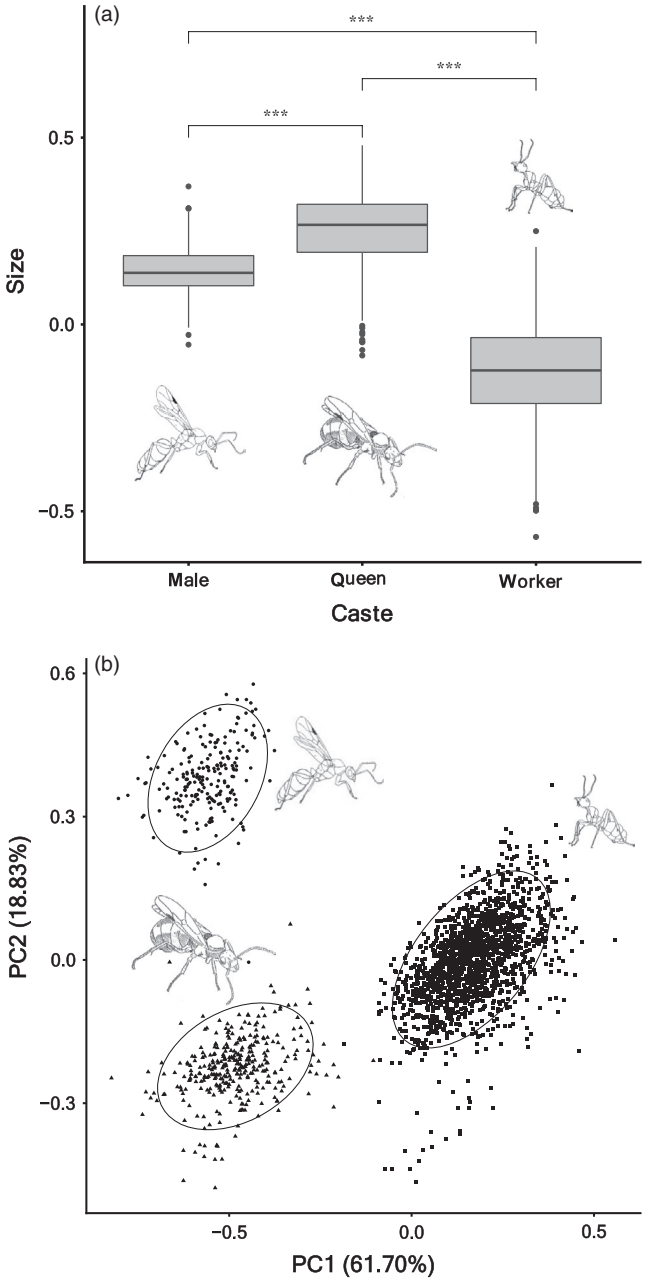

FIGURE 2 (a) Boxplots representing size in queens, workers and males. Lower and upper hinges of boxplots correspond to the first and third quantiles. Upper and lower whiskers extend from the closest hinge to the largest and lowest value no further than 1.5 times the inter-quantile range respectively. Data beyond the whiskers (i.e. outliers) are plotted as single points. Significant *p* values for ANOVA comparisons marked with asterisks (***$p < 0.001$). (b) Principal component analyses using 12 log-transformed morphometric measurements to visualize how (a) castes and (b) species of *Formica* segregate in the morphospace. The level of confidence ellipses shown is 0.95. Each ellipse represents a caste

TABLE 1 Summary of selected models for interspecific patterns using size, shape PC1 and shape PC2 as the response variables, environmental predictors as fixed effects (MAT, MAP and TS) and species as a random variable. Models with the lowest scores were chosen. When multiple models were within two AIC units the most parsimonious model was used

