Body size, colony size, and range size in ants (Hymenoptera: Formicidae): are patterns along elevational and latitudinal gradients consistent with Bergmann's Rule?

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Abstract

Body size of organisms often increases with latitude and elevation, a pattern commonly called Bergmann's Rule. Though this pattern has been documented in many endothermic taxa, relatively few insect taxa have been examined, with some taxa showing strong support and other taxa showing little or no support for the rule. For colonial organisms (social insects, corals, bryozoans) size can also be estimated as the number of sub-units. Consequently, for ants the number of workers per colony should also increase with latitude or elevation. Here, we test whether body size or colony size is related to latitude and elevation for ants in eastern North America. We found no positive relationship between body size or colony size and elevation or latitude. However, species with large latitudinal ranges also had large elevational ranges, suggesting that species that are able to tolerate broad climatic conditions have the largest ranges. In addition, species with high latitudinal maxima also had high elevational maxima. Taken together, our results do not support Bergmann's Rule in ants, in contrast to other studies on ants. But climate imposes limits on ant distributions in similar ways along both elevational and latitudinal gradients.

Key words: Range size, elevational gradient, latitudinal gradient, social insects, colony size, worker size.

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Introduction

The body size of organisms is associated in diverse ways with range size and geographic patterns of distribution and diversity (GASTON & BLACKBURN 2000, GASTON 2003, BROWN & al. 2004). One of the most well-known macroecological patterns relating body size to geographic distributions is Bergmann's Rule. Bergmann's Rule (BERGMANN 1847) posits that body size tends to be larger at higher latitudes than at lower latitudes within endothermic species. The pattern and its underlying mechanisms are controversial for both endothermic vertebrates (BLACKBURN & al. 1999, MEIRI & DAYAN 2003) and ectothermic invertebrates (VAN VOORHIES 1996, MOUSSEAU 1997, PARTRIDGE & COYNE 1997). In some species, body size increases with increasing latitude, while in others body size decreases with latitude (MOUSSEAU & ROFF 1989). To date, relatively few insect taxa have been tested for Bergmann's Rule, with some taxa showing strong support (ants: CUSHMAN & al. 1993, KASPARI & VARGO 1995) while other taxa show only weak or no support for the rule (termites: PORTER & HAWKINS 2001; bees: HAWKINS 1995; butterflies: HAWKINS & LAWTON 1995, HAWKINS & DEVRIES 1996; moths: BREHM & FIEDLER 2004).

Size in colonial organisms (e.g., social insects, corals, bryozoans, etc.) can also be measured as the number of the colony's subunits (HUGHES & HUGHES 1986, KASPARI 2005). In ants, colony size can range from < 10 individuals to hundreds of millions per colony (HÖLLDOBLER & WILSON 1990, KASPARI & VARGO 1995, KASPARI 2005). In the Western Hemisphere, KASPARI & VARGO (1995) found that temperate ant species have larger colonies (more workers) than do tropical ant species at lower latitudes. However, in another group of social insects, PORTER & HAWKINS (2001), found no relationship between colony size and latitude among termite species.

If temperature drives the macroecological relationships among body size, colony size and geographic location along latitudinal gradients, then the same patterns observed along latitudinal gradients ought to be mirrored along elevational gradients because, on average, temperature drops 1 °C for every 100 m increase in elevation (BROWN & LOMOLINO 1998). To date, few studies have examined interspecific variation in body size along elevational gradients, relative to the number that have examined latitudinal variation in body size (JANZEN & al. 1976, HAWKINS & DEVRIES 1996, BLACKBURN & RUGGIERO 2001, ASHTON 2002, CHOWN & KLOCK 2003, HAUSDORF 2003, FU & al. 2004, BREHM & FIEDLER 2004), and no studies have examined body size or colony size variation along elevational gradients in the social insects, or more generally in colonial organisms.

Here, we quantify the relationships among size (both worker size and colony size) along both elevational and latitudinal gradients for ants in eastern North America. The latitudinal gradient we examine extends almost 26 degrees, and the elevational gradient extends almost 1500 m. To our knowledge, this is the first time these relationships along both latitudinal and elevational gradients have been assessed in social insects, and it is one of the first such assessments for any taxon (BLACKBURN & RUGGIERO 2001, HAUSDORF 2003, FU & al. 2004).

