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Life-History Correlates of Taxonomic Diversity

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LIFE HISTORY CORRELATES OF TAXONOMIC DIVERSITY[1]

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Abstract. One of the most pervasive, nonrandom evolutionary patterns is extreme domination of a taxon by one subtaxon or only a few subtaxa. Domination refers to taxonomic diversity and the fraction of the taxon that is classified in the most diverse subtaxon. We attempt to explain how subtaxa come to dominate their phyletic counterparts by examining correlations between taxonomic diversity and life history traits such as age of first reproduction, longevity, fecundity and partitioning of reproduction, and resource availability in a variety of vertebrate, invertebrate, and plant groups. Regardless of taxonomic group or rank, the number of taxa within an assemblage, or the school of taxonomy employed, diverse taxa were characterized by short generation time (early age of first reproduction and short life-span) and the ability to contact many resources (high mobility and high resource availability). We suggest that the intrinsic character of short generation time increases diversity because it promotes speciation and reduces extinction. Extrinsic factors such as resource availability and environmental complexity and variability may have a secondary influence on diversity by constraining or enhancing speciation for taxa with short generation times.

Key words: colonization ability; diversity; extinction; fecundity; generation time; life history; longevity; speciation.

INTRODUCTION

Robert MacArthur (1972) challenged ecologists to search out, document, and explain nature's general and often iterative patterns. One such pattern, which has repeatedly been documented, but remains poorly understood, is the extreme domination of a phylogenetic assemblage by one taxon or a few taxa. Given your favorite taxonomic group, is it not true that one taxon or at most a few taxa are much more speciose than the other taxa? This general pattern has been documented in a wide variety of vertebrate, invertebrate, and plant assemblages regardless of the taxonomic rank considered or the school of taxonomy employed (Willis 1922, Williams 1964, Anderson 1974, Bock and Farrand 1980, Dial and Marzluff 1988, 1989). A familiar example is found in the Class Mammalia where the Order Rodentia contains 40% of all mammal species (Dial and Marzluff 1989). Similarly, the Phylum Arthropoda contains over 80% of all animal species, and more than 40% of all Monocotyledoneae species are found in the plant family Orchidaceae (Dial and Marzluff 1989).

Despite this pattern's ubiquity, few authors have addressed the issue of why only a few taxa are responsible for the bulk of the diversification within an assemblage. An appropriate starting point in understanding any

widespread pattern is to ask whether or not it could reasonably be generated by random processes. Diversity results from differential rates of speciation and extinction. Investigations into diversity, therefore, must address these two key processes. A variety of probabilistic models simulate speciation and extinction and can be used to generate assemblages by randomly increasing or decreasing the diversity of taxa through time. Qualitatively, simulated assemblages appear quite similar to real assemblages (Raup et al. 1973, Anderson 1974, 1975, Anderson and Anderson 1975, Gould et al. 1977, Flessa and Thomas 1985). However, the diversity attained by the most diverse (dominant) taxon in natural assemblages is statistically greater than predicted by several random models, including those used by the above authors (Dial and Marzluff 1989). Random processes, therefore, seem to have played a minor role in the spectacular radiations exhibited by dominant taxa (Flessa and Levinton 1975, Stanley et al. 1981, Gilinsky and Bambach 1986, Dial and Marzluff 1989).

If random speciation and extinction events cannot generate the extreme diversity exhibited by dominant taxa, then intrinsic properties of taxa or properties of the environments they inhabit must be responsible for most diversification. Commonly, such properties are identified by searching for a "key character" possessed by a dominant taxon that enabled it to radiate more extensively than the other members of its assemblage (Van Valen 1971, Raikow 1986). For example, flight

is supposed to be the key character that enabled bats to attain the second highest diversity within the mammals (Hill and Smith 1984).

In order to understand why virtually *all* assemblages come to be dominated by a limited number of taxa we need to move beyond an assemblage-by-assemblage approach and look for attributes held in common by a vast array of diverse taxa. Cracraft (1982, 1985) has made such a move by suggesting that the environment inhabited by a taxon is the primary determinant of its diversity. Taxa evolving in complex, but climatically benign, environments are predicted to dominate their assemblages because environmental complexity (the number of geologic and climatic barriers) enhances speciation, and benign environments (warm temperatures, abundant and evenly distributed rainfall) reduce the probability of extinction.

Ever since MacArthur and Wilson (1967), ecologists have demonstrated associations between life history attributes of organisms and their ability to colonize new habitats and avoid extinction. It is a common observation that low rates of reproduction, long generation times, and life in the upper trophic levels are shared attributes of extinction-prone species (e.g., Wilson and Willis 1975). The link between life history and extinction suggests that intrinsic attributes of a taxon may also influence its relative taxonomic diversity. However, correlations between evolved life history traits and taxonomic diversity have not been investigated in a wide variety of organisms. Failure to identify a strong relationship between speciation rate and reproductive potential (Zeuner 1931, Simpson 1953, Kurten 1968, Stanley 1979) and general statements that intrinsic characteristics, by themselves, cannot adequately explain most macroevolutionary patterns (Cracraft 1982) may have reduced interest in the influence of life history and ecology on diversity. We hope to rekindle this interest by showing that within a variety of vertebrate, invertebrate, and plant assemblages diverse taxa share similar life history traits and ecological characteristics.

In this paper we investigate correlations between diversity and reproductive potential, longevity, and resource availability for a wide variety of organisms. Elsewhere we have shown that some properties of organisms are correlated with diversity (e.g., body size, Dial and Marzluff 1988), whereas other attributes appear to be unrelated to diversity (e.g., sociality, Marzluff and Dial, *in press*). We shall use these previous tests along with the ones presented herein to develop a unified theory of how evolved life history traits and ecological traits correlate with, and therefore may influence, evolutionary diversification.

