Latitudinal patterns in European ant assemblages: variation in species richness and body size

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Abstract. Using published distributions of 65 species from the British Isles and northern Europe, we show that ant assemblages change with latitude in two ways. First, as commonly found for many types of organisms, the number of ant species decreased significantly with increasing latitude. For Ireland and Great Britain, species richness also increased significantly with region area. Second, although rarely demonstrated for ectotherms, the body size of ant species, as measured by worker length, increased significantly with increasing latitude. We found that this body-size pattern existed in the subfamily Formicinae and, to a lesser extent, in the Myrmicinae, which together comprised 95% of the ant species in our study area. There was a trend for formicines to increase in size with latitude faster than myrmicines. We also show that the pattern of increasing body size was due primarily to the ranges of ant species shifting to higher latitudes as their body sizes increased, with larger formicines becoming less represented at southerly latitudes and larger myrmicines becoming more represented at northerly latitudes. We conclude by discussing five potential mechanisms for generating the observed body-size patterns: the heat-conservation hypothesis, two hypotheses concerning phylogenetic history, the migration-ability hypothesis, and the starvation-resistance hypothesis.

Key words: Ants – Worker body size – Species richness – British Isles – Northern Europe

A central problem in ecology is to identify and understand large-scale patterns in communities and regional biotas (MacArthur 1972; Brown 1981; Brown and Maurer 1989). Many ecological patterns occur along environmental gradients, such as those associated with latitude, and involve variation in species richness and body size. Body size is

possibly the most fundamental trait of an animal (McMahon and Bonner 1983; Peters 1983; Calder 1984; Schmidt-Neilsen 1984). Every aspect of its life is influenced by body size – its interactions with the abiotic environment, the rates of its physiological processes, and the outcomes of its interactions with other organisms. Thus, body size should have considerable influence on the organization of ecological communities (Lawton 1990).

The study of variation in body size along latitudinal gradients has attracted considerable attention and debate (e.g., Bergmann 1847; Scholander 1955; Mayr 1956; Ray 1960; Lindsey 1966; Schoener and Janzen 1968; Brown and Lee 1969; James 1970; McNab 1971; Searcy 1980; Blau 1981; Murphy 1985; Geist 1987). Much of this work has centered around Bergmann's 'rule' which states that body size in endotherms (within species or among closely related species) varies inversely with ambient temperature and thus increases with latitude (Mayr 1956; McNab 1971). For example, mean weight of breeding land bird species roughly doubles from the south to north of Great Britain (Cousins 1989). Although commonly overlooked, Bergmann's rule only concerns empirical patterns of increasing body size with latitude and makes no statement about the mechanism(s) responsible for such variation (Mayr 1956). Nevertheless, despite its prevalence in the literature, the validity of Bergmann's rule has been severely criticized by Scholander (1955, 1956) and more recently by Geist (1987), who concluded that "Bergmann's rule has no basis in fact or theory". This view results largely because body-size patterns in endotherms are quite variable (e.g., see McNab 1971), and some ectotherms, such as fish and amphibians, also exhibit larger body sizes at higher latitudes (Lindsey 1966).

Here, we consider large-scale patterns in European ant assemblages. We focus on ants because they are dominant members of terrestrial communities and their distributions in Europe are comparatively well known. They vary in body size in three ways: 1) the size of workers, queens, and males differ within species; 2) the sizes of individuals in each of these castes varies within species; and 3) the average size of each caste varies among species (Brian 1973; Hölldöbler and Wilson 1990). In this paper, we focus

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exclusively on interspecific body-size variation in worker ants (3), although worker size is strongly correlated with the size of queens and males of the same species, at least for the European ant fauna (Pearson correlation coefficients are 0.857 and 0.884, respectively).

We examine the latitudinal patterns in species richness and body size exhibited by ant faunas of the British Isles and a large portion of northern Europe. We also assess how body-size patterns arise and the possibility that patterns vary within the Formicinae. We conclude by discussing five potential mechanisms for generating body-size variation in ant assemblages.

Methods

We assembled data from Barrett (1979) and Collingwood (1979) on the known ant fauna of the British Isles (Great Britain and Ireland) and northern Europe (Denmark, Sweden, Norway, Finland, and two regions in Russia). The data came from range maps and provincial species lists. In total, this data consisted of 65 species along a latitudinal gradient, from 50° to 70° north.

