CHAPTER TWO

Latitudinal Variation of Body Size in Land Snail Populations and Communities

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Bergmann's rule states the tendency for body size to positively correlate with latitude within groups of closely related animals (Bergmann 1847; Rensch 1938; Mayr 1956; James 1970). While there has been much discussion about the appropriate taxonomic groups and scales where this pattern is expected to operate, there is little question that it applies to most endothermic vertebrates (e.g., Blackburn et al. 1999). However, not only are the underlying mechanisms still the subject of considerable debate (Ashton et al. 2000), but it is also less clear if this pattern should be expected for ectothermic invertebrates. This is because while larger ectothermic bodies experience lowered heat loss rates due to smaller surface-to-volume ratios, they will also experience correspondingly lower heat absorption rates (Cushman et al. 1993).

It should thus not be surprising that general body size vs. latitude relationships have not been forthcoming for these species. While positive body size–latitude relationships have been identified in ants (Cushman et al. 1993; Kaspari and Vargo 1995), marine isopods (Poulin 1995b), copepods (Poulin 1995a), amphipods (Poulin and Hamilton 1995), and monogoneans (Poulin 1996), marine bivalves tend to have largest body sizes at midlatitudes (Roy and Martien 2001). While Northern Hemisphere butterflies possess positive body size correlations with increasing latitude, Southern Hemisphere taxa demonstrate a negative relationship (Barlow 1994; Hawkins and Lawton 1995). Eastern North American

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bees demonstrate no latitudinal patterns in body size within state faunas and five of eight investigated families. Of the three families that do demonstrate significant patterns, two actually become smaller with increasing latitude (Hawkins 1995). Regional land snail faunas in northwest Europe also demonstrate a negative correlation between body size and latitude, though this pattern may be related to phylogenetic constraints (Hausdorf 2003).

A potential limitation of these prior analyses is that local faunas (i.e., 100 × 100 km regions or greater) are typically generated from geographic range maps. This leads to two important potential sources of error. First, all taxa will contribute equally to calculated statistics, no matter their actual abundance in that local region. This will bias results in favor of rare species, which will typically be more frequent than common taxa in a metacommunity (Hubbell 2001). Second, as species will never completely saturate their range (Hurlbert and White 2005), it should not be assumed that all mapped taxa will actually be present within a given region or locality. One way to address these problems is to investigate body size relationships at the grain of individual populations or communities, where empirical determination of body sizes and composition patterns is possible via field observations.

This chapter documents the nature and underlying mechanisms for body size vs. latitude relationships in land snail populations and communities observed across large extents (>2,500 km) in northwestern Europe, eastern North America, and New Zealand. As these regions possess little phylogenetic overlap (even at higher taxonomic levels), they represent fairly independent tests for latitudinal control of body size. Interregional comparisons are appropriate, however, as each supports similarly rich community assemblages (e.g., >30 taxa/0.1 ha; Barker 2005; Nekola 2005; Pokryszko and Cameron 2005). The following four questions will be addressed: (1) Does individual body size within a species positively correlate with latitude? (2) Are communities of high latitude represented by a greater proportion of large taxa? (3) Are communities of high latitude represented by a greater proportion of large individuals? (4) Does altitudinal variation in community body size mimic latitudinal relationships?

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Materials and Methods

Datasets

Within-species analysis of body size vs. latitude was conducted on seven North American taxa: *Carychium exiguum, C. exile, Gastrocopta procera, G. rogersensis, Cochlicopa lubrica, C. lubricella*, and *C. morseana*, representing 99–5,177 individuals from 25–126 sites spread across 472–1,094 km extents (table 2.1). These taxa represent three families (Carychiidae, Pupillidae, and Cochlicopidae) within two orders (Basommatophora and Stylommatophora; Hubricht 1985). Specific methods used to sample these populations are provided in Nekola and Coles (2001) and Nekola and Barthel (2002). The height and width of all undamaged adult shells collected from each population was measured in increments of 0.02 mm using a dissecting microscope with a calibrated ocular micrometer. The latitude-longitude coordinates for each population were determined through digitization of USGS (or equivalent) 7.5 minute topographic maps, or use of a handheld GPS unit. To minimize statistical bias from use of polar coordinates, site locations were converted to Cartesian UTM Zone 16 coordinates using ARCINFO.

