

VARIATION IN SPECIES DIVERSITY AND SHELL SHAPE IN HAWAIIAN LAND SNAILS: IN SITU SPECIATION AND ECOLOGICAL RELATIONSHIPS

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Abstract.—The native land-snail fauna of the Hawaiian islands was investigated from a combined perspective of ecological and historical, vicariant, and dispersalist biogeography. There were more than 750 described, valid species; almost all were endemic to the archipelago, many to single islands. Path analysis showed that island area, per se, had the strongest influence on numbers of species. Island altitude and number of plant communities, both strongly related to area and both dimensions of habitat diversity, also had major influences. The influence of island age was complex. A direct effect, older islands having more species, was more than counterbalanced by the strong indirect effects of age on area and altitude: older islands are smaller and lower, and smaller, lower islands had fewer species. Distance of an island from a source of colonization was of minor importance. Species richness thus appears to be related almost exclusively to evolutionary radiation in situ and not to an equilibrium between immigration and extinction. Islands need not be extremely isolated for evolutionary radiation to be more important than immigration/extinction dynamics in determining species richness, but isolation is a relative term dependent on the dispersal abilities of the organisms in question. Numbers of recorded species were also strongly correlated with collecting effort on each island, a result that stands as a warning to others involved in such studies. Numbers of species in different families were not evenly distributed across islands. Notably, Kauai had more amastrids and heliciniids and fewer achatinellids than predicted; Oahu had more amastrids but fewer pupillids and succineids than predicted; Hawaii exhibited the opposite pattern from Oahu. These patterns may partly reflect the vagaries of collecting/describing effort, but some may be due to the combined effects of historical factors and competitive exclusion. The distribution of shell height/diameter was bimodal with a distinct absence of more or less equidimensional species, a general pattern seen in other faunas. Among the pulmonates, tall species predominated, suggesting a relative lack of opportunity for globular/flat species. Notably, amastrids occurred in both modes, evidence that, at least in part, ecological not taxonomic factors underlie the bimodality. The proportions of tall and globular/flat species did not vary among islands. Prosobranchs were mostly low-spined but generally less flat than the pulmonates in the low-spined mode. The islands were probably colonized originally by small taxa. Large, tall shells are found only on Kauai and Niihau, the oldest of the main islands, suggesting that opportunities for such species are probably available on other islands.

Key words.—Biogeography, dispersal, islands, path analysis, species-area relationships, vicariance.

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Islands have always been important in evolutionary biology (Williamson 1983; Cain 1984), but the theory of island biogeography developed by MacArthur and Wilson (1963, 1967) to explain the numbers of species on islands has been of especially seminal significance. The theory has been invoked to account for both ecological and historical patterns (Rosen 1988), but its mathematics ignores vicariance and phylogenetic relatedness and depends fundamentally on dispersal from a center (or centers) of origin to account for variation in species richness. Although intra-island evolution was not included in the mathematics (Williamson 1981; Rosenzweig 1995), evolutionary radiation was acknowledged as important in some situations (see also Wilson 1969). Although the theory has been criticized heavily (e.g., Simberloff 1976; Gilbert 1980), it has led to considerable achievements (Schoener 1988) and remains of heuristic value for the study of island biotas (e.g., Ricklefs and Schluter 1993; Rosenzweig 1995).

The MacArthur and Wilson theory predicts an equilibrium between immigration and extinction that depends on island area and distance from a presumed source of immigrants. Although centers of origin have been heavily criticized by vicariant biogeographers (e.g., Croizat et al. 1974), dispersal from one or more source areas is probably the predominant mode of origin of Pacific island biotas (Vagvolgyi 1975; Kay 1980; Thornton 1983).

The myriad islands of the tropical Pacific have assumed special significance in evolutionary biology. Classic examples of evolutionary radiation include Hawaiian honeycreepers (Freed et al. 1987), Galápagos finches (Grant 1986), Hawaiian Drosophilidae (e.g., Carson 1987; Tompkins et al. 1993), and Society Island land snails (Cowie 1992; Johnson et al. 1993).

The extensive basic knowledge of Pacific island snails, albeit incomplete, provides a unique opportunity for approaching unanswered questions about patterns of distribution. Preliminary analyses, following the MacArthur and Wilson theory, were attempted by Peake (1969, 1978, 1981) for the land snails of Melanesia, and Solem (1973, 1983) for selected families and islands of Micronesia and Polynesia. Chambers (1991), using multivariate statistics, analyzed the distributions of Galápagos land snails. The Hawaiian fauna has not been analyzed from this perspective yet offers many advantages. It is one of the most speciose in the world for its area (cf. Solem 1984) and is probably the best documented land-snail fauna of a major Pacific archipelago. Sadly, much of the fauna is now extinct (Hadfield 1986; Solem 1990). Nonetheless, the fauna may still help answer a number of general questions about island systems. How important is isolation? What process predominates in generating the immense diversity of Pacific island biotas; the immigration/extinction dynamics of the equilibrium theory, or in situ ra-

diation? Received wisdom suggests the latter, but to what extent?

Using a nomenclatural catalog of all described native land-snail species (Cowie et al. 1995a), I analyzed patterns of species richness in the Hawaiian archipelago in relation to island area, maximum altitude, age, distance from possible sources of colonizers, and habitat diversity. In addition, I incorporated the effect of differential collecting effort on the different islands, as a possible reflection of systematic study of the faunas. I used path analysis (Sokal and Rohlf 1981; Cohen and Cohen 1983), a relatively rarely used but potentially powerful statistical tool, to explore the contributions of these factors.

Because of what appears to have been extensive in situ radiation, the Hawaiian fauna also offers a valuable opportunity to test ideas about shell-shape evolution in land snails. The fauna contains a large number of species; many are extremely small, but some are large; shell shape ranges from tall, thin forms to flat, discoidal forms; Hawaiian habitats are diverse, ranging from xeric scrubland to tropical rain forest to high-altitude aeolian habitats; and prosobranchs, as well as pulmonates, are well represented. (I retain the term prosobranchs, for convenience, while acknowledging the paraphyletic status of Prosobranchia; cf. Bieler 1992).

Following the approach established by Cain (1977), I examined shell shape variation using the spire index (the ratio of shell height to shell diameter, or width). The spire index in faunas of free-crawling, pulmonate land snails that can retract the body fully into the shell is not randomly distributed. In many faunas, it exhibits a bimodal distribution, with most, if not all species falling into a tall, thin mode or a subglobular to flat mode (Cain 1977, 1980, 1983 and references therein; Heller 1987; Cameron and Cook 1989; Roth 1991). Terrestrial prosobranchs in most, but not all faunas also exhibit the bimodality (Cain 1978, 1983). Is this non-random pattern, exhibited by both prosobranchs and pulmonates, related to phylogeny, or does it signal the existence of two rather different functional roles? Field observations and laboratory experiments (Cain and Cowie 1978; Cameron and Cook 1989 and references therein) have suggested functional explanations, including different microhabitat preferences for snails with shells of different size and shape (see also Cain 1983). Exceptions exist (Cain 1983; Solem and Climo 1985); although many factors no doubt play a role, the very general bimodal distribution of shell shape begs a simple and general explanation.