METHODS

We have attempted to standardize taxonomic terminology with respect to taxonomic diversity by employing the following definitions (Dial and Marzluff

1988, 1989). A *subunit* is the taxon counted within a *unit* (e.g., species/genus, species = subunit and genus = unit). An *assemblage* is an entire collection of units and their subunits (e.g., all species/genera within an assemblage of families). A *dominant* (or *most diverse*) *unit* is the unit within an assemblage having the most subunits.

We selected 33 taxonomic assemblages, which cover a wide variety of vertebrate, invertebrate, and plant groups, to study the relationship between diversity and various ecological factors. Because the ecology of birds and mammals is particularly well known, our analyses focus on data acquired from these two assemblages.

Properties of taxonomic units are characters such as fecundity, longevity, and age of first reproduction. Our statements about units should be interpreted as statements about average properties held by *individuals* within a taxon (see Vrba 1983 for a similar view). We based all statistical tests and summaries on the average values of subunits within units for life history factors and each ecological factor.

Demography

To relate diversity to demography, we ranked the units within an assemblage according to their demographic statistics and then calculated the relative rank of the most diverse unit. Relative ranks were calculated by dividing the number of units with a lower demographic value than the most diverse unit by the total number of units minus 1 (see Dial and Marzluff 1988 for calculation of relative rank, but note in the example that the divisor should be $N - 1$, not N). Multiplication by 100 produces a scale from 0 to 100%. For example, Didelphidae is the most diverse family of marsupials in terms of the number of species (Appendix 1), and has the earliest age at first reproduction for the $N = 5$ marsupial families with available data (Eisenberg 1981). Therefore, the calculated relative age of first reproduction is $0/4 \times 100 = 0\%$. A value of 0% indicates that the most diverse group also had the smallest value of a life history factor, whereas a value of 100% indicates it had the largest. Relative scores enable us to summarize one aspect of a dominant unit's ecology with a single value which, regardless of assemblage size, is indicative of its position within an assemblage, and is comparable between assemblages, including those that are distantly related and of unequal size. We have relied on published accounts of demography within the assemblages we investigated. A complete list of references for all demographic values used and the relative ranking of each dominant unit is given in Appendix 1.

We investigated the interdependence of life history factors and diversification in three ways. First, we assessed the overall goodness of fit between the observed distribution of relative ranks and the distribution expected if dominance and a particular life history trait were unrelated. Observed distributions were generated

A.

EARLIEST
REPRODUCTION

MOST DELAYED
REPRODUCTION

**PERCENT RELATIVE AGE
OF FIRST REPRODUCTION**

B.

SHORTEST
LIFESPAN

LONGEST
LIFESPAN

PERCENT RELATIVE LONGEVITY

C.

LEAST
FECUND

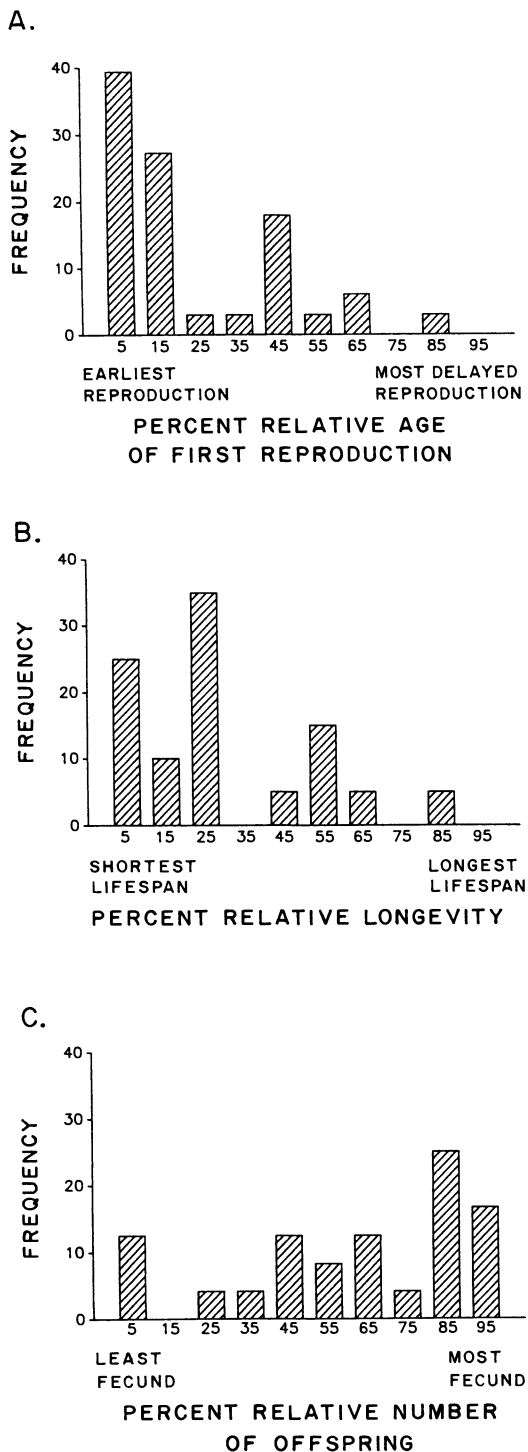MOST
FECUND

**PERCENT RELATIVE NUMBER
OF OFFSPRING**

FIG. 1. Frequency distributions of: (A) percent relative age of first reproduction, (B) percent relative longevity, and (C) percent relative annual fecundity of the dominant taxon in 33, 20, and 24 assemblages, respectively. Raw data for each plot can be found in Appendix 1. Labelled points on the x axis equal the midrange for each category (e.g., 5 = category that includes 0–9.9%).