Analysis of community body size vs. latitude patterns was based on 128–2,476 sites sampled within each landscape (table 2.1). European samples extended from Scotland and western Ireland to Ukraine and Finland. In this region data were available at two scales. Species presence/absence data from the 46 areas discussed in Pokryszko and Cameron (2005) were used to analyze size class frequency variation within site faunas. Species abundance data from the 128 sites used to generate most of the above species lists were used to document size class frequency variation within the individuals encountered at each site. North American samples extended from the western shore of Hudson's Bay to the Ozark Plateau, New England, and the South Carolina coastal plain. New Zealand samples were collected throughout the archipelago, including the outlying island systems of the Antipodes, Auckland, Bounty, Campbell, Chatham, Kermadec, Snares, and Three Kings. The latitude-longitude coordinates for each site were determined through digitization of topographic maps or use of a handheld GPS. As before, data were converted to Cartesian UTM coordinates using ARCINFO. To allow more direct comparison of Northern and Southern Hemisphere latitudinal patterns, UTM northing coordinates for the New Zealand sites were

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TABLE 2.1 **Overview of Datasets Used in Analyses**

a. Within Species

Species	No. of Sites	No. of Individuals	Latitudinal Extent (km)	Source
Carychium exiguum	35	1,178	586	Nekola and Barthel 2002
Carychium exile	116	5,177	1,094	Nekola and Barthel 2002
Gastrocopta procera	24	343	997	Nekola and Coles 2001
Gastrocopta rogersensis	25	415	955	Nekola and Coles 2001
Cochlicopa lubrica	108	961	764	Nekola unpublished
Cochlicopa lubricella	126	621	780	Nekola unpublished
Cochlicopa moreseana	25	99	472	Nekola unpublished

b. Within Communities—Latitude

Region	No. of Sites	No. of Taxa	No. of Individuals	Latitudinal Extent	Total Extent	Source
Europe	128	140	70,175	1,676	2,778	Pokryszko and Cameron 2005
North America	898	167	423,322	1,771	2,508	Nekola 2005
New Zealand	2,476	790	2,379,991	2,557	2,807	Baker 2005

c. Within Communities—Altitude

Region	No. of Sites	No. of Taxa	No. of Individuals	Altitudinal Extent	Source
New Mexico, USA	120	45	23,434	2,050	Dillon and Metcalf 1997

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converted to UTM southing coordinates by subtraction of each from 9,997,823 m.

Specific methods used to document communities at each site are presented in Pokryszko and Cameron (2005), Nekola (2005), and Barker (2005). Although minor methodological variations exist, in each region all communities were analyzed through standardized litter sampling augmented by hand searching for larger taxa within approximately 0.1 ha areas, as outlined in Cameron and Pokryszko (2005). All recovered identifiable shells were assigned to species, subspecies, or morphospecies.

Approximate adult shell height and width for each encountered taxon were determined from median sizes reported by Kerney et al. (1983), Pilsbry (1948), Nekola (unpublished data) and Barker (unpublished data). Each taxon was then placed into one of five size classes based on maximum shell dimension: micro (≤ 2 mm), minute (2.1–5 mm), small (5.1–10 mm), medium (10.1–20 mm), and large (>20 mm). To better reflect the faunas of these landscapes, size classes were modified from Emberton (1995) by breaking his "minute" (<5 mm) class in two, and by lumping together his "large" (20.1–40 mm) and "giant" (>40.1 mm) classes.

The contribution of each size class to the taxa and individuals present within each community was then determined. The contribution of a given size class to the taxa observed on a given site was calculated by dividing the number of taxa falling into each size class by the site's total richness. Contribution of a given size class to the individuals encountered on a given site was calculated by dividing the abundance of individuals falling within each size class by the total number of encountered individuals from that site. These metrics may provide slightly different insights. While the taxa-based metric will be a more conservative measure because of the greater replicatability of taxa lists vs. abundance data within sites (Cameron and Pokryszko 2005), the individual-based metric may provide better insight into the nature of environmental control, as each individual represents a separate sample unit.

Because of the similarity often observed between latitudinal and altitudinal body size relationships (Hausdorf 2003), analyses were also conducted on the variation in size class frequency within site taxa lists and individual abundances along elevation gradients in New Mexico (USA) mountain land snail communities using data presented in Dillon and Metcalf (1997). Communities were sampled at 61 m elevation intervals from 1,700–3,600 m in the Mogollon, Sierra Blanca, Sangre de Cristo, and Mt. Taylor ranges, and at 90 m intervals from 1,600–2,900 m along the Rio

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Peñasco and Tularosa River in the Sacramento Mountains. Data analysis was conducted as for latitudinal relationships, with maximum shell dimension being based on median size data reported in Pilsbry (1948).

