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INSULAR BIOGEOGRAPHY OF MAMMALS IN THE GREAT SALT LAKE

Michael A. Bowers¹

ABSTRACT.— The distribution of 21 species of nonvolant mammals among nine islands in the Great Salt Lake was analyzed for biogeographic patterns. The number of species inhabiting an island is closely correlated with island area. That the slope of the regression line describing this relationship (z or b) is relatively shallow compared to (1) totally isolated island systems or (2) island systems where an equilibrium between rates of colonization and extinction have been attained suggests that isolation plays little role in accounting for the variation in mammalian species diversity among islands. Stepwise multiple regression confirms this, while demonstrating that area alone accounts for 88 percent of the variation in species diversity among islands. However, endemic subspecies comprise a significant proportion of the insular mammalian fauna, suggesting that isolation for small mammals restricted to certain habitats may be substantial. A general scenario of the processes determining insular mammalian diversity and endemism is discussed for the Great Salt Lake, where the dynamic lake level creates a potential for different biogeographic processes over time.

Analysis of the distribution of nonvolant mammals among oceanic (Carlquist 1965, Wright 1981), landbridge (Hope 1973, Southern 1964, Bloeker 1967, Wright 1981), and montane (Brown 1971, 1978) islands has played a significant role in the development and testing of contemporary biogeographic theory (reviews by Brown 1978, Wright 1981). However, most emphasis in the current biogeographic literature focuses on the distribution of reptiles and birds (Carlquist 1965, Simberloff 1974, Wright 1981). Although the conspicuousness of these vertebrates facilitate the quantification of species in insular habitats, the poor dispersal abilities of nonvolant mammals (Carlquist 1965, Brown 1971, 1978, Wright 1981) make them particularly interesting subjects for biogeographic analysis.

Isolated habitats in the Intermountain Region of western North America have provided several good tests of biogeographic theory (review by Harper and Reveal 1978). Rigorous interpretation of such patterns have been possible because the paleoclimatic history of the region is well understood (Hubbs and Miller 1948, Martin and Mehringer 1965, Wells and Berger 1967, Wells and Jorgensen 1964).

This paper discusses the distribution of nonvolant mammals among islands in the Great Salt Lake in relation to the theory of

insular biogeography. Special emphasis relates distributional patterns to the process of extinction and dispersal, which appear to reflect historical events rather than equilibrium processes.

METHODS

The distribution of nonvolant mammalian species among nine islands in the Great Salt Lake was compiled from published literature (Stansbury 1852, Fremont 1850, Durrant 1936, 1952, Goldman 1939, Marshall 1940). One source (Marshall 1940), which reported the findings of an extensive mammal survey of the Great Salt Lake in the late 1930s, not only documented the distribution of species (and subspecies) by islands, but also characterized in detail the islands proper. Both historical (age of island, number of years connected to the mainland between 1850 and 1940) and physical (area, island height, distance to mainland) features were included in the general description of each island. Marshall (1940) and Durrant (1936, 1952) were particularly interested in the distribution of subspecies restricted to certain islands in the Great Salt Lake. Although both of these authors invoked historical explanations to account for the distribution of mammals in general and endemic subspecies in particular, little emphasis was given to the quantitative

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analysis of determinants affecting the dispersion of species and subspecies over the nine islands. In the present paper I reanalyze the baseline data reported by Marshall (1940) in a quantitative manner and interpret the results in light of recent contributions to the general theory of biogeography. The general taxonomy follows Goldman (1939) and Durrant (1952). Introduced mammalian species and all chiropterans were excluded from the analysis. For a more detailed account of the islands, see Marshall (1940).

RESULTS AND DISCUSSION

As of 1938, 21 species of nonvolant mammals were distributed among the nine islands (Table 1) of the Great Salt Lake. Moreover, nine subspecies were totally restricted in distribution to these islands.

The number of mammalian species (Table 1) inhabiting an island is closely correlated with the area (Table 2) of the island (Fig. 1). When both variables are plotted logarithmically, the data are well described ($r = .74$) by a straight line with a slope (z) of .19. Traditionally, biogeographers have expressed this relationship as $S = CA^z$, where S is the number of species inhabiting an island and A is the insular area. The value of the constant (C) and slope (z) have been shown to be dependent on the specific taxon and group of islands under consideration (MacArthur and Wilson 1967, Preston 1962, Wright 1981). Widespread use of the power function has proved beneficial in that it facilitates the comparison of slopes and, in an *a priori* sense, biogeographical processes that are impacting insular systems (reviews by Brown 1978, Wright 1981).