Detailed information for the British Isles allowed us to analyze ant faunas in 30 latitudinal bands, each 50 km wide and assigned the latitude of its midpoint. For the other 77 regions, we analyzed ant faunas by province, with each assigned the latitude of its midpoint. Where possible, we excluded small islands from the analysis to avoid adding insular effects into the species-richness data.

As a measure of size, we used the midpoint of the range in worker body lengths reported in Collingwood (1979; see Table 1). Three species lack workers and were thus included in the richness analysis but not in the body-size analysis. Although all ant species are variable in size (Hölldöbler and Wilson 1990), only the four *Camponotus* species are known to be polymorphic in size (B. Bolton, personal communication).

Throughout this paper, we have evaluated the relationship between species richness or worker body size and latitude. In the past, community ecologists and biogeographers have used standard regression analysis to assess such relationships, testing for slopes significantly different from zero. However, this approach is valid only if each species occurs once in the data. In our ant data, there is considerable redundancy, as each species occurs in from 1 to 107 latitudinal provinces. Biologically, this redundancy is interesting, and was the primary focus of our paper. However, statistically, it violated assumptions of independence and thus invalidated the significance tests of standard regression methods.

We dealt with the problem of redundancy in two ways. In a few analyses, we treated each species as a single observation, thereby removing the redundancy, and used standard regression analysis. In all other cases, we used statistical tests that could tolerate the species redundancy: logistic regression and randomization tests.

Species-richness analyses

We used logistic regression to relate the presence and absence of 65 ant species in 107 provinces to the latitude and area of each province. With this approach, we assumed that the probability of species i being present at latitude j was given by

$$P_{ij} = \exp(S_i + \alpha A_j + \tau L_j)/\{1 + \exp(S_i + \alpha A_j + \tau L_j)\},$$

where S_i was a parameter to account for the fact that some species were naturally more widespread than others, α was a parameter to allow for area effects, A_j was the area for province j, τ was a parameter to allow for latitude effects, and L_j was the midpoint latitude of province j. While area data were not available for the northern European provinces, the logistic model could still be used with the S_i and τ parameters only.

Table 1. Worker body lengths of 62 ant species from the British Isles and northern Europe. Data are from Collingwood (1979) and consist of midpoint body lengths and ranges (mm). *Myrmica hirsuta*, *Sifolinia karavajevi*, and *Anergates atratulus* do not have a worker caste and were thus excluded. *Leptothorax unifasciatus* and *Lasius emarginatus* were also excluded because they occur exclusively on small islands

Species	Subfamily	Worker body length (mm) Midpoint	Range
Hypoponera punctatissima	Ponerinae	2.85	2.5– 3.2
Ponera coarctata	Ponerinae	3.25	3.0– 3.5
Tapinoma erraticum	Dolichoderinae	3.4	2.6– 4.2
Myrmica gallieni	Myrmicinae	4.7	4.5– 5.0
lobicornis		4.5	4.0– 5.0
rubra		4.25	3.5– 5.0
ruginodis		5.0	4.0– 6.0
rugulosa		3.65	4.0– 4.3
sabuleti		4.5	4.0– 5.0
scabrinodis		4.5	4.0– 5.0
schencki		4.75	4.0– 5.5
specioides		3.75	3.0– 4.5
sulcinodis		5.0	4.0– 6.0
Stenamma westwoodii	Myrmicinae	3.75	3.5– 4.0
Diplorhoptrum fugax	Myrmicinae	2.25	1.5– 3.0
Myrmecina graminicola	Myrmicinae	3.3	3.0– 3.6
Leptothorax acervorum	Myrmicinae	4.15	3.8– 4.5
muscorum		2.8	2.4– 3.2
nylanderi		2.85	2.3– 3.4
corticalis		2.85	2.5– 3.2
interruptus		2.85	2.3– 3.4
tuberum		2.85	2.3– 3.4
Formicoxenus nitidulus	Myrmicinae	3.1	2.8– 3.4
Harpagoxenus sublaevis	Myrmicinae	4.5	3.5– 5.5
Strongylognathus testaceus	Myrmicinae	2.8	2.0– 3.6
Tetramorium caespitum	Myrmicinae	3.25	2.5– 4.0
Camponotus fallax	Formicinae	6.5	4.0– 9.0
vagus		9.0	6.0–12.0
herculeanus		8.5	5.0–12.0
ligniperda		10.0	6.0–14.0
Lasius flavus	Formicinae	3.5	2.2– 4.8
alienus		3.6	3.0– 4.2
brunneus		3.85	3.2– 4.5
niger		4.25	3.5– 5.0
fuliginosus		5.0	4.0– 6.0
umbratus		4.65	3.8– 5.5
meridionalis		4.25	3.5– 5.0
bicornus		4.25	4.0– 4.5
mixtus		4.0	3.5– 4.5
carniolicus		3.6	3.5– 3.7
Formica fusca	Formicinae	5.75	4.5– 7.0
gagatoides		5.1	4.2– 6.0
lemani		5.75	4.5– 7.0
transkaucasica		5.25	4.5– 6.0
cinerea		5.25	4.0– 6.5
cunicularia		5.25	4.0– 6.5
rufibarbis		5.75	4.5– 7.0
exsecta		6.0	4.5– 7.5
foreli		5.75	4.5– 7.0
forsslundi		5.25	4.0– 6.5
pressilabris		5.1	4.2– 6.0
suecica		5.5	4.5– 6.5
uralensis		6.25	4.5– 8.0
sanguinea		7.5	6.0– 9.0
truncorum		6.25	3.5– 9.0
rufa		16.75	4.5– 9.0
polyctena		6.25	4.0– 8.5
aquiloni		6.25	4.0– 8.5
lugubris		6.75	4.5– 9.0
pratensis		7.0	4.5– 9.5
nigricans		7.0	4.5– 9.5
Polyergus rufescens	Formicinae	6.0	5.0– 7.0