Statistical Procedures

As all analyzed relationships appeared approximately linear, with variance along the best-fit lines being both normal and homoscedastic, least-squares linear regression was used to characterize variation with latitude/altitude in: (1) shell size within species; and (2) size class frequencies for taxa/individuals within sites. As five regressions were performed separately on each community dataset (one for each size class), a Bonferroni correction was used to adjust the critical value in these analyses to $p = 0.01$. Because of differences in substrate, landscape position, and sampling intervals in the seven New Mexican elevational transects, a mixed model was used to block transect site effect prior to analysis of altitudinal patterns. In this analysis, partial r^2 values of size class frequency vs. altitude, given transect effects, were reported.

Because the European datasets exist at two sampling scales (46 presence/absence lists generated from summation of multiple sites collected within a locality, and abundance lists from 128 separate sites), these data may not be easily comparable to the North American and New Zealand datasets, in which taxa lists and abundances are known from each site. To attempt to compensate for this discrepancy, sites from North America and New Zealand were geographically grouped into 300 × 300 km square regions. Average size class frequencies were then calculated within each region, and regression statistics were repeated on these average responses.

Results

Latitudinal Size Variation within Species

Only one of the seven analyzed taxa (*Gastrocopta rogersensis*) did not demonstrate significant ($p = 0.876$) variation in size with latitude (fig.2.1; table 2.2). Of the remaining taxa, four (*Carychium exiguum, C. exile, Cochlicopa lubrica, C. lubricella*) exhibited significant ($p < 0.0005$) increases in shell size with latitude, while the remaining two (*Gastrocopta procera, Cochlicopa morseana*) demonstrated significant ($p < 0.0005$)

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decreases. The amount of variation accounted for by latitude varied from 14% (*Carychium exile*) to 38% (*Gastrocopta procera*), while the magnitude of changes ranged from approximately 10% of shell height per 1,000 km in *Cochlicopa morseana* to 22% in *Carychium exile.*

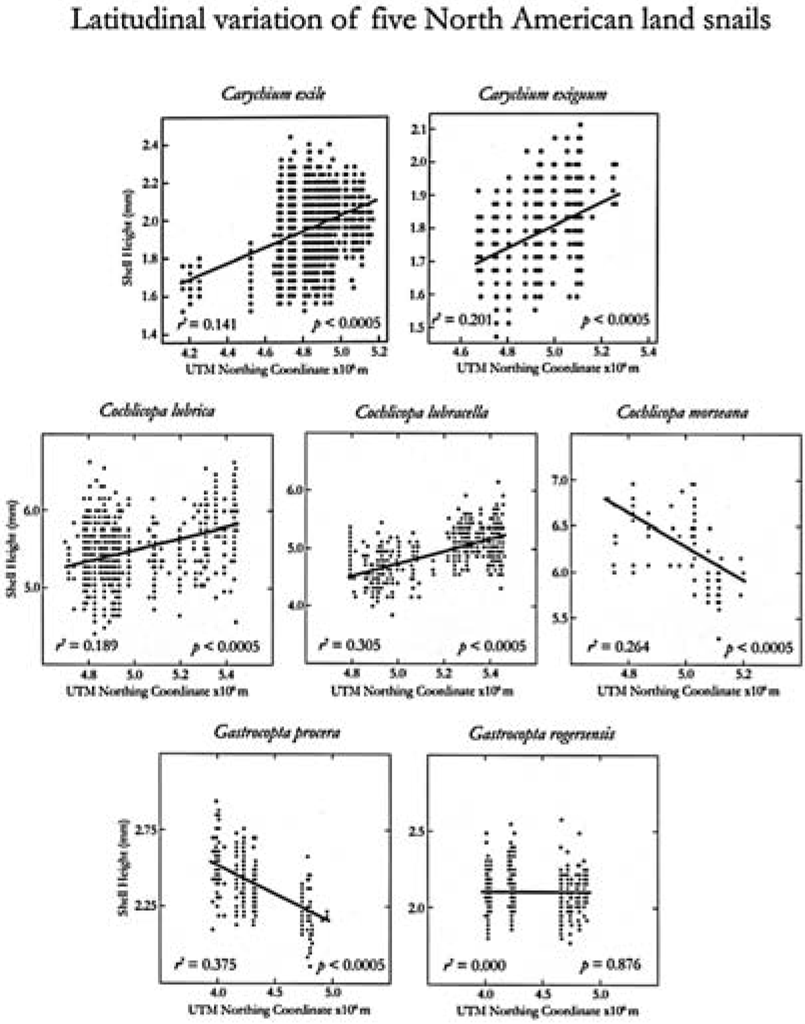

FIGURE 2.1. Shell height vs. latitude with associated least-squares regression statistics and best-fit lines for six North American land snail species: *Carychium exile, Carychium exiguum, Cochlicopa lubrica, Cochlicopa lubracella, Cochlicopa morseana, Gastrocopta procera*, and *Gastrocopta rogersensis*.