TABLE 1. Distribution of subspecies, by island, for mammals in the Great Salt Lake. Taxonomy from Goldman (1939) and Durrant (1952).

	Dolphin	Gunnison	Bird (Hat)	Sand bar	Carrington	Badger	Stansbury	Antelope	Fremont
<i>Dipodomys microps russeolus</i> °	X								
<i>Dipodomys microps alfredi</i> °		X							
<i>Dipodomys microps subtenuis</i>					X	X	X		
<i>Dipodomys ordii marshalli</i>			X		X	X	X		
<i>Dipodomys ordii cineraceus</i> °	X								
<i>Dipodomys ordii utahensis</i>								X	
<i>Perognathus parvus plerus</i> °					X		X		
<i>Thomomys bottae minimus</i> °							X		
<i>Thomomys bottae nesophilus</i> °								X	
<i>Eutamias minimus pictus</i>							X		
<i>Spermophilus townsendii mollis</i>	X						X	X	X
<i>Erethizon dorsatum epixanthum</i>	X						X		
<i>Peromyscus crinitus pergracilis</i>							X		
<i>Peromyscus maniculatus sonoriensis</i>	X		X	X	X	X	X	X	
<i>Peromyscus maniculatus gunnisoni</i> °		X							
<i>Peromyscus maniculatus inclarus</i> °									X
<i>Reithrodontomys megalotis rarus</i>							X		
<i>Neotoma lepida marshalli</i> °					X	X	X		
<i>Neotoma lepida lepida</i>	X							X	
<i>Onychomys leucogaster utahensis</i>							X		
<i>Sylvilagus nuttalli grangeri</i>					X	X	X	X	
<i>Lepus californicus deserticola</i>							X	X	X
<i>Odocoileus hemionus hemionus</i>							X	X	
<i>Antilocapra americana americana</i>								X	
<i>Lynx rufus pallescens</i>							X	X	
<i>Mustela frenata nevadensis</i>								X	
<i>Taxidea taxus taxus</i>							X		
<i>Mephitis mephitis major</i>							X	X	
<i>Canis latrans lestes</i>	X		X		X	X	X	X	
Total species	7	2	3	1	7	6	19	13	3

°Subspecies not found on the mainland.

The z-value (.19) for nonvolant mammals inhabiting islands in the Great Salt Lake is slightly lower than insular biotas where an equilibrium between rates of colonization and extinction have been attained (.20-.35, MacArthur and Wilson 1967). However, the z-value for insular habitats in the present analysis is larger than those commonly reported for continental situations (.12-.17, MacArthur and Wilson 1967) and is comparable to two decimal places the value reported in a recent vegetational analysis of a pinyon-juniper ecosystem where nested quadrants were used as islands (Harner and Harper 1976).

The slight deviation from predicted z-values for continental and equilibrial insular systems can be elucidated through stepwise multiple regression analysis of island characteristics (Table 2) on the number of resident mammal species (Table 1). Similar multivariate techniques have been extremely powerful when investigating the significance of interdependent island characteristics (Table 3) on the variation in insular species diversity (Brown 1971, 1978, Harper et al. 1978).

That (a) approximately 88 percent of the variation in insular mammalian diversity can be accounted for by island area (Table 4), and (b) there appears to be little impoverishment of species number resulting from isolation by distance to the mainland (Table 4) suggest that colonization rates are high and that there is little effect of insular isolation on species richness. These results appear to be consistent with those of others (Johnson 1975,

Brown 1978) studying boreal birds in intermountain habitats where avian diversity is attributable primarily to the diversity of available habitats and not area per se. Specifically, the overwhelming dominance of area in the multiple regression analysis (Table 4) is in all probability an illusion. Wyckeroff (1973) and Harner and Harper (1976) have demonstrated that both environmental favorability and heterogeneity exert a strong influence on the number of vascular plant species per unit area. Because area alone subsumes all these variables, it by itself accounts for several variables that *a priori* could account for a significant amount of the variation in mammalian species diversity. Unfortunately, data on environmental favorability and heterogeneity are not available for the islands in the Great Salt Lake. Quantification and analysis of habitat diversity patterns of the islands would be a strong test of the effect of area, per se, on variation in the number of mammalian species in this system of islands.

