THE ECOLOGICAL BASIS OF LIFE HISTORY VARIATION IN MARSUPIALS

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Abstract. Our understanding of the diversity of mammalian life histories is based almost exclusively on eutherian mammals, in which the slow–fast continuum persists even after controlling for effects of body size and phylogeny. In this paper, we use modern comparative methods to test the extent to which this eutherian-based framework can be extrapolated to metatherian mammals. First, we examine the pattern of covariation among life history traits, and second, we test for correlations between variation in life history and variation in six candidate ecological variables: type of diet, extent of intraspecific competition, risk of juvenile mortality, diurnal pattern of activity, arboreality, and rainfall pattern. Even when controlling for body size and phylogeny, we observe a slow–fast continuum in metatherian mammals. Some parameters involved are different from those identified by studies of eutherians, but the underlying relationships among longevity, fecundity, and age at maturity persist. We also show that overall variation in a key life history variable, reproductive output (measured by annual reproductive rate and litter size), is significantly related to variation in type of diet, with a foliage-rich diet being associated with low fecundity. This is interesting because, although ecological correlations have been found within some eutherian subgroups, modern comparative approaches have failed to reveal robust ecological correlates of overall life history diversity in eutherians.

Key words: body size; comparative analysis; diet; eutheria; independent contrasts; life history; mammals; marsupialia; metatheria; reproductive rate; trade-off.

INTRODUCTION

Comparative analyses of eutherian mammals and other taxa have revealed a ''slow–fast continuum'' in life history traits: larger body size is associated with larger neonate size, slower metabolic rate, slower growth, longer gestation period, delayed sexual maturity, lower fecundity, and greater longevity (Harvey et al. 1989, Read and Harvey 1989, Promislow and Harvey 1990, Purvis and Harvey 1995). In eutherian mammals, previous explanations for the slow–fast continuum assumed that life history traits are constrained by allometry to correlate with body size, brain size, or metabolic rate (e.g., Western 1979, Western and Ssemakula 1982). Brain size has been suggested as the key variable because rate of growth of the brain is a rate-limiting factor in development (Sacher and Staffeldt 1974). It has also been proposed that life history traits could be directly limited by maternal metabolic rate, which is dependent on body size (Stearns 1992). However, such constraints are not complete explanations because the fast–slow continuum persists even after controlling for variation in body size and phylogenetic ancestry (Harvey et al. 1989). Explaining this ''resid-

ual'' pattern of variation in life histories is the current challenge (Promislow and Harvey 1991, Owens and Bennett 1995).

Theory predicts that the residual variation in life histories might be correlated with ecological factors such as the availability of energy, the degree of intraspecific competition, or risk of predation (Partridge and Harvey 1988, Promislow and Harvey 1991). For example, Owens and Bennett (1995) showed that life histories of birds diversified at the same time as a dichotomy appeared in nesting habit, a trait associated with variation in nestling mortality rates in modern species (see also Martin and Li 1992, Martin 1995). However, such correlations have proven difficult to demonstrate among eutherian mammals. Life history variation among particular subgroups of eutherians, such as ungulates and canids, has been found to be correlated with ecological variables such as habitat type or diet (e.g., Ross 1987, Harvey et al. 1989, Sæther and Gordon 1994, Geffen et al. 1996), but no single ecological factor has been shown to correlate with life history variation across the entire eutherian clade (Purvis and Harvey 1995). One plausible explanation for this failure to find a general ecological correlate of life history variation in eutherians is provided by Charnov's unified model of mammalian life history evolution. Charnov's model proposes that life history traits are adaptations to age-specific mortality rates because

a relatively high juvenile mortality rate favors early sexual maturity, large litters, rapid growth, and small body size (Charnov 1991, 1993). If this mechanism applies, then links between life history and ecology will be idiosyncratic to particular clades, because a given life history response could result from different ecological causes of mortality in different species. Nevertheless, it is puzzling that it has also proven difficult to find ecological correlates of the key parameters in Charnov's model (Harvey et al. 1989, Charnov 1993, Purvis and Harvey 1995). Is life history diversity among mammals really due to the effects of a different ecological factor in each clade?

In contrast to eutherian mammals, life history diversity among marsupials has been subjected to little modern quantitative analysis. Although marsupials are conservative in terms of body size, ecology, and social organization, and generally have "slower" life histories than eutherians of similar body size (Lee and Cockburn 1985, Tyndale-Biscoe and Renfree 1987), they nevertheless show a great diversity of life history tactics. Females of extant species have adult body masses of 4 g–31 kg (Strahan 1995). The "fast" end of the continuum includes Didelphids and Dasyurids with maximum litter sizes of 10–16 and typical life-spans of a year or less. At the "slow" end of the continuum, koalas (*Phascolarctos cinereus*) and wombats (*Vombatus* and *Lasiorhinus* spp.) have a single offspring every two or three years and may live >25 yr. Diversity of life histories within the subclass often has been attributed to variation in diet, with an energy-poor or patchily distributed diet being linked to low fecundity. However, life history variation may also be explained by other variables that are correlated with diet and with each other (Russell 1982, Lee and Cockburn 1985, Eisenberg 1988). Quantitative tests of these ideas are needed, because the most recent synthesis of marsupial life history and ecology was attempted 15 yr ago, when many fewer species and habitats had been studied, and before modern comparative methods and molecular phylogenies were available (Lee and Cockburn 1985).