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TABLE 2.2 **Latitudinal Variation in Adult Shell Height for Seven North American Land Snail Species**

Species	Average Height (mm)	Change per 1,000 km N	Percent Change per 1,000 km N	r^2	p
Carychium exiguum	1.95	0.347	19.6	0.201	<0.0005
Carychium exile	1.77	0.424	21.7	0.141	<0.0005
Gastrocopta procera	2.40	−0.367	−15.3	0.375	<0.0005
Gastrocopta rogersensis	2.11	−0.003	−0.1	0.000	0.876
Cochlicopa lubrica	5.50	0.738	13.4	0.189	<0.0005
Cochlicopa lubracella	4.95	0.964	19.4	0.305	<0.0005
Cochlicopa morseana	6.29	−0.609	−9.7	0.264	<0.0005

Latitudinal Variation of Size Class Frequencies within Communities

In northwestern Europe the frequency of micro and minute taxa demonstrated significant ($p < 0.0005$ and $p = 0.002$) positive correlations with latitude, while the frequency of medium and large taxa showed significant ($p < 0.0005$ and $p = 0.001$) negative correlations (table 2.3). Latitude explained 20%–30% of observed variation in these size classes. The frequency of small-sized taxa did not demonstrate a statistically significant ($p = 0.098$) correlation with latitude. While southern sites were dominated by medium taxa (ca. 40% of a site fauna list), northern sites were characterized by minute (ca. 30%), micro (ca. 30%), and small (20%) taxa (fig. 2.2). The frequency of minute northwestern European individuals also demonstrated a significant ($p < 0.0005$) positive correlation with latitude while the frequency of medium and large individuals both exhibited significant ($p < 0.0005$) negative correlations (table 2.4). Latitude explained 10%–40% of observed variation in these size classes. The frequency of both micro and small-sized individuals demonstrated no significant ($p = 0.534$ and $p = 0.276$) correlation with latitude. While micro and medium individuals dominated southern sites (each representing ca. 35% of total), northern sites were characterized by minute (ca. 45%) and micro (35%) individuals (fig. 2.2).

In eastern North America the frequency of minute taxa demonstrated a significant ($p < 0.0005$) positive correlation with latitude, while the frequency of micro, medium, and large taxa showed significant ($p < 0.0005$) negative correlations (table 2.3). Latitude explained 1.6%–3.6% of observed variation in these size classes, with up to 24% of observed variation being accounted for by latitude when sites were grouped into 300 × 300 km regions. The frequency of small-sized taxa did not demonstrate a

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TABLE 2.3 **Variation in Shell Size Class Frequency of Taxa within Site Faunas of Increasing Latitude**

Region and Size Class	Constant	Slope	r^2	p
Northwestern Europe:				
Micro	−20.805	5.961	0.302	<0.0005
Minute	−6.966	5.513	0.203	0.002
Small	6.287	3.418	0.061	0.098
Medium	101.923	−12.083	0.254	<0.0005
Large	19.561	−2.808	0.232	0.001
Eastern North America:				
Micro	48.211	−4.198	0.016	<0.0005
Minute	15.647	6.547	0.034	<0.0005
Small	11.670	1.390	0.003	0.120
Medium	11.014	−1.824	0.036	<0.0005
Large	13.458	−1.916	0.020	<0.0005
New Zealand:				
Micro	−10.700	8.920	0.060	<0.0005
Minute	60.449	−0.821	0.001	0.255
Small	43.356	−7.735	0.074	<0.0005
Medium	−0.448	1.195	0.008	<0.0005
Large	7.344	−1.559	0.031	<0.0005

Note: Values are summary statistics generated via least-squares linear regression, with values scaled by 10^3 km.

significant ($p = 0.12$) correlation with latitude. Southern sites were most often represented by minute (ca. 40%) and micro (ca. 30%) taxa, while northern sites were dominated by minute (ca. 60%) taxa (fig. 2.2). The frequency of minute eastern North American individuals also exhibited a significant ($p < 0.0005$) positive correlation with latitude, while the frequency of micro and medium individuals demonstrated significant ($p < 0.0005$ and $p = 0.001$) negative correlations (table 2.4). Latitude explained 1.4%–5.4% of observed variation in these size classes, with up to 24% of variation being accounted for by latitude when sites were grouped into 300 × 300 km regions. The frequency of both small and large-sized individuals demonstrated marginal correlations with latitude ($p = 0.026$ and $p = 0.012$), with small individuals tending to increase and large individuals tending to decrease in frequency with increasing latitude. Micro and minute individuals dominated the communities of southern sites (ca. 55% and 30% of total), while northern sites were characterized by minute (ca. 60%) and small (20%) individuals (fig. 2.2).