MATERIALS AND METHODS

The Hawaiian Islands

The Hawaiian islands derive from volcanic activity associated with an approximately stationary hot spot under the Pacific plate (Clague and Dalrymple 1987). As the plate moves northwestward, islands are formed consecutively, resulting in a chain running from the oldest islands in the northwest to the youngest, over the hot spot, in the southeast. As the plate moves, the older, northwestern islands are gradually eroded and submerged, eventually being subducted under or accreted onto the adjacent plate.

This study considers the entire Hawaiian archipelago,

which spans a distance of approximately 2500 km. The chain is broken into two groups: the Northwestern Hawaiian islands, running from the oldest, Kure, in the northwest, to Nihoa; and the eight main Hawaiian islands, from the oldest, Niihau and Kauai, through Oahu, Molokai, Maui, Lanai, and Kahoolawe, to the youngest island in the southeast, the island of Hawaii itself.

Land-Snail Species Richness by Island

Data on the distributions of native land-snail species by island were obtained from the catalog of Cowie et al. (1995a), which lists all species-group names that have been applied to the native Hawaiian fauna. It provides distribution data for all nomenclaturally valid species currently accepted (according to the latest revisionary works). Only these nomenclaturally valid species were considered here, except when a subspecies other than the nominate was the only representative of that species on a particular island. The supralittoral Ellobiidae were excluded as being essentially associated with the marine environment. Also excluded were taxa of unknown systematic placement and species that may not be Hawaiian (explained in Cowie et al. 1995a).

Although the Hawaiian fauna is the best known of a major Pacific archipelago, two general taxonomic problems remain (Solem 1990). First, species concepts change. Especially in groups exhibiting great variation in color pattern and shell morphology, early conchologists tended to describe almost every minor variety as a species. Subsequent revisions have in some cases greatly reduced these numbers. For instance, the genus *Achatinella* probably comprises but 12 to 16 species (USFWS 1993), yet a staggering 314 names have been used in it, 39 of which remain nomenclaturally valid species (Cowie et al. 1995a). In addition, although all but two to four of the native land-snail species (plus a number of Ellobiidae) are endemic to the archipelago as a whole, single-island endemism was often assumed, and although it is clearly the dominant pattern, this bias may also have inflated numbers. Second, many species probably remain undescribed. For instance, Solem (1973, 1976, 1990) believed about 200 species of Endodontidae occurred in the Hawaiian islands, but only 41 names have been proposed, of which 34 represent species considered valid (Cowie et al. 1995a). These two examples (*Achatinella* and Endodontidae) are probably extreme but illustrate the limitations of the Cowie et al. (1995a) catalog. Nonetheless, it is the most complete synopsis of the fauna available. Given that the two above problems will tend to work in opposite directions, and given that I was looking for general patterns, I used the catalog data, without modification.

Certain species are known only as "fossils" or "subfossils." Use of these terms in the early systematic literature for Hawaii was vague and frequently based simply on the species having been found only as dead, bleached shells. Human-induced extinctions probably have been occurring since arrival of the first Polynesians (Hadfield 1986), but many of these "fossil/subfossil" species may have become extinct since the arrival of Europeans in 1778. Because the time since these extinctions seems short relative to probable land-snail speciation rates, few if any of the "fossil" and

“subfossil” species can be discounted as not belonging to the recent fauna. All are included in this analysis.

The total numbers of species on each island were analyzed in relation to island area, maximum altitude, age, distance from the nearest older island (or seamount in the case of Kure, the northwesternmost island), and habitat diversity. Island areas and maximum altitudes were obtained from Armstrong (1983, p. 218) and island ages from Clague and Dalrymple (1987, table 1.4, fig. 1.5). Distance to the nearest older island was measured on appropriate maps. The number of native plant communities on each island (from Gagné and Cuddihy 1990) was used as an index of habitat diversity. The number of communities currently extant may be fewer than occurred naturally because of habitat destruction and modification by human activities, but Gagné and Cuddihy (1990) attempted to include all components of the flora predating Polynesian arrival, and their account is the best available (see also Athens et al. 1992). In addition to these natural variables, the effort of taxonomists in collecting and describing species may not have been evenly spread across the archipelago (cf. Connor and Simberloff 1978; Chambers 1991; Lewinsohn 1991). An index of this possible differential effort was obtained from the Bishop Museum (Honolulu) malacology collection catalog ledgers by recording the island from which the first lot on every tenth page was collected (total 261 lots). The number of counts for each island was used as an index of collecting effort, with the supposition that this may also roughly reflect taxonomic effort.

The proportions of species in each family on each of the eight main Hawaiian islands were compared with the proportions in the overall land-snail fauna.

Statistical Analysis of Species Richness by Island

Overall Species Richness.—The untransformed data for all variables (except distance to the nearest older island) departed significantly from normality. Log transformation (using $\log(x + 1)$ for collecting effort because of zero values) normalized all variables except collecting effort (Kolmogorov-Smirnov-Lilliefors tests (Vaudor 1991): $P > 0.05$ in all cases except collecting effort for which $P = 0.012$). Although the biological justification for log transformation is not clear (Connor and McCoy 1979; Abbott 1983), all analyses were performed on the transformed data. This approach follows Connor and McCoy (1979) who recommended selecting the model that provides the best fit to a linear regression (see also Williamson 1988).

Although often used to explore the association of species numbers with other variables, multiple regression was inappropriate because the present variables were strongly intercorrelated (see, e.g., Connor and Simberloff 1978; Kleinbaum et al. 1988; Rosenzweig 1995). Therefore, as a preliminary analysis, separate bivariate regressions of number of species on each of the other variables were calculated. Model I regressions are more generally used but may be less appropriate in species-area and similar studies as measurement error in all variables is uncontrolled (Connor and McCoy 1979; Williamson 1988). This issue is complex (McArdle 1988; Blackburn et al. 1993 and references therein); thus, both ordinary model I least-squares (OLS) regressions and

model II reduced-major-axis (RMA) regressions (Sokal and Rohlf 1981) were computed to allow comparison with other studies.

The bivariate regressions could not indicate the relative contribution of each variable to variation in species numbers. To address this, path analysis (Sokal and Rohlf 1981; Cohen and Cohen 1983; and see Kohn and Walsh 1994 and references therein) was performed using the program of Vaudor (1991). Path analysis involves establishment of a hypothetical model of causalities among variables. It then provides path coefficients, which indicate the relative importance of the various interactions originally introduced in the model. It distinguishes direct and indirect effects of the predictor variables on the criterion variables (terminology after Sokal and Rohlf 1981). Path analysis offers a major advantage over multiple regression because it sets up and tests a hypothesis of interactions rather than simply describing patterns. However, the outcome of the analysis depends heavily on the design of the model. Hence, the rationale and hypothesized causal interactions behind a particular model must be carefully considered.