The goal of our study was to use modern comparative methods and a new database to determine (1) the pattern of relationships among life history traits, and (2) if there are consistent associations between life history and ecology in metatherians. We focus on ecological factors suggested as explanations for diversity in marsupial life histories: type of diet, extent of intraspecific competition, risk of juvenile mortality, pattern of diurnal activity, extent of arboreality, and rainfall pattern. "Slow" marsupial life histories have been predicted to be associated with intense competition for food (Eisenberg 1988), high juvenile mortality due to predation (Russell 1982, Lee and Cockburn 1985), arboreality (Eisenberg 1988), more diurnal habits (Eisenberg 1988), or low, unpredictable rainfall (Lee and Cockburn 1985, Ward 1998). In this study, we concentrate on patterns across the subclass metatheria, focusing on

females. We do not attempt to examine specializations that have risen only a few times within particular families, such as male semelparity within the Dasyuridae, ant-eating within the Notoryctidae and Myrmecobiidae, or fungi eating in the Potoroidae. We also leave quantitative comparisons between the life history strategies of marsupials and eutherians for the future.

METHODS

Data collection and definitions

We compiled a database on Australian, Papua New Guinean, and South American species of marsupials for which life history data were available, including both field and captive studies, but preferring field data (see Appendix in *Ecological Archives*). Age-related life history traits were gestation length (days), age at weaning (days), age at maturity (age at first conception, in days), and life-span of females (years). Mass-related variables were mean mass of adult females (grams), and mass (averaged across both sexes) at birth, permanent exit from the pouch (PEP), and weaning (grams). Litter size was defined as the mean number of young born per reproductive event, excluding supernumary young (i.e., young in excess of the number of teats, as these have no possibility of survival). The number of young per year was calculated by multiplying mean litter size by mean number of reproductive events per female per year. Type of diet was ranked in terms of energy and protein content: 4, >50% invertebrates or vertebrates; 3, nectar or fruit with invertebrates; 2, seeds, grass, roots, leaves, fruit, and invertebrates; 1, >50% grass or browse (see Sæther and Gordon 1994, Owens and Bennett 1995). Strength of intraspecific competition was estimated by collecting data on population density and mean group size. Intensity of intraspecific competition was assumed to be positively related to both of these indices (Purvis and Harvey 1995). Population densities were from mark–recapture, radiotelemetry, or line-transect data, considered at the scale of the study site (i.e., ecological densities). Mean group size was based on observations of feeding groups. Risk of juvenile predation was assumed to be associated with the "safety" of the type of shelter (Owens and Bennett 1995). Shelter type was ranked: 1, protected (burrow or constructed nest in tree hollow); 2, intermediate (tree canopy, hollow log, under rock, nest on ground or in soil crack); or 3, open (under shrubs, in grass or shade of tree). Diurnality categories were: 0, strictly nocturnal; or 1, not strictly nocturnal. Species reported to be both arboreal and terrestrial were classed as "arboreal," and rockpile dwellers as "terrestrial." Rainfall pattern was characterized by mean rainfall per year (in millimeters). For mainland Australian species and Papua New Guinean species, respectively, mean annual rainfall data reported in AUSLIG (1980) and McAlpine et al. (1975) were compared with geographical ranges in Strahan (1995) and Flan-

nery (1990) to obtain values at the center of a species' range. For South American families and species studied only in restricted areas, such as offshore islands, we used values of annual rainfall reported in published ecological studies. Data were collected from the primary literature, reports, theses and unpublished studies. If data from more than one study were available, we used the arithmetic mean.

Statistical analyses

We analyzed both raw species data and phylogenetically independent contrasts, as both types of analysis are likely to be informative (Price 1997, Harvey and Rambaut 2000). Before each procedure, we tested assumptions of normality and homoscedasticity using Shapiro-Wilks' tests and Barlett's tests, respectively, and $\log_{10}$-transformed all allometric data (body size, all other life history variables, and density). Because multiple comparisons addressing the same broad hypotheses were carried out on different combinations of variables (between 42 and 81 for each type of analysis), the α value of tests was corrected using the Dunn-Sidák procedure (Sokal and Rohlf 1981). All analyses were performed using the software package SAS (SAS Institute 1989).

