MULTIVARIATE ANALYSIS OF DESERT SNAIL DISTRIBUTION IN AN ARIZONA CANYON

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ABSTRACT

Multiple discriminant analysis and principal component analysis were found quite useful in interpreting distributions of two land snails in a desert canyon in Arizona. Snail presence and abundance in small, arbitrarily chosen sites can be accurately predicted from five environmental variables: elevation, slope angle, slope aspect, percent vegetational cover, and substrate type. Though correlation among the environmental variables was high, vegetational cover was found to account for most of the variance in snail presence. Independent of vegetation, slope aspect, slope angle, and elevation were not demonstrated to affect the presence of snails. The two snail species commonly found living in the canyon, Discus cronkhitei and Sonorella baboquivarlensis cossi, differ significantly in their preference of slope angle and substrate. It is suggested that Sonorella was found more commonly on steep rocky slopes because it requires rocks for shelter. Discus, a much smaller snail, can find adequate shelter in loosely packed humus and thus inhabits shallower slopes where humus accumulates.

INTRODUCTION

Boycott (1934) suggested that the major factors influencing habitat selection by land snails are shelter (protection from desiccation and predation) and availability of lime. More recent work has emphasized a third important consideration, food availability. There is evidence of correlation between snail abundance and both the amount of calcium and organic matter in soil samples (Burch, 1955). In the western U.S.A., many land snails are more often found associated with certain deciduous trees than with pines or grasses, implying that the litter from deciduous trees serves as food (Karlin, 1961). Grime & Blythe (1969) found two species of snails inhabiting opposite slopes of the same pass and feeding on different plants, but they suggested that climatic rather than vegetational differences were responsible for the separation. Differences in the sites of activity of several land snails have been interpreted as adaptations facilitating coexistence (Cameron, 1978).

Perhaps the major difficulty in all of these studies has been that of dealing with environmental variables often unmeasured or correlated with each other. Cover, moisture, food, lime, competition and predation are surely only a few of the factors potentially influencing the local distribution of land snail populations.

In this investigation I examine the abundance of individuals of two snail species in quadrat samples from a canyon in southern Arizona. Since rainfall is quite low in the area, measures reflecting cover, moisture, and temperature should account for a large part of the variance in snail distribution observed. The importance of unmeasured factors such as lime were not addressed by this study.

How accurately can snail presence at a small site in the desert be predicted from altitude, slope angle, slope aspect, percent vegetational cover and substrate? Which of these variables is most important in explaining the variance? Do the two species differ in their local distributions, and if so, which variables seem best correlated to these differences? I have employed multivariate analysis to address these questions. If multivariate statistical techniques can be demonstrated useful in the relatively simple desert environment, their application to more complex sets of distributions or to environments where important variables are more difficult to identify will seem promising.

METHODS

Arch Canyon is located in Organ Pipe Cactus National Monument, Arizona, about

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TABLE 1. Environmental variables measured at each site.

Variable	Mean	Standard deviation	Maximum	Minimum
Altitude (feet (meters))	3160 (963)	230(70)	3700 (1128)	2700 (883)
Slope aspect (degrees)	73	66	180	0
Slope angle (degrees)	21	12	50	0
Substrate type (coded)	4.4	1.6	6	1
Vegetational cover (%)	56	29	100	0

21 km from the Mexican border (32°02′ N, 112°42′ W). Its mouth at 2560 ft (780 m) altitude is well within the limits of the Sonoran Desert, and cacti comprise a large portion of the vegetation, but at the top of the canyon (4000 ft., 1219 m) shrubs and trees dominate. On 5 to 10 January, 1978, quadrat samples 4 m² each were made at 129 arbitrarily chosen sites in the canyon. Smaller sample areas might have permitted better estimation of the actual environment experienced by the snails, but a sample size of at least 4 m² was dictated by the scarcity of individuals.