Caste	Model AIC	Response variable	Fixed effects	Estimate	*p* Value
Worker	4,424.80	Size	MAT	0.11809	3.82^{-04}***
			MAP	0.03810	0.14107
			MAT × MAP	0.06730	7.17^{-03}**
	2,937.14	Shape PC1	MAT	−0.10263	2.32^{-05}***
			TS	−0.09227	4.86^{-05}***
			MAT × TS	−0.03664	1.81^{-02}*
	4,029.12	Shape PC2	MAP	0.0707	0.004**
			TS	0.1175	3.62^{-05}***
Queen	670.01	Size	MAT	0.23744	1.79^{-05}***
			MAP	−0.02337	0.5562
			MAT × MAP	0.10741	0.0117*
Male	433.36	Size	MAT	0.15459	0.0161*
			MAP	0.05003	0.3438
			MAT × MAP	−0.06665	0.1703
	550.81	Shape PC2	MAT	−0.19438	0.046*
			TS	−0.29278	0.001**
			MAT × TS	−0.13088	0.008**

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; TS, temperature seasonality.

Significant *p* values marked with asterisks (***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$).

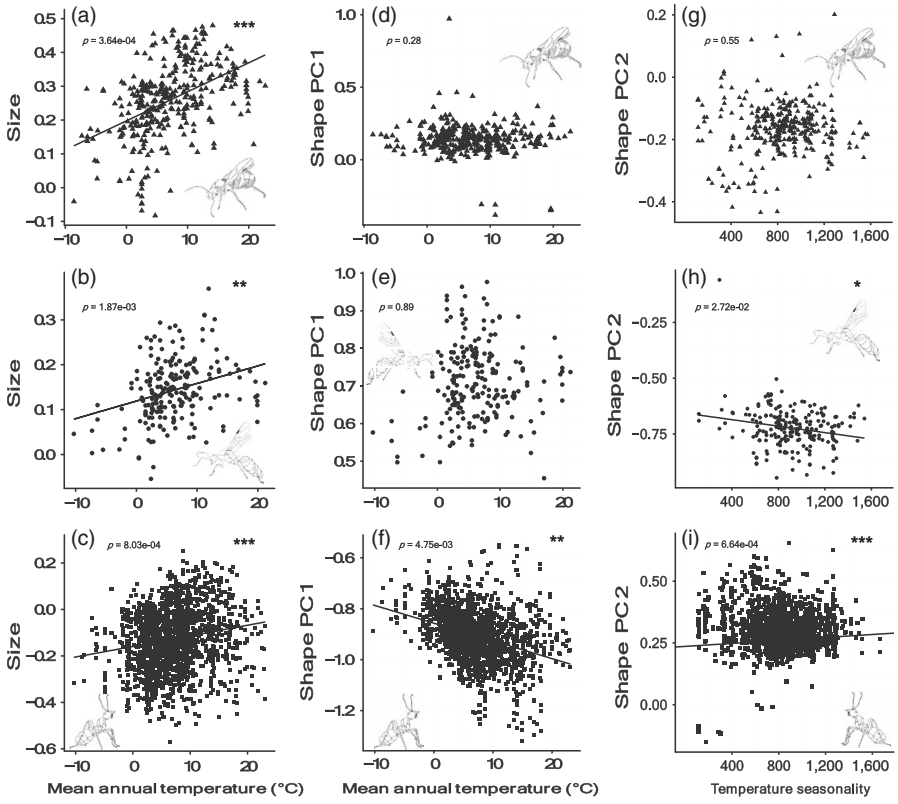

FIGURE 3 Relationship between size and variation in mean annual temperature (°C) in (a) queens, (b) males and (c) workers. Size represents a shape-free variable produced by using the Aitchison transformation on 12 morphological traits. Relationship between shape and variation in mean annual temperature (°C) in (d–g) queens, (e–h) males and (f–i) workers. Here, shape is the PC1 and PC2 of the 12 size-free shape variables produced by using the Aitchison transformation on 12 morphological traits. Significant *p* values for linear mixed models marked with asterisks (***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$)

