



CHICAGO JOURNALS



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Source: *The American Naturalist*, Vol. 174, No. 6 (December 2009), pp. 898-905

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/646604>

Accessed: 21/05/2015 15:08

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Notes and Comments

Ecological Opportunity in Adaptive Radiation of Galápagos Endemic Land Snails

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Submitted October 31, 2008; Accepted August 5, 2009; Electronically published October 22, 2009

ABSTRACT: The classic evolutionary hypothesis of ecological opportunity proposes that both heterogeneity of resources and freedom from enemies promote phenotypic divergence as a response to increased niche availability. Although phenotypic divergence and speciation have often been inferred to be the primary consequences of the release from competition or predation that accompanies a shift to a new adaptive zone, increased phenotypic variation within species is expected to represent the first stage resulting from such a shift. Using measures of intraspecific morphological variation of 30 species of Galápagos endemic land snails in a phylogenetically controlled framework, we show that the number of local congeners and the number of local plant species are associated with lower and higher intraspecific phenotypic variation, respectively. In this clade, ecological opportunity thus explicitly links the role of competition from congeners and the heterogeneity of resources to the extent of intraspecific phenotypic divergence as adaptive radiation proceeds.

Keywords: adaptation, diversification, ecological release, intraspecific variation, shell morphology.

Introduction

When a species is released from interspecific competition by colonizing a vacant adaptive zone, competition among conspecific individuals for limiting resources is predicted to promote divergence in phenotype and resource use, leading to an increase in intraspecific phenotypic variation (Van Valen 1965; Roughgarden 1972; Lister 1976; Bolnick 2004; Svanback and Bolnick 2007). As the adaptive radiation proceeds and the lineage diversifies into multiple species, the total range of resources used expands, and interspecific competition between newly formed species promotes phenotypic divergence among species but constrains it within species (Arthur 1987). Species therefore decrease in phenotypic diversity because of stabilizing selection as species accumulate in the same zone. Under this

scenario, species should exhibit a maximum degree of intraspecific phenotypic variation because of diversifying selection soon after they first invade an empty adaptive zone, when the phenotypic consequences of intraspecific competition are not yet constrained by interspecific competition. The relative contributions of interspecific competition and resource heterogeneity in determining phenotypic divergence within species as a lineage undergoes adaptive radiation have yet to be explicitly evaluated in the context of adaptive radiation, although both mechanisms are key to phenotypic shifts in adaptive radiation.

Adaptive radiations on oceanic archipelagos provide ideal systems to test the predictions of the ecological opportunity hypothesis since colonization of each new island corresponds to the invasion of an empty but often similar adaptive zone. Moreover, given the ecological simplicity of insular systems, competition and resource heterogeneity can be readily estimated for each island assemblage. In this study, we use the radiation of Galápagos endemic land snails of the genus *Bulimulus* to test for the relative contributions of competition and resource heterogeneity in determining intraspecific phenotypic variation.

The native land snail fauna of Galápagos includes 88 described species, and the genus *Bulimulus* constitutes approximately 80% of this diversity (Chambers 1991). Bulimulids (represented on Galápagos exclusively by the genus *Bulimulus*) form the most species-rich radiation of any animals or plants on this archipelago (Parent et al. 2008). Other land snail lineages have not diversified extensively on the islands (the next most diverse group has four species), are generally much smaller than bulimulids, and have distribution ranges restricted to certain islands or habitats (Smith 1966; Chambers 1991). Bulimulids colonized all major islands, roughly in the same sequence as their geological formation, and successful colonization was followed by independent radiation within islands so that island assemblages are composed of one or few independent lineages. Although some species were originally described as occurring on more than one island, the combination of current morphological and molecular evidence

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Am. Nat. 2009. Vol. 174, pp. 898–905. © 2009 by The University of Chicago. 0003-0147/2009/17406-50836\$15.00. All rights reserved.
DOI: 10.1086/646604

suggests that all studied species are single-island endemics. Bulimulid species richness on a given island is positively associated with island area, maximum elevation, plant (habitat) diversity, and island geological age (Parent and Crespi 2006).