On the islands of the Great Salt Lake, recurrent colonization appears to be much more important than local extinction. This contention can be examined in more detail by looking at ecological attributes of the 21 species that are distributed among the nine islands. In particular, the documentation of characteristics that might increase the probability of local extinction could produce a finer degree of resolution than examining entire island compositions.

TABLE 2. Historical and physical data for the nine islands in the Great Salt Lake. Data adapted from Marshall (1940).

Island	Area (hectares ²)	Distance ¹ (km)	Height ² (m)	Corridor ³ height (m)	Years ⁴ connected	Age ⁵ (years)
Dolphin	20.7	5.67	18.5	.77	18	20,000
Gunnison	67.4	24.30	46.2	-1.23	0	20,000
Bird (Hat)	9.1	32.40	12.3	.31	12	20,000
Sand bar	.2	37.26	.6	.31	7	6
Carrington	730.2	32.40	123.0	.31	12	20,000
Badger	2.5	35.64	3.1	.31	13	50
Stansbury	7,977.3	19.44	769.2	3.01	76	70,000
Antelope	10,766.9	5.27	737.8	.92	19	70,000
Fremont	1,216.9	24.30	244.9	.46	2	70,000

¹Distance (km) from island to the nearest mainland area.

²Maximum height (m) of an island relative to zero (= 1291.3m) on the Saltair gage.

³Height (m) of connecting bar on the Saltair gage.

⁴Years an island was connected to the mainland between 1850 and 1938.

⁵Probable age of an island (see Marshall 1940).