3.3 | Assessing the environmental determinants of ant shape

At the interspecific level, the drivers of shape differed among castes (Table 1; Tables S6–S7). None of the abiotic factors affected the shape PC1 of queens and males, whereas temperature and seasonality affected the shape PC1 of workers (Table 1; Figure 3). Specifically, temperature had the strongest influence on worker shape (Table 1; Figure 3). In our best model, seasonality similarly affected the first axis of worker shape as temperature, as well as

TABLE 2 Summary of significant models for intraspecific patterns of the first and second axes of shape (size is not included because ANCOVAs showed that responses do not differ among species within each caste). Simple linear regressions using shape (size was not included here since no models were significant after applying the FDR correction) as the response variable, and with the fixed factor set as the best environmental predictor of shape found at the interspecific level (MAT, MAP or TS), were done for workers ($n = 23$ species), queens ($n = 9$ species) and males ($n = 8$ species). Adjusted p values were obtained using the FDR correction. Only the models still significant after using the FDR correction were chosen for display

Caste	Species	Response variable	Term	Estimate	*SE*	*t* value	*df*	*p* Value	*p* adjusted	Multiple r^2	Adjusted r^2
Worker	*browni*	Shape PC1	MAT	2.29^{-02}	5.87^{03}	3.90	17	0.001**	0.021*	0.47	0.44
	neorufibarbis	Shape PC1	MAT	-3.27^{-03}	1.04^{-03}	−3.15	208	0.002**	0.021*	0.05	0.04
	podzolica	Shape PC1	MAT	-2.48^{-03}	8.91^{-04}	−2.78	217	0.005**	0.044*	0.03	0.03
	xerophila	Shape PC1	MAT	-6.50^{-03}	1.86^{-03}	−3.49	8	0.008**	0.047*	0.60	0.55
	argentea	Shape PC2	TS	1.25^{-04}	2.83^{-05}	4.43	190	1.58^{-05}***	3.62^{-04}***	0.09	0.08
Queen	*argentea*	Shape PC2	TS	-1.07^{-04}	3.11^{-05}	−3.45	21	0.002**	0.022*	0.36	0.33
Male	*occulta*	Shape PC2	TS	-9.30^{-04}	2.04^{-04}	−4.56	10	0.001**	0.008**	0.68	0.64

Abbreviations: FDR, false discovery rate; MAP, mean annual precipitation; MAT, mean annual temperature; TS, temperature seasonality.
Significant p values marked with asterisks (***$p < 0.001$, **$p < 0.01$ and *$p < 0.05$).

intensified its effect. Namely, with increasing temperatures *and* seasonality, the relative length of their antennae, legs and mesosomas increased, whereas their relative head width diminished (Table 1; Figure 3).

Abiotic factors differentially affected the shape PC2 of each caste. Seasonality had the strongest effect on the shape PC2 of males, as well as a weak effect on the shape PC2 of workers, but none on the shape of queens (Table 1; Figure 3). In our best model for workers, precipitation also affected their shape PC2. Namely, their relative head length and eye diameter decreased with increasing seasonality and precipitation, whereas the relative minimal width of their head increased (Table 1; Figure 3). In contrast, in our best model for males, temperature similarly affected, as well as intensified, the effect of seasonality on the shape PC2 of males. Namely, the relative width and length of the males' head became relatively smaller with increasing seasonality and temperature, whereas the relative width of their pronotum increased (Table 1; Figure 3).

At the intraspecific level, relationships between shape and environmental variables differed, with few species following a clear trend (Table 2). The interaction between species and temperature was significant for the first shape axis of queens (ANCOVA, $F_{20,\ 290} = 2.16$, $p < 0.01$) and workers (ANCOVA, $F_{27,\ 1598} = 2.84$, $p < 0.001$), but not for males (ANCOVA, $F_{13,\ 177} = 1.22$, $p = 0.27$). As for the second axis of shape, ANCOVAs show that species respond differently to seasonality variation in queens ($F_{20,\ 290} = 1.839$, $p < 0.05$), males ($F_{13,\ 177} = 3.88$, $p < 0.001$) and workers ($F_{27,\ 1598} = 6.77$, $p < 0.001$).