Bulimulids are found in all described vegetation zones, except the lava boulder and sandy coastal zones (Dall 1896; Dall and Ochsner 1928; Smith 1966; Coppo 1984; C. E. Parent, personal observation). Although vegetation on Galápagos has been traditionally categorized into up to seven vegetation zones (Wiggins and Porter 1971), in this study we follow the simple three-level zonation (coastal, dry lowland, and humid highland zones) of McMullen (1999) and classify the snail species and plant species accordingly. Bulimulids are mostly found on vegetation or on the ground near vegetation. Although *Bulimulus* species are not host-plant specific, when found in sympatry the species are typically distributed in space among different local microhabitats, according to substrate, plant species, vegetation type, and resting elevation and angle (e.g., under rocks vs. particular heights on particular plant species; Dall and Ochsner 1928; Smith 1966; Coppo and Glowacki 1983; Coppo 1984; C. E. Parent, personal observation). Increased plant species diversity is thus one important dimension of habitat complexity that provides increased ecological space for snails to exploit. We therefore use native and endemic plant species as a proxy of habitat heterogeneity.

There is evidence that Galápagos bulimulid land snails have adapted to the different habitat and vegetation zones they inhabit (Parent 2008). Specifically, shell shape is associated with elevational variation in moisture levels, so that bulimulid species with more slender shells (and a smaller shell opening relative to shell size) tend to be found at lower elevations, whereas species that are more conical in shape tend to be found at higher elevations where humidity levels are higher (Parent 2008). Shell morphology (especially shape and size) has been associated with adaptation to the environment in other snail taxa (e.g., Goodfriend 1986; Schilthuizen et al. 2006; Conde-Padin et al. 2007; Johnson and Black 2008; Guerra-Varela et al. 2009). Other studies of land snails have also demonstrated that species compete for microhabitat, such that interactions within and between species mediate diversification in ecological and morphological traits (Baur and Baur 1990; Chiba 1996, 1999, 2004; Lee and Silliman 2006).

We quantified the effect of ecological opportunity on intraspecific phenotypic variation for each bulimulid species as (1) the number of congeners (interspecific competition) and (2) the number of native plant species (proxy for resource and habitat heterogeneity) found in the vegetation zone where the species occurs. We use multiple regression analyses to test for the relative contribution of

the number of congeners and habitat heterogeneity in a given vegetation zone on bulimulid land snail intraspecific variation in shell shape and shell size.

Material and Methods

Sampling

Between 11 and 133 adult specimens of each of 30 bulimulid land snail species (median = 20; total = 816) were sampled across their range on eight Galápagos islands from November 2000 to April 2005. The same sampling strategy was used at all collecting sites; the ground and the vegetation were carefully searched for specimens over an area of approximately 10 m × 10 m for at least 30 min. Since the exact distribution ranges of species are unknown, we sampled to cover the greatest area possible on the islands, given the time available. All specimens were preserved in 75% ethyl alcohol.

Shell Radiography and Geometric Morphometric Analysis

Since bulimulid land snails have determinate shell growth (they stop growing once they are adults), we used only adult specimens. They were radiographed using an H. G. Fischer x-ray machine (Model FP200) at 70 kV, 20 mA exposed for 0.9 s at 60-cm focus-film distance. Specimens were held in place with mounting putty on a sheet of photographic emulsion (Kodak Ultra-speed DF-58 dental film). The shells were always positioned in the same orientation, with the axis of the shell on the Y-axis and the aperture upward and parallel to the photographic film. Each radiograph was scanned and saved in a tag image file format. The shell images obtained were digitized by recording the X and Y coordinates of six morphological landmarks on the shells in TPSDIG2 (Rohlf 2006). The geometric morphometric approach that we used partitions morphological variation into components of size and shape. Shape includes all features of a configuration of landmarks that are invariant to scaling (variation in size), translation (variation in the X-Y position of the shell on the radiograph), and rotation (variation in the orientation of the specimen on the plane of the radiograph). We used Procrustes superimposition to characterize shape variation of individuals within each species. This method extracts the shape information from the landmark configurations by scaling to the unit centroid size, superimposing the centroids of all configurations, and rotating the configurations to a position of optimal fit according to a least squares criterion. The scaling, superimposition, and rotation steps were performed for all specimens of a given species simultaneously (we used a full Procrustes fit and projection onto a tangent space) in TPSSUPER (Rohlf