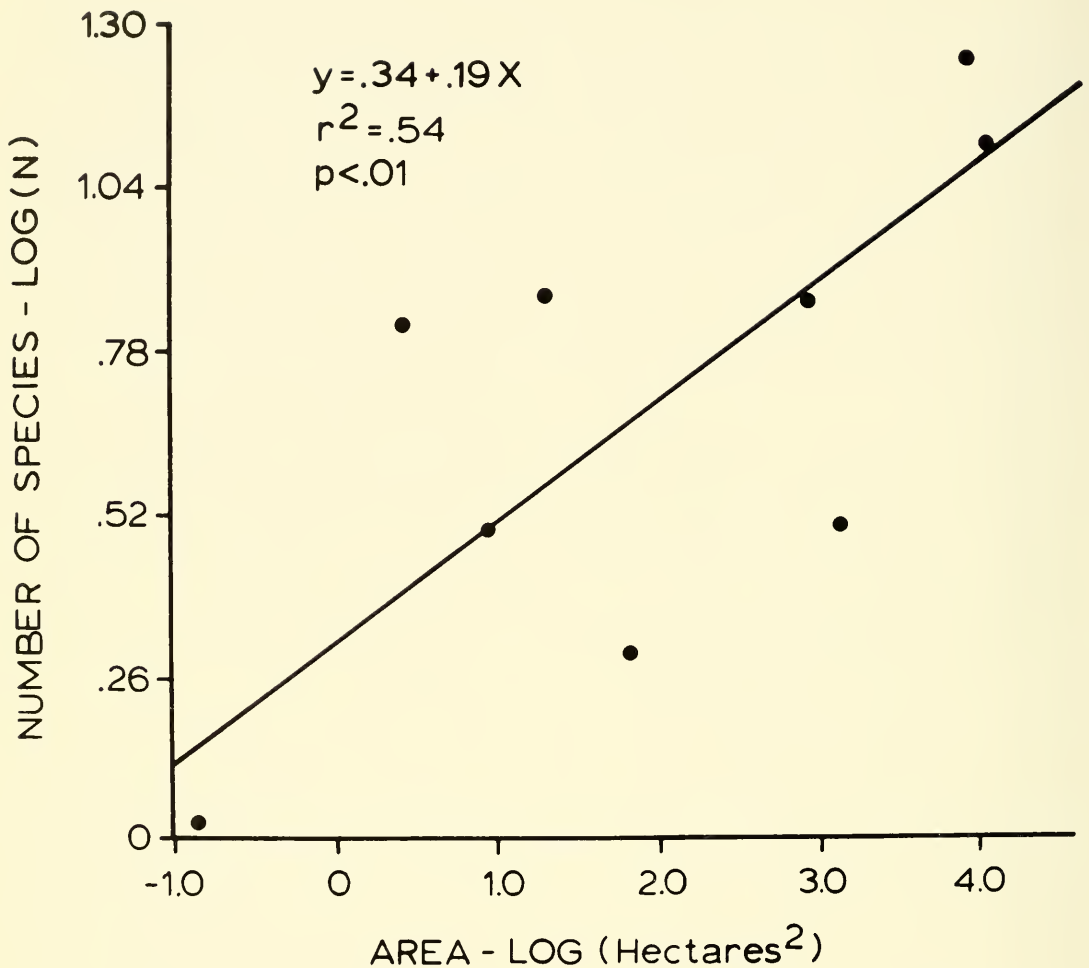


Fig. 1. The relationship between insular area and the number of nonvolent mammal species for the nine islands in the Great Salt Lake. The equation for the fitted regression and the amount of variance in mammalian species diversity accounted for by area (r^2) are indicated.

The probability of a species becoming extinct appears to be directly dependent on local population size (MacArthur and Wilson 1963, 1967). In addition to island size, three ecological variables appear to be particularly important in determining insular population size. These variables—body size, trophic status, and degree of habitat specialization—affect the distribution of mammalian species among the Great Salt Lake islands in the manner we would expect from considerations of their effects on population size: small mammals are found on more islands than large ones (Fig. 2), herbivores are better represented than granivores, insectivores, or

carnivores, and species that can live only in restricted habitats inhabit fewer islands than species with the same trophic affinities but who are habitat generalists. Figure 2 shows the relationship between the number of islands inhabited by a particular species and the logarithm of body weight. Generally these variables do not covary to any significant extent ($r = -.28$). However, within the herbivore guild (Fig. 2) the number of islands inhabited by a species is negatively ($P < .04$) correlated with the logarithm of body weight ($y = .64 - .09x$, $r = -.65$, $df = 7$). Within this guild, the species of largest body size occur only on the larger islands (Tables 1 and 2),

TABLE 3. Correlation coefficients (r) between variables for the nine islands in the Great Salt Lake. Matrix is computed with untransformed data. Note that the number of total species and endemic subspecies are not always closely correlated with the same variables.

	Area	Distance	Height	Corridor height	Years connected	Age	Number of species
Area	—						
Distance	-.593	—					
Height	.970	-.547	—				
Corridor height	.630	-.279	.677	—			
Years connected	.610	-.272	.705	.941	—		
Age	.772	-.583	.859	.402	.466	—	
Number of species	.938	-.605	.924	.789	.766	.676	—
Number of endemic subspecies	.240	.013	.395	.663	.820	.663	.467

suggesting the importance of matching body size (and, hence, population size) with suitable habitat patch size, which appears to covary with island area. In fact, those species of both large and small body size that occur on only a few islands usually are found only on large islands (Tables 1 and 2). Thus, it appears that, for mammals on islands in the Great Salt Lake, insular area not only affects the number of species but also can be used to predict some ecological attributes of the denizens.

The preceding analyses suggest that isolation of insular habitats in the Great Salt Lake is relatively unimportant in determining mammalian diversity. However, the fact that such a high proportion of the island faunas are composed of endemic subspecies strongly suggests that isolation has been a prominent factor, at least in the past, in the evolution of these insular biotas. The determinants promoting endemism can be examined by using the proportion of subspecies endemic on each island (Table 1) as the dependent variable and island characteristics as the independent variables (Table 2) in a stepwise multiple regression. The results of this analysis (Table 5) show that two variables (height of the corridor connecting the various islands with the mainland and number of years between 1850

and 1938 that an island was connected to the mainland) explain 76 percent of the variation in the proportion of insular subspecies that are endemic. Obviously, the degree of isolation as reflected by corridor height and years connected to the mainland are imminently important in producing and maintaining endemic subspecies in insular mammalian faunas. It should be noted that in this particular analysis subspecies are considered endemic if the corresponding mainland species are of different subspecies. Consequently, endemic subspecies can and do occur on several islands.