Materials and methods

Elevational gradient data

We sampled ant assemblages at 22 sites in Great Smoky Mountains National Park (GSMNP), USA in 2004 and 2005 during periods of peak ant activity (June - September). The sites were in mixed hardwood forests away from roads, heavily visited trails or other human disturbances and ranged in elevation from ~300 m to ~1800 m. All worker ants were extracted from 16 1-m^2 plots at each of the 22 sites and then identified and enumerated. In total, we collected 38 leaf litter ant species at the 22 sites. The number of species per m^2 ranged from 0 - 10, and the number of species per 50×50 m plot varied from 2 - 22. Chao2 estimates of site richness ranged from 4 - 34 species. In 20 of the 22 sites, the estimators reached an asymptote, indicating that further sampling with the same methods would probably have added no new species (SANDERS & al. 2007a). Because our sampling approach appeared to yield nearly complete samples of the ant fauna, we are confident that we are accurately estimating the elevational ranges of species. Voucher specimens are stored in N. Sanders's ant collection at the University of Tennessee. For more details of the sampling regime, sites, and keys we used to identify the specimens, see SANDERS & al. (2007a) and LESSARD & al. (in press).

Latitudinal gradient data

We assessed latitudinal range sizes and positions of species by searching for community-level studies of ant diversity in the eastern US and Canada (DUNN & al. 2007b). The criteria for selection included (1) studies had to assess diversity using quantitative techniques, e.g., pitfall traps, leaf litter samples, etc., and (2) the data had to be available either in the published or gray literature. In addition, we obtained data on latitudinal ranges from the Global Biodiversity Information Facility (www.gbif.org, 2.VII.2007; most of the data were supplied by the California Academy of Sciences and the Ohio State University Collection). GBIF, to date, consists of 128,112 ant records with coordinates for ant species from 427 genera. For each species that we collected in GSMNP along the elevational gradient, we searched www.gbif.org for the maximum and minimum latitude at which that species was collected in the eastern North America (east of the Mississippi River). Then, to obtain the latitudinal maximum for each species, we used whichever value was greater: the value from www.gbif.org or from our literature searches. To obtain the latitudinal minimum for each species, we used whichever value was smaller: the value from www.gbif.org or from our literature searches.

Latitude and elevation

In addition to the main variables we were concerned with, we also considered the relationship between the elevational and latitudinal ranges of species. Latitudinal ranges and elevational ranges could be tightly coupled if the species that are tolerant of cold northern conditions, for example, are also tolerant of cold, high elevation conditions. Such a coupling would suggest that the mechanisms which shape the relationships among body size, colony size, and range size operate in similar ways along both latitudinal and elevational gradients, as has long been suggested for many macroecological patterns (JANZEN 1967, BLACKBURN & RUGGIERO 2001, RAHBEK 2005).

Colony size and body size

We used the average number of workers as an estimate of colony size. Estimates came from books (primarily HÖLL-DOBLER & WILSON 1990), journal articles (e.g., KASPARI & VARGO 1995), and our own collections in Great Smoky Mountains National Park. For our own collections, we tried to obtain as many nests as possible for each species. The total ranged from 2 - 8 nests per species. For two species, more than one data source from different geographic locations existed. In these cases, we used the source location nearest to the Great Smoky Mountains National Park.

For each species, we estimated body size by measuring Weber's Length, the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum (BROWN 1953) for six randomly selected individuals of each species. Weber's length is a commonly used metric in studies of ant body size (GOTELLI & ELLISON 2002, NIPPERESS & BEATTIE 2004, WEISER & KASPARI 2006, SANDERS & al. 2007b).

For both colony size and body size, intraspecific variation undoubtedly exists (e.g., HEINZE & al. 2003). However, in this study, we do not examine how body size and colony size vary within species, both because such data for single species do not exist at macroecological scales and because tests for the mechanisms underlying interspecific and intraspecific patterns in life history traits are not necessarily the same.

Analyses

This dataset includes thirty-six species from six subfamilies. We measured or estimated six traits for each of the species: (1) body size, as described above; (2) colony size, as described above; (3) the maximum and minimum elevation at which a species was collected in GSMNP; (4) the elevational range of each species in GSMNP; (5) the maximum and minimum latitude at which a species was collected in eastern North America; and (6) the latitudinal range of each species in eastern North America. We were able to obtain colony size information for 26 of the species included here. For the remaining species, we used average values from congeneric species from our own study and from published records.