Two types of associations were analyzed: relationships between pairs of life history traits, and between each life history trait and the ecological variables. For each of these types of association, three different approaches were taken. We first analyzed relationships using the raw, species-specific data by performing least squares linear regression on continuous variables, and ANOVAs on ecological categories vs. life history variables. Relationships between litter size, group size, and the other continuous variables were analyzed using Spearman rank correlation tests. Secondly, we repeated these analyses on residual data to control for the effects of variation in body size. Residuals were calculated from regressions on body mass of adult females. Thirdly, we repeated the analyses using residual evolutionarily independent contrasts to control for variation in both body size and degree of shared phylogenetic ancestry (Felsenstein 1985, Harvey and Pagel 1991, Pagel 1992). For this third set of analyses, phylogenetically independent contrasts were initially obtained using the software package CAIC 2.0, with the CRUNCH algorithm for continuous data and the BRUNCH algorithm for categorical ranked data (Purvis and Rambaut 1995). For contrasts in continuous data, we then calculated residuals using linear regression, with contrast in body mass of adult females as the independent variable and the intercept forced through the origin (Harvey and Pagel 1991, Garland et al. 1992). We then analyzed relationships between the resulting residuals of contrasts using standard regression as before.

Contrasts based on categorical variables.—To examine the relationship between each ecological category and contrasts in life history traits relative to body mass, we fitted the regression between contrasts in each life history trait relative to body mass (as before) to the data set of contrasts in life history traits relative to each ecological category. This was done by calculating contrasts of a life history variable and body mass relative to an ecological category using the BRUNCH algorithm in CAIC, then taking the slope of the original relationship between contrasts in life history and contrasts in body mass, and subtracting the contrasts in the life history trait from the contrasts in body mass (relative to the ecological category) multiplied by the slope of the original regression (see Sæther and Gordon 1994, Owens and Bennett 1995). We then tested if the new mean residual contrasts were significantly different from zero using a one-sample t test (Owens and Bennett 1995, Purvis and Harvey 1995).

Concentrated-changes randomization tests.—Where our analyses based on independent comparisons suggested that there was a significant correlation between life history variation and an ecological factor, we checked the robustness of these relationships using Maddison's (1990) concentrated-changes tests. This method tests whether changes in life history are more likely than expected by chance to occur in phylogenetic lineages with particular ecological characteristics, given the total number of changes in life history traits and overall phylogenetic distribution of ecological traits (see Maddison 1990, Maddison and Maddison 1992). To perform the test, however, we had to reduce life history and ecological variables to binary states.

Phylogenies.—For analyses based on evolutionary independent contrasts and the concentrated-changes tests, we used Johnson's (1998) composite phylogeny based primarily on Kirsch et al. (1997), incorporating recent studies (Burk et al. 1998, Springer et al. 1998, Blacket et al. 1999) and some extra data on South American taxa from Patton et al. (1996). Because branch lengths for many taxa were unknown, we assumed that branch lengths were equal, as recommended by Purvis and Rambaut (1995). We used MacClade (Maddison and Maddison 1992) to infer values of ancestral traits and map changes onto the family-level phylogeny.

Results

Raw species data

With the exception of gestation length, all of the raw life history traits were strongly related to each other (Table 1). The most closely correlated were age at weaning with annual reproductive rate (inversely related), life-span with annual reproductive rate (inversely related), and life-span with age at weaning. Litter size was highly negatively correlated with all other life history traits except for gestation length, mass of young at permanent exit from the pouch (PEP), and weaning. Differences in body mass of adult females explained a significant percentage of the variation in annual repro-

TABLE 1. Pattern of covariation among marsupial life history traits, based on raw species-specific data. Values are correlation coefficients, with sample sizes (no. species) in parentheses.

Trait†	Age at maturity	Life-span	Age at weaning	Gestation length	Annual reproductive rate
Life-span	**0.41** (94)				
Age at weaning	**0.51** (100)	**0.69** (97)			
Gestation length	**0.25** (78)	**0.08** (74)	**0.15** (82)		
Annual reproductive rate	−**0.52** (98)	−**0.72** (93)	−**0.74** (102)	0.13 (80)	
Neonatal mass	**0.40** (40)	**0.76** (37)	**0.76** (41)	0.109 (34)	−**0.62** (40)
Mass at PEP	**0.28** (60)	**0.64** (57)	**0.75** (66)	**0.18** (46)	−**0.62** (60)
Mass at weaning	**0.26** (67)	**0.63** (63)	**0.77** (61)	0.088 (50)	−**0.55** (67)
Body mass	**0.24** (111)	**0.61** (115)	**0.72** (113)	0.04 (85)	−**0.50** (111)
Litter size	−ve* (108)	−ve* (109)	−ve* (11)	NS (83)	* (113)

Notes: Associations between two continuous variables were tested using regression models; boldface indicates a significant positive or negative association. Associations between a continuous variable and a categorical variable were tested using Spearman rank correlations. A single asterisk indicates a significant association ($P < 0.05$); NS indicates a nonsignificant association; and "−ve" indicates a negative association.