Each variable was assumed to have a direct causal effect on land-snail species numbers. Some variables were also considered to have indirect effects. For instance, area, per se, may have a direct effect, but it may also have a more, or less, important indirect effect via habitat diversity.

Direct Effects.—1. Island age. Younger islands may not have received their full complement of colonizing species and/or the colonizing species may not have fully radiated.

2. Island area. Larger islands will offer more opportunities for chance fragmentation of populations to lead to evolution of new taxa by allopatric or peripatric speciation, unrelated to other variables such as habitat diversity.

3. Island altitude. Altitude, per se, may not have a direct influence but as a measure of climatic, particularly temperature, range it may have an indirect effect (cf. Williamson 1988). Altitude, as an indicator of climatic range, was therefore considered in the present model to have a direct influence on numbers of snail species.

4. Distance to the nearest older island. This was used as a crude measure of distance from a source of colonization. If the numbers of species follow a MacArthur and Wilson (1967) immigration/extinction-equilibrium model, islands further from a source will have fewer species.

5. Number of plant communities. This was used as a measure of biological habitat diversity.

6. Collecting effort. Greater effort in collecting and taxonomic study of the fauna of certain islands will lead to description of more species from those islands. Because this study was constrained to use numbers of described species (considered the best approximations of the real numbers, which could not be determined), collecting effort (assumed to parallel taxonomic effort) will have a direct influence on numbers.

Indirect Effects.—1. Island age influences island area. Older islands are more eroded and hence smaller than younger islands.

2. Island age influences island altitude. Older islands are more eroded and hence lower than younger islands.

3. Island age influences number of plant communities. By

TABLE 1. Numbers of native, valid land-snail species on the Hawaiian Islands, excluding Ellobiidae, taxa of unknown systematic placement, and taxa that may not, in fact, be Hawaiian (data from Cowie et al. 1995). Records for the Northwestern Hawaiian Islands (NWHI) are combined. Main island abbreviations are Niihau, N; Kauai, K; Oahu, O; Molokai, Mo; Maui, M; Lanai, L; Kahoolawe, Kah; Hawaii, H. Species not definitively recorded from a particular island, only from the archipelago as a whole, are listed in the column "Not located." Total number is the combined number of species per island; this exceeds the number of species in the fauna as a whole (in parentheses) because some species occurred on more than one island. The percent endemic is the percent of the fauna of that island that is endemic to that island.

	NWHI	Main Hawaiian Islands								Not located	Total	% of total
		N	K	O	Mo	M	L	Kah	H			
Hydrocenidae			2								2 (2)	0.2 (0.3)
Helicinidae		2	9	5	2	2	1	1	2		24 (14)	2.7 (1.9)
Achatinellidae	4	2	11	92	42	59	10	3	30	4	257 (209)	28.6 (27.8)
Amastriidae		1	56	118	42	54	21	1	24	14	331 (325)	36.9 (43.2)
Pupillidae		1	11	24	16	16	10	3	27		108 (56)	12.0 (7.4)
Endodontidae	2		8	9	4	4	3		5	1	36 (33)	4.0 (4.4)
Punctidae				1					1		2 (1)	0.2 (0.1)
Succineidae			6	7	4	7	2		21	3	50 (42)	5.6 (5.6)
Helicarionidae			10	25	7	9	5	2	13		71 (60)	7.9 (8.0)
Zonitidae			5	1	2	3	2		3		16 (10)	1.8 (1.3)
Total	6	6	118	282	119	154	54	10	126	22	898 (752)	
% endemic	83.3	33.3	82.2	86.9	63.9	75.3	57.4	10.0	73.8			

allowing longer time for colonization and radiation, island age will influence plant diversity and hence number of plant communities.

4. Island area influences number of plant communities. Very small islands will have predominantly maritime communities, but the interior of larger islands will be less affected by oceanic influences, allowing the development of other communities.

5. Island altitude influences number of plant communities. Again, altitude is an indicator of climatic range. The plant community classification used here (Gagné and Cuddihy 1990) explicitly categorizes communities on the basis, among other things, of altitude.

6. Distance to nearest older island influences number of plant communities. Just as distance to the nearest older island is hypothesized to influence land-snail species richness, so will it influence plant diversity and hence complexity and number of plant communities.

7. Maximum altitude influences collecting effort. High altitude parts of the islands are difficult to access; thus, collecting effort will have been disproportionately less on higher islands.

Within-Family Species Richness.—The island-by-island distributions of species richness within families were tested against the overall distribution of species in the fauna using log-likelihood *G*-statistic analyses, with Williams' correction (Sokal and Rohlf 1981). The Northwestern Hawaiian islands and the islands of Niihau and Kahoolawe were ignored as having too few species. To obtain high enough expected values, the following families were combined: Endodontidae and Punctidae ("endodontoids"), Helicarionidae and Zonitidae ("zonitoids"), and Hydrocenidae and Helicinidae (proso-branches).

Shell-Shape Variation

As in the analysis of species distribution patterns, some taxa were excluded: Ellobiidae, taxa that may not be Hawaiian, and taxa of unknown systematic placement. Follow-

ing Cain (1977 and other references in Cain 1983), but contrary to Cain (1980), Succineidae (42 species) were also excluded because for at least some Hawaiian species, as elsewhere, the body is not fully retractable into the shell, and they must be considered semislugs. Exclusion of Succineidae was adopted for comparability with earlier studies (see references in Cain 1983) and had no major influence on the general patterns detected. No slugs are native to the Hawaiian islands.

For every currently accepted valid species, values of *h* (shell height) and *d* (shell diameter or width) were obtained, from the original descriptions (cited by Cowie et al. 1995a) where possible, or from subsequent treatments in the Manual of Conchology, Solem (1976), and other revisionary works if necessary. The data and sources are held by the author. Although different authors may not have measured *h* and *d* in exactly the same manner (e.g., maximum diameter or diameter perpendicular to the columella), the variation is small relative to the differences among species.

RESULTS

Overall Species Richness and Species-Area Relationships

Valid species in the native Hawaiian land-snail fauna, according to the latest taxonomic revisions, numbered 752 (table 1), excluding Ellobiidae (10 species) and taxa whose systematic placement is unknown and/or whose native status is questionable (17 species). These represented 10 families (as classified by Cowie et al. 1995a). Only 2 to 4 of these 752 species were considered native but not endemic to the archipelago; and most occurred on only one island (table 1). Islands from which no land snails have been recorded are not listed in table 1 and were excluded from the analyses.

All the variables (table 2) were intercorrelated, except distance to the nearest older island, which was correlated only with island age (table 3). Number of species was strongly correlated with five of the six variables (table 4, fig. 1). Together, these variables explained 99.0% of the variance in

TABLE 2. Area, maximum altitude, age, distance to the nearest older island, number of plant communities, collecting effort, and total number of species for each of the Hawaiian Islands known to harbor land snails. Derivation of the data is explained in the text.