The above equation was estimated from data using the logistic regression option in GLIM (Payne 1987). It automatically set up a model where species were treated as levels of a factor and area and latitude were treated as quantitative variables. The program computed maximum likelihood estimates of the model parameters together with approximate standard errors. The model's goodness of fit was measured by the deviance statistic, with associated degrees of freedom equal to the number of dependent variable values minus the number of estimated parameters (see Manly 1992 for additional details).

For the species-richness data, the dependent variable was the presence or absence of each species in each latitude. We fitted three models to the Irish and British data and two models to the northern European data: model 1 estimated the deviance attributable to the fact that some species were naturally more widespread than others (S_j); model 2 added the estimated effect of area (α) to model 1 (omitted for the northern European data); and model 3 added the estimated effect of latitude (τ) to model 2 (or model 1 for the northern European data). The differences between the deviances of these three models was used to determine whether the addition of extra terms resulted in a significant reduction in deviance, as assessed by chi-squared tests. The signs of α and τ indicated whether the probability of occurrence increased or decreased with area and latitude, respectively. We plotted the observed and predicted ant species richness, with the latter determined by combining the P_{ij} equation estimates for all species at each latitude.

Body-size analyses

Our data consisted of 62 body sizes (i.e., species) paired with 62 subsets of the 107 provinces. Using the raw data, we determined the slope of the least-squares regression line relating body size to latitude. We then generated 10,000 randomizations (sampling without replacement) of the 62 pairings of body size and province subset and, for each randomization, determined the slope of the regression line for body size on latitude. The P-value for the test was that proportion of the randomly generated slopes which were larger than the observed slope. Our null hypothesis was that the present distribution of ant species was independent of worker body size. This meant that each ant species occurring in a given subset of provinces was equally likely to have any of the body sizes present in the data. Therefore, any assignment of body sizes to species ranges was equally likely to have occurred as the actual assignment, and thus any of the randomly generated slopes were just as likely as the observed (see chapter 6 in Manly 1991).

In addition to the overall size analysis, we carried out two analyses to assess whether body-size patterns varied within the Formicidae. For both analyses, we focused on the subfamilies Formicinae and Myrmicinae, as together they comprised 95% of the ant species in this data set. In the first analysis, we performed separate randomization tests on each subfamily, as described previously, to assess the effects of latitude on body size.

The second within-family analysis considered the hypothesis that the two subfamily regression equations relating body size to latitude had significantly different slopes. To address this possibility, we performed an approximate randomization test using the following procedure. First, to remove the average size and latitude differences of the subfamilies (without altering any relationships that existed between size and latitude), we standardized the body sizes of all species by replacing their lengths with the deviation of this length from the mean for the appropriate subfamily. We also standardized latitudes by replacing them with the deviation from the mean for the appropriate subfamily. Second, we regressed the standardized body sizes on the standardized latitudes for each subfamily and calculated the difference in slope. Third, we then generated 10,000 random reallocations of the records for each species to the two subfamilies and compared the differences in slope with the one that we observed. We estimated significance levels as discussed previously.