We use ordinary least squares regression to examine the relationships among body size, colony size, elevation, and latitude. We incorporated phylogeny into preliminary analyses using CAIC (Comparative Analysis by Independent Contrasts, PURVIS & RAMBAUT 1994). The results from the CAIC were not qualitatively different from the analyses presented here, but are not considered further because they were limited by the modest number of comparisons possible using existing ant phylogenies.

There is some question as to whether Bergmann's Rule should be tested intra- or interspecifically (BLACKBURN & al. 1999). It seems clear from the original text and translations (JAMES 1970) that Bergmann's original notion applied interspecifically. In addition, it is not uncommon to see studies testing for Bergmann's Rule both intra- and inter-specifically, especially in ants and termites (CUSHMAN & al. 1993, KASPARI & VARGO 1995, PORTER & HAWKINS 2001).
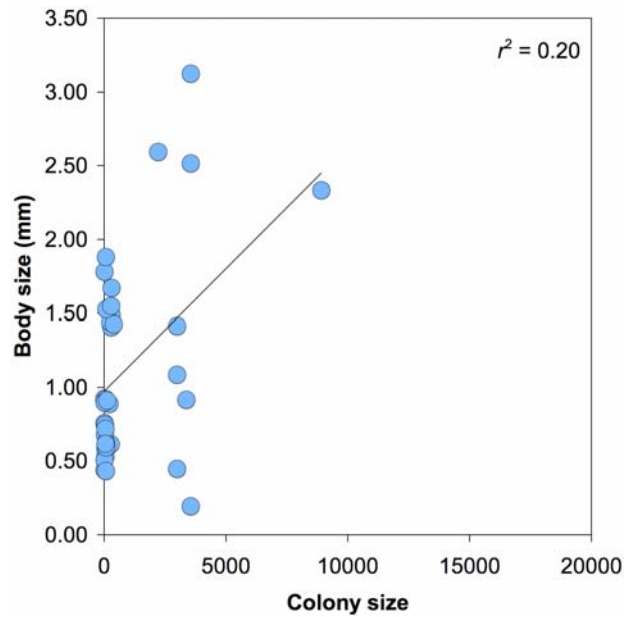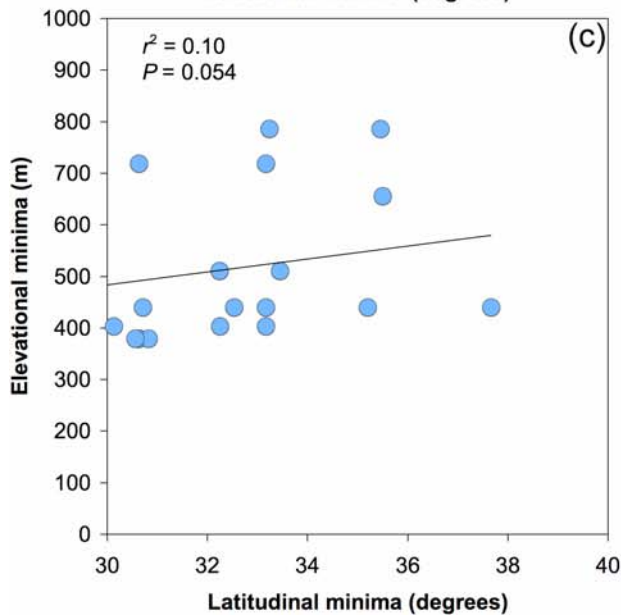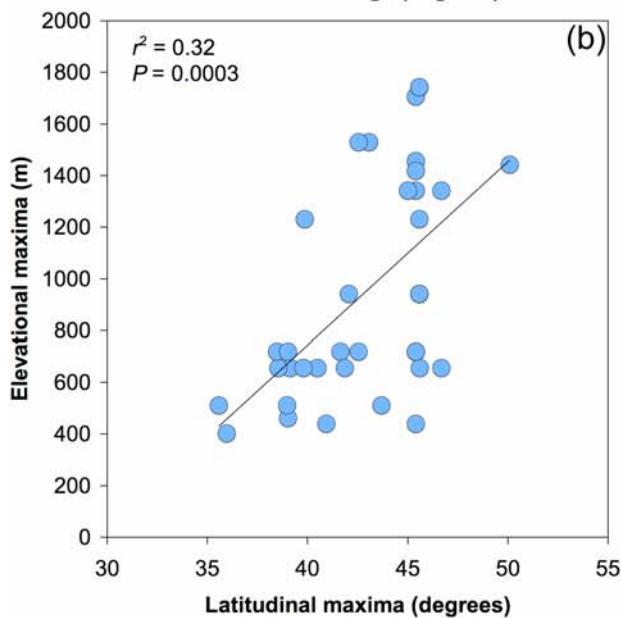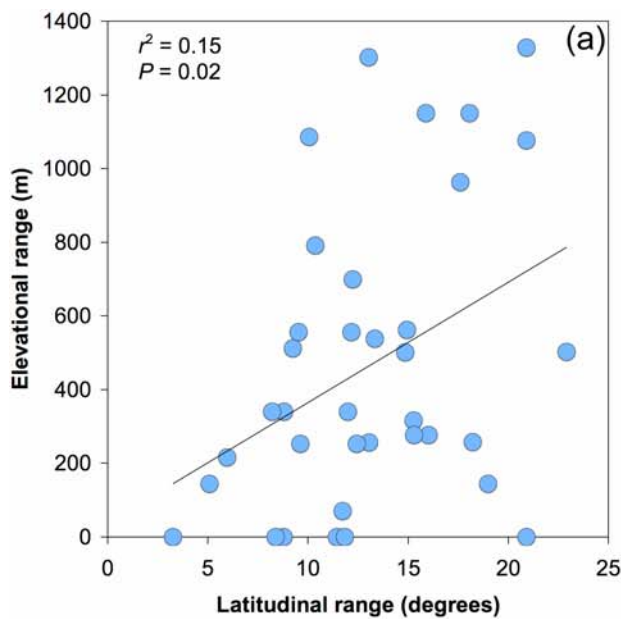
Fig. 2: The relationship between body size (in mm, measured as Weber's Length) and colony size (estimated as the number of workers) for 36 forest ant species in eastern North America. In the figure, each symbol represents a single species, and the line is the best-fit regression line.