by assigning each dominant unit's relative rank to the appropriate 10%-wide interval on a scale from 0 to 100% (Fig. 1). If dominance and life history are unrelated, then each interval should contain an equal 10% of the dominant units. Thus, the expected distribution equals $(0.1) \times (N)$ units per interval. Observed and expected distributions were compared with the Kolmogorov-Smirnov goodness-of-fit test because this test is appropriate for interval or ratio scale data (Zar 1974: 56). Second, when there were four or more units within an assemblage, we correlated diversity with the average value of a life history factor for the subunits in that unit. Third, we compared the conditional and unconditional probabilities of selecting the most diverse unit out of its assemblage. The unconditional probability equals the chance of randomly selecting the most diverse unit from among all other units in an assemblage. It is simply $1/N$, where N equals assemblage size. The conditional probability is the chance of randomly selecting the most diverse unit from among those units possessing a specified condition. Our criterion for a unit to meet a particular condition was that it be in the upper 10% of the range for a given factor exhibited in its assemblage. For example, with fecundity as a factor ranging from 1 to 5 in an assemblage, units that scored 4.5 or greater met the condition of "high fecundity." We empirically calculated this probability by dividing the number of times the dominant unit satisfied the condition by the number of assemblages investigated. The importance of a given factor to diversification is indicated by its ability to improve our predictive ability. Improvement in predictive ability is the ratio of conditional probability to random probability.

Resource availability

We investigated correlations between resource availability, or the variety of adaptive zones an organism is likely to encounter, in two ways. First, we investigated correlations between mobility and diversity. We quantified mobility using: (1) Eisenberg's (1981) indices of mobility for mammals, (2) Bellrose's (1980) migration distance for waterfowl, and (3) flight ability for beetles, following Arnett (1963). Second, we selected four examples where resource availability was quantifiable and demography was known. We then calculated the improvement in predictive ability gained by knowing how a taxon used a particular resource.

We used trophic status as an indication of resource availability for 12 mammalian orders and 12 avian families. We assume primary consumers have high resource availability because of the approximately 10-fold higher productivity of plants relative to resources of higher trophic status (e.g., Whittaker 1975).

Chiropteran families can be used to test for a correlation between diversity and the ability to contact abundant resources. Only three families of bats are able to enter nightly torpor (Oxberry 1979, McNab 1982).

This ability has allowed them to colonize temperate regions as well as tropical ones, and we therefore assume they have higher resource availability than families constrained metabolically to the tropics.

Nesting requirements indicate resource availability for genera of waterfowl. Most waterfowl build nests out of vegetation and place them on land, in emergent vegetation, or on floating mats of vegetation (Bellrose 1980). Some, however, use naturally occurring cavities in trees as nest sites. "Hole nesters" should have fewer nesting resources available than species not requiring the presence of cavities ("open nesters"). This is demonstrated by the fact that individual open nesters show greater behavioral flexibility by using a greater range of nesting locations than hole nesters (open: $\bar{X}$ = 3.03 locations, N = 34; hole: $\bar{X}$ = 1.86 locations, N = 7; t = 1.84, 12 df, one-tailed P < .05; data from Bellrose 1981).

Traditional vs. phylogenetic classifications

Investigation of diversity patterns among supraspecific groups defined by evolutionary classifications has two major biases (Cracraft 1984): (1) such groups have not necessarily had equal geologic time for diversification, and (2) monophyly is not assured. We reduced these biases in two ways. First, we investigated patterns at a variety of taxonomic levels. This reduces bias because time-dependent changes in diversity are expected to be more apparent among higher taxonomic ranks than lower ones because rediversification after extinction is more likely to occur in lower categories (Valentine 1980). Second, we analyzed differences in the life history strategies of phylogenetically defined sister groups of birds and mammals. Such sister groups are assumed to be monophyletic and of equal age (Cracraft 1983). We obtained avian sister groups from Cracraft (1982, Table 2) and mammalian sister groups from Eisenberg (1981, who primarily relied on McKenna 1975).

RESULTS

Demography

Early age of first reproduction was the life history trait most strongly correlated with high taxonomic diversity. On average, dominant units reproduced before 80.6% of the units in their assemblage, and had the earliest age of reproduction in 39.4% of assemblages (Fig. 1A). We would only expect 10% of the dominant taxa to have the earliest age of reproduction by chance if diversity and age of first reproduction were unrelated. The observed distribution of the dominant units' relative ages of reproduction was significantly different from the expectation that 10% of the units should occur in each of the 10 relative age intervals (Kolmogorov-Smirnov D = 0.47, N = 10, P < .001). Relative age of reproduction was equally correlated with diversity in bird and mammal assemblages (birds: median relative

age = 95%, N = 6; mammals: median relative age = 82%, N = 18; W = 210, P = .33, Mann-Whitney U test). The influence of early reproduction was not affected by type of taxonomic unit analyzed (species: median relative age = 87%, N = 19; genera: median relative age = 77.5%, N = 8; W = 286, P = .30, Mann-Whitney U test). Importance of relative reproductive age was not dependent on assemblage size (r = 0.04, N = 33, P > .10).

Dominant taxa tended to have short life-spans relative to less diverse taxa. Mean life-spans of dominant units were on average shorter than those of 73.7% of the other units in their assemblages, and were shortest in 25% of assemblages (Fig. 1B). More dominant units had relatively shorter life-spans than expected by chance (Kolmogorov-Smirnov D = 0.40, N = 10, P < .005). Longevity was correlated equally well with diversity in birds and mammals (mammals: median relative longevity = 20%, N = 13; birds: median relative longevity = 22%, N = 5; W = 116, P = .49, Mann-Whitney U test). The taxonomic unit considered did not influence the effect of longevity on diversity (species: median relative longevity = 20%, N = 13; genera: median relative longevity = 21%, N = 6; W = 129, P = .97, Mann-Whitney U test). The importance of relative longevity was the same regardless of assemblage size (r = 0.004, N = 20, P > .10).