In the analysis of species distributed among islands, isolation played little role in accounting for the patterns. In contrast, the occurrence of endemic subspecies is highly correlated with the degree of isolation. These differences can be reconciled by examining ecological attributes of the endemic subspecies. That all endemic subspecies are herbivores, granivores, or omnivores and are relatively small (<300g) when compared with the other species that are distributed among the nine islands suggests that population size may effect the rate of local genotypic differentiation from mainland populations. Specifically, the data suggest that species capable of maintaining large insular populations per

TABLE 4. Summary of stepwise multiple regression of the influence of island characteristics on the number of mammalian species on islands in the Great Salt Lake.

Variable*	Order entered in equation	Contribution to R ²	F-value	Significance level
Area	1	0.882	52.16	.0001
Corridor height	2	0.065	7.36	.035
Distance	3	0.008	.96	.373

*Data from Table 2 (untransformed).

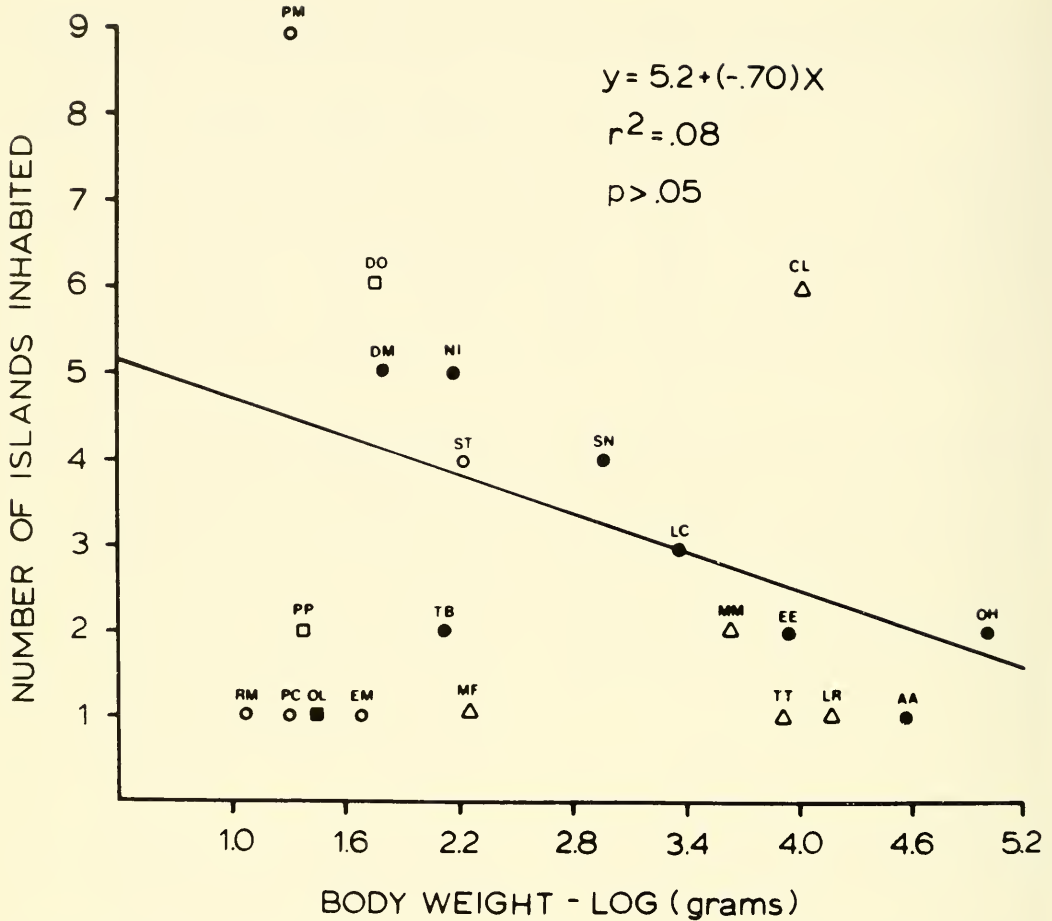


Fig. 2. Frequency of occurrence of species of nonvolent mammals on the nine islands in the Great Salt Lake plotted against body weight; solid circles represent herbivores, hollow circles represent omnivores, hollow squares represent granivores, hollow triangles represent carnivores, and solid squares represent insectivores. Letters adjacent to each point refer to species names that can be identified by reference to Table 1.

unit area are more likely to show substantial differentiation from the mainland populations than species with smaller populations.