Results and discussion

Ant species with large latitudinal ranges also had large elevational ranges ($r^2 = 0.15$, $P = 0.02$; Fig. 1a). Additionally, species with high elevational maxima also had high latitudinal maxima ($r^2 = 0.32$, $P = 0.0003$; Fig. 1b), and species with low elevational maxima tended to have low latitudinal maxima ($r^2 = 0.10$, $P = 0.054$; Fig. 1c). In other words, species with broad environmental tolerances along elevational gradients also had broad environmental tolerances along the latitudinal gradient, if range size is correlated with the ability to tolerate climatic variation. Additionally, those species with high-latitude ranges also had high elevational ranges, and those species with ranges at low latitudes tended also to have low elevational ranges. Taken together, this suggests that, if the distribution of ant species is set by climate, and climate varies systematically along elevational and latitudinal gradients, then climate operates in similar ways to shape species distributions along both latitudinal and elevational gradients.

Larger colonies tended to have larger workers ($r^2 = 0.20$, $P = 0.006$; Fig. 2, Tab. 1). Even if we remove from our analyses the single point for the species with the largest colony size (*Formica subsericea* SAY, 1836) with > 8000 workers), the pattern still holds ($r^2 = 0.13$, $P = 0.037$). It is a bit surprising that species with large workers tend to have

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← Fig. 1: (a) The relationship between latitudinal range and elevational range for 36 forest ant species in eastern North America. (b) The relationship between elevational and latitudinal maxima. (c) The relationship between elevational and latitudinal minima. In each figure, each symbol represents a single species, and the line is the best-fit regression line.

Tab. 1: Data for each of 36 forest ant species in eastern North America, including latitudinal maxima, latitudinal minima, latitudinal range, elevational maxima, elevational minima, elevational range, body size (measured as Weber's Length), and colony size. The Source column indicates the literature source from which we derived the estimate of colony size.