4 | DISCUSSION

We investigated how geographic variation in climate relates to the morphology of 32 closely related ant species in the genus *Formica*. Although much of ant community ecology and macroecology focuses on workers, here we assessed the influence of the abiotic environment on the morphology of the worker and reproductive castes.

4.1 | Assessing the environmental determinants of ant body size

The reproductive and worker castes of *Formica* ants occupy different portions of the morphospace. Queens and males are not only larger than workers, they differ in shape. As such, they may respond differently to selective pressure from abiotic, or even biotic factors.

Here our results show that queens, males and workers increase in size with increasing temperatures among species, but not within species. The direction, but not the strength, of the relationship between size and temperature is consistent among castes. Thus, contrary to our initial prediction and the pattern found in previous ant studies (Bernadou et al., 2016; Cushman et al., 1993; Heinze et al., 2003; Purcell et al., 2016), *Formica* ants follow the converse of Bergmann's rule as they are increasingly smaller in colder environments. This result appears counter-intuitive since, in laboratory experiments, cold temperatures cause ants to mature at a larger size (Molet, Péronnet, Couette, Canovas, & Doums, 2017; Oms, Cerdá, & Boulay, 2017). However, the pattern we find here might reflect longer term thermal dynamics playing out across seasons. Specifically, if we consider MAT as a proxy for the number of degree days in a locality (i.e. growing season length), our results concur with the mechanism thought to drive the converse to Bergmann's rule—shorter growing seasons in cold environments constrain the size ectotherms can reach. *Formica* ants are univoltine (Kipyatkov, 1993), and their development time increases rapidly with decreasing temperatures (Penick, Diamond, Sanders, & Dunn, 2017). In effect, this makes short and cold summers

especially restrictive to attain a large size because they simultaneously diminish growth rates and limit the time available to reach maturity. The different responses of the workers and reproductive castes support this explanation. Namely, temperature affects the size of queens and males more than the size of workers, which is expected since they are larger and thus take more time to mature (Porter, 1988). Note that this pattern was even stronger when considering precipitation; queens and workers were largest in warm and wet climate.

Research on ant body size has focused largely on workers (Cerdá & Retana, 1997; Kaspari, 1996; Powell & Franks, 2006; Schöning, Kinuthia, & Franks, 2005); few studies examined size variation in males (Abell et al., 1999; Stürup, den Boer, Nash, Boomsma, & Baer, 2011) or queens (Helms & Godfrey, 2016; Rüppell & Heinze, 1999; Wiernasz & Cole, 2003) despite their crucial role within the colony. Here we find that members of the reproductive castes are smaller in colder environments, which could lower their fecundity (Vargo & Fletcher, 1989; Wiernasz, Sater, Abell, & Cole, 2001 but see Stürup et al., 2011), longevity (Calabi & Porter, 1989), and dispersal ability (Helms, 2018; Sundström, 1995 but see Davidson, 1982). Moreover, it could lower the ability of queens to found colonies independently (Wiernasz & Cole, 2003), which may partially explain why polygynous colony structures and dependent colony founding strategies are more prevalent in cooler environments (Heinze, 1993; Heinze & Rueppell, 2014).

Our expectation was that intraspecific patterns of size variation would reflect those found at the interspecific level. However, this was not the case. We posit that this could be because the range of temperature experienced by different populations within species may be too small to produce a detectable variation in size. Indeed, the range of sizes of all species as well as the range of temperature experienced by all species is substantially larger than that of any singular species (Figure 4). As such, to detect intraspecific variation in size across the distribution of a single species may require data with higher spatial resolution. Indeed, our data's resolution is relatively low considering the potential effects of microclimatic variation. For instance, *Formica* ants can select nest locations according to their thermal capacities (Mccaffrey & Galen, 2011), thermoregulate their nests (Jílková, Cajthaml, & Frouz, 2015) and selectively move brood along a thermal gradient within their nest to optimize their development (Kadochová & Frouz, 2013). Each of these strategies could partially compensate for the harsher conditions of colder climates and diminish the strength of the relationships observed between size and temperature. Nevertheless, in *Formica*, the converse to Bergmann's rule may solely be an interspecific phenomena, where larger species are found in warmer environments and smaller species in colder environments (see Figure 4).