† All traits are continuous variables except for litter size, which is a categorical variable.

ductive rate, and 24% (age at maturity) to 72% (age at weaning) of the variation in all of the age-related life history traits except gestation length. Marsupial young leave the pouch and are weaned at a fixed percentage of maternal mass; mass of the mother explained 93% of the variation in mass at permanent exit from the pouch ($F_{1,63} = 824$), and 96% of the variation in mass at weaning ($F_{1,69} = 1487$). Neonatal mass was not as closely correlated with adult body size ($F_{1,39} = 129$, $r^2 = 0.77$).

Group size and diet were significantly associated with most life history traits (except gestation length
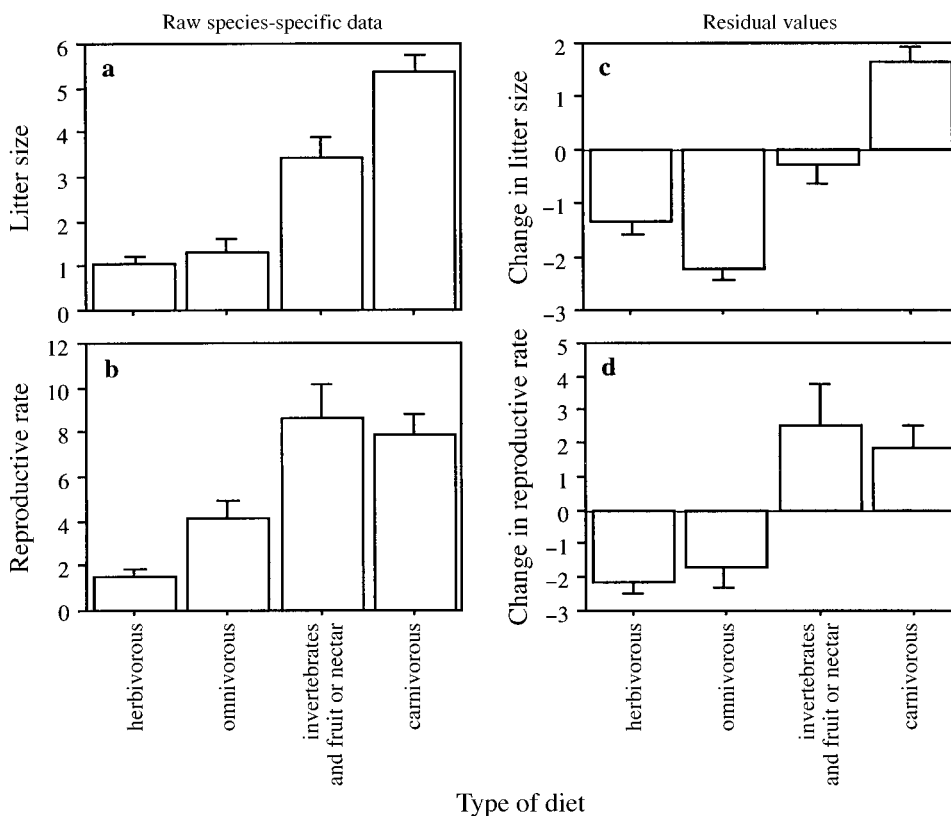

FIG. 1. Associations between marsupial life history variables and diet types. Data are means + 1 SE. Figures based on raw species-specific data show relationships between diet categories and (a) litter size and (b) annual reproductive rate. Figures based on residual values, after controlling for variation in body size, show relationships between diet categories and (c) residual litter size and (d) residual annual reproductive rate. Diet categories are the four-point scale described in detail in *Methods: Data collection and definitions.*

TABLE 1. Extended.

Neonatal mass	Mass at PEP	Mass at weaning	Body mass
0.90 (32)			
0.85 (31)	**0.97** (49)		
0.77 (40)	**0.93** (65)	**0.96** (71)	
−**ve*** (40)	NS (65)	NS (71)	−**ve** (160)

and neonatal mass, in the case of group size, and gestation length in the case of diet), such that more herbivorous species, and those occurring at lower densities, were further toward the "slow" end of the slow–fast continuum (Table 2; Fig. 1a, b). Shelter type was negatively associated with annual reproductive rate and litter size, and was positively associated with mass-related life history traits such that marsupials sheltering in more open sites were further toward the slow end of the slow–fast continuum (Table 2). Non-nocturnal species (30 of 134 species) showed delayed weaning and maturity in comparison with strictly nocturnal species (Table 2). There was no difference in any life history traits according to rainfall or between arboreal and terrestrial species.