| Subfamily: species	Latitude			Elevation			Body size (mm)	Colony size	Source
	maximum	minimum	range	maximum	minimum	range			
Amblyoponinae:									
Amblyopone pallipes (HALDEMAN, 1844)	43.08	27.18	15.90	1530	379	1151	1.78	12	FRANCOEUR (1965), BURRILL & SMITH (1919)
Dolichoderinae:									
Tapinoma sessile (SAY, 1836)	46.69	27.70	18.99	656	511	145	1.67	300	BLACKER (1992)
Formicinae:									
Brachymyrmex depilis EMERY, 1893	50.10	27.18	22.92	1443	941	502	0.44	22	GRUNDMANN (1952)
Camponotus americanus MAYR, 1862	40.50	24.48	16.02	656	379	277	2.52	3560	
Camponotus chromaiodes BOLTON, 2000	41.87	32.25	9.62	656	403	253	3.13	3560	
Camponotus nearcticus EMERY, 1893	45.39	27.18	18.21	719	461	258	1.88	69	VAN PELT (1958), WHEELER (1910)
Camponotus pennsylvanicus (DEGEER, 1773)	45.57	30.63	14.94	941	379	562	2.59	2222	PRICER (1908)
Camponotus subbarbatus EMERY, 1893	40.93	37.67	3.26	440	440	0	0.20	3560	
Formica subsericea SAY, 1836	45.60	33.17	12.43	656	403	253	2.33	8916	
Lasius alienus (FOERSTER, 1850)	46.69	29.08	17.61	1342	379	963	1.42	3000	BLACKER (1992)
Lasius umbratus (NYLANDER, 1846)	45.39	30.13	15.26	719	403	316	1.09	3000	
Paratrechina faisonensis (FOREL, 1922)	39.79	24.48	15.31	656	379	277	0.61	268	
Prenolepis imparis (SAY, 1836)	42.05	28.72	13.33	941	403	538	0.91	3370	TALBOT (1943), TSCHINKEL (1987)
Myrmicinae:									
Aphaenogaster fulva ROGER, 1863	41.65	28.60	13.05	719	462	257	1.41	281	HEADLEY (1949), VAN PELT (1958)
Aphaenogaster rudis ENZMANN, 1947	45.39	24.48	20.91	1707	379	1328	1.48	303	HEADLEY (1949), TALBOT (1951)
Crematogaster minutissima MAYR, 1870	35.96	27.18	8.78	403	403	0	0.89	208	VAN PELT (1958), COLE (1940)
Monomorium minimum (BUCKLEY, 1867)	39.87	30.64	9.23	1231	719	512	0.45	3000	VAN PELT (1958)
Myrmica latifrons STÄRCKE, 1927	43.68	32.24	11.44	511	511	0	1.44	255	TALBOT (1945)
Myrmica pinetorum WHEELER, 1905	39.13	33.17	5.96	656	440	216	1.43	396	
Myrmica punctiventris ROGER, 1863	45.57	30.71	14.86	941	440	501	1.53	86	SNYDER & HERBERS (1991)
Myrmica spatulata SMITH, 1930	38.53	33.45	5.08	656	511	145	1.55	296	
Myrmecina americana EMERY, 1895	42.56	24.48	18.07	1530	379	1151	0.76	24	TALBOT (1957), COLE (1940)
Pyramica clypeata (ROGER, 1863)	35.57	27.18	8.39	511	511	0	0.53	62	BROWN (1953)
Pyramica ohioensis (KENNEDY & SCHRAMM, 1933)	38.48	29.68	8.80	719	379	340	0.58	53	BROWN (1953)
Pyramica ornata (MAYR, 1887)	38.98	27.26	11.72	511	440	71	0.51	20	WESSON & WESSON (1939)
Pyramica rostrata (EMERY, 1895)	39.03	30.83	8.20	719	379	340	0.62	72	BROWN (1953)
Stenamma brevicorne (MAYR, 1886)	45.39	33.24	12.16	1342	786	556	0.92	70	TALBOT (1957)
Stenamma diecki EMERY, 1895	45.57	32.54	13.03	1742	440	1302	0.75	41	FRANCOEUR (1965)
Stenamma impar FOREL, 1901	45.57	35.50	10.07	1742	656	1086	0.72	54	TALBOT (1957)
Stenamma meridionale SMITH, 1957	45.00	35.46	9.54	1342	786	556	0.90	15	TALBOT (1957)
Stenamma schmitti WHEELER, 1903	45.39	33.17	12.23	1419	719	700	0.91	121	TALBOT (1957)
Temnothorax curvispinosus (MAYR, 1866)	42.56	30.56	12.00	719	379	340	0.59	84	HEADLEY (1943)
Temnothorax longispinosus (ROGER, 1863)	45.57	35.21	10.36	1231	440	791	0.62	47	HEADLEY (1943)
Ponerinae:									
Ponera pennsylvanica BUCKLEY, 1866	45.39	24.48	20.91	1456	379	1077	0.92	5	
Proceratiinae:									
Proceratium pergandei (EMERY, 1895)	39.02	27.18	11.84	462	462	0	0.68	28	KENNEDY & TALBOT (1939), DENNIS (1938)
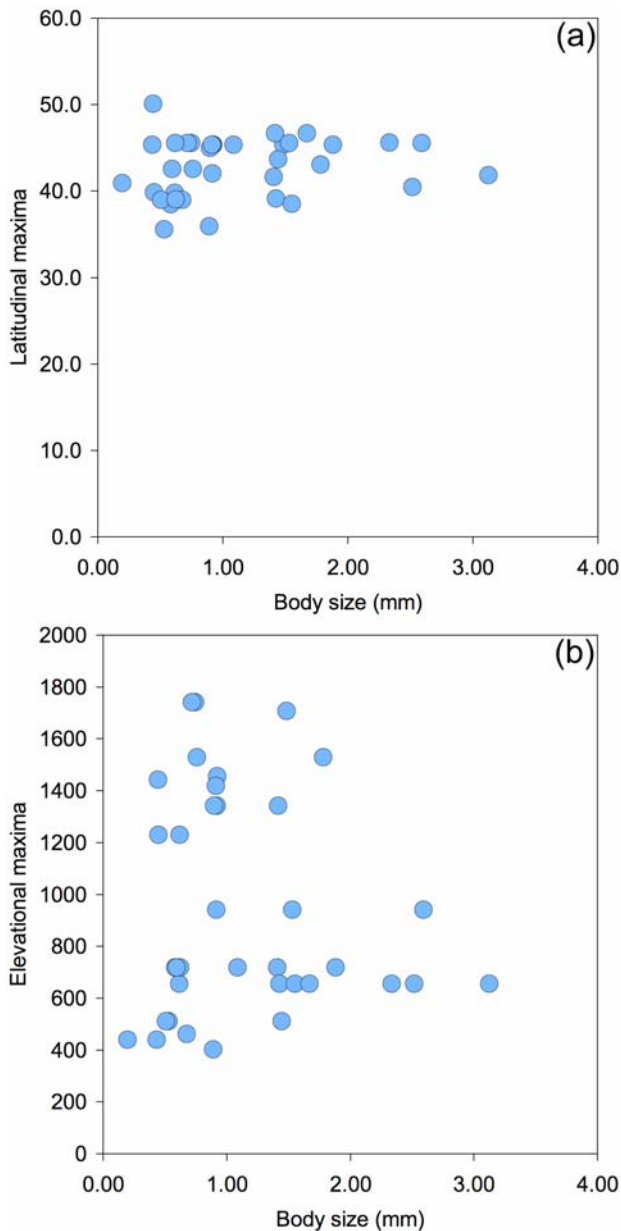
Fig. 3: The relationship between (a) body size and latitude and (b) body size and elevation. In the figures, each symbol represents a single species.