Island	Area (km ²)	Maximum altitude (m)	Age (myr)	Distance to nearest older island (km)	Number of plant communities	Collecting effort	Number of snail species
Northwestern Hawaiian Islands							
Kure	1.0	6	29.1*	72	1	0	1
Midway	5.2	4	27.7	96	2	0	2
Lisianski	1.7	6	23.5*	278	4	1	1
Laysan	4.0	11	19.9	223	4	0	2
Necker	0.2	84	10.3	147	2	0	1
Nihoa	0.8	277	7.2	284	6	0	2
Main Hawaiian Islands							
Niihau	189	390	4.9	218	8	1	6
Kauai	1433	1598	5.1	248	36	19	118
Oahu	1574	1225	3.7	116	42	178	282
Molokai	676	1515	1.9	43	40	22	117
Maui	1888	3055	1.3	14	55	18	154
Lanai	361	1027	1.3	14	27	5	54
Kahoolawe	117	450	1.0	29	13	1	10
Hawaii	10,458	4205	0.4	48	56	16	126

* Estimated values from the least-squares cubic fit line of Clague and Dalrymple (1987, fig. 1.5).

species numbers (table 5). Of this, 35.7% was explained causally by the direct and indirect effects of the variables in the path-analysis model (fig. 2, table 5), whereas the remaining 63.3% was due to noncausal components resulting from correlation among variables and from common causality of variables (cf. Cohen and Cohen 1983; Schemske and Horvitz 1988; Lewinsohn 1991).

Adequate significance tests in path analysis, particularly for indirect coefficients, are unavailable or difficult to interpret (Cohen and Cohen 1983; Lewinsohn 1991). The following therefore focuses on the relative magnitude rather than significance of the coefficients.

Area, altitude, and collecting effort all had significant positive direct effects, of similar magnitude, on numbers of snail species (table 5). In addition, area and altitude had indirect effects on numbers of species through their large direct effects (significant in the case of area) on number of plant communities. Island age had a positive direct effect on species richness (older islands had more species) but a much greater negative indirect effect through its effects on island area and altitude (lower and smaller islands had fewer species). Hence, the overall effect of island age was negative: older islands had fewer species. The number of plant communities (introduced into the model as an index of habitat diversity) made a smaller positive contribution (direct only).

Distance to the nearest older island had a negative direct effect and a very small indirect effect but, because of its low correlation with numbers of snail species, explained only a very small amount of the overall variance.

Given the data available, the path-analysis model used (fig. 2) seemed the most logical. However, because the outcome of path analysis is sensitive to the constraints established in the model, a number of modified models were tested. One model excluded distance to the nearest older island, the variable with the lowest path coefficients (table 5). This modified model explained less of the overall variance in land-snail species numbers. In addition, a number of models were tested using all the variables but excluding certain paths (e.g., altitude to collecting effort) or including additional paths (e.g., collecting effort to number of plant communities), but none increased the overall variance in snail species numbers explained. The model in figure 2 is therefore considered robust, under the constraints of the data set available.

Because the number of data points were few, the above strong correlations may have been overinfluenced by a concentration of points for very small, low islands with very few species, essentially all the Northwestern Hawaiian islands. In addition, areas of high altitude, aeolian habitats with virtually no vegetation on the islands of Hawaii and Maui seemed unsuitable for snails. All land above the somewhat

TABLE 3. Product moment correlation coefficients between log-transformed variables.

	Area	Maximum altitude	Age	Distance to nearest older island	No. of plant communities	Collecting effort
Maximum altitude	0.820***					
Age	-0.802***	-0.898***				
Distance to nearest older island	-0.490	-0.445	0.659**			
No. of plant communities	0.925***	0.912***	-0.846***	-0.457		
Collecting effort	0.830***	0.734**	0.581*	-0.311	0.859***	
No. of snail species	0.943***	0.867***	-0.770**	-0.499	0.956***	0.932***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 4. Regression statistics for ordinary least-squares (OLS) and reduced-major-axis (RMA) regressions of number of species on each variable (see fig. 1). Because the OLS regression of number of species with distance to nearest older island was not significant, the RMA regression was not calculated (cf. McArdle 1988). Statistical significances are not presented for RMA regressions because of the difficulty or impossibility of calculating and interpreting them (McArdle 1988; and cf. Blackburn et al. 1993).

Variable	OLS			RMA	
	Intercept	Slope (z)	F	Intercept	Slope (z)
Area	0.082	0.586***	95.607***	-0.021	0.622
Altitude	-0.679	0.766***	36.367***	-0.951	0.883
Age	1.933***	-1.236**	17.453**	2.221	-1.606
No. of plant communities	-0.463*	1.523***	127.409***	-0.535	1.593
Collecting effort	0.285	1.242***	78.775***	0.226	1.333
Distance to nearest older island	3.098*	-1.035	0.070	—	—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

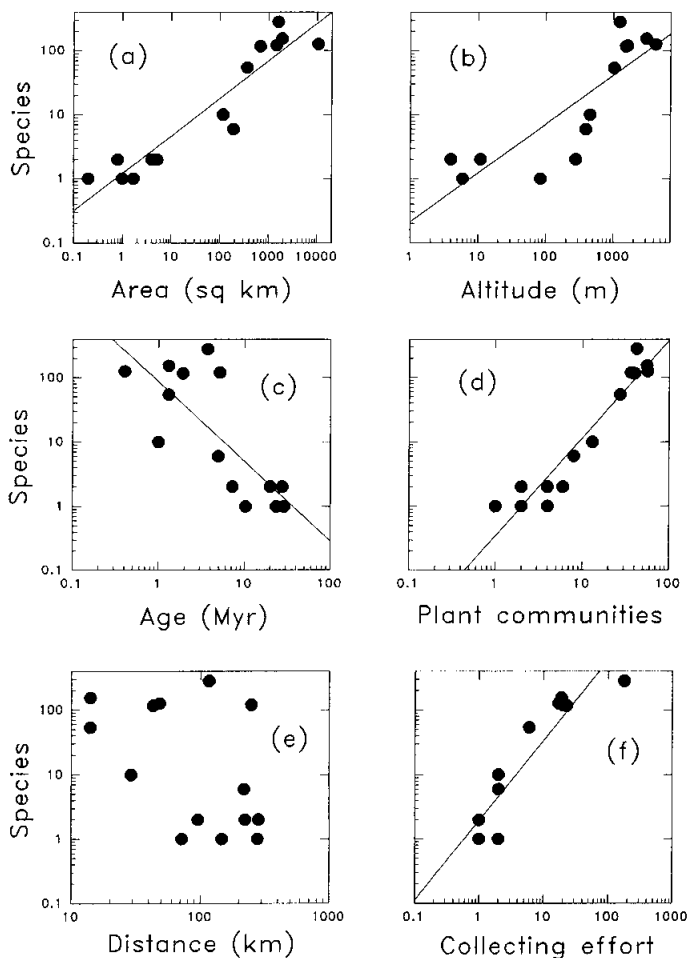


FIG. 1. Log-log plots of numbers of species of land snails on the Hawaiian Islands (all islands on which snails have been recorded) against (a) island area, (b) maximum island altitude, (c) island age, (d) number of plant communities, (e) distance to the nearest older island, and (f) collecting effort (plus one because of zero values in the raw data; see text for explanation of units). The OLS regression lines (see table 4) are drawn in, except that for distance to the nearest older island, which is not significant. (Some points are coincident in [a] and [f]).

arbitrary contour of 2800 m was therefore excluded; thus, reducing the area of Hawaii to 9797 km² and that of Maui to 1881 km². The area of Hawaii was further reduced to 9169 km² to account for the large areas of barren lava. These adjusted data, and an analysis restricted to only the eight main islands, led to similar correlations among the variables, although the significance of most was reduced (presumably largely because of the reduced number of data points) and island age was no longer correlated with either number of snail species or number of plant communities. With seven variables but only eight data points, path analysis was precluded.