Table 1: Regression results of intraspecific phenotypic variation

Phenotypic variable (standardized contrast)	Independent variable (standardized contrast)	<i>N</i>	β	SE of β	<i>t</i>	<i>t</i> _{PIC}
Shell shape	Number of congeners	30	-.00366	.0012	-3.05**	-10.21***
Shell shape	Number of plant species		.000000382	.000000145	.264	4.84***
Shell size	Number of congeners	30	.279	.230	1.21	1.98*
Shell size	Number of plant species		-.0000299	.0000278	-1.08	.80

Note: Values of *t* and associated *P* values are presented for standard and phylogenetically controlled (*t*_{PIC}) multiple regression models. Separate multiple regression analyses were performed for each component of intraspecific morphological variation (size and shape), with number of congeners and number of plant species included as separate independent variables in the final model. Shell shape: $R^2 = 0.349$, $F_{2,27} = 7.23$, $P = .003$; shell size: $R^2 = 0.056$, $F_{2,27} = 0.804$, $P = .46$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

2004). Each specimen could then be described by a size (unidimensional) and a shape component (multidimensional). Intraspecific variation in shell size was then assessed as the coefficient of variation in centroid size for each species, and intraspecific variation in shell shape was assessed as the mean euclidean distance between each specimen's shape vector and the species' mean shape vector.

Multiple Regression Analyses

Six of the 30 species had a sample size smaller than 20, the median. To make sure that we did not introduce bias by including these species in our analysis, we tested for an association between sample size and the number of congeners found with a species in a given vegetation zone, as well as the habitat heterogeneity. We found no significant correlation ($r = -0.12$, $P = .54$ and $r = 0.062$, $P = .75$, respectively), and we therefore included all species in the multiple regression analyses.

Some bulimulid species had no congener in the same vegetation zone, so we added 1 to the number of congeners to enable data transformation to meet assumptions of normality. Number of congeners, number of plant species, and the coefficient of variation in shell size data were Box-Cox transformed (Box-Cox parameter $\lambda = 0.2$, 2, and -0.3 , respectively). We first ran a standard multiple regression analysis with shell shape variation and shell size variation as the dependent variables and Box-Cox-transformed values of habitat heterogeneity and numbers of congeners as predictor variables. We then computed phylogenetic generalized least squares models (Garland and Ives 2000), an approach that is functionally identical to independent contrasts regressions. These models allow the inclusion of detailed information on the taxonomic relations among the species investigated but have the restriction of assuming linear relations between response and all predictor variables. We used topology and branch lengths of the phylogeny of Parent and Crespi (2006) to generate

a phylogenetic distance matrix among species. This phylogeny is the best maximum likelihood tree obtained from combined nuclear (internal transcribed spacer) and mitochondrial (cytochrome oxidase subunit I) sequence data sets. It is well resolved, with good nodal support. Multiple linear generalized least squares models with shell shape variation and shell size variation as the dependent variables and Box-Cox-transformed values of habitat heterogeneity and numbers of congeners as predictor variables were computed with the R library PHYLOGR (Díaz-Uriarte and Garland 2006). Because collinearity between independent variables might confound the analyses, we checked for redundancy by investigating tolerance levels for resource heterogeneity and competition intensity. Tolerance value for resource heterogeneity regressed on competition intensity (tolerance = $1 - R^2 = 0.6$) was adequately high (Quinn and Keough 2002), and both variables could therefore be included in the regression models.