In New Zealand the frequency of micro and medium taxa exhibited significant ($p < 0.0005$ and $p = 0.008$) positive correlations with latitude, while the frequency of small and large taxa demonstrated significant ($p < 0.0005$) negative correlations (table 2.3). Latitude explained 1%–

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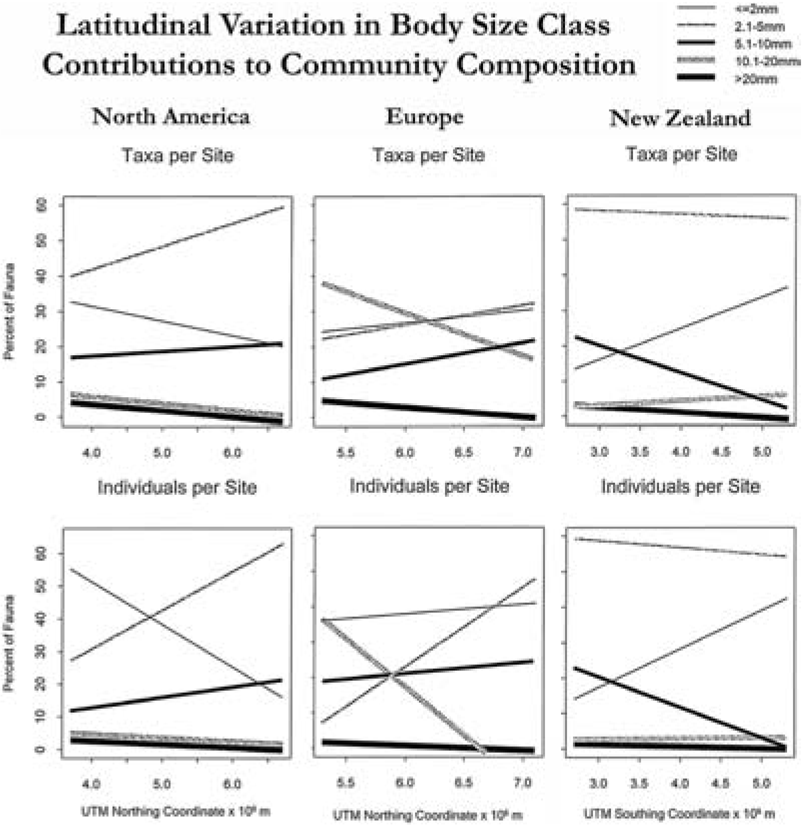

FIGURE 2.2. Average change in the contribution of five shell size classes (<2 mm = micro; 2.1–5 mm = minute; 5.1–10 mm = small; 10.1–20 mm = medium; >20 mm = large) for northwestern European, eastern North American, and New Zealand land snail community composition with increasing latitude, as represented by best-fit lines generated from least-squares linear regression. *a*, Variation in the frequency of size classes among taxa. *b*, Variation in the frequency of size classes among individuals.

7.4% of observed variation in these size classes, with up to 14% of variation being accounted for by latitude when sites were grouped into 300 × 300 km regions. The frequency of minute taxa did not demonstrate significant ($p = 0.255$) correlations with latitude. While northern sites were most often represented by minute (ca. 60%) and small (ca. 25%) taxa, southern sites were dominated by minute (ca. 60%) and micro (ca. 35%) taxa (fig. 2.2). The frequency of New Zealand micro individuals demonstrated a significant ($p < 0.0005$) positive correlation

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TABLE 2.4 **Variation in Shell Size Class Frequency of Individuals within Site Faunas of Increasing Latitude**

Region and Size Class	Constant	Slope	r^2	p
Northwestern Europe:				
Micro	21.155	2.799	0.003	0.534
Minute	−112.570	22.601	0.363	<0.0005
Small	2.040	3.162	0.009	0.276
Medium	180.745	−27.238	0.386	<0.0005
Large	8.629	−1.323	0.105	<0.0005
Eastern North America:				
Micro	103.593	−13.067	0.054	<0.0005
Minute	−16.882	11.912	0.054	<0.0005
Small	0.017	3.164	0.006	0.026
Medium	5.892	−0.979	0.014	0.001
Large	7.371	−1.029	0.007	0.012
New Zealand:				
Micro	−15.174	10.853	0.047	<0.0005
Minute	63.989	−1.823	0.001	0.058
Small	45.992	−8.584	0.062	<0.0005
Medium	2.309	0.135	0.000	0.599
Large	2.882	−0.580	0.011	<0.0005