Partitioning of Species Richness among Families and Islands

If species were distributed randomly among islands, the proportions of species in each family on individual islands should be the same as for the archipelago as a whole. *G*-statistic analysis of the data in table 1, ignoring islands with ten or fewer species, and after combining families into seven groups (see Materials and Methods), indicated significant overall heterogeneity ($G = 112.60$, $df = 30$, $P < 0.001$). When each family or group of families was treated separately, significant departures from the expected distributions were observed for five out of seven (Achatinellidae, $G = 29.86$, $P < 0.001$; Amastridae, $G = 18.06$, $P < 0.005$; Pupillidae, $G = 13.68$, $P < 0.025$; "endodontoids," $G = 3.23$, not significant; Succineidae, $G = 25.43$, $P < 0.001$; "zonitoids," $G = 3.59$, not significant; prosobranchs, $G = 16.79$, $P < 0.005$; $df = 5$ in all cases). The major contributions to this heterogeneity included a relative paucity of Achatinellidae on Kauai, of Amastridae on Hawaii, and of Pupillidae and perhaps Succineidae on Oahu; and a relative abundance of Achatinellidae on Maui, of Amastridae on Kauai and Oahu, of Pupillidae and Succineidae on Hawaii, and of prosobranchs on Kauai.

Shell-Shape Variation

Shell-shape variation in both pulmonates and prosobranchs, exhibited a bimodal distribution, as seen in other faunas (fig. 3). High-spired species predominated and the relatively fewer low-spired species were all small. The proportions of high-spired and low-spired species on each of the

TABLE 5. Path analysis of numbers of species according to the model in figure 2. The program used for this analysis (Vaudor 1991) gives probabilities for only the correlation coefficients (r) and the path coefficients (p). Statistical significance in path analysis is not well understood (see text).

Criterion	Variables	Predictor	Coefficients			Determination		
			Correlation (r)	Direct (p)	Indirect (i)	Effect (e)	Effect ($e \times p$)	Total ($r \times p$)
No. of snail species		Area	0.943***	0.335*	0.143	0.478	0.160	0.316
		Altitude	0.867***	0.311*	0.128	0.439	0.137	0.270
		Age	-0.770**	0.301	-0.769	-0.468	-0.141	-0.232
		No. of plant communities	0.956***	0.259	0	0.259	0.067	0.248
		Collecting effort	0.932***	0.323*	0	0.323	0.104	0.301
		Nearest older island	-0.499	-0.176*	0.003	-0.173	0.030	0.088
							Total R^2	0.357
No. of plant communities		Area	0.925***	0.551**	0	0.551	0.304	0.510
		Altitude	0.912***	0.492	0	0.492	0.242	0.449
		Age	-0.846***	0.029	-0.883	-0.854	-0.025	-0.025
		Nearest older island	-0.457	0.012	0	0.012	0.000	-0.005
							Total R^2	0.521
Area	Age	-0.802***	-0.802***	0	-0.802	0.643	0.643	
Altitude	Age	-0.898***	-0.898***	0	-0.898	0.806	0.806	
Collecting effort	Altitude	0.734**	0.734**	0	0.734	0.539	0.539	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

eight main islands were not quite significantly heterogeneous ($G = 13.81$, $df = 7$; for $\alpha = 0.05$, $G = 14.07$).

Pulmonates.—The high-spired mode ($h > d$) was composed of Achatinellidae, Amastridae, and Pupillidae. Considering the fauna of the archipelago as a whole, the h/d distributions of these families overlapped extensively (fig. 3). Pupillidae were the smallest taxa but overlapped the smallest Achatinellidae, and the Achatinellidae as a whole overlapped broadly with the Amastridae. The highest concentration (in h/d space) of amastrids fell in the middle of the achatinellid distribution, an area relatively sparsely occupied by achatinellids. Particularly notable was the almost complete lack of overlap of any group with the amastrid genus *Carelia* (fig. 3). Considering each island separately (fig. 4), the faunas of Oahu, Molokai, Maui, Lanai, and Hawaii all exhibited the same overall pattern, although Lanai had rather few large and mid-sized achatinellids. Kauai lacked large and midsized achatinellids (no Achatinellinae or *Au-*

riculella), this part of the high-spired mode being occupied solely by amastrids. In addition on Kauai, small achatinellids hardly overlapped at all with the pupillids, and the large end of the scatter was extended by the virtually endemic *Carelia* (one other *Carelia* species on Niihau). The distinction between the two spire index modes was less clear on Kauai than on the other islands, although this may have been related to the relatively larger number of prosobranchs on Kauai (see below). Niihau, Kahoolawe, and the Northwestern Hawaiian Islands had too few species to detect trends.

Three groups occupied the low-spired mode and overlapped extensively: Amastridae with $h < d$, "endodontoids" and "zonitoids." The Amastridae were notable because (1) they occurred in both modes, and (2) a number of them fell between the modes. However, amastrids with $h < d$ were represented strongly only on Oahu, where they tended to be flatter than the "endodontoids" and "zonitoids," although overlapping considerably. The "zonitoids" tended to be larger than the "endodontoids" (figs. 3, 4).

Prosobranchs.—Helicinid species were most numerous on Kauai and Oahu, and only on these islands, and perhaps Molokai, did the helicinids and pulmonates tend not to overlap, the former lying closer to the line of equidimensionality (fig. 4). On the other islands (Maui, Hawaii, and perhaps Lanai), the very few helicinids fell within the pulmonate distributions. The Hydrocenidae (Kauai only) were notably smaller than the Helicinidae and lay just above the line of equidimensionality (fig. 3).