Residual data

Strong relationships persisted between all of the age-related life history traits (except for gestation length) after we controlled for body mass of adult females (Table 3). The most closely correlated traits were age at weaning and annual reproductive rate ($F_{1,101} = 84.2$,

$r^2 = 0.46$), and life-span and annual reproductive rate ($F_{1,91} = 68.2$, $r^2 = 0.43$). Annual reproductive rate and litter size were both inversely related to mass at PEP and weaning, after we accounted for maternal body mass. Litter size explained more than one-half of the variation in mass at PEP, but only around one-fourth of the variation in neonatal mass. Most relationships between ecological variables and categories did not persist after the effect of body mass was removed (Table 4). Life-span and neonatal mass were still correlated with group size, and annual reproductive rate was still inversely related to density, but only diet continued to be strongly related to a range of age- and rate-based life history traits (age at maturity, age at weaning, annual reproductive rate, and litter size) independently of body size. Again, a herbivorous diet was associated with a relatively "slow" life history (Fig. 1c, d). Arboreality was associated with age at maturity after adult female body mass has been statistically removed, but not before, indicating that arboreal species have relatively delayed sexual maturity compared to terrestrial species of equivalent size (Table 4).

Residuals of independent contrasts

Only three relationships between life history traits persisted after body mass of adult females and the effects of non-independence due to phylogeny were controlled, and the Dunn-Sidák correction for multiple comparisons was performed. Annual reproductive rate remained closely inversely correlated with life-span and age at weaning, and positively correlated with litter size (Table 5).

Before the α correction for multiple comparisons, type of diet and annual reproductive rate, and type of diet and litter size were related ($t = -2.33$, df = 13, $P = 0.036$; and $t = -2.845$, df = 12, $P = 0.013$, respectively) such that the number of young born an-

TABLE 2. Pattern of covariation between marsupial life history traits and seven ecological variables, based on raw species-specific data. Values are correlation coefficients, with samples size (no. species) in parentheses.

Trait†	Continuous variables				Categorical variable		
	Group size	Rainfall	Density	Diet	Arboreality	Diurnality	Shelter
Age at maturity	**0.08** (104)	0.02 (105)	0.03 (86)	−**ve*** (111)	NS (105)	* (102)	NS (105)
Life-span	**0.11** (100)	0.01 (106)	0.11 (77)	−**ve*** (115)	NS (108)	NS (104)	NS (108)
Age at weaning	**0.06** (104)	0.05 (109)	−**0.16** (83)	−**ve*** (112)	NS (109)	* (106)	* (108)
Gestation length	0.02 (81)	0.01 (83)	<0.01 (60)	NS (84)	NS (82)	NS (83)	NS (82)
Annual reproductive rate	−**ve*** (106)	<0.01 (110)	0.06 (84)	* (109)	NS (110)	NS (109)	−**ve*** (108)
Neonatal mass	NS (41)	0.02 (41)	0.24 (36)	−**ve*** (42)	NS (40)	* (41)	* (40)
Mass at PEP	* (63)	0.01 (63)	−**0.30** (54)	−**ve*** (65)	NS (63)	NS (63)	* (63)
Mass at weaning	* (69)	<0.01 (68)	−**0.31** (59)	−**ve*** (70)	NS (68)	NS (67)	* (68)
Litter size	−**ve*** (134)	NS (139)	NS (99)	* (153)	NS (149)	NS (132)	−**ve*** (149)

Notes: Associations between two continuous variables were tested using regression models; boldface indicates a significant positive or negative association. Associations between a continuous variable and a categorical variable were tested using either ANOVA models (for diet, arboreality, diurnality, and shelter categories) or Spearman rank correlations (for group size and litter size). Single asterisks indicate significant differences or association ($P < 0.05$); NS indicates nonsignificant differences or association; "−ve" indicates a negative association. Associations between group size and annual reproductive rate, neonatal mass, mass at PEP (permanent exit from the pouch), and mass at weaning were also tested using Spearman rank correlation tests.

† All traits are continuous variables except for litter size, which is a categorical variable.

TABLE 3. Pattern of covariation among marsupial life history traits, based on residual species-specific data, after controlling for variation in body size. Values are correlation coefficients, with sample sizes (no. species) shown in parentheses.