4.2 | Assessing the environmental determinants of ant shape

We found that temperature drives variation along the main shape axis of the worker caste, but not the reproductive castes, and that this effect was exacerbated by seasonality. We also found that seasonality drove variation in the second shape axis of both the worker and male castes, but not the queen caste. Moreover, precipitation had a similar, albeit weaker, effect on workers, whereas temperature similarly affected and intensified the effects of seasonality on the shape of males. We speculate that this dichotomy between the worker and the reproductive castes originates from their different functions within a colony.

Selective pressures on the reproductive success (Fjerdingstad & Boomsma, 1997), and the flight ability (Keller, Peeters, & Beldade, 2014) of queens and males might prevent drastic shape variations despite change in body size along climatic gradients. Indeed, they need large gasters to contain their reproductive organs (Trible & Kronauer, 2017), but also large thoraxes to accommodate their flight muscles (Keller et al., 2014), and metabolic reserves, especially in claustral species (Peeters, 2012). Thus, for the reproductive castes, an increase in gaster size might be counterbalanced by an increase in thorax size to conserve a similar flight muscle to weight ratio (Helms & Godfrey, 2016), thus heightening fecundity while minimizing drawbacks on dispersal ability.

Accordingly, we found that queen shape did not vary across abiotic gradients. We posit that queens could break the flight/fecundity trade-off by adopting different colony founding strategies (i.e. budding or social parasitism), since they would no longer need large wing muscles. In *Formica*, queens use both dependent and independent founding strategies, as well as multiple forms of social parasitism (Buschinger, 2009). Data on the founding strategy of species within this study were unavailable, but all species for which we had information on their social parasitism (66%) revealed that they act as hosts (Table S9), which indicates their queens are independent founders (i.e. claustral). This could partially explain why their shape was consistent across environmental gradients.

The reproductive behaviour of male ants is found along a continuum between two syndromes—the male aggregation (MA) and female calling syndromes (FC; Hölldobler & Bartz, 1985), which may promote different morphologies (Shik, Donoso, & Kaspari, 2013). In *Formica*, both behaviours are known, such as FC in *F. montana* (Kannowski & Johnson, 1969), and MA in *F. subpolita* (O'Neill, 1994) and *F. sanguinea* (Mori & Moli, 1998). Here we found that males had relatively smaller heads, but larger pronotums in more seasonal environments. This may represent an increased investment in dispersal ability, since larger pronotums would allow larger wing muscles (Keller et al., 2014). More capable male flyers may be essential when they are the primary dispersers, such as in *Formica exsecta* (Vitikainen, Haag-Liautard, & Sundström, 2015). Moreover, we found that males' scapes do not vary consistently along environmental gradients. We interpret this as evidence, as the species we assessed do not shift from one mating syndrome to another along environmental gradients, but invest relatively more energy in their flight (i.e. larger pronotums) instead of their seeking (i.e. smaller heads) ability in more seasonal environments. Lastly, because we found no clear pattern in eye size variation along environmental gradients, we interpret this as evidence that males do not shift the time of day at which they fly (Narendra et al., 2011).