DISCUSSION

The native land-snail fauna of the Hawaiian islands is predominantly ancient in origin (Solem 1983, 1990; Cowie 1992) and generally can be considered a relict fauna isolated in the Pacific and having evolved not only on the islands currently above sea level but also on islands long-ago submerged and subducted as the Pacific plate moved north-

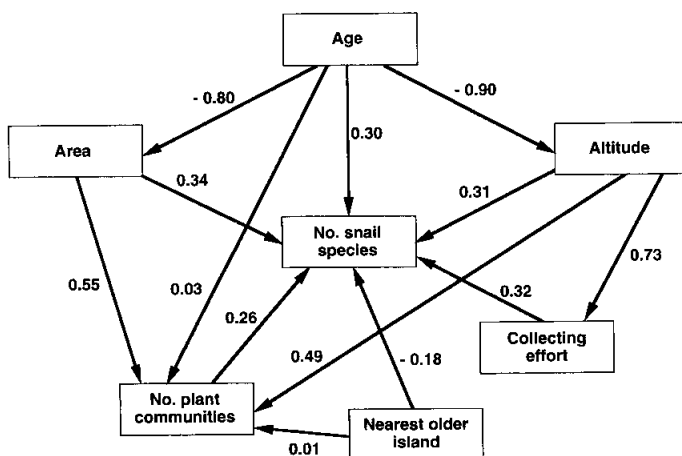


FIG. 2. The path-analysis model with values of path coefficients.

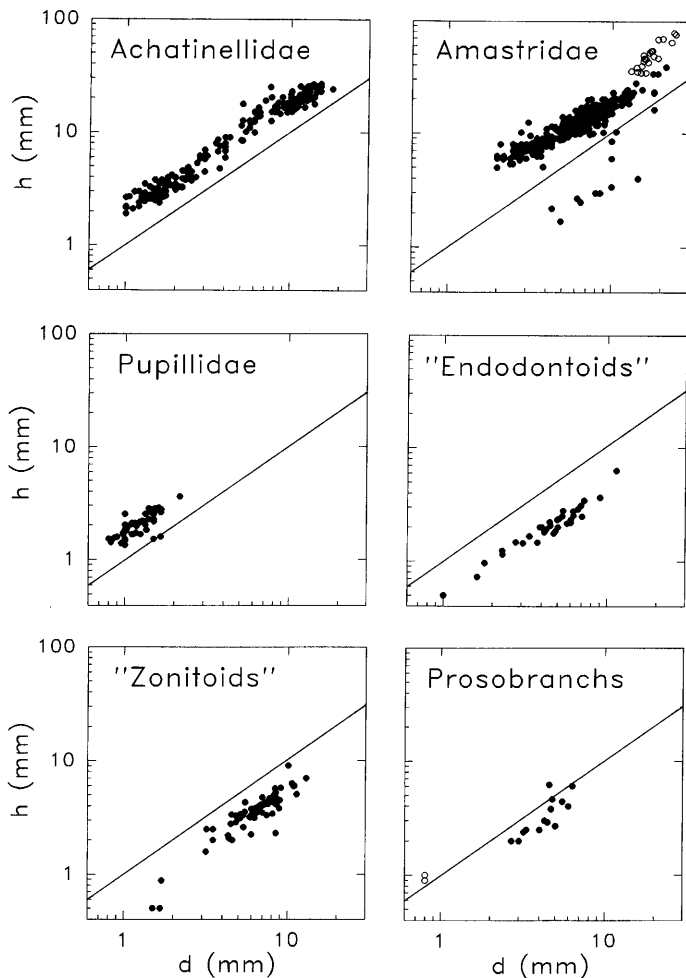


FIG. 3. The distribution of shell spire index (h/d) for the land snail families or family groups (excluding Succineidae and Ellobiidae) of the Hawaiian Islands (log scale). In the figures for Amastridae and prosobranchs, *Carelia* spp. and Hydrocenidae, respectively, are distinguished by open symbols. The diagonal line is the line of equidimensionality ($h = d$).

westward. The present fauna probably derives mainly from dispersal of progenitors along the chain from these now submerged or subducted islands followed by radiation in situ on the present islands.

Overall Species Richness

MacArthur and Wilson (1967) acknowledged that eventually speciation and radiation would occur in island biotas. They suggested that the proportion of nonendemic species would be a measure of species turnover and that the more isolated the island or archipelago the greater would be the contribution of radiation to species richness. Their mathematical model, however, focused on the immigration/extinction equilibrium and the degree of isolation from a source of immigration, essentially excluding intransland evolution as a contributor to species richness. On extremely isolated islands, the rate at which new species evolve may be considerably greater than the rate at which they arrive as new colonists (Williamson 1981); thus, species-area relationships for highly

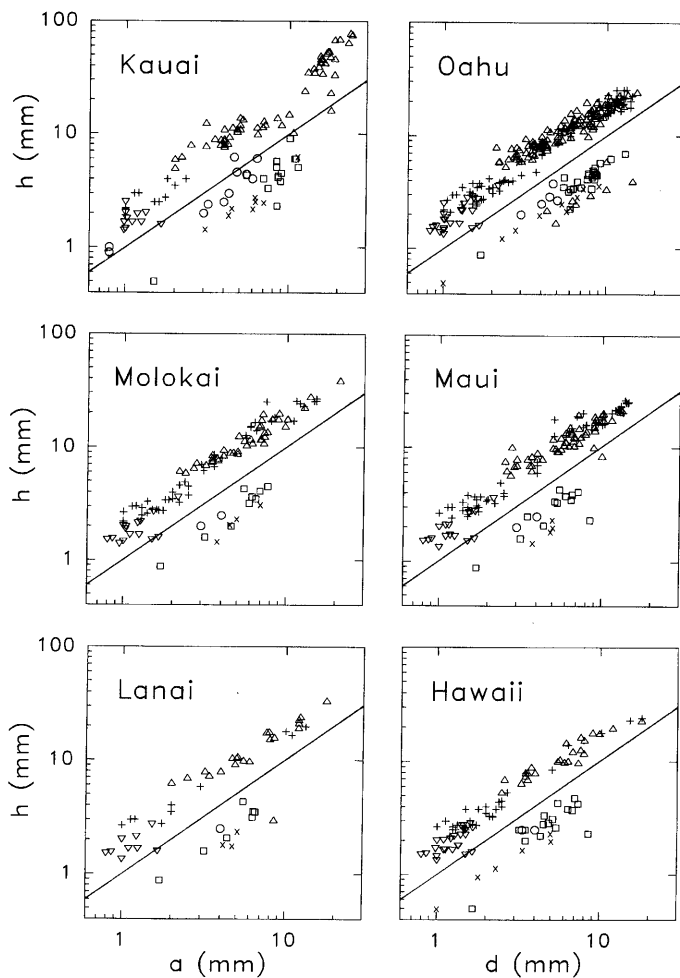


FIG. 4. The distribution of shell spire index (h/d) on each of the main Hawaiian Islands (excluding Niihau, Kahoolawe, and the Northwestern Hawaiian Islands), symbolized by family or family group (log scale). Achatinellidae, vertical/horizontal crosses; Amastridae, upward-pointing triangles; Pupillidae, downward-pointing triangles; "endodontoids," diagonal crosses; "zonitoids," squares; prosobranchs, circles. The diagonal line is the line of equidimensionality ($h = d$).

isolated archipelagos will be determined predominantly by evolution and not by the immigration/extinction equilibrium. The biota of the Hawaiian archipelago, despite its extreme isolation, is extremely species rich and exhibits high levels of endemism. Among the land snails (excluding 10 Ellobiidae), all but 2 to 4 of the 752 native species are endemic to the archipelago. Such extreme endemism indicates immense local radiation and an almost imperceptibly low turnover rate between the archipelago and its source areas, which for the land snails are unknown.