Trait†	Age at maturity	Life-span	Age at weaning	Gestation length	Annual reproductive rate	Neonatal mass	Mass at PEP	Mass at weaning
Life-span	**0.22** (94)							
Age at weaning	**0.40** (100)	**0.25** (97)						
Gestation length	**0.20** (78)	0.06 (74)	**0.22** (82)					
Annual reproductive rate	**−0.36** (98)	**−0.43** (93)	**−0.46** (102)	0.11 (80)				
Neonatal mass	0.01 (40)	**0.26** (37)	**0.19** (41)	0.20 (34)	0.16 (40)			
Mass at PEP	0.01 (60)	**0.19** (57)	**0.39** (66)	0.14 (46)	**−0.27** (60)	**0.78** (32)		
Mass at weaning	0.10 (67)	**0.21** (63)	**0.18** (61)	0.13 (50)	**−0.36** (67)	**0.37** (31)	**0.51** (49)	
Litter size	**−0.25** (108)	**−0.20** (109)	**−0.08** (11)	0.03 (83)	**0.41** (113)	**−0.27** (40)	**−0.51** (65)	**−0.25** (71)

Notes: All variables were continuous. Associations were tested using regression models; boldface indicates a significant positive or negative association.

nually and in each litter decreased more at nodes where the degree of herbivory increased (Table 6). However, the BRUNCH method of analyzing categorical variables using phylogenetically independent contrasts inevitably gives very small sample sizes and low power, so these significant associations disappeared after we corrected for the number of multiple comparisons. Nevertheless, multiple changes in the cladogram (Fig. 2) also strongly suggest that the evolution of herbivory in the diprotodonts lead to much slower life histories, and lineages that became secondarily more carnivorous increased their reproductive rates relative to herbivorous families, regardless of body size. Species in polyprotodont families (Caenolestidae, Didelphidae, Dasyruridae, Thylacinidae, Notoryctidae, Peramelidae, and Myrmecobiidae) produce more than three times as many offspring per year, on average, than do species in diprotodont lineages (mainly herbivorous: Phascolarctidae, Vombatidae, Potoroidae, Macropodidae, Pseudocheiridae, Phalangeridae, Burramyidae, Acrobatidae, and Tarsipedidae) (Fig. 2). Other than these associations with diet, no other relationships between ecological variables and life history traits approached

significance after the effects of both body mass and phylogeny were taken into account.

Concentrated-changes tests

Our randomization tests confirmed the relationship between diet and life history. Diet was scored as a binary variable by giving a value of ''zero'' to all families in categories 1 and 2 of the original four-point dietary scale, and ''one'' to all other families. Litter size was made a binary variable by giving a value of ''zero'' to families with mean litter size of less than two, and a value of ''one'' to other families. Annual reproductive rate was made a binary variable by giving of ''zero'' to families with mean annual fecundity of less than two, and a value of ''one'' to other families.

In total, there were four changes from ''fast'' to ''slow'' life history in terms of number of young per year (in the lineage containing the Phascolarctidae and Vombatidae; and in the families Macropodidae, Phalangeridae, and Pseudocheiridae), and all four changes occurred in lineages with ''herbivorous'' diets (concentrated-changes test, $P = 0.0019$). With respect to litter size, there were again four changes in life history,

TABLE 4. Pattern of covariation between marsupial life history traits and seven ecological variables, based on residual species-specific data, after controlling for variation in body size. Values are correlation coefficients, with sample sizes (no. species) in parentheses.

Trait†	Group size†	Rainfall†	Density†	Diet‡	Arboreality‡	Diurnality‡	Shelter‡
Age at maturity†	0.01 (104)	0.01 (105)	0.01 (86)	* (111)	* (105)	NS (102)	NS (105)
Lifespan†	**0.07** (100)	0.03 (106)	0.02 (77)	NS (115)	NS (108)	NS (104)	NS (108)
Age at weaning†	0.01 (104)	0.01 (109)	0.02 (83)	**−ve*** (112)	NS (109)	NS (106)	NS (108)
Gestation length†	0.01 (81)	<0.01 (83)	0.06 (60)	NS (84)	NS (82)	NS (83)	NS (82)
Annual reproductive rate†	0.23 (106)	0.01 (110)	**−0.05** (84)	* (109)	NS (110)	NS (109)	NS (108)
Neonatal mass†	**0.35** (41)	0.06 (41)	0.06 (36)	NS (42)	NS (40)	* (41)	* (40)
Mass at PEP†	0.05 (63)	<0.01 (63)	0.03 (54)	NS (65)	NS (63)	NS (63)	* (63)
Mass at weaning†	0.01 (69)	0.12 (68)	<0.01 (59)	NS (70)	NS (68)	NS (67)	* (68)
Litter size†	0.02 (134)	0.01 (139)	0.03 (99)	* (153)	NS (149)	NS (132)	NS (149)

Notes: Associations between two continuous variables were tested using regression models; boldface indicates a significant positive or negative association. Associations between a categorical ecological variable and a continuous life history variable were tested using ANOVA models. Asterisks indicate significant differences ($P < 0.05$); NS indicates nonsignificant associations; and ''−ve'' indicates negative associations.

† Continuous variable.

‡ Categorical variable.