Measurements of five environmental variables were made at each site (Table 1). Altitude was estimated to the nearest 50 ft (15.2 m) from a topographic map. Slope aspect was determined to the nearest 45° on a scale from 0° to 180°, evaluating both east and west at 90°. I measured slope angle with an inclinometer set on a meter stick lying flush with the ground and oriented upslope. Substrate type was scored on a scale from 1 to 6, with 1 designating solid rock; 2, coarse cobble (diameter more than 25 cm); 3, fine cobble (diameter less than 25 cm); 4, sand; 5, dirt; and 6, humus. Vegetational cover was estimated to the nearest 25%. Notice that the distributions of these variables at best only approximate normality, for each variable is broken into a small number of discrete values. The results of my analyses are therefore only approximations.

Each quadrat was thoroughly searched for snails by turning rocks and sorting through humus. The two snail species commonly found living were the helminthoglyptid Sonorella baboquivariensis cossi Miller and the endodontontid Discus cronkhitei (Newcomb). Sonorella was occasionally observed

in the morning actively foraging on the surface, but *Discus* was only seen lying dormant in sheltered areas. Forty individuals of *Sonorella* were found in 21 quadrats, while 59 *Discus* inhabited 32 quadrats. Rocks were replaced and all snails returned to the quadrats after sampling.

The multivariate analytical methods I used will be briefly described by example. Each of my 129 sample sites can be imagined as a point plotted in five dimensional space, where the axes are measures of the five environmental variables. Using factor analysis, new axes (factors) running through this five dimensional space can be described. In principal component analysis, a type of factor analysis, the axes are generally uncorrelated with one another and chosen to maximize the variance explained. Thus if correlation among the original variables is high, the data can be expressed in much fewer than 5 axes with little loss of information. In discriminant function analysis, the axes chosen are those that maximize the separation of two or more groups of points. Thorough discussions of these techniques are given by Morrison (1967), Harman (1967), and Pielou (1969).

RESULTS AND DISCUSSION

Principal component analysis is a useful tool for simplifying complex data sets and identifying latent regularities. It has been used extensively in vegetational studies (e.g., Austin, 1968; Peet & Loucks, 1977) where each collection site is characterized by its species composition. I applied principal component analysis based on the correlation matrix of the five environmental variables

TABLE 2. Correlations among environmental variables. Elements of the matrix above the diagonal are simple correlation coefficients, while those below the diagonal are partial correlation coefficients.

	Altitude	Aspect	Angle	Substrate	Cover
Altitude	1.00	236**	.177	026	.000
Aspect	192*	1.00	−.306**	085	0 9 7
Angle	.104	313**	1.00	268**	1 96*
Substrate	026	085	200*	1.00	.795**
Cover	.023	037	.011	.780**	1.00

^{*}Significant at the 95% confidence level.

(BMDP4M, Dixon, 1977) to the 129 sample sites. Factors were rotated orthogonally to maximize the variance.

Both simple and partial correlation coefficients (all other variables held constant) are presented in Table 2. There is a very high positive correlation between cover and substrate, demonstrating that those sites with high vegetational coverage tend to have dirt and humus below. There is also an inverse correlation between substrate and slope angle, reflecting the tendency of dirt and humus to collect in flat areas and the tendency for rocks to be exposed on steeper slopes. The correlation between cover and slope angle disappears in the partial correlation analysis, suggesting that this correlation is secondary to the one between substrate and slope angle. The high correlations between slope angle and slope aspect, and between slope aspect and altitude reflect peculiarities of Arch Canyon. The canyon's northfacing slope is dissected by several steep washes, and at high elevations the canyon itself steepens and turns toward the south making south-facing sites rare. Hence higher elevations and higher slope angles both tend to have lower (more northerly) slope aspects.

Two principal components had eigenvalues greater than one, and together they accounted for 67.5% of the total variance. The factor loadings on these two principal components (PC's) are presented in Table 3, and the 129 sample sites are plotted by their factor scores in Fig. 1. Notice that substrate and cover are very highly loaded on PC 1 and relatively unimportant in PC 2, while slope aspect and altitude are highly correlated with PC 2 but not with PC 1. Fig. 1 shows that snail-containing sites had uniformly high PC 1 scores but occupied the range of PC 2. This suggests that snails can be found at almost all elevations and all slopes within the canyon, but they

localize at places with high vegetational cover and humus.