Very diverse taxa were not consistently more fecund than less diverse ones. Dominant units were on average more fecund than 60.5% of the units in their assemblage, and were most fecund in 12.5% of assemblages (Fig. 1C). The distribution of relative fecundity of dominant units did not differ from random (Kolmogorov-Smirnov D = 0.22, N = 10, .20 > P > .10). The weak relationship between fecundity and diversity was not due to assemblage size, or the particular taxa or taxonomic units we investigated. Dominant units of birds and mammals did not differ significantly in relative fecundity (birds: median relative fecundity = 50%, N = 6; mammals: median relative fecundity = 80%, N = 16; W = 194.5, P = .46, Mann-Whitney U test). Median relative fecundity of species did not differ from relative fecundity of genera (species: median relative fecundity = 62.5%, N = 15; genera: median relative fecundity = 80%, N = 6; W = 166.0, P = .67, Mann-Whitney U test). There was no significant correlation between assemblage size and relative fecundity of dominant units (r = -0.25, N = 24, P > .10).

Diversity was rarely *linearly* correlated with age of reproduction, longevity, or fecundity within assemblages (Table 1). The signs of correlations within assemblages support the previous tests on the relative values of life history traits of dominant units. Negative correlations predominated when age of reproduction or longevity was related to diversity, suggesting that diverse taxa reproduced earlier and died sooner than less diverse taxa. Positive correlations predominated when fecundity was correlated with diversity, suggest-

TABLE 1. Pearson product-moment correlations (r) between diversity and life history traits with assemblages with four or more units. Sample size (N) and significance level († P < .10, * P < .05, ** P < .01) follows each correlation.

| | | Correlation between number of subunits and: | | | | | | | | |
| | Subunit/ unit‡ | Age of first reproduction | | | Fecundity | | | Longevity | | |
Assemblage		r	N	P	r	N	P	r	N	P
Mammals										
Chiroptera	S/F	−0.59	9	†	+0.82	7	*	...	...	...
	G/F	−0.49	9		+0.28	6		...	...	...
Vespertilionidae	S/G	−0.25	9		...	...	...	...	...	...
Marsupialia	S/F	−0.04	5		+0.66	7		−0.59	7	...
	G/F	+0.20	5		+0.24	7		−0.67	7	†
Rodentia	S/F	−0.64	6		+0.64	12	*	−0.67	7	†
	G/F	−0.56	6		+0.43	12		−0.63	7	
Peromyscus	SS/S	−0.43	10		+0.77	10	**	...	...	...
Carnivora	S/F	−0.57	6		+0.53	6		−0.70	7	†
	G/F	−0.29	6		+0.29	6		−0.56	7	
Primates	S/G	−0.72	11	*	...	...	...	...	...	...
Artiodactyla	S/F	−0.35	6		−0.20	6		−0.39	6	
	G/F	−0.34	6		−0.18	6		−0.38	6	
Bovidae	S/SF	+0.28	12		+0.48	13	†	+0.32	12	
	G/SF	+0.70	12	*	+0.64	13	*	+0.61	12	*
Overall	S/O	−0.50	12	†	+0.44	10		−0.38	10	
	G/O	−0.41	12		+0.44	10		−0.37	10	
	F/O	−0.34	12		+0.28	10		−0.32	10	
Birds										
North American waterfowl	S/G	−0.05	15		+0.01	15		−0.16	10	
(open nesters)	S/G	−0.39	10		+0.37	10		−0.03	6	
(hole nesters)	S/G	+0.46	5		+0.10	5		+0.54	4	
North American Galliformes	S/G	...	...	...	−0.31	9		−0.09	7	
Corvidae	S/G	...	...	...	+0.01	21		+0.55	10	†
Seabirds	S/G	−0.22	16		...	...	...	...	...	...
Overall	S/F	−0.64	11	*	−0.10	15		...	...	...
Amphibians										
Salamanders	S/G	−0.51	16	*	...	...	...	...	...	...
Frogs and toads	S/F	+0.59	4		...	...	...	...	...	...
Reptiles										
Overall	S/O	−0.97	4	*	...	...	...	...	...	...
Plants										
North American trees										
(Gymnosperms)	S/G	−0.30	10		...	...	...	−0.60	6	
(Angiosperms)	S/G	−0.21	19		...	...	...	+0.14	19	
Overall plants	G/F	−0.27	16		...	...	...	...	...	...

‡ Subunit and unit abbreviations are: SS = subspecies, S = species, G = genus, SF = subfamily, F = family, O = order.

ing that diverse taxa had higher reproductive output than less diverse taxa.

Partitioning reproduction into single (semelparous) or repeated (iteroparous) events was not consistently associated with high diversity. Birds and mammals are rarely semelparous, therefore our sample is restricted to fish and plant assemblages. The genus *Onchorhynchus,* within the Salmonidae, is made up of the Pacific salmon, which characteristically mature at sea before their single reproductive bout. This semelparous genus is only the fifth most diverse of seven salmonid genera. The plant genera *Agave, Digitalis, Bambusa, Sasa,* and *Arundinaria* contain predominantly semelparous species (Smith 1977). *Agave* is one of the most diverse genera of lilies, having 300 species (Smith 1977). However, the iteroparous lily genera: *Smilax, Asparagus,* and *Allium* also each contain 300 species. In the

Scrophulariaceae, 12 genera are more diverse than *Digitalis,* which contains only 21 species. In contrast, the dominant iteroparous genera *Pedicularis* and *Calceolaria* contain 600 and 500 species, respectively (Smith 1977). *Bambusa, Sasa,* and *Arundinaria* include semelparous grasses. *Arundinaria* is the most diverse of these, having 100 species; however, 15 iteroparous grass genera have equal or greater diversity. *Panicum* is the most diverse grass genus, having 600 species.

Correlates of diversity in phylogenetic classifications

Relative age of first reproduction was the only significant correlate of diversity in taxa assembled by phylogenetic taxonomic schemes (Appendix 2). Diverse sister groups reproduced earlier than less diverse sister groups in 21 of 29 pairs (P = .004, binomial test). On

average, units in diverse sister groups reproduced 0.59 yr before those in less diverse groups (paired $t = 2.06$, $P = .05$).