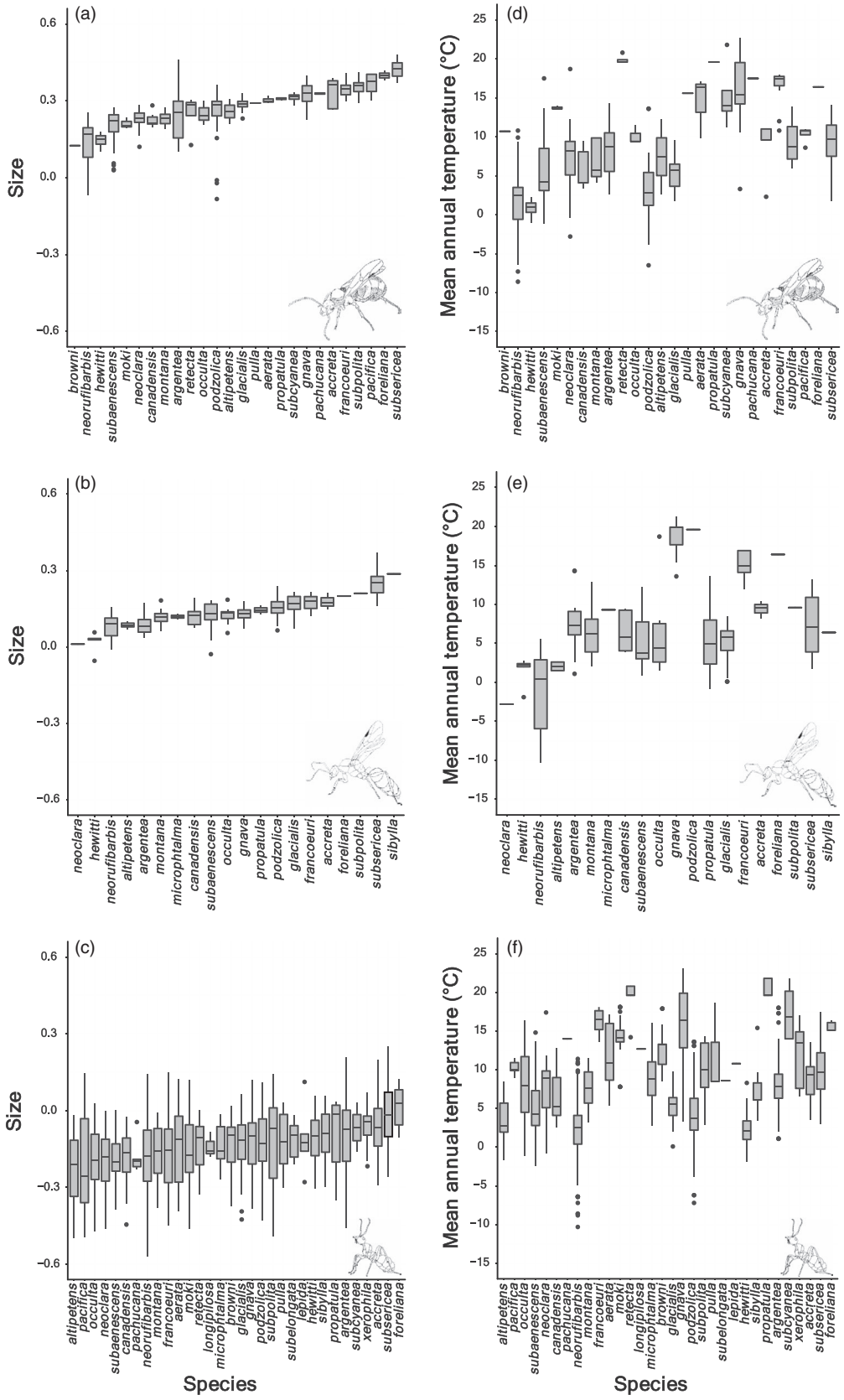

FIGURE 4 Boxplots of the size of queens (a), males (b) and workers (c) for each *Formica* species used in our analyses, and boxplots of the mean annual temperature range of the locations at which the queens (d), males (e) and workers (f) of each *Formica* species were collected from. Boxplots are ordered by the mean value of the size of the caste and species it represents. Lower and upper hinges of boxplots correspond to the first and third quantiles. Upper and lower whiskers extend from the closest hinge to the largest and lowest value no further than 1.5 times the inter-quantile range respectively. Data beyond the whiskers (i.e. outliers) are plotted as single points