To verify this result, I employed stepwise discriminant function analysis (BMDP7M, Dixon, 1977) on the 41 snail-containing sites versus the 88 sites without snails. Strahler (1978) used a similar technique to investigate the relationship between woody plant species and underlying rock type. Percent cover and substrate were the only two variables with any power to identify snail-containing sites, and once the cover variable was entered into the function, the discriminating power of substrate was rendered insignificant. Table 4 shows the

TABLE 3. Factor loadings on the first 2 principal components in analysis of 129 sample sites.

	PC 1	PC 2
Altitude	123	630
Slope aspect	.013	.799
Slope angle	48 9	- 579
Substrate	.924	~.176
Cover	.901	231
Eigenvalue	1.92	1.45
% variance explained (cumulative)	38.4	67.5

TABLE 4. F ratios for environmental variables in discriminant function analysis of snail presence.

	At outset of stepwise procedure	After first step
Vegetational		
cover	52.27	entered
Substrate	42.84	2.62
Slope angle	3.76	.76
Slope aspect	3.38	2.14
Altitude	1.42	1.99
Degrees of		
freedom	1 and 128	1 and 127

^{**}Significant at the 99% confidence level.

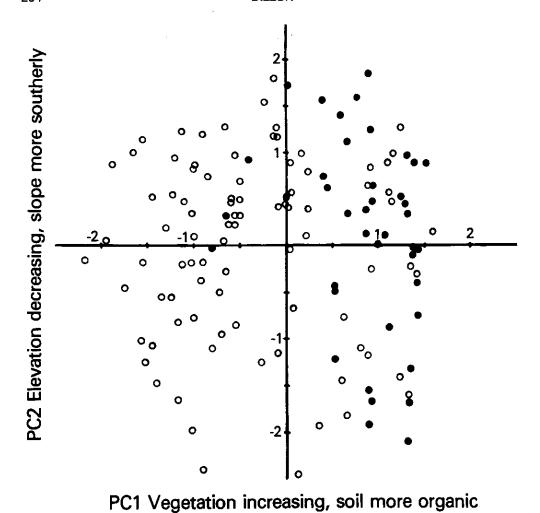


FIG. 1. Principal component analysis of environmental variables at 129 sample sites. Darkened points

FIG. 1. Principal component analysis of environmental variables at 129 sample sites. Darkened points are samples that contained snails.

F ratios for the five variables at the outset of the discriminant function analysis and the F ratios of the four remaining variables after "cover" was entered in the first step of the procedure. On the basis of vegetational cover alone snail presence can be predicted in all sites with 78% accuracy (Fig. 2). Altitude, slope angle, and slope aspect were not demonstrated to have any significant influence on the presence of snails at small sites in Arch Canyon.

Stepwise discriminant analysis was also used to identify differences in the distributions of Sonorella and Discus within the canyon. The occurrence of each species in any particular site was weighted by its abundance at

that site. Discriminant analysis has been used widely in studies of community structure (M'Closkey, 1976; Dueser & Shugart, 1978). Green (1971, 1972) used multiple discriminant analysis to determine the factors important in separating the habitats of 10 species of freshwater bivalves. Harner & Whitmore (1977) have proposed methods to calculate niche overlap from discriminant function scores. They used the program BMDO7M to rank 10 environmental variables by their ability to discriminate between bird species pairs.

I obtained a discriminant function significant at the 99% confidence level (F=13.4, d.f.=2, 97) capable of classifying 72% of the cases correctly. The F ratios for variables not in-

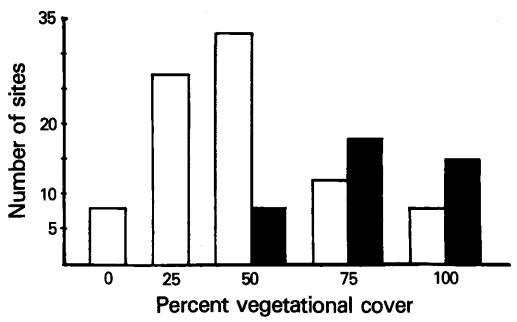


FIG. 2. Histogram showing the 129 sample sites categorized by their percent vegetational cover. Snail-containing sites are darkened.