Note: Values are summary statistics generated via least-squares linear regression, with values scaled by 103 km.

with latitude while the frequency of small and large individuals exhibited significant ($p < 0.0005$) negative correlations. Latitude explained 1%–6.2% of observed variation in these size classes, with up to 10% of variation being accounted for by latitude when sites were grouped into 300 × 300 km regions. The frequency of both minute and medium individuals did not significantly ($p = 0.058$ and $p = 0.599$) correlate with latitude. While minute and small individuals dominated northern sites (ca. 60% and 25% of total), southern sites were characterized by minute (ca. 55%) and micro (40%) individuals (fig. 2.2).

Altitudinal Variation of Size Class Frequencies within Communities

Few significant elevational trends in size class frequency of either taxa or individuals were noted within New Mexican mountain faunas (table 2.5). Only the micro class demonstrated significant variation, with these taxa becoming marginally less frequent ($p = 0.013$), and individuals becoming less frequent ($p = 0.003$) with increasing altitude. This altitudinal relationship explained an additional 7.1% and 10.1% of observed variation, following blocking for transect effects.

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TABLE 2.5 **Variation in Shell Frequency with Increasing Elevation (Scaled by 10^3 m) in Seven New Mexico, USA, Mountain Transects**

Size Class	Constant	Slope	Partial r^2	p
a. Taxa within faunas:				
Micro	22.518	−5.280	0.071	0.013
Minute	35.447	4.308	0.001	0.782
Small	18.327	3.929	0.019	0.208
Medium	26.229	−2.013	0.005	0.532
Large	1.120	0.621	0.037	0.075
b. Individuals within faunas:				
Micro	27.073	−9.418	0.101	0.003
Minute	37.600	5.607	0.009	0.384
Small	14.633	6.613	0.021	0.178
Medium	21.084	−2.974	0.008	0.421
Large	−0.393	0.174	0.021	0.184

Note: Values are summary statistics based on mixed GLM models where site effects were blocked. Partial r^2 values represent the additional explanatory contribution of elevation following blocking of site effects.

Discussion

In contrast to the positive relationship between body size and latitude posited by Bergmann's rule, land snails exhibited strong but inconsistent patterns. Positive, negative, and no correlations with latitude were observed within species. At the community level, analyses from the three disparate regions demonstrated that small taxa and individuals tend to increase in frequency, whereas large taxa and individuals tend to decrease in frequency with increasing latitude.

Body Size Patterns within Species

The lack of consistent body size relationships with latitude mirrors previous studies that have been unable to identify general environmental correlates to land snail shell size. Shell size variation in *Albinaria idaea* and *Albinaria terebra* from Crete appear uncorrelated with contemporaneous precipitation, temperature/insolation, substrate chemistry, and elevation (Welter-Schultes 2000, 2001). However, a historical component appears important, because populations with greatest size variation are found in the oldest habitats (Welter-Schultes 2001). Lack of correlation between shell size and current environmental conditions, but apparent correlation of variance with population age, has also been noted for *Helix aspersa* in North Africa (Madec et al. 2003). Goodfriend (1986) could not identify universal ecological predictors for shell size in an extensive

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literature review, with individualistic responses being noted along moisture, temperature/insolation, and calcium availability gradients. He did document, however, positive correlations between shell size and moisture in ten of twelve taxa. Similar moisture vs. body size patterns have been more recently noted for *Cochlicopa lubrica* in Europe (Armbruster 2001) and in the fauna of the Kikai Islands of Japan over a 40 ka time frame (Hayakaze and Chiba 1999; Marui et al. 2004).

Cushman et al. (1993) suggest that positive body size correlations with latitude in ectotherms may be related to a greater capacity for larger organisms to store food, allowing for increased starvation resistance. This may be important in seasonal climates where individuals are forced to experience prolonged periods of low resources. The generality of this mechanism for land snails, however, is unclear as water may be a more important limiting resource than food (Riddle 1983; Goodfriend 1986). This would suggest that body size should also increase with frequency and severity of moisture stress. While this hypothesis cannot be tested via the current data, it is interesting to note that this prediction runs counter to the moisture vs. body size trends discussed above. Additionally, large snails in the arid southwestern USA are typically restricted to montane "islands" of higher and more regular precipitation, while lowland taxa that experience increased water stress tend to be of minute or micro size (e.g., Bequaert and Miller 1973; Metcalf and Smartt 1997). Starvation avoidance may thus not be an important general factor influencing land snail body size.