To document specifically how the body-size patterns occurred, we performed a series of analyses to assess the relationship between worker body length and the midpoint, lowest, and highest latitude at which ant species were present. These consisted of regressing the three latitudes against body size for all 62 ant species together, and for species in the Formicinae and Myrmicinae considered separately.

Results

Species-richness patterns

Ants of the British Isles exhibit a classic north-south gradient in species richness, with the number of species decreasing with increasing latitude (Fig. 1). For Ireland, there was a significant reduction in deviance between model 1 and model 2, indicating that the probability of a species being present in a region depended on its area (model 1 deviance − model 2 deviance = 12.23, $df = 1$, $p < 0.01$). There was also a significant reduction in deviance between model 2 and model 3, giving strong evidence that the probability of a species being present in a region depended on its latitude (model 2 deviance − model 3 deviance = 54.75, $df = 1$, $p < 0.01$; $P_{ij} = \exp(S_i + 0.0098A_j - 0.475L_j)/\{1 + \exp(S_i + 0.0098A_j - 0.475L_j)\}$; standard errors associated with the estimated coefficients A_j and L_j were 0.0074 and 0.306, respectively). The positive coefficient of A_j and negative coefficient of L_j indicate that the probability of species occurrence increased with region area and decreased with latitude. As illustrated in Fig. 1, the species richness predicted by the model closely paralleled the observed values, both when area was included and excluded from the model.

For Great Britain, we also found that the probability of species occurrence increased significantly with area (model 1 deviance − model 2 deviance = 80.46, $df = 1$, $p < 0.001$) and decreased significantly with latitude (model 2 deviance − model 3 deviance = 99.18, $df = 1$, $p < 0.001$; $P_{ij} = \exp(S_i + 0.0201A_j - 1.654L_j)/\{1 + \exp(S_i + 0.0201A_j$
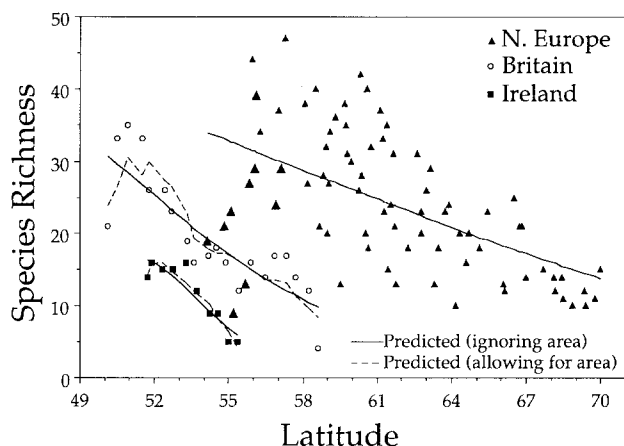

Fig. 1. Species richness of ants for 107 regions in Great Britain, Ireland, and northern Europe plotted as a function of latitude. *Solid lines* correspond to the species richness predicted by a logistic regression model when latitude was considered and area was ignored. *Dashed lines* correspond to the predicted richness of Great Britain and Ireland when both latitude and area were considered. The enlarged *triangle symbols* indicate the species richness for the 10 Danish provinces

$-1.654L_j$); standard errors associated with the coefficients A_j and L_j were 0.0021 and 0.054, respectively). As before, the predicted species richness was very close to the observed (Fig. 1).

The ants of northern Europe exhibited a similar pattern of species richness as that detected for the British Isles (Fig. 1). While area data were not available, we found that the probability of species occurrence was significantly related to latitude (model 1 deviance — model 3 deviance = 254.0, $df = 1$, $p < 0.001$; $P_{ij} = \exp(S_i - 0.155L_j)/\{1 + \exp(S_i - 0.155L_j)\}$; the standard error of the coefficient L_j was 0.01). The predicted species richness paralleled the observed, but not as closely as for the British Isles (Fig. 1).

Body-size patterns

While the ant fauna of the British Isles and northern Europe exhibited substantial interspecific variation in worker size (Table 1), the distribution of these sizes was greatly influenced by latitude. The body lengths of ant workers increased significantly with latitude ($S = 1.114 + 0.063L$; $p = 0.007$, one-sided test; Fig. 2a). We also found that this body-size pattern persisted in the subfamily Formicinae ($S = 1.246 + 0.075L$, $p = 0.048$, one-sided test) and, to a lesser extent, in the Myrmicinae,

although this latter trend was not significant at the 0.05 level ($S = 2.916 + 0.022L$, $p = 0.0695$, one-sided test; Fig. 2b). Thus, our analysis provides strong evidence for a positive relationship between ant body size and latitude.