Two interdependent factors may account for these differences. First, as a consequence of larger body size, and thus mobility, more colonists of large-bodied species probably disperse to islands than smaller species. Thus, the amount of gene flow from mainland to island populations would be relative to body size: e.g., because of intrinsic differences in dispersal ability insular populations of large species would be expected to have gene frequencies closer to those mainland populations when compared to smaller species. Second, given that a single colonist did disperse to an island from the mainland, the in-

corporation and ultimate fixation of its genes into the genepool of the population would be a negative function of population size. Specifically, the larger the population the greater the likelihood that a single colonist's contribution of novel genes will be swamped: e.g., the infusion of new genetic material from one act of colonization will be much greater in a population of 10 individuals when compared to a population of 100.

Although the analyses presented in this present paper generally suggest that isolation has not been important in limiting the distribution of nonvolant mammals among the islands in the Great Salt Lake, a caveat should be interjected. Specifically, the survey by Marshall (1940) was conducted when the lake

TABLE 5. Summary of stepwise multiple regression of the influence of island characteristics on the proportion of subspecies that are endemic for the nine islands in the Great Salt Lake.

Variable*	Order entered in equation [†]	Contribution to R ²	F-value	Significance level
Corridor height	1	.16	1.32	.287
Years connected	2	.60	14.64	.009
Age	3	.07	2.08	.208

*Data from Table 2 (untransformed).

level was near a 100-year minimum. Colonizations by mammals just prior to the survey could effectively obscure patterns of local extinctions, thereby downplaying the role of isolation. Since that time, the lake level has remained relatively high.

A strong test of the result presented here would be to re-census the islands while testing for the effects of isolation. Not only would this yield valuable biogeographical information, but it would serve as one of the few instances where island relaxation rates (Diamond 1972, 1975) could be precisely quantified because the exact year of isolation by island is known through the detailed documentation of the lake level (U.S. Weather Bureau).

GENERAL DISCUSSION

The distribution of nonvolant mammals among nine islands in the Great Salt Lake appears to reflect the effect of recurrent colonizations rather than the equilibrium processes of extinction and immigration. Consequently, islands appear to be "saturated" with species and the distribution of species among islands is probably determined by the distribution of amicable habitats that are extensive enough to support populations of the colonists. However, isolation of insular habitats does appear to be important for some species of small body size. This is supported by a high degree of endemism for these species.

The failure of the equilibrium theory of biogeography (MacArthur and Wilson 1963, 1967) to account for the distribution of mammals among insular habitats studied here supports a general trend that contrasts intermountain insular habitats with oceanic island systems. Specifically, the distribution of birds (Johnson 1975, Behle 1978), mammals (Brown 1971, 1978), fish (Smith 1978) and even plants (Harper et al. 1978) among insular

habitats in western North America rarely conform to equilibrium predictions. In contrast, the biotas of oceanic islands often exhibit equilibrium distributions (Simberloff 1974, Wright 1981). This difference is correlated with contrasting paleoclimatic and geological processes impacting the two types of insular systems. Over the last million years extensive climatic and geological changes have drastically changed and, for islands in the Great Salt Lake, are still changing the landscape of western North America (see earlier citations of Hubbs, Martin, Wells). Oceanic systems, however, have a long history of isolation and relative environmental stability (MacArthur and Wilson 1967, Simberloff 1974). It is possible that these differences in the underlying environmental patterns (both past and present) account for the contrasting biogeographic tendencies. As pointed out by Brown (1978), these dynamic environmental factors should differentially affect species with contrasting vagilities. Because mammals in general are relatively poor dispersers across unsuitable habitats (Brown 1971, 1978) and aquatic barriers (Carlquist 1965), it is interesting to speculate what biogeographic model the Great Salt Lake islands would conform to if the islands were isolated for long periods of time. In all probability the maintenance of a high lake level would create a system analogous to that of boreal mammals on mountain tops (Brown 1971, 1978), where extinctions are dependent on insular size and colonizations are rare. Such processes may currently be in effect with the higher lake level.

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