TABLE 5. F ratios in discriminant function analysis of Discus and Sonorella distribution.

	At outset of stepwise procedure	After first step	After second step
Slope angle	20.25	entered	entered
Substrate	10.71	5.56	entered
Slope aspect	8.13	.27	.41
Altitude	5.51	.95	.40
Vegetational cover	.11	.08	.92
Degrees of freedom	1, 99	1, 98	1, 97

cluded in the function are listed for each step in Table 5. Slope angle was the best discriminator between the two species. Fig. 3 shows that Sonorella is found on significantly steeper slopes than Discus (P < .001, Mann-Whitney U test). One likely explanation for the differing abundances of the two species on different slope angles involves the great difference in their sizes. An average Sonorella has a shell 19 mm in diameter while a typical Discus has a shell only 4 mm across. Thus Discus can find adequate shelter during dry periods in interstitial spaces of the humus that collects in flat areas, but Sonorella requires rocks more common on steeper slopes. In the course of this survey, individuals of Sonorella were indeed found most frequently under rocks,

while *Discus* was most often encountered while sifting through deep, loosely packed humus.

Table 5 shows that the substrate variable also had significant discriminating power even after "angle" was entered into the function (Discus scores higher, as expected). It is important to notice, however, that the cover variable had no discriminating power, even though cover and substrate are very highly correlated (Table 1). Cover, it has been demonstrated, is a good predictor for the presence of both species. But apparently Discus is to be expected where the vegetation grows in flat areas so that humus accumulates, while Sonorella is most common in the few places where vegetation grows on steep-

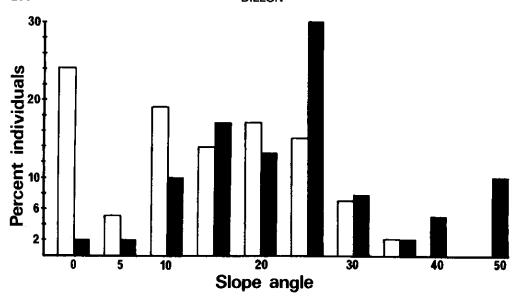


FIG. 3. Abundance of *Discus* and *Sonorella* at sites of varying slope angle. *Sonorella* is darkened and *Discus* is left unshaded.

er slopes and humus does not collect, leaving rocks and cobble exposed. Differences of this nature decrease the probability that individuals of different species occur at the same site, and thus could reduce competition.

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RESUMEN

ANALYSIS MULTIVARIADO DE LA DISTRIBUCION DE LOS CARACOLES DEL DESIERTO EN UN CAÑON DE ARIZONA

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El análisis discriminatorio múltiple y el análisis de componentes principales resultaron bastante útiles para interpretar la distribución de dos especies de caracoles en un cañón desértico. En sitios pequeños, elegidos al azar, es posible predecir con precisión la presencia y abundancia de las especies a partir de las siguientes variables ambientales: altitud, ángulo de la pendiente, orientación de la pendiente, porcentaje de cobertura vegetal y tipo de substrato. Aunque la correlación entre las variables ambientales fue alta, la cobertura vegetal explicó la mayor parte de la varianza en la presencia de las especies. La orientación y ángulo de la pendiente, y la altitud, no afectan la presencia de las especies cuando se les considera en forma independiente de la vegetación. Las dos especies que viven en el cañón, *Discus cronkhitei* y *Sonorella baboquivariensis cossi*, difleren significativamente en sus preferencias en substrato y ángulo de la pendiente. Se sugiere que *Sonorella* fue encontrada más frecuentemente en pendientes rocosas inclinadas debido a que requiere la protección de las rocas. *Discus*, una especie mucho más pequeña, puede encontrar abrigo adecuado en humus suelto y así habitar en pendientes más leves, donde el humus se puede acumular.