large colonies because a colony's investment in growth is thought to manifest itself as either an increase in worker number or in the size of workers (KASPARI 2005). Our results suggest that some species seem to break this trade-off by having both large-bodied workers and many workers. There is likely to be considerable intraspecific variation in colony size that our methods do no account for, but accounting for such variation is unlikely to change the qualitative result that the ant species with the largest individuals in our study region also have the largest colonies. Interestingly, three of the largest species in our study sites were *Camponotus* species, suggesting that the response variables (species) are not phylogenetically independent of one another. Another study in the same region has also shown strong phylogenetic constraint for another life-history trait, the timing of reproductive flights (DUNN & al.

2007a). Phylogenetic constraints on many complex life history traits may be sufficient within biogeographic regions to swamp the effects of selection due to environmental gradients. In contrast, for traits more directly linked to environmental tolerance (latitudinal range, maximum latitude, minimum latitude, elevational range, maximum elevation, minimum elevation; Tab. 1), there appears to be no strong phylogenetic signature and also stronger biogeographic patterns.

Bergmann's Rule predicts that body size increases with latitude and perhaps elevation. We found no relationship between body size in ants and latitudinal maxima ($r^2 = 0.03$, $P = 0.32$; Fig. 3a). Similarly, body size did not increase with elevational maxima ($r^2 = 0.003$, $P = 0.77$; Fig. 3). We obtained similar results when we plotted body size against latitudinal and elevational midpoints, so we do not present those results. Our results along the latitudinal gradient contrast with those of CUSHMAN & al. (1993) who found that ant body size decreased with latitude for ants in Europe. In a similar vein, KASPARI (2005) found that worker size (measured as mass) increased with decreasing temperature. The studies of CUSHMAN & al. (1993) and KASPARI (2005) covered a greater latitudinal extent than did our study. It could be the case that if our dataset extended from the equator to the poles, then we might have detected a significant increase in body size with latitude. Perhaps we simply did not sample enough variation in latitude to detect the pattern.