Intraspecific variation in shell morphology could be a function of mean shell size through an allometric scaling relationship, with larger shells potentially being more variable, and we therefore tested for an association between mean shell size and the variation in shell morphology within species. Furthermore, since vegetation zones on different islands vary in the number of species for which morphological data were available, we also used the mean intraspecific morphological variation per vegetation zone and further investigated the relationship between intraspecific phenotypic variation and competition and resource heterogeneity. Because the results did not change when this procedure was used, it is unlikely that our results are confounded by the number of species for which we have been able to collect morphological data.

Results

The number of congeners inhabiting the same vegetation zone was strongly negatively correlated with the degree of

intraspecific variation in shell shape, and in the best model determined by forward stepwise multiple regression analyses, resource heterogeneity was positively associated with intraspecific variation in shell shape (table 1). Dividing the number of plant species by the number of congeners yields an index of ecological opportunity, and this metric was positively correlated with the degree of intraspecific variation in shell shape (fig. 1). By contrast, intraspecific variation in shell size was significantly explained by competition from congeners only when we controlled for the phylogenetic relationship among species (table 1). We find that ecological opportunity is greatest on younger islands, where vegetation zones exhibit a combination of relatively high resource heterogeneity and low intensity of interspecific competition (fig. 2). Intraspecific variation in shell shape was not significantly associated with shell size ($R^2 = 0.070$, $P = .16$); therefore, the pattern of ecological release observed is not a reflection of allometric scaling.

Discussion

The main findings of this study are a significant negative relationship between intraspecific phenotypic variation and number of congeners and a significant positive relationship between intraspecific phenotypic variation and resource heterogeneity. These results support the combined role of competition and resource heterogeneity in generating ecological release during diversification and support niche-filling models of diversification (Simpson 1953; Freckleton and Harvey 2006).

For bulimulids on the Galápagos archipelago, levels of competition and resource heterogeneity are functions of island age, island size, and local species diversity. Bulimulid species diversity is significantly higher on older islands and on islands with greater plant species diversity (resource heterogeneity; Parent and Crespi 2006). However, the relationship between island age and bulimulid species diversity is not significant when analyzed at the level of a