The two ant subfamilies differed in slope by 0.0539 for the regression of body size on latitude. After subfamily body lengths and latitudes were standardized, an approximate randomization test revealed that the two-sided significance of such a difference occurring was 0.0837. Thus, while there was a trend for formicines to increase in size with latitude faster than for myrmicines, this pattern was not significant at the 0.05 level.

The ranges of ant species increasingly shifted to higher latitudes as body size increased. This pattern was revealed by the significantly positive relationship between midpoint latitude range and body length (Fig. 3a; $M = 54.08 + 0.84S$, $t_{60} = 3.93, p = 0.0002, r = 0.453$). In addition, for the entire Formicidae, both the lowest and highest latitude at which species occurred increased significantly with body size (Fig. 3b; $L_{lowest} = 49.5 + 0.646S$, $t_{60} = 2.79$, $p = 0.0071$, $r = 0.339$; $L_{highest} = 58.61 + 1.040S$, $t_{60} = 2.59$, $p = 0.0121$, $r = 0.318$). However, the two subfamilies exhibited patterns different from each other and from those of the family as a whole. In the Formicinae, there was a trend for the lowest latitude of occurrence to increase with body size ($L_{lowest} = 49.76 + 0.641S$, $t_{34} = 1.8$, $p = 0.0811, r = 0.295$), while this
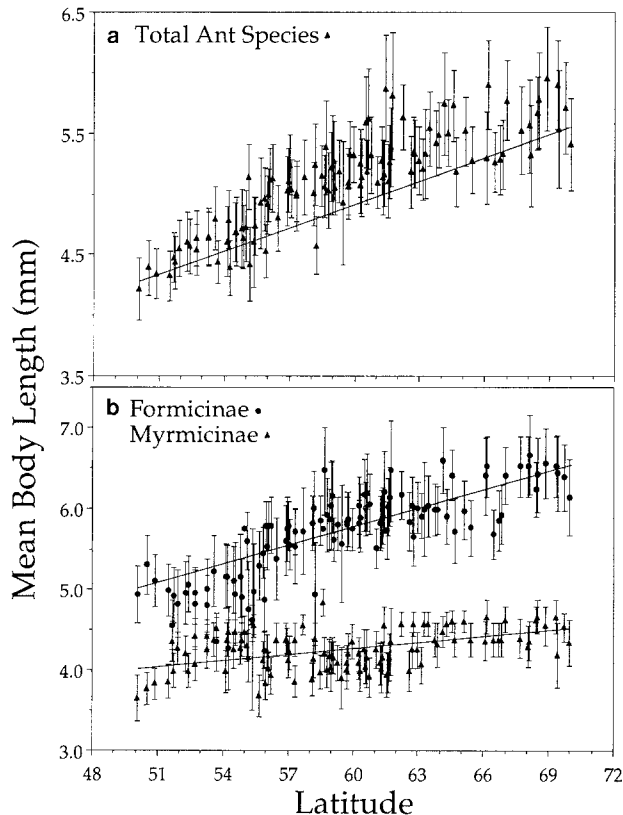

Fig. 2a, b. Mean worker body length of ant species in the British Isles and northern Europe plotted as a function of latitude. **a** shows the relationship for all 62 ant species in the study region, while **b** presents the relationship for the subfamilies Myrmicinae and Formicinae. All regressions lines were calculated from the raw data rather than the means. Vertical bars correspond to ± 1 standard error
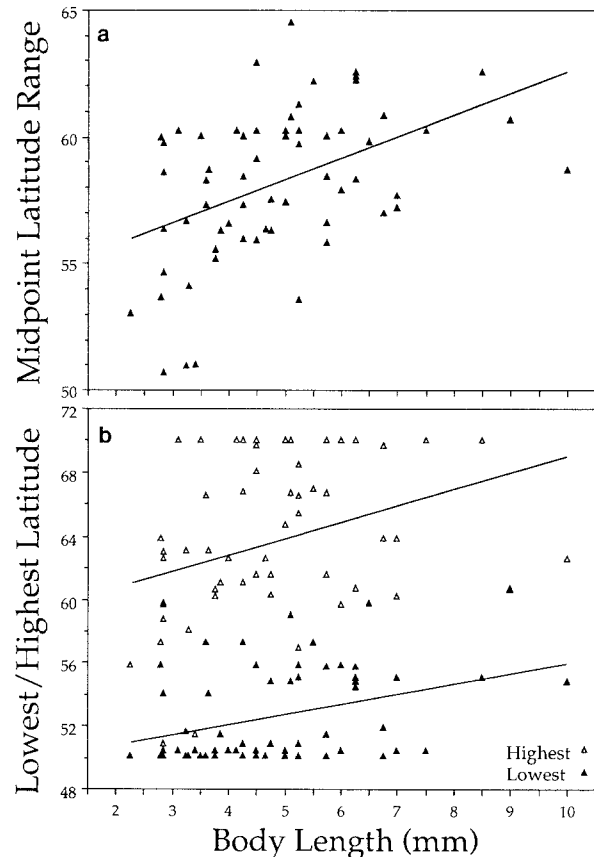