Turner and Lennon (1989) suggest that because of limited resources, smaller ectotherms will be more likely to maintain minimally viable populations at high latitudes, thus leading to a negative correlation between body size and latitude. This mechanism also does not apply to these data, as neither *Cochlicopa morseana* nor *Gastrocopta procrea* demonstrated a positive correlation between population size and latitude. Additionally, both of these taxa have closely related siblings that demonstrated positive body size correlations with latitude, even though these siblings presumably share similar resource demands and minimum viable population sizes. What does differentiate these two taxa from their siblings, however, is their lower latitude of geographic range (Hubricht 1985). As will be discussed below, if these species have a more limited ability to depress their freezing point, increased supercooling and winter survival abilities will be imparted by a reduction in body size.

The only consistent predictor of shell size identified by Goodfriend

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(1986) was population density, which has been found to correlate inversely with adult shell size in European *Arianta arbustorum, Candidula intersecta, Cepaea nemoralis, Cochlicella acuta*, and *Helicella itala*. This relationship has also been observed in North American *Mesodon normalis* (Foster and Stiven 1996; Stiven and Foster 1996), though no impact was found on fecundity rates (Foster and Stiven 1994). Increased environmental heavy metal concentration may also correlate negatively with shell size in some species (Tryjanowski and Koralewska-Batura 2000).

These factors, too, are probably not responsible for the body size variation observed in the present study. All but one of the investigated species demonstrated population sizes that were independent of latitude (Nekola, unpublished data). And the lone taxon that did show a significant trend (*Cochlicopa lubricella*) had both significantly larger populations and shell sizes at higher latitudes. Additionally, heavy metal concentrations do not monotonically vary across eastern North America: pollution levels peak at midlatitudes along the industrial corridor extending from Chicago to New York.

Body Size Patterns between Communities

Contrary to Bergmann's rule, across all three regions small-sized taxa and individuals tended to become more frequent at higher latitude, while larger-sized taxa and individuals tended to demonstrate a negative correlation. Variation in size class frequency of individuals within communities tended to follow the patterns observed for taxa. This general pattern was expressed somewhat differently in each region. The magnitude of micro and/or minute taxa increase and medium and/or large taxa decrease with increasing latitude was strongest in northwestern Europe. This general pattern differed in eastern North America, with the frequency of micro species decreasing at higher latitudes, and in New Zealand, with the frequency of medium species increasing at higher latitudes.

These variations do not invalidate the general pattern, as they probably represent differences in sampling protocols, regional ecological histories, gradients, and/or component phylogenies. The greater magnitude of variation in frequency of medium-sized taxa/individuals in Europe appears at least partially related to phylogenetic constraint due to the presence of the Clausiliidae, which has undergone significant radiation in the east and south of Europe (Kerney et al. 1983; Pokryszko and Cam-

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eron 2005). This family and its morphological niche (medium-sized individuals that are taller than wide) are essentially absent from both eastern North America and New Zealand. The stronger correlations with latitude found in Europe (as compared to the other two regions) are probably due to a more narrowed sampling regime, with only upland woods being observed. The lack of change in frequency for minute taxa/individuals in New Zealand appears related to in situ radiation of the Charopidae and Punctidae, which generated large numbers of minute taxa throughout the archipelago (Barker 2005). Additionally, the positive correlation between frequency of medium-sized taxa and latitude in New Zealand at best only weakly influences community composition, with less than 1% of observed variation being accounted for by this relationship. Additionally, medium-sized individuals did not demonstrate a corresponding significant correlation with latitude. The reduction of frequency of micro taxa/individuals in eastern North American communities, however, is not a phylogenetic or statistical artifact, as this size class includes taxa from seven different families, and as the relationship is equally significant for taxa and individuals. A possible explanation for this unique pattern is that only the North American dataset includes continental arctic climates. Thus, the highest-latitude northwestern Europe and New Zealand sites will be exposed to comparatively less severe winter temperatures.

Generally no body size vs. elevation relationships were noted from New Mexican montane faunas. Micro-sized taxa and individuals tended to decrease in frequency with increasing elevation, mirroring the latitudinal pattern seen in the eastern North American fauna. The lack of strong correlation between altitude and snail body size is not surprising, however, because in New Mexico elevation is strongly negatively correlated with precipitation levels (Metcalf and Smartt 1997). The confounding of elevation and precipitation in this region makes it unlikely that simple body size correlations will exist.

Two non-mutually-exclusive mechanisms can be advanced to account for the positive correlation between frequency of smaller-sized taxa/individuals in land snail communities and latitude: increased winter survival and dispersal ability with decreasing shell size.