A limited number of studies have examined body size patterns along elevational gradients. Most to date have found no support for an elevational Bergmann's Rule (HAWKINS & DEVRIES 1996, BLACKBURN & RUGGIERO 2001, HAUSDORF 2003, BREHM & FIEDLER 2004), so it is not surprising that inter-specific body size patterns of ants along an elevational gradient in Great Smoky Mountains National Park do not support Bergmann's Rule either.

Here, we found no relationship between colony size and latitude for a subset of the ants of eastern North America ($r^2 = 0.005$, $P = 0.67$; Fig. 4). Similarly, colony size did not increase with elevation ($r^2 = 0.02$, $P = 0.42$; Fig. 4).

The "Fasting Endurance Hypothesis" (KASPARI & VARGO 1995), which is equivalent to the "starvation resistance hypothesis" described by BLACKBURN & al. 1999 (and first suggested by BRODIE 1975), predicts that colony sizes are larger in areas with extended periods of low food availability, as may be the case at high latitudes and elevations where cold winter temperatures prohibit foraging. KASPARI & VARGO (1995) compared colony sizes of ants in temperate and tropical regions and found support for the Fasting Endurance Hypothesis. KASPARI (2005) showed that worker number in ants tended to decrease with increasing productivity, which seems counter to the Fasting Endurance Hypothesis. However, a hump-backed relationship, with worker number peaking at intermediate levels of net primary productivity (NPP) is also a possibility (and undetectable with KASPARI & VARGO's 1995 methods). PORTER & HAWKINS (2001) compiled data on termites along latitudinal gradients and found no support for the Fasting Endurance Hypothesis. Thus, it is unclear what the relationship between colony size and latitude or elevation (or some environmental variable, such as NPP, that is correlated with latitude or elevation) should be, if there should be any relationship at all.
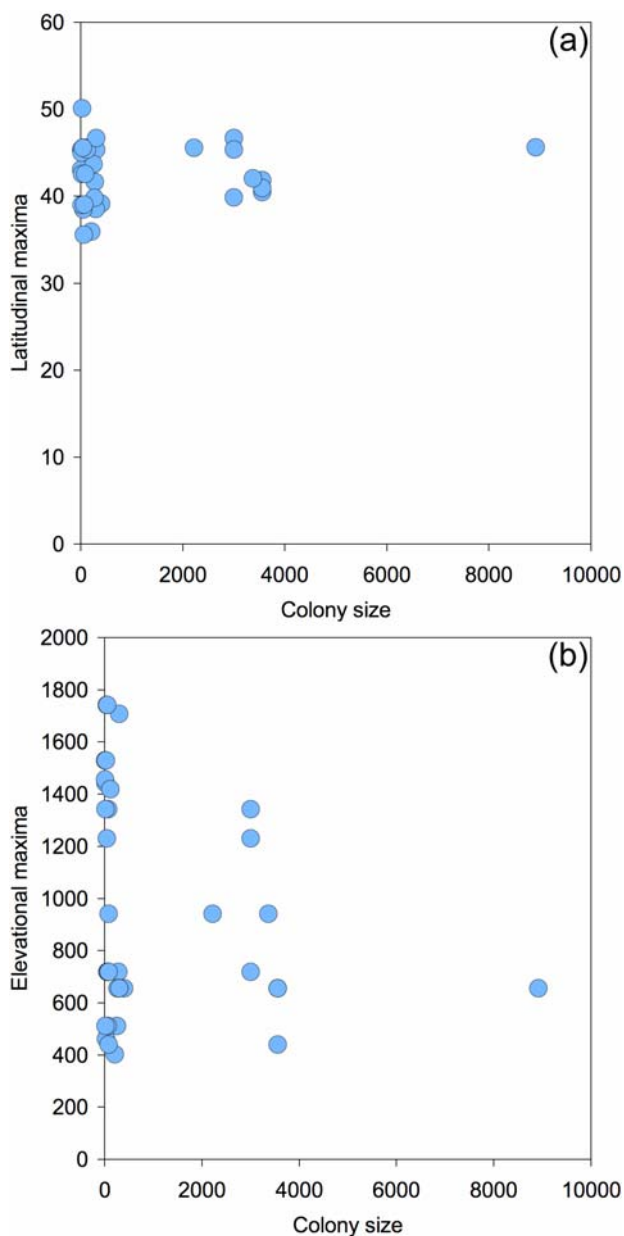
Fig. 4: The relationship between (a) colony size and latitude and (b) colony size and elevation. In the figures, each symbol represents a single species.