Fig. 3a, b. Midpoint of the range in latitude for workers of 62 ant species (**a**) and the highest and lowest latitude attained by workers of these species (**b**) plotted as a function of their respective body lengths

was not the case for the highest latitude ($L_{highest} = 62.89 + 0.324S$, $t_{34} = 0.62$, $p = 0.54, r = 0.106$). In the Myrmicinae, the highest latitude of occurrence increased significantly with body size ($L_{highest} = 48.41 + 3.99S$, $t_{21} = 3.58, p = 0.0018$, $r = 0.616$), while the lowest latitude did not ($L_{lowest} = 52.58 + 0.27$, $t_{21} = -0.40, p = 0.69, r = 0.087$). In total, these results indicate that the body-size pattern illustrated in Fig. 2 was jointly due to the under-representation of larger formicines at more southerly latitudes and the over-representation of larger myrmicines at more northerly latitudes.

Discussion

Species-richness patterns

Our analysis of latitudinal patterns in the European ant fauna revealed that species richness decreased with latitude (Fig. 1). There was substantially more unexplained variation in species richness for northern Europe than for the British Isles. The most likely explanation for this difference is that the provinces in northern Europe were, on average, much larger than the latitudinal bands in the British Isles. Not only were we unable to remove area effects for northern Europe, but each province occurred over a greater latitudinal range. For example, the latitude of Jamtland, Sweden ranges from approximately 62.5° to 65.0° north, with an assigned latitude of 63.75°. Thus, the use of midpoint latitude was a cruder measure of latitude for northern Europe than for the British Isles.

The species-richness pattern found in Denmark is another source of variation. As can be seen in Fig. 1, the 10 provinces of this country exhibit a trend in the opposite direction to that of all other regions (symbols for Denmark are enlarged in Fig. 1 only for the purposes of illustration). The pattern clearly deserves further attention, as it does not seem to be explained by area differences.

There are at least four other studies of species-richness patterns in ants. Using different methods, Baroni Urbani and Collingwood (1976, 1977) detected a similar gradient for the ants of the British Isles and northern Europe, although they did not consider area effects or analyze the latitudinal trends statistically. However, they did present data indicating that species richness in these regions was positively correlated with hours of bright sunshine, July temperatures, length of the growing season, and proximity to the coast. In the third study, Kusnezov (1957) provided a preliminary global analysis which indicated that ant species richness increased towards the tropics, although the data set was very small and again he did not consider area effects or analyze the pattern statistically. Lastly, on 10 plots matched for habitat, elevation, and size, Jeanne (1979) showed that the number of ant species increased toward the tropics.

Body-size patterns

The second major pattern that we detected was that regional ant assemblages become increasingly dominated by species with large-bodied workers at higher latitudes (Fig. 2). This pattern persisted for species in both the Formicinae and Myrmicinae, although the significance level in the latter case marginally exceeded 0.05. In addition, formicines increased in size with latitude faster than myrmicines, although again the significance level marginally exceeded 0.05.

As can be seen in Figures 2 and 3, the relationship between body size of ants and latitude showed considerable variation. While some degree of variation undoubtedly occurs naturally, our methods contributed significantly to the large amount of error that we observed. The first source of error, as discussed earlier, involved our measure of the latitude for each region (latitudinal midpoints). For equally narrow latitudinal bands, such as those for the British Isles, the use of midpoints caused minimal error. However, for large provinces, such as those in northern Europe, this could create significant error. Thus, if there was body-size variation within this province attributable to latitude, it would appear as error and bias our analysis away from accepting the hypothesis that body size increases with latitude.