Contrary to our initial hypothesis that workers of *Formica* would have relatively larger heads in warmer environments, here we find that, at the interspecific level, workers have relatively thinner heads, but relatively longer antennae, legs and thoraxes in warm *and* seasonal environments. This is not altogether surprising, because larger heads may not allow *Formica* workers to better defend their colony since they rely heavily on spraying formic acid for defence. Instead, where workers can grow to larger sizes it might be advantageous to invest more energy in other structures than head size. For instance, longer legs allow workers to move faster (Kaspari & Weiser, 1999), whereas longer antennae are more efficient to follow pheromone trails (Couzin & Franks, 2002; Schöning et al., 2005). Also, a longer mesosoma may allow workers to carry larger loads (Davidson, Cook, & Snelling, 2004; Keller et al., 2014). Consequently, as *Formica* workers grow larger along an increasing temperature gradient, they may invest relatively more energy in traits relating to foraging efficiency.

Patterns of shape variation within species, contrary to our prediction, generally did not reflect patterns found among species. As hypothesized for size, this could result from single species experimenting les environmental variation than the sum of all species assessed. Yet, we found intraspecific patterns for shape in some instances (workers: 4 of 23 species; queens: 1 of 9 species; males: 1 of 8 species). This could indicate that constraints on shape variation within species are weaker than for size.

In summary, our results suggest that environmental constraints, especially in temperature and seasonality, relate to shape variation across *Formica* species. In colder environments, workers have shapes that may be less efficient for foraging, whereas in more seasonal environments males have shapes that may optimize their flight ability. Meanwhile, the shape of queens generally did not relate to environmental variation. As such, how the shape of an ant responds to environmental variation depends on the caste it belongs to.

4.3 | Caveats

Across our models relating morphology to environmental gradients, fixed effects (i.e. abiotic factors) explained relatively little variation in comparison to our random effect (i.e. species). This corresponds to the observation that *Formica* species differ in size, and suggests that species in colder environments are smaller than species in warmer environments, especially for the reproductive caste (Figure 4). It also reinforces the fact that interspecific, rather than intraspecific, effects largely drive the clines we observe. It is therefore not surprising that the abiotic environment alone does not explain much variation in morphology after accounting for differences between species. Nevertheless, linear models using solely environmental variables as fixed effects (i.e. without species as a random effect) explained approximately 15%–20% of the variation in morphology (Table S8), which shows that this pattern is not spurious. However, *Formica* represents a small fraction of the functional diversity of ants. Future studies should assess other genera to verify the replicability of our results within the Formicidae.

5 | CONCLUSIONS

Our study suggests that climatic variations may constraint an organism's morphology. Thus, evaluating how the functional traits of species, and groups within species, vary along gradients may highlight what restricts their distribution, and subsequently help identify key habitats for their conservation. This is also relevant to other non-eusocial taxa including morphologically distinct groups such as species with sexual dimorphism, or for which different populations show diverging morphologies. Nevertheless, despite the difficulties of collecting data on males and queens, progress in ant ecology and biogeography clearly requires a more holistic, caste-specific approach.

ACKNOWLEDGEMENTS

A NSERC Discovery Grant (RGPIN-2015-06081) and a FRQNT New University Researchers Start-up Grant (2016-NC-189273) to J.-P.L. funded this study.

DATA AVAILABILITY STATEMENT

Data are available for download in the Dryad Digital Repository https://doi.org/10.5061/dryad.dncjsxkx3 (Brassard, Francoeur, & Lessard, 2020).

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SUPPORTING INFORMATION

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

How to cite this article: Brassard F, Francoeur A, Lessard J-P. Temperature drives caste-specific morphological clines in ants. *J Anim Ecol*. 2020;00:1–14. https://doi.org/10.1111/1365-2656.13330