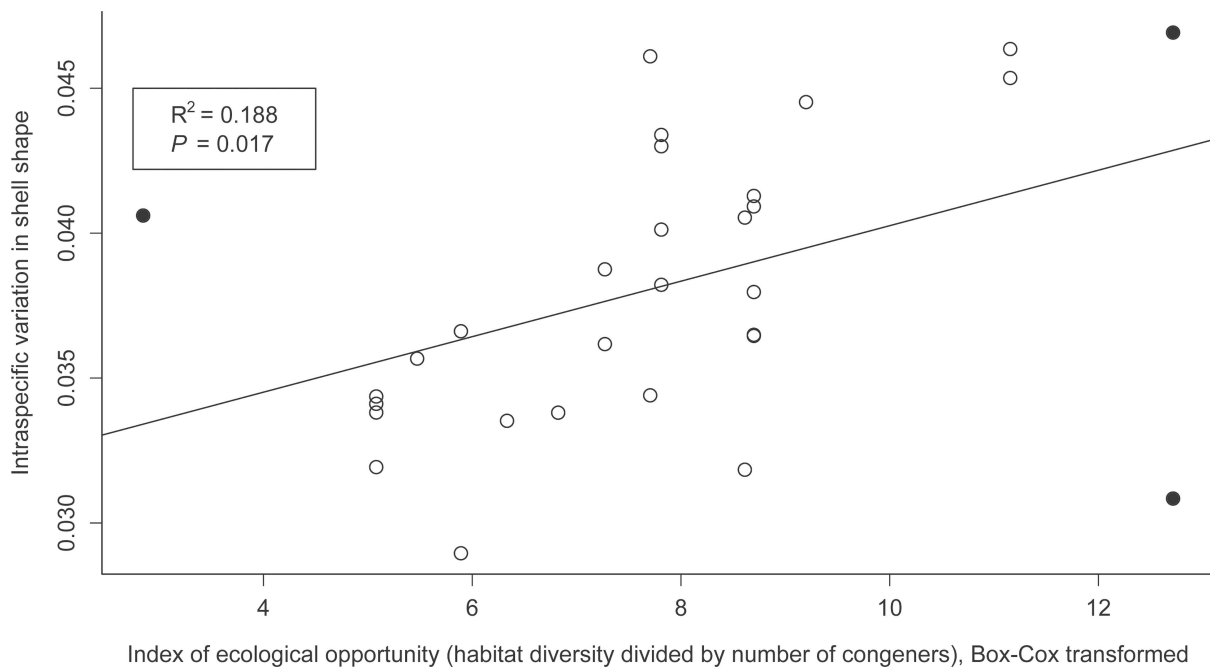


Figure 1: Positive relationship between intraspecific morphological variation in shell shape and ecological opportunity (measured as the number of plant species divided by the number of congeners found in a given vegetation zone). Because three data points (*Bulimulus pinzonopsis* and two undescribed species from the volcano Sierra Negra on Isabela Island, depicted by filled circles) had a disproportionate influence on the regression slope and fit (influence analysis: hat = 0.195, 0.199, and 0.199, respectively; $DF_{betaslope} = -0.818, 0.452, \text{ and } -1.577$, respectively; and $DF_{fit} = 0.898, 0.495, \text{ and } -1.728$, respectively), we also retested the model after omitting these three data points and found it to be much stronger ($N = 27$, $R^2 = 0.491$, $P < .001$). Similar results were obtained by regressing the mean intraspecific morphological variation in shell shape for all species for which morphological data are available within a given vegetation zone against ecological opportunity ($N = 14$, $R^2 = 0.369$, $P < .05$; see “Material and Methods”). It is unclear why the outliers show considerably higher (for *B. pinzonopsis*) or considerably lower (for one of the undescribed species on Sierra Negra) intraspecific morphological variation than the ecological opportunity on these islands predicts.