Diverse sister groups had marginally shorter longevity and statistically equal fecundity compared to less diverse sister groups. Diverse groups had the shortest life-spans in 15 of 26 comparisons ($P = .16$, binomial test). Taxa in diverse groups lived on average 2.93 yr less than their less diverse sister groups (paired $t = 1.88$, $P = .07$). Only 15 of 29 diverse groups exhibited higher fecundity than less diverse sister groups ($P = .36$, binomial test), whereas 8 of 29 sister groups had equal fecundity regardless of differences in diversity. On average, diverse sister groups had annual clutches (litters) 1.25 eggs (young) larger than less diverse sister groups (paired $t = .82$, $P = .42$).

Resource availability

Mobility (one index of a taxon's ability to contact resources) was not significantly correlated with mammalian diversity. Bats are the most mobile mammals, and they rank second in diversity, suggesting a positive relationship between diversity and mobility. This was not generally the case within assemblages of mammals. For example, the correlation between indices of mobility and the number of genera per order of mammals was only 0.08 ($N = 12$, NS). In addition, within the orders Marsupialia ($r = 0.11$, $N = 7$ families), Rodentia ($r = -0.66$, $N = 4$), and Carnivora ($r = 0.38$, $N = 5$) mobility was not significantly correlated with the number of species per family.

Mobility was correlated with diversity in waterfowl and insects. Waterfowl migrate variable distances (Bellrose 1980) and hence can be viewed as being mobile to differing degrees. There was a weak increase in the number of species per genus with migration distance, measured as degrees latitude ($r = 0.48$, $N = 15$, $P < .10$). Tenebrionid beetles of the United States can be classified as having wings or being apterous (Arnett 1963). Tribes of winged beetles had significantly more genera than apterous tribes (apterous: $\bar{X} = 7.8$ genera, $N = 25$; winged: $\bar{X} = 31.9$, $N = 19$; $T = 3.46$, $P = .002$). This relationship also holds among tribes within the subfamily Tenebrioninae (apterous: $\bar{X} = 7.09$ genera, $N = 11$; winged: $\bar{X} = 35.6$ genera, $N = 15$; $T = -3.37$, $P = .004$).

Knowledge of resource availability increased our ability to pick the most diverse unit in an assemblage. The chances of picking the most diverse unit from 12 orders of mammals or birds is 0.08 (1/12). The probability of picking the most diverse from among those with high resource availability (primary consumers) is 0.17 (1/6) for mammals, and 0.25 (1/4) for birds (Fig. 2A, B). This represents a twofold and threefold increase in predictive ability, respectively. Within nine families of bats knowledge of their ability to enter torpor, increased predictive ability threefold from 0.11 to 0.33 (Fig. 2C). Resource availability, as measured by avail-

ability of nest sites, was less important to waterfowl diversification. Within 14 genera of waterfowl, knowledge of nest sites only increased our predictive ability from 0.07 to 0.10 (Fig. 2D).

Combined influence of demography and resource availability

Knowledge of demography coupled with information on resources further increased our ability to pick the most diverse unit in an assemblage. In assemblages of mammalian orders, avian families, and waterfowl genera, only two units, one of which was the most diverse in the assemblage, satisfied the conditions of high resource availability and early age of reproduction (Fig. 2A, B, D). Thus, knowing these two conditions gives us a 50:50 chance of picking the most diverse unit out of an entire assemblage. This represents a sixfold increase in predictive ability over random chance and 2-, 3-, and 4.7-fold improvements in predictive ability over those attained knowing only resource availability for avian families, mammalian orders, and waterfowl genera, respectively. Only one family of bats, the most diverse, Vespertilionidae, had high resource availability and early age of reproduction (Fig. 2C). Thus, knowing resource availability and age of reproduction identifies the most diverse unit of bats. This is a ninefold increase in predictive ability over chance and a 6.1-fold increase in predictive ability over that attained knowing resource availability alone.

DISCUSSION

We have identified correlations between the modern life history traits of organisms and the taxonomic diversity they have attained throughout the course of evolution. The most diverse taxa can be characterized as those with short generation times (early age of first reproduction and short life-spans) and with an ability to colonize new resources (high mobility and/or high resource availability). Partitioning of reproduction and annual fecundity were less closely correlated with diversity.