Tab. 2: Results from an ANCOVA examining the effects of subfamily, latitude, and elevation on body size and colony size for 36 ant species in eastern North America.

Body size				
Effect	df	SS	F	P
Latitude	1	0.001	0.002	0.96
Subfamily	1	3.160	7.09	0.01
Effect	df	SS	F	P
Elevation	1	0.052	0.12	0.73
Subfamily	1	3.190	7.18	0.01
Colony size				
Effect	df	SS	F	P
Latitude	1	688395	0.2812	0.6
Subfamily	1	43726913	17.86	0.0002
Effect	df	SS	F	P
Elevation	1	869304	0.36	0.56
Subfamily	1	40380206	16.54	0.0004

So what does explain body and colony size variation? We used an Analysis of Covariance (ANCOVA) to ask whether subfamily identity (here, we use only Myrmicinae and Formicinae because we collected only one species each from the subfamilies Amblyoponinae, Ponerinae, Proceratiinae, and Dolichoderinae) as the main factor and latitudinal maxima of the species as a covariate explained colony size and body size. Subfamily identity, but not latitude, explained most of the variation in colony size and body size (Tab. 2). An ANCOVA analysis with subfamily as the main factor and elevational maxima as the covariate indicated that subfamily identity, but not elevational maxima, explained most of the variation in colony size and body size along the elevational gradient examined here (Tab. 2). Together, these results suggest that phylogeny and evolutionary constraints have a greater influence on colony size and body size along latitudinal gradients than does any ecogeographic mechanism.

Conclusions

We found no evidence for a latitudinal or elevational gradient in ant body or colony size, in contrast to other studies on latitudinal gradients (CUSHMAN & al. 1993, KASPARI & VARGO 1995). Though there are limitations and biases in our approach, namely we did not account for intra-specific variation in body or colony size and we did not sample the entire latitudinal gradient, we argue that the lack of an ecogeographic pattern in these data is real. In addition, the effect of subfamily on body size and colony size along the latitudinal and elevational supports the assertion that the strength of phylogenetic niche conservatism in ants (e.g., ants in Chile and California of the same genera share very similar life histories, HUNT 1973), necessitates consideration of macrecological patterns in an evolutionary context.

Acknowledgements

Zusammenfassung

Die Körpergröße von Organismen nimmt oft mit der geographischen Breite und der Höhenlage zu; dies wird meist als Bergmannsche Regel bezeichnet. Während diese Regel für viele endotherme Taxa nachgewiesen worden ist, ist sie bei nur wenigen Insekten untersucht worden – für

einige von diesen trifft sie eindeutig zu, für andere kaum oder nicht. Für Kolonien bildende Organismen (soziale Insekten, Korallen, Bryozoen) kann Größe auch als die Zahl der Untereinheiten einer Kolonie gemessen werden. Im Sinne der Bergmannschen Regel würde das bei Ameisen eine Zunahme der Zahl der Arbeiterinnen pro Kolonie mit zunehmender geographischer Breite oder Höhenlage bedeuten. Wir haben getestet, ob Körper- oder Koloniegröße von Ameisen im östlichen Nordamerika mit geographischer Breite oder Höhenlage in Beziehung stehen, und konnten keine positive Beziehung feststellen. Jedoch wiesen Arten mit großer Nord-Süd-Verbreitung auch eine große Amplitude der besiedelten Höhenlagen auf, woraus wir folgern, dass Arten mit großer klimatischer Toleranz auch die am weitesten verbreiteten sind. Hinzu kommt, dass Arten, die weit im Norden vorkommen, auch hoch oben leben. Insgesamt zeigt unsere Studie nicht, dass die Bergmannsche Regel auf Ameisen zutrifft – im Gegensatz zu anderen Studien an Ameisen –, aber das Klima limitiert die Verbreitung von Ameisenarten hinsichtlich geographischer Breite und Höhenlage auf ähnliche Weise.

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