TABLE 5. Pattern of covariation among marsupial life history traits based on residual contrasts, after controlling for variation in body size and extent of shared phylogenetic ancestry. Values are correlation coefficients, with sample sizes (no. contrasts) in parentheses.

Trait	Age at maturity	Life-span	Age at weaning	Gestation length	Annual reproductive rate
Life-span	0.16 (54)				
Age at weaning	0.14 (54)	0.07 (54)			
Gestation length	<0.01 (54)	0.03 (54)	0.13 (54)		
Annual reproductive rate	0.11 (54)	**−0.22** (54)	**−0.30** (54)	0.01 (54)	
Litter size	<0.01 (54)	<0.01 (54)	0.09 (54)	0.03 (54)	**0.47** (54)

Notes: All variables were continuous. Associations between variables were tested using regression models; boldface indicates a significant positive or negative association.

in this case one change from fast to slow (the poly-protodont vs. diprotodont divide) and three changes in the opposite direction (in the families Acrobatidae, Burramyidae, and Tarsipedidae). Of these, the change from fast to slow was associated with a lineage with equivocal ecology, whereas all three changes from slow to fast were associated with "omnivorous" lineages. Given that the ancestral state for life history in this clade is fast, the probability of this pattern occurring by chance is $P = 0.027$ (concentrated-changes test).

DISCUSSION

Our analyses confirm that marsupials show a slow–fast continuum in life histories similar to that found in eutherians, and that this pattern is independent of body size and phylogeny. When we controlled for variation in body size and shared ancestry, most relationships weakened, and the only consistently correlated traits were size and age at weaning, age at maturity, life-span, and annual fecundity. We conclude, therefore, that these are key variables for describing life history diversity in marsupials.

As previously described for eutherian mammals, off-spring size, age at maturity, and longevity were positively correlated in marsupials, and there was a negative correlation between these factors and annual fecundity. Life-span is the best predictor of annual fecundity in eutherians, as it is in metatherians (Read and

Harvey 1989). Most analyses of eutherians identify birth mass and gestation period as key life history traits (Harvey et al. 1989, Read and Harvey 1989, Promislow and Harvey 1990); however, our analyses suggest that mass and age at weaning are more important in marsupials. This is probably because most fetal development occurs in the pouch and uterine development times vary less in marsupials. Indeed, Russell (1982) suggested that maternal investment in neonates is ecologically unimportant in marsupials, because birth occurs at an embryonic stage. Despite the fact that gestation length was generally unrelated to other life history traits, neonatal mass is nevertheless an informative life history trait in marsupials because it is correlated with other life history traits, and particularly with mass at PEP (Table 1).

Finally, our results also confirm that life history patterns in marsupials are linked to ecology. In contrast to earlier suggestions by Eisenberg (1988) and Lee and Cockburn (1985), we found no associations between arboreality or rainfall patterns and life history traits. In our analyses of the raw data, type of diet, extent of intraspecific competition, risk of juvenile predation, and diurnality were all significantly associated with key life history variables in the direction predicted previously (Russell 1982, Lee and Cockburn 1985, Eisenberg 1988, Promislow and Harvey 1991). However, after controlling for the effects of body size and an-

TABLE 6. Pattern of covariation between marsupial life history traits and seven ecological variables, based on residual contrasts, after controlling for variation in body size and extent of shared phylogenetic ancestry. Values are correlation coefficients, with sample sizes (no. contrasts) in parentheses.

Traits (continuous variables)	Continuous variables			Categorical variables			
	Group size	Rainfall	Density	Diet	Arboreality	Diurnality	Shelter
Age at maturity	0.045 (45)	0.072 (45)	0.003 (45)	NS (14)	NS (11)	NS (23)	NS (13)
Life-span	0.072 (45)	0.016 (45)	0.043 (45)	NS (14)	NS (11)	NS (27)	NS (15)
Age at weaning	0.024 (45)	<0.001 (45)	0.005 (45)	NS (23)	NS (11)	NS (21)	NS (14)
Gestation length	0.024 (45)	0.031 (45)	0.139 (45)	NS (11)	NS (12)	NS (20)	NS (12)
Annual reproductive rate	0.004 (45)	0.007 (45)	0.008 (45)	NS† (15)	NS (11)	NS (26)	NS (11)
Litter size	0.016 (45)	0.056 (45)	0.036 (45)	NS‡ (14)	NS (12)	NS (25)	NS (17)

Notes: Associations between continuous variables were tested using regression models; boldface indicates significant associations. Associations between categorical ecological variables and continuous life history variables were tested using one-sample *t* tests.