Generation time and colonization ability could be important to diversification because they directly influence the likelihood of speciation and extinction. In Fig. 3 we model a causal scenario suggested by the correlations we reported between ecological traits and diversity. Reduced generation time is a key to diversification because it is a very effective way to increase a population's intrinsic rate of increase (r) (Cole 1954, Lewontin 1965, MacArthur and Wilson 1967). Populations with high growth rates, especially very mobile ones, are expected to be good colonists and therefore often encounter new resources (MacArthur and Wilson 1967). Rapid turnover of individuals in the population can lead to strong selection and rapid evolution (Stanley 1979). Founding populations may therefore speciate rapidly as they adapt to new resources. Similarly, they may withstand extinction in the face of environ-
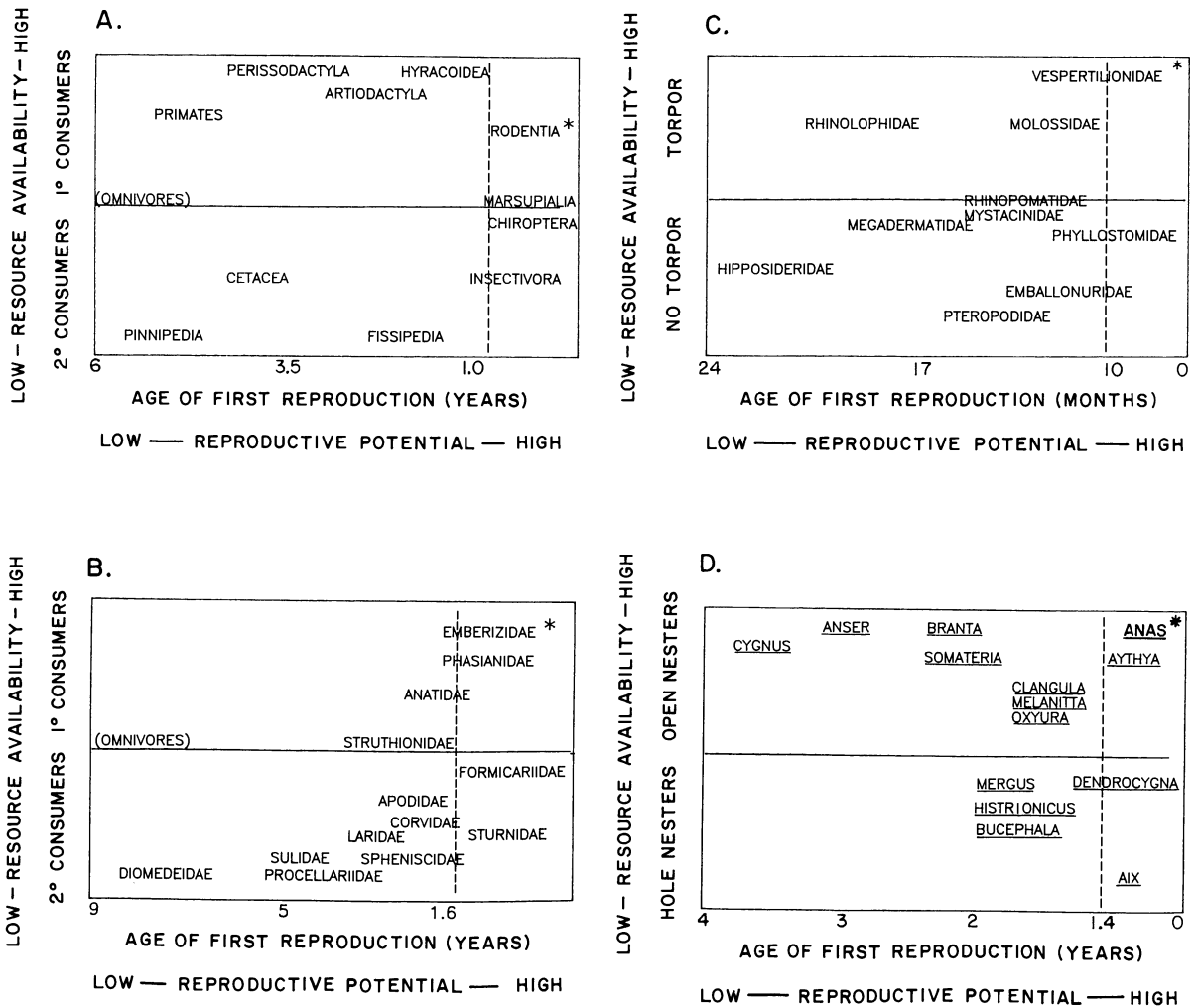
FIG. 2. Interaction of resource availability and age of first reproduction on relative diversity of: (A) mammalian orders, (B) avian families, (C) chiropteran families, and (D) waterfowl genera. The solid horizontal line separates high from low resource availability. Dashed vertical line divides taxa that reproduce before 90% of the taxa in their assemblages from taxa with more delayed ages of first reproduction. * denotes the dominant unit.

mental deterioration because they can adapt to environmental changes and quickly attain large population sizes over broad geographic ranges (Van Valen 1973a, b, Goodman 1974, Hansen 1978, Brown 1984, Flessa and Thomas 1985, Jablonski 1985). High mobility and rapid population growth rates also reduce extinction by enabling populations to recolonize areas in their range that experienced local extinctions (Carr and Kitchell 1980). Short generation time also increases the rate of recombination and mutation (Simpson 1953: 129–132), which may provide the raw material for the evolution of a unique key character commonly associated with adaptive breakthroughs (Simpson 1944, 1953, Van Valen 1971).

Our model differs from other models of diversification by specifically tying life history traits to speciation and extinction probabilities. Other models of diversity have relied extensively on fossil taxa where little

is known about life history. Accordingly, only two life history traits (dispersal ability and ecological specialization) have received much attention. Most studies concur with ours by suggesting that high dispersal ability increases geographic range and increases the ability to recolonize former ranges, thereby reducing extinction (Van Valen 1973b, Gould and Eldridge 1977, Hansen 1978, Carr and Kitchell 1980, Flessa and Thomas 1985, Jablonski 1985). However, most studies also indicate that widespread populations exhibit low speciation rates (Mayr 1963, Bush et al. 1977, Hansen 1978, Stanley 1979, Vrba 1980). Our results suggest that reduction in extinction overwhelms reduced speciation in many cases because taxa with high population growth rates commonly attain high diversity. Moreover, broad geographic range and the ability to colonize new resources may actively promote speciation while simultaneously reducing extinction. This has
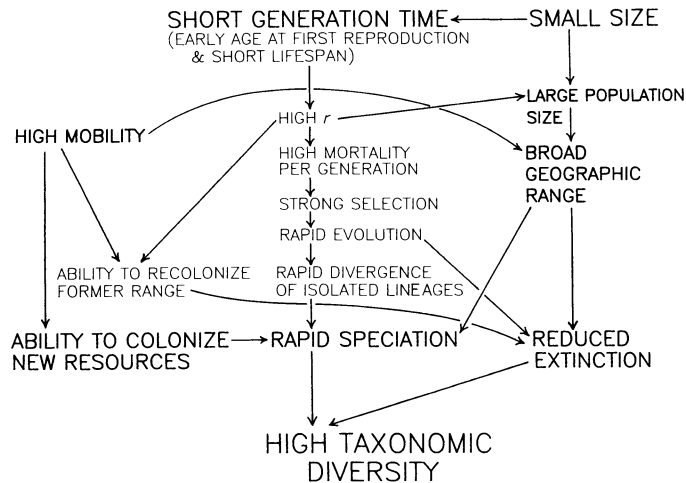
FIG. 3. Summary model of the deterministic influence of life history traits and colonization ability on taxonomic diversity. See *Discussion* for explanation.

been suggested for a few taxa (cockles: Stanley 1975, Bovidae: Vrba 1980). However, our results suggest that it is a common occurrence.