Within the archipelago, dispersal has been of greater significance, as indicated by the presence of some species on more than one island, although the majority are endemic to single islands, and by the fact that the six largest islands have representatives of all except the two least speciose families (table 1). In addition, vicariant events may have had an influence on some islands. As sea levels fluctuated during the formation of the Hawaiian archipelago, the adjacent islands

of Maui, Molokai, Lanai and Kahoolawe have at various times coalesced into a single island, "Maui-nui." Increased likelihood of allopatric, vicariant speciation might have led to a greater number of species than expected for the single Maui-nui island. Alternatively, since the total land area of the separate islands is currently much less than that of Maui-nui, and if the periods of island separation were insufficient for complete speciation such that incipient species coalesced when sea levels dropped, fewer species than expected may occur there. The hint of lower levels of single-island endemism on the islands of Maui-nui (table 1) perhaps supports this latter explanation. Although dispersal and perhaps vicariance within the archipelago have had some influence, in situ evolution on individual islands has been the main determinant of species richness.

Adaptive radiation (and hence local endemism) related to habitat diversity is assumed to increase not only with isolation but also with increasing island area (MacArthur and Wilson 1967). On extremely isolated islands, area-related habitat diversity, combined with an effect of area per se, are therefore likely to dominate determination of species richness. The path analysis confirmed this for the Hawaiian land-snail fauna. Island area, per se, had the largest direct effect on species richness and, of all the predictor variables, explained the largest proportion of the variance. Number of plant communities, as a measure of habitat diversity, made an important contribution to the variance explained, probably because it was strongly determined directly by island area. In addition, island altitude made a major contribution, perhaps because its direct effect was considered in the path analysis as an effect of climatic range, in turn an additional dimension of habitat diversity. The direct effect of island age, per se, was also important, suggesting that the islands may not be fully colonized and that the fauna has not had time to radiate fully. This may partially explain the relative paucity of species on the youngest island, the island of Hawaii, as suggested for Hawaiian Drosophilidae by Williamson (1981, p. 195). However, island age has a much greater negative indirect effect because of its strong direct influence on area and altitude. Although the path analysis indicated a small direct effect of island isolation on snail species richness, more isolated islands indeed having fewer species, the number of species on a particular island was at best weakly correlated with its distance from the nearest older island, and the proportion of the overall variance explained by this factor was small (table 5). Distance from the nearest older island was used as the measure of isolation under the probably only partially valid assumption (cf. Hawaiian Drosophilidae; Carson 1987) that most immigration would be along the developing island chain from older to younger islands. Other measures of isolation could have been used, but given the high level of single island endemism and the inferred very low turnover rate and hence minor importance of dispersal, it seems unlikely that any measure of isolation would have made an important contribution to the variance explained by the analysis.

The path analysis allowed the disentangling of natural effects on perceived species richness from the effect of collecting effort, which may parallel taxonomic effort. The major effect of collecting effort is remarkable and should stand

as an important caveat for all studies of this kind (cf. Connor and Simberloff 1978; Chambers 1991; Lewinsohn 1991). It almost certainly accounts for the disproportionately high number of species on Oahu, the island with the great majority of the human population. It may also help account for the low numbers on the island of Hawaii, which is much larger than the other islands, with major areas remaining poorly known malacologically (Cowie et al. 1995b).

Species-area relationships in Pacific island land-snail faunas have been investigated by Cooke (1928), Peake (1969, 1978, 1981), and Solem (1973, 1983), all of whom concluded that species numbers did not correlate positively with area for the isolated islands of the central Pacific. Nevertheless, Peake did demonstrate a relationship between number of species and both island area and isolation in Melanesia; and simple regression analysis of Solem's plots (Solem 1983: figs. 140, 141) would clearly indicate a positive relationship. Chambers (1991) reanalyzed unpublished data of R. P. Smith for the Galápagos land snails by multiple regression. Smith's data suggested that number of plant species and island area were the best predictors of snail species richness, but when Chambers incorporated number of collecting trips this variable made the only significant contribution to the overall regression. As indicated above, however, multiple regression is inappropriate when variables are strongly intercorrelated. Nevertheless, these studies, and the present analysis of the Hawaiian fauna, reveal fairly clear relationships between island area and land-snail species richness in Pacific islands.

The value of the slope (z) of the regression of log-log species-area relationships has been the subject of debate, but its biological significance is still not fully understood (e.g., Abbott 1983; Connor et al. 1983; Williamson 1988; Wissel and Maier 1992; Rosenzweig 1995). MacArthur and Wilson (1967), followed by Peake (1981), suggested that highly isolated archipelagos should exhibit higher z -values. Connor and McCoy (1979) thought the reverse might be the case (see also Williamson 1988) but remained skeptical about whether z -values had any biological meaning. The z -values of both the ordinary least-squares (OLS) and reduced major-axis (RMA) regressions in the present study (0.586 and 0.622, respectively; table 4) were higher than in many other studies of islands and higher than the value of about 0.26 that is, perhaps wrongly, taken as the biologically expected value (e.g., Connor and McCoy 1979; Connor et al. 1983). Williamson (1988) suggested that high values may be related to high levels of single-island endemism resulting from in-trailand radiation, as in the Hawaiian land-snail fauna. Rosenzweig (1995) took this suggestion further by arguing that regions whose biota originated mostly from in situ radiation are not islands, according to his biological definition of islands, but should be considered provinces. His examples of provinces had z -values consistently higher than those for islands. But, as he made clear, the island/province dichotomy is in reality a continuum, on which the position of a locality is measured by its z -value, which will differ among taxa. He explicitly considered the Hawaiian islands a province on the basis of the endemicity of their biota. The z -values in the present study conform with his interpretation.

Although the land-snail fauna of the Hawaiian islands is highly speciose, only 10 families are represented (table 1)

out of about 70–100 recognized worldwide. Representation of these 10 families is very uneven. Of the 752 species (table 1), 534 (71%) belong to but 2 families: the Amastridae, which are endemic to the archipelago, and the Achatinellidae, which are Pacific island endemics but have an endemic Hawaiian subfamily and a number of endemic Hawaiian genera. A further 191 species (25%) belong to only 4 other families, and the remaining 4 families are represented by only small numbers of species. In contrast, the native land-snail fauna of, for example, the much less isolated islands of Vanuatu (plus the Santa Cruz islands), although less well-known, contains only 65 species (a few perhaps introduced by pre-European human travelers), but these represent 17 families with no more than 10 species in any one family (Solem 1959). Clearly, a rather small number of initial immigrations to the Hawaiian islands were followed by immense speciation. Even within the archipelago, dispersal seems to have played a minor, although not negligible, role (see above), emphasizing the extremely limited dispersal capabilities of land snails. Clearly, isolation is a relative term dependent on the dispersal abilities of the organisms in question.