† $P = 0.0367$; ‡ $P = 0.013$; NS indicates associations that are nonsignificant after multiple comparisons have been taken into account.
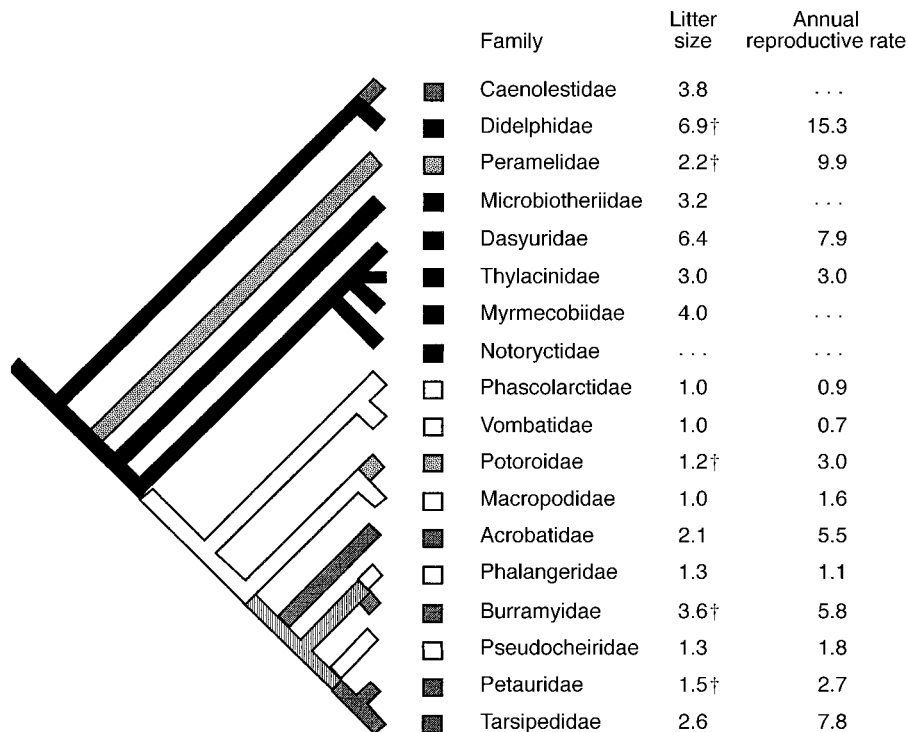
Family	Litter size	Annual reproductive rate
Caenolestidae	3.8	...
Didelphidae	6.9†	15.3
Peramelidae	2.2†	9.9
Microbiotheriidae	3.2	...
Dasyuridae	6.4	7.9
Thylacinidae	3.0	3.0
Myrmecobiidae	4.0	...
Notoryctidae	...	...
Phascolarctidae	1.0	0.9
Vombatidae	1.0	0.7
Potoroidae	1.2†	3.0
Macropodidae	1.0	1.6
Acrobatidae	2.1	5.5
Phalangeridae	1.3	1.1
Burramyidae	3.6†	5.8
Pseudocheiridae	1.3	1.8
Petauridae	1.5†	2.7
Tarsipedidae	2.6	7.8

FIG. 2. Phylogenetic distribution of types of diets among families of marsupials. Black represents insectivorous or carnivorous species, gray represents species consuming invertebrates with nectar or fruit and nectarivorous species, light gray fill represents omnivorous species, and white denotes foliage- and grass-eating species. Hatching shows lineages with ambiguous diets. Ellipses indicate that data are not available for any species in the family. The Papua New Guinean bandicoots (Peroryctidae) are included within the Peramelidae.

† Families with more than one type of diet among species.

cestry, only type of diet showed robust evidence of a link, confirming the popular view that decreased fecundity has been associated with increased herbivory during the evolutionary history of marsupials (Lee and Cockburn 1985). Russell (1982) hypothesized that, not only does herbivory impose nutritional constraints on fecundity, but also carnivorous marsupials benefit from having small young that can be left in the nest sooner and not impede maternal hunting, allowing them to increase litter sizes. Eisenberg (1988) considered that longer life-spans and smaller litters are associated with specialization on patchy or low-energy food, and the exceptionally fast life histories of bandicoots (Peramelidae) have been linked with exploitation of abundant food in early-successional habitats (Lee and Cockburn 1985). Several authors have pointed out that the mechanism linking diet to life history in marsupials is not metabolic rate, or at least not basal metabolic rate (McNab 1986, Cockburn and Johnson 1988, Harder and Fleck 1997). Rather, our results support the long-held idea that life history diversity in marsupials is a simple consequence of energy constraints. Relative to body mass, species with energy-rich diets have more energy to invest in offspring and can sustain higher reproductive rates; other life history variables are accordingly

traded off against reproductive rate (Lee and Cockburn 1985, Harder and Fleck 1997). Reductions in reproductive rate have occurred more often than expected by chance at nodes where the diet of marsupials changed to include more vegetation, particularly browse and grass, and secondary increases in reproductive rate have accompanied increased carnivory (