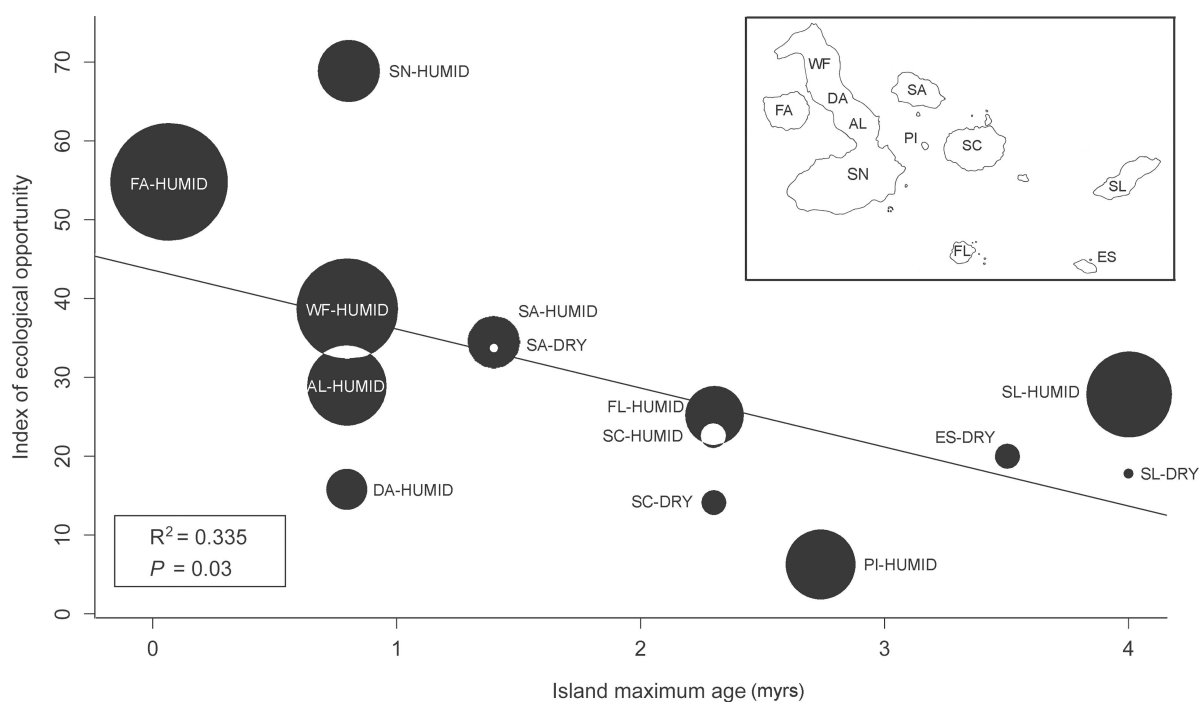


Figure 2: Negative relationship between ecological opportunity (measured as the number of plant species divided by the number of congeners found in a given vegetation zone) and island maximum age (D. Geist, H. Snell, C. Goddard, and M. Kurz, unpublished data). The radius of each data point is proportional to the average intraspecific variation in shell shape for all bulimulid species found in a given vegetation zone. *AL*, volcano Alcedo; *DA*, volcano Darwin; *ES*, Española; *FA*, Fernandina; *FL*, Floreana; *PI*, Pinzon; *SA*, Santiago; *SC*, Santa Cruz; *SL*, San Cristobal; *SN*, volcano Sierra Negra; *WF*, volcano Wolf. “Humid” and “dry” designate the vegetation zones.

vegetation zone rather than island ($R^2 = 0.21$, $P = .09$). Larger islands have significantly more resource heterogeneity (Parent and Crespi 2006) and harbor vegetation zones with significantly more resource heterogeneity ($R^2 = 0.48$, $P < .01$). The combined effects of island age on the number of competitors and island area on resource heterogeneity result in a distribution of ecological opportunity across the archipelago, where younger islands have vegetation zones presenting greater ecological opportunity (fig. 2). Consequently, we find that species show high levels of intraspecific morphological variation in vegetation zones that present a combination of few competitors and considerable resource heterogeneity, mainly on younger islands. Conversely, species that are found in vegetation zones with high land snail diversity (mainly on older islands) and relatively low habitat heterogeneity (mainly on smaller islands) are generally less variable in intraspecific morphology. This predictable variation in intraspecific morphology is consistent with the evolutionary process of ecological opportunity, leaving a morphological signature of intraspecific variation in contemporary species associated with the ecological context in which they occur.

Release from interspecific competition has been sug-

gested to result in expansion of resource use in lineages invading depauperate environments such as islands. For example, Hawaiian silverswords and *Bidens* are two plant groups that are more variable than their mainland relatives (Schluter 2000). Similarly, Schluter (1988) found accelerated morphological divergence in Hawaiian and Galápagos finches compared to their mainland relatives. These patterns are consistent with the hypothesis that adaptive radiation on islands is mediated in part by release from competition. Another potential explanation for the increased phenotypic variability in environments with fewer competitors is competitive displacement, which has the causality reversed, such that morphologically more variable species preclude the accumulation of new species in the same habitat (Gause 1934; Arthur 1978, 1982). This scenario involves the process of interspecific competition in determining community assembly, and in this study it implies that phenotypically more variable species would outcompete less variable species. Both competitive exclusion and ecological opportunity imply competition between species and are not necessarily mutually exclusive scenarios. It will not be possible to clearly differentiate the potential role of these two processes until further infor-

mation about the possible association between competitive value and intraspecific phenotypic variation is available.

Other studies have shown that snails compete within and between species, in the laboratory and in nature (Fenchel and Kofoed 1976; Cowie and Jones 1987; Baur and Baur 1990; Cross and Benke 2002). Furthermore, inter- and intraspecific competition in snails have been inferred to result in both character displacement (Fenchel 1975; Grahame and Mill 1989; Cowie 1992; Barker and Mayhill 1999; Chiba 1999; Marko 2005; Davison and Chiba 2006; De Weerd et al. 2006) and competitive displacement (Arthur 1982). Although the limiting factors over which species or individuals compete are often unspecified in these studies, authors usually point to food and suitable resting or feeding microsites, although predator-free space could also be important. The ecology of Galápagos land snails has yet to be studied in detail, but bulimulids appear to feed primarily on lichens growing on the vegetation, as well as decaying matter on the ground, and individuals may compete for a suitable microhabitat to feed and to avoid desiccation. Snails are indeed often observed in dense groups under rocks, at the base of trees, or under bark.