Even though a positive relationship between reduced generation time and evolutionary rate has been repeatedly searched for there are no convincing arguments as to its existence. Species with low r have not evolved slower than ones with high growth rates (Zeuner 1931, Simpson 1953, Kurten 1968, Stanley 1979), and Vrba (1980) cites several examples where the opposite is true. How are these results compatible with our claim that taxa with high growth rates attain high diversity? These apparently contradictory findings are explained by the difference between diversity and evolutionary rate. High evolutionary rates stem from high rates of speciation and high rates of extinction, which produce rapid species turnover, whereas, high diversity results from high rates of speciation and *low* rates of extinction. Speciation rates and extinction rates are positively correlated (Stanley 1979), but this linkage must be minimal for very diverse taxa. Our results indicate that the difference between speciation rate and extinction rate is maximized in taxa with high rates of population growth and this is why they can attain high diversity and yet not exhibit extraordinarily high evolutionary rates.

Allopatric speciation is presumably the primary mode of speciation producing the diversity patterns we have investigated (Mayr 1963, Bush 1975, Stanley 1979, Vrba 1980). Our results suggest that intrinsic properties of organisms (e.g., high colonization ability, large and widespread populations) directly influence the probability of allopatric speciation. Speciation need not be controlled primarily by extrinsic properties of the environment (physiographic complexity and environmental harshness [Cracraft 1982, 1985], geographic complexity [Stanley 1979], continental fragmentation [Valentine and Moores 1970]). We expect complex,

dynamic environments where semi-isolated habitats are common ("crucibles of diversification," Stanley 1979) to contain taxa with different intrinsic properties. Those with high reproductive potential are predicted to take full advantage of this extrinsic complexity by successfully colonizing many habitats and diversifying before those with low reproductive potential.

Our model in Fig. 3 applies to the majority of assemblages we investigated. However, small size and short generation time are not sure tickets to high taxonomic diversity. Differences in environmental variability through the course of evolution may explain why all assemblages are not dominated by those taxa with the highest r or smallest body size. Elsewhere we argued that small-sized taxa with high intrinsic rates of increase may dominate assemblages in variable environments, but may be outcompeted by large-sized taxa with slower growth rates in constant environments (Dial and Marzluff 1988).

An interesting twist in the link between body size and diversity is that very diverse taxa are usually composed of small, but not the smallest organisms (Dial and Marzluff 1988). This may occur because environments change in variability as assemblages evolve, which constrains diversification of extreme-sized taxa (Dial and Marzluff 1988). In addition, because age of reproduction correlates more strongly with diversity than does body size it appears that all life history traits may not be monotonically related to size. Instead small, but not the smallest, organisms may often have the highest r values (a conclusion supported by the models of Roff [1981] and the large amount of variation in measures of r not accounted for by linear correlations with body size, e.g., in Peters [1983] the average r^2 for 39 allometric relationships describing individual and population production was only 0.64).

Our deterministic model contains a stochastic element, but it differs from traditional stochastic models

(e.g., Raup et al. 1973, Anderson and Anderson 1975, Osman and Whitlatch 1978). In our model, speciation and extinction events do not occur at random with respect to units differing in body size, mobility, intrinsic rate of increase, or resource availability. Instead, nonrandom speciation and extinction among groups differing in these factors accounts for much of the difference in present-day taxonomic diversity. Diversity is not linearly related to the factors we investigated (note there is often a lack of correlation between diversity and selected life history traits within an assemblage; Table 1). Instead, the fact that dominant taxa had consistently early ages of reproduction and short life-spans (Fig. 1), but few of the correlations in Table 1 were significant, indicates that a step function describes the relationship between these life history traits and diversity better than a linear function. Alternatively, the rarity of significant correlations may simply reflect the small sample sizes underlying most of these tests. However, few tests within even the largest assemblages were significant. Our results suggest that there is commonly a pool of units with approximately equal diversification potential from which only one dominates the assemblage. Taxa in these pools have early ages of reproduction and high resource availability (Fig. 2). In our model, stochastic events may determine which of the units in such a pool dominates.

We have only scratched the surface in our investigation of the relative importance of ecological factors to diversification. Many other factors not investigated may also influence diversity. A promising avenue of future research may be to incorporate a taxon's degree of ecological specialization into our deterministic model of diversification. Ecological generalists may persist in spite of changing environmental conditions that should reduce their chances of extinction and promote diversification. Many have suggested that the degree of specialization influences diversity in specific assemblages (Fryer and Iles 1969, Kohn 1971, Stanley 1973, Jackson 1974, Hallam 1975, Hansen 1978, Vrba 1980). However, to test the relative importance of specialization we require comparative data from a wide range of taxa. As such data accumulate for attributes such as specialization we will be able to construct a more complete model of the interplay between ecology and evolutionary diversification.

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APPENDIX 1

Assemblages investigated, units dominating them, and relative age of first reproduction (rel age), fecundity (rel fecund), and longevity (rel life) of dominant units. N equals the size of the assemblage (number of units with available data).