The second source of error involved our measure of worker size for each species (midpoint of the range in reported body length). While adequate for our purposes, this practice ignored intraspecific variation in worker size, which is known to occur in most species (Hölldöbler and Wilson 1990). Unfortunately, we were unable to test for intraspecific latitudinal trends in body size for wide-ranging species, due to lack of data. If worker size increases with latitude within (as well as among) species, use of midpoint size would be a conservative measure.

While there are many studies that purport to demonstrate increasing body size of endotherms with latitude (see above), only a handful of studies consider such patterns in ectotherms. In a substantial review of ectothermic taxa, Ray (1960) showed that over 75% of all species studied to date reached larger adult size when inhabiting low-temperature environments. Lindsey (1966) demonstrated that amphibian and reptilian faunas increase in body size with latitude. This latter study is especially important because it is one of the few that evaluated interspecific body-size patterns exhibited by entire faunas over a substantial latitudinal gradient.

Only one other study has presented body-size data for ants. Schoener and Janzen (1968) found that the mean length of workers in ant faunas at four sites in Costa Rica ranged from 4.2–5.3 mm, compared with 3.3–4.3 mm for the fauna at a single site in Massachusetts, USA. While the authors did not test the significance of this pattern, the trend is in the opposite direction to that found in the British Isles and northern Europe. One interpretation of these data is that the body-size patterns we found are restricted to Europe or temperate regions as a whole. Alternatively, it may be that Schoener and Janzen's data are not comparable with ours due to methodological differences. Their data were from sweep-net samples made during a single year. In contrast, the species-distribution data for Europe were obtained by compiling collection records over the past 100 years. Thus, it is possible that short-term, sweep-net methods underestimate the species composition of sample regions.

Our analyses deal exclusively with the presence or absence of ant species and not the relative abundances of species in the 107 regions. Thus, while we have shown that ant species with large-bodied workers are more common at northern latitudes, it is possible that these species are rare in terms of numbers of individuals per colony, numbers of colonies, and/or total biomass. Unfortunately, we do not know of any studies that present data on the relationship between worker body size and these variables.

Mechanisms for latitudinal variation in body size

There are a range of mechanisms that could generate interspecific patterns of increasing body size with latitude, and below we discuss five that we think are most relevant. However, before doing so, it is worth mentioning that Turner and Lennon (1989) recently predicted that ectotherms should decrease in body size with latitude, rather than increase as we observed. Their proposed mechanism for this pattern was based on latitudinal changes in energy availability and population size. Building on Wright's (1983) species-energy theory, they predicted that larger ectotherms will be less represented at higher latitudes because larger species should have smaller population densities which make them more vulnerable to local extinction events associated with the reduced availability of energy at these latitudes. While this proposed mechanism may operate for some taxa, there is no evidence that it does so for ants.

Heat-conservation hypothesis. The usual mechanism put forth to explain patterns of increasing body size with increasing latitude (i.e., Bergmann's rule) concerns thermoregulation. Here, large size is hypothesized to be adaptive in cold environments because animals expend less energy on thermoregulation due to reduced surface-to-volume ratios. Heat conservation may be an important mechanism for some body-size patterns in endotherms, where heat is (by definition) generated internally and reducing its loss is a major selective force. However, heat conservation by itself is unlikely to explain the latitudinal trends in body size reported for ectotherms, and thus is unlikely to be a general explanation for these patterns. This is because heat gain and loss should be equally important selective pressures on ectotherms. While increasing body size reduces the rate of heat loss, it also reduces the rate of heat gain. Nevertheless, the heat-conservation hypothesis may be applicable at the colony level, if worker body size is positively correlated with colony size and if larger colony size is correlated with thermoregulatory capabilities. Unfortunately, there are insufficient data to evaluate these relationships (see Hölldöbler and Wilson 1990).

Phylogenetic hypotheses. The second and third mechanisms use phylogenetic history of ant taxa to explain increasing body size with latitude. The second mechanism states that the observed body-size patterns resulted from random colonization of regions by ancestral lineages of differing size, such that large-bodied species inhabited high latitudes while small-bodied species inhabited low latitudes. The lineages subsequently speciated and each became dominant in their own region. Such a pattern could have persisted due to minimal dispersal by the respective lineages and reduced subsequent colonization by other ant taxa.