Predation appears to play a minor role, if any, in mediating the evolution of diversity within and between bulimulid species on Galápagos. The only known predators of bulimulid land snails on the islands are mockingbirds and possibly rats (Smith 1966). Mockingbirds are found on all major islands and are not likely a source of differential selection. Coppo (2000) has suggested that introduced rats prey on bulimulid snails, and it is possible that endemic rats, where they still occur, do so as well. Although once found on several major islands, Galápagos endemic rats have suffered extinction, and the four species that remain are distributed on three islands only. Undoubtedly, some of the other land birds prey on bulimulids occasionally, but given the shell thickness of most species, as well as their size, birds are probably more likely to prey on the smaller-sized snail species in other genera. Snail predators have never been observed in action in the field, and we follow Smith (1966) in concluding that Galápagos bulimulids are not subject to appreciable levels of predation.

The mechanistic basis linking shell shape with competition and resource use in this study has yet to be investigated, but associations between shell shape (but not size) and vegetation zone or microhabitat have been described for Galápagos bulimulids (Coppo and Glowacki 1983). Furthermore, there is an association between interspecific shell shape (and not size) variation and elevation across multiple islands of the archipelago (Parent 2008), suggesting that species have repeatedly adapted to the variation in moisture levels across the archipelago.

Shell shape can mediate habitat use via effects on mobility, exploitation of different food sources, use of different types of shelter, and resistance to desiccation (Cook and Jaffar 1984; Goodfriend 1986; Heller 1987). Inter- and intra-specific populations of *Mandarina* land snails on the Bonin Islands appeared to differ more markedly in shell shape (compared to shell size) in association with habitat (Chiba 1996).

The genetic basis of the measured intraspecific morphological variation in bulimulid land snails is unknown. Many studies have found a genetic component to morphological variation in gastropods, particularly in the case of discrete characters, such as color and pattern (e.g., Cain et al. 1960; Atkinson and Warwick 1983; Palmer 1984, 1985a). Control of variation in continuous morphological characters, such as shape, is less well understood, although there is evidence for both plastic (Phillips et al. 1973; Kemp and Bertness 1984; Boulding and Hay 1993; Gibbs 1993) and genetic (Newkirk and Doyle 1975; Crothers 1980; Palmer 1985b; Johannesson and Johannesson 1996; Parsons 1997) components of variation.

It is possible that the morphological variation we observed in bulimulids is not (entirely) genetically based. The release from competition following the colonization of an empty vegetation zone could potentially induce a plastic response that would increase the morphological variation within land snail species faced with an increased wealth of resources. However, the type of phenotypic response (genetic, plastic, or a combination of both) to ecological opportunity would not alter the main conclusion of this study; that is, competition and resource heterogeneity are significant determinants of intraspecific phenotypic variation in the context of adaptive radiation. However, until we can determine the relative contribution of genes and environment to the morphological variation observed, the link between this intraspecific variation and the remarkable interspecific phenotypic variation observed among species in this group remains to be established.

Competition between closely related species is often considered to be an important factor in driving phenotypic diversification and speciation (Schluter 2000). Our results are consistent with competition between closely related species limiting phenotypic variation within species. The constraining role of competition between species is particularly important in adaptive radiation since the competing species are likely to be phenotypically very similar, given their recent common ancestry.

Acknowledgments

We thank D. Bolnick, J. Joy, A. Mooers, L. Snowberg, and four anonymous reviewers for comments on this manuscript. We thank the FAB-lab at Simon Fraser University

for discussion. D. C. Adams and F. J. Rohlf provided advice on geometric morphometric and statistical methods, and S. Stone helped with shell radiography. We thank the Charles Darwin Research Station and the Galápagos National Park Service for fieldwork permits and logistical support. Financial support was provided by the Natural Science and Engineering Research Council of Canada.

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