Partitioning of Species Richness by Family and Island

Although there is some heterogeneity, the general trends clearly follow the overall pattern of distribution of numbers of species in the archipelago as a whole (table 1). Over- and underrepresentation of particular families on particular islands may partly relate to the history of collecting and describing. Nonetheless, as suggested by Henshaw (1904) in an insightful footnote, the vagaries of the sequence of colonization and radiation by particular taxa may have led, at least in part, to the apparently anomalous representations of families on particular islands. Once a family became established and radiated on an island, subsequent immigrants of different families may have been excluded competitively. Thus, although present on other islands, the Succineidae, for example, might not have been able to radiate extensively because of competition with other taxa. However, if, by chance, they were one of the earliest immigrants to the island of Hawaii, they could have radiated easily in the absence of competition. This possibility remains purely speculative.

Cameron and Cook (1992) also ascribed differences in distribution of families and genera in the islands of the Madeiran archipelago in part to differing habitat preferences among the taxa. No adequate information is available for the Hawaiian fauna to address this possibility and further speculation on the apparent over- and underrepresentation of certain families on certain islands seems unjustified (but see below for the genus *Carelia* and the prosobranchs on Kauai).

Shell-Shape Variation

Variation in shell shape (fig. 3), even among very small taxa, follows the widespread bimodal pattern first noted by Cain (1977). Solem and Climo (1985) suggested that very small snails might be less constrained in *h/d* space than larger species, based on their interpretation of the spire index distribution of a new Zealand fauna as unimodal. However, although their fauna included some approximately equidimensional species, most species fell below the line of equidi-

mensionality, that is, corresponding to the low-spined mode (Solem and Climo 1985, figs. 2–4, 8). Although the relative lack of high-spined species is notable, their fauna may not be as anomalous as suggested. The Hawaiian fauna included many very small species but nonetheless conformed to the general pattern. Shell size seems not to complicate the generality of the bimodal spire index distribution.

Cain (1977, 1983 and references therein) suggested that ecological explanations might account for the bimodal pattern, with shell shape tied evolutionarily to niche characteristics. These niche characteristics remain unknown, although a few studies (Cain and Cowie 1978; Cameron and Cook 1989 and references therein) have tentatively confirmed Cain's idea that shell shape may be related to the preferred angles of inclination on which the snails crawl and that these might be related to the mechanics of carrying a shell of a certain shape. In addition, burrowing and arboreal species tend to be high-spined (Cain 1978, 1983). Further investigation of these ideas requires field observations, which for much of the Hawaiian fauna are no longer possible as the majority of species are extinct.

Cain (1977 and references in Cain 1983) also suggested that within a fauna, families tend to be mutually exclusive within each of the two modes. In the Hawaiian fauna, however, families overlap broadly in both modes and the overlap only partly disappears when islands are considered separately (fig. 4). Cain suggested that where families overlap in *h/d* space, other ecological differences may allow coexistence. Prosobranchs and pulmonates have different feeding habits (Cain 1978) and in the Hawaiian fauna overlap broadly (fig. 3). Among the pulmonates, the wide overlap of amastrids and achatinellids in *h/d* space may be permitted by the generally ground-dwelling habits of the former and arboreal habits of the latter. Among the low-spined pulmonates (amastrids with $h < d$, "endodontoids," "zonitoids"); most are ground-dwelling, with the exception of certain "zonitoids"; their food preferences are virtually unknown; different groups do tend to occupy slightly different regions of *h/d* space within each island (fig. 4). However, although shell shape may be broadly constrained to two modes by the mechanics of carrying a shell, the mechanisms by which families could evolve to partition the two modes are unclear.

Kauai appears to differ from the other main islands in a number of notable respects. The genus *Carelia* (Amastridae) includes large, high-spined snails that are larger than all but three other Hawaiian species, and there is a clear gap in the scatter (fig. 3) between these very large species and the next largest species in the $h > d$ mode. *Carelia* is a well-defined, unquestionably amastrid genus that is almost endemic to Kauai (one other species on the neighboring island of Niihau). Kauai is the oldest of the main islands and therefore has been available for colonization and evolutionary radiation for the greatest time. Assuming that colonizing species tend to be small (Peake 1969; Vagvolgyi 1975), perhaps only Kauai (and Niihau) have had sufficient time for such large species to evolve and radiate. Opportunities for a large, tall, *Carelia*-like snail are probably available on the other islands, at least the older ones, especially because of the three other large species (*Amastra hitchcocki*, *Amastra magna*, and *Kauaia knudsenii*, all amastrids), one is from Molokai and another

is from Lanai. Insufficient time may have elapsed since colonization either for the chance dispersal of *Carelia* from Kauai to the other islands, or for the evolution and radiation of similar large, tall taxa in situ. If *Carelia* is removed from the analysis of amastrid distribution by island, the observed number of amastrids remaining on Kauai (36) is close to the predicted number (35.4). Cameron and Cook (1989) suggested a similar explanation for deficiencies in the Madeiran land-snail fauna, involving vacant niches and insufficient time for radiation.

Kauai is also the only island to lack large and midsized Achatinellidae, and the large end of the $h > d$ mode is occupied only by Amastridae. Because Kauai is the oldest main island, the absence of Achatinellinae and *Auriculella* is an anomaly that has long provoked comment but that has not been resolved (Pilsbry and Cooke 1912–1914; Zimmerman 1948). The family Achatinellidae is ancient, pre-dating by far the present main Hawaiian Islands, but the subfamily Achatinellinae and the genus *Auriculella* may have evolved more recently, perhaps on the Maui-nui complex (Zimmerman 1948). Their absence from Kauai may be a purely historical accident due to the vagaries of dispersal, or they may have been excluded by the more numerous amastrids.

In addition, the h/d distribution on Kauai appears less clearly bimodal than on the other islands (fig. 4). Although a small number of amastrids lie close to the line of equidimensionality, this lack of clear bimodality seems to be due to the presence of prosobranchs (helicinids and hydrocenids). Prosobranch species richness increased roughly with increasing island age (table 1), and the high number on Kauai may simply relate to the greater time that has been available for speciation on that island. The presence of hydrocenids only on Kauai, despite their frequent occurrence elsewhere in the Pacific, is unexplained.

Most land-snail families are confined to one or other of the two h/d modes. The presumed adaptive trough between the two modes may well be difficult to cross, but, as Cain (1977) argued, enough families contain species in both modes to show that this is not impossible. The Amastridae, which are endemic to the Hawaiian islands and which seem to have radiated entirely within the archipelago, are one of the best examples of a well-defined family with representatives in both modes. In addition, some amastrids fall between the modes. An ecological explanation, at least in part, for the very general bimodal distribution of land-snail shell shape seems inescapable.

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