Assemblage	Subunit/ unit*	Dominant unit	Demographic data†					
			Rel age	N	Rel fecund	N	Rel life	N
Mammals								
Chiroptera	S/F	Vespertilionidae	0	9	1.0	7	...	...
	G/F	Phyllostomatidae	.13	9	0	6	...	...
Vespertilionidae	S/G	*Myotis*	.38	9	...	...	...	...
Marsupialia	S/F	Didelphidae	0	5	1.0	7	.17	7
	G/F	Dasyuridae	.25	5	.83	7	0	7
Rodentia	S/F	Cricetidae	0	6	.64	12	0	7
	G/F	Cricetidae	0	6	.64	12	0	7
Peromyscus	SS/S	*P. maniculatus*	0	10	0	10	...	...
Carnivora	S/F	Viverridae	.40	6	.40	6	.50	7
	G/F	Viverridae	.40	6	.40	6	.50	7
Primates	S/G	*Cercopithecus*	0	11	...	...	...	...
Artiodactyla	S/F	Bovidae	.40	6	.80	6	.2	6
	G/F	Bovidae	.40	6	.80	6	.2	6
Bovidae	S/SF	Gazellinae	.45	12	0	13	.18	12
	G/SF	Caprinae	.82	12	1.0	13	.64	12
Overall	S/O	Rodentia	.18	12	.89	10	.22	10
	G/O	Rodentia	.18	12	.89	10	.22	10
	F/O	Rodentia	.18	12	.89	10	.22	10
Birds								
North American waterfowl	S/G	*Anas*	0	15	.71	15	.22	10
(open nesters)	S/G	*Anas*	0	10	1.0	10	.20	6
(hole nesters)	S/G	*Mergus*	.50	5	.50	5	0	4
North American Galliformes	S/G	*Callipepla*	0	15	.50	9	.50	7
Corvidae	S/G	*Corvus*	...	...	.50	21	.89	10
Seabirds	S/G	*Larus*	.13	16	...	...	...	...
Overall	S/F	Emberizidae	.10	11	.21	15	...	...
Amphibians								
Salamanders	S/G	*Plethodon*	.67	16	.71	8	...	...
Frogs and toads	S/F	Hylidae	.67	4	...	...	...	...
Reptiles								
Crotaphytus	SS/S	*C. collaris*	0	2	...	...	...	...
Eumeces	SS/S	*E. egregius*	0	5	...	...	...	...
Sceloporus	SS/S	*S. undulatus*	0	6	...	...	...	...
Overall	S/O	Sauria	0	4	.33	4	...	...
Plants								
North American trees								
(Gymnosperms)	S/G	*Pinus*	.10	11	...	...	.40	6
(Angiosperms)	S/G	*Salix*	.15	21	...	...	0	21
Overall plants	G/F	Compositae	.19	17	...	...	...	...

* SS (subspecies), S (species), G (genera), SF (subfamily), F (family), O (order).

† Demographic data are from Walker 1975 and Eisenberg 1981 (mammals), Asdell 1964 and Layne 1968 (Rodentia), Tuttle and Stevenson 1982 (Chiroptera), Haltenorth and Diller 1980 (Artiodactyla), Bellrose 1980 (waterfowl), Johnsgard 1976 (galliforms), Goodwin 1986 (corvids), Nelson 1979 (seabirds), Taylor and Guttman 1977 (amphibians), Tinkle 1969 (reptiles), Fowells 1965 (gymnosperms), and Farrell 1985 (overall plants). We supplemented each of these sources with additional data from Altman and Dittmer 1972.

APPENDIX 2

Ecological characteristics of phylogenetically defined sister taxa. Differing letters separate monophyletic sister groups that are adjacently listed. Sources for phylogeny are listed in *Methods*.

Sister groups	Diversity (no. species)	Age of 1st reprod. (yr)	Average longevity (yr)	Avg. annual fecundity (offsp.·$♀^{-1}$·yr^{-1})
Mammals*				
A) Rhinopomatidae	4	1.33	...	1.0
B) Crasconycteridae + Emballonuridae	44	1.0	12	1.0
A) Rhinolophidae	127	1.67	23	1.0
B) Hipposideridae	40	2.0	...	1.0
A) Cervidae	32	2.25	17.5	1.0
B) Giraffidae	2	3.00	24.0	1.0
A) Cervidae + Giraffidae	34	2.63	20.8	1.0
B) Bovidae + Antilocapridae	100	1.45	15.3	1.0
A) Hippotraginae	5	2.15	19.3	1.0
B) Bovinae	12	3.00	26.0	1.0
C) Caprinae	16	2.00	18.0	1.5
A) Muridae	457	0.18	4.4	55.5
B) Cricetidae	567	0.10	3.1	13.9
A) Viverridae	72	1.90	13.3	3.1
B) Felidae	35	3.10	16.2	2.3
A) Canidae	35	2.00	11.3	5.6
B) Mustelidae	67	1.00	12.1	4.6
C) Ursidae	7	3.30	28.4	1.2
D) Procyonidae	18	1.50	12.8	2.4
A) Ferae	240	2.12	15.3	3.5
B) Insectivora	343	0.36	3.2	6.2
C) Archonta	1129	2.56	16.2	1.3
D) Ungulata	304	4.93	20.5	1.2
A) Polyprotodontia	125	0.73	4.4	11.4
B) Diprotodontia	136	1.04	9.1	2.0
A) *Cercopithecus*	12	2.50	24.0	1.0
B) *Erythrocebus*	1	3.00	20.0	1.0
A) *Cynopithecus + Macaca*	13	4.00	30.0	1.0
B) *Papio + Mandrillus*	8	4.50	28.0	1.0
A) *Cynopithecus + Macaca + Papio + Mandrillus +* *Cercocebus + Theropithecus*	27	4.50	26.3	1.0
B) *Cercopithecus + Erythrocebus*	13	2.75	22.0	1.0
Birds†				
A) Diomediae	11	8.10	39.0	1.0
B) Procellariae	29	6.25	30.0	1.0
A) Corvidae	106	2.00	15.6	4.33
B) Grallinidae	4	4.00	15.4	4.25
A) Phaethontidae	3	4.50	...	1.00
B) Other Pelecaniformes	59	5.00	29.3	1.80
A) Accipitridae + Falconidae	279	3.10	22.3	2.90
B) Pandionidae	1	3.50	21.0	2.50

* Demographic data are from Eisenberg 1981.

† Demographic data are from Altman and Dittmer 1972, Nelson 1979, Newton 1979, and Goodwin 1986.