We do not think this phylogenetic hypothesis explains the body-size patterns in our system. Except for the extreme south of Ireland and parts of south, east, and central England, the British Isles were covered by ice 15,000 years ago (Godwin 1975). Where ice was absent, conditions were periglacial and extremely harsh. Northern Europe was completely ice-covered, with extensive polar deserts extending as far south as the Netherlands (Coope 1986 and references therein). Therefore, the entire ant fauna of these regions must have colonized the area within the last 10,000 years. Thus, it seems highly improbable that the body-size patterns resulted from speciation after colonization. In addition, ants are not generally regarded as having low dispersal abilities (see Hölldöbler and Wilson 1990).

The third hypothesis focuses on associations between body size and other behavioral, morphological, and/or physiological traits. It states that the observed body-size patterns resulted from the selective advantage of non-size traits that were randomly coupled with body-size traits. Large-bodied lineages would come to inhabit northern latitudes, not because of their size, but because they possessed randomly associated traits that allowed them to more effectively withstand and exploit the colder, harsher environments at such latitudes. We do not think this scenario is likely for ant assemblages, because both formicine and myrmicine ant species exhibit increasing body size with latitude; for this phylogenetic hypothesis to be correct, random associations between size and advantageous traits would need to have occurred in both subfamilies.

Migration-ability hypothesis. A fourth mechanism to explain increasing body size with latitude is based on the migrating abilities of ant species. It states that small-bodied species migrate less rapidly than large-bodied species, and thus will be under-represented at northern latitudes because they fail to colonize such regions. Although rigorous data on this hypothesis are not available, we doubt its importance, given that colonization ability does not appear to be dependent on worker size (see Hölldöbler and Wilson 1990).

Starvation-resistance hypothesis. A fifth mechanism to explain increasing body size with latitude is based on the risks of starvation in seasonal and/or unpredictable environments (see Lindsey 1966; Blau 1981; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Lindstedt and Boyce 1985; Forsman 1991). This mechanism is suggested by two empirical relationships. First, metabolic rates scale as M^b where M is body mass and b is typically less than 1 and usually about 0.75. Second, although less well studied, body reserves appear to scale as M^a where a is approximately 1 (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Because energy stores increase with size faster than metabolic rate, resistance to starvation should increase with body size, roughly as $M^1/M^{0.75}$. Thus, in seasonal and/or unpredictable environments, large-bodied species should

be able to ride out longer periods of unfavorable conditions before succumbing to starvation. This hypothesis therefore predicts that seasonal and/or unpredictable environments should favor large-bodied species over small-bodied species. We strongly suspect that differences in foraging behavior, habitat use, food supply, and local climate will dictate that this pattern is not absolute; rather, large-bodied species should make up a larger proportion of the taxa at higher latitudes.

While the assertion of size-dependent resistance to starvation is supported by many studies of both endo- and ectotherms (intraspecific comparisons – Brodie 1975; Boyce 1978; Murphy 1985: interspecific comparisons – Threlkeld 1976; Goulden and Hornig 1980; Lindstedt and Boyce 1985), only one study considers this subject for ants. Kondoh (1977) assessed the affect of body size, as measured by head width, on the ability of starved workers to withstand different humidity regimes. For the polymorphic *Camponotus japonica*, the author found that, within each humidity regime, worker survival increased with increasing head width. For the monomorphic *Formica japonica*, Kondoh reported that such positive size effects occurred only at extremely small and large worker sizes. Thus, at least for these species, there is evidence for size-dependent resistance to starvation.

We find the starvation-resistance hypothesis to be the most likely explanation for the observed body-size patterns, but the shortage of relevant data on ants makes it impossible to rigorously assess the validity of this hypothesis. It may be that the harsher climates at higher latitudes lead to more rapid starvation of ant species with small-bodied workers and thus favor species with large-bodied workers. However, the allometric relationships upon which this hypothesis is based have been generated for organisms other than ants. In addition, as currently formulated, the hypothesis only explains why small-bodied species should be under-represented at higher latitudes, and does not explain why large-bodied species should be under-represented at lower latitudes (as suggested by our data). Further, this hypothesis ignores the fact that ants live in colonies, and that energy reserves of the colony may be more important than the reserves of the individual. Clearly, much more information is needed on the relationships among starvation resistance, worker size, and body reserves – and how these variables translate into colony viability.

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