Land snails have, at best, only a moderate ability to lower their freezing temperature. Many species apparently do not have cryoprotective chemicals (Riddle 1983), while those that do can only depress freezing temperatures to a limited degree (Ansart et al. 2002; Ansart 2002). For

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example, even though larger *Helix aspersa* individuals are able to depress freezing temperature more than small individuals, all perished within 16 hours of exposure to –50 C temperatures (Ansart and Vernon 2004). The principal avenue used by land snails to survive freezing is an increase in supercooling ability via gut clearance, prevention of debris contact with mantle tissue, and reduction of an individual's water mass (Riddle 1983). This last factor is probably the most important in terms of body size relationships, as the greater the water volume, the greater the likelihood that ice nucleation will occur, leading to freezing of tissues and mortality (Lee and Costanzo 1998; Ansart and Vernon 2003). Smaller land snails with lower water mass thus have greater abilities to supercool than larger individuals (Riddle and Miller 1988; Ansart and Vernon 2003). This pattern is common to most ectothermic invertebrates (Lee and Costanzo 1998). Additionally, because small snails experience greater water loss through their shells than larger taxa (Arad and Avivi 1998; Arad et al. 1998), they will have a greater ability to decrease water mass prior to the winter season.

Differential migration abilities of small vs. large snails, in combination with Pleistocene glaciation history, may also underlie this pattern. Active dispersal rates for land snail individuals are very low (10^1–10^2 m/yr; Hausdorf and Hennig 2003) with individuals being unable to cross barriers of 10^2–10^3 m (Baur 1988; Schilthuizen and Lombaerts 1994). While there is a positive correlation between body size and distance moved over a single day, this relationship disappears by day 2 (Popov and Kramarenko 2004). Landscape migration of land snails is thus solely related to passive dispersal abilities (Hausdorf and Hennig 2003). Smaller-sized individuals have greater capabilities of long-range passive dispersal by wind (Kirchner et al. 1997) and animal (Pfenninger 2004) vectors. Additionally, while small snails have a lower fecundity per individual, they have much higher reproductive outputs when calculated on a per-volume basis. For example, while *Arianta arbustorum* individuals (16 × 21 mm) will lay 800 eggs during a lifetime and *Punctum pygmaeum* (0.7 × 1.4 mm) only six, *Punctum* produces 50 times the number of eggs per standard cubic unit of animal mass (data from Heller 2001). Such increased fecundity will increase the number of individuals capable of passive dispersal. Also, as the frequency of uniparental reproduction is inversely correlated with body size (Pokryszko and Cameron 2005), smaller taxa have the capability of founding new colonies via dispersal of only single individuals into new stations. Small-sized snails would

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thus be expected to be the most rapid colonizers of previously glaciated terrain, accounting for the positive correlation between the frequency of small snails in communities and latitude. A similar mechanism has been invoked to explain the disproportionate presence of small-shelled taxa as colonists of Pacific islands (Vagvolgyi 1975; Marui et al. 2004). Large-size snails of Pacific islands have largely developed from in situ evolution of small taxa into unfilled niches (Cowie 1995).

Conclusions

These analyses demonstrate that (1) general body size relationships with latitude do not exist within a species; (2) communities of high latitude tend to be represented by a greater proportion of small taxa; (3) communities of high latitude tend to be represented by a greater proportion of small individuals; and (4) altitudinal variation in community body sizes is weak and probably obscured by other strong local environmental gradients such as precipitation.

Thus, Bergmann's rule appears to not apply as a general feature of land snail biogeography. The reasons for this are related to the unique physiology and biology of land snails: as they possess limited capabilities for lowering their freezing temperature and are not capable of active dispersal across landscapes, small forms will be favored at high latitudes, as they will maintain better supercooling abilities and will more rapidly and effectively colonize deglaciated landscapes.

This result cautions that general latitudinal body size predictions for ectotherms must consider more than heat balance issues if they are to reflect real world patterns. For instance, ectotherms not exposed to freezing temperatures, or with better abilities to generate cryoprotection compounds or to actively disperse, may exhibit different body size relationships from those seen in land snails. The prevalence of Bergmann-style body size variations in marine invertebrates (Poulin 1995b, 1995a; Poulin and Hamilton 1995; Poulin 1996) may be due to the fact that these populations are never exposed to freezing temperatures. Additionally, the colonial nature of ants may buffer individuals against winter temperatures, allowing this taxa group to follow predictions of Bergmann's rule (Kaspari and Vargo 1995). It is thus imperative that the unique physiology, reproductive biology, behavior, and environments of ectothermic groups be considered when formulating body size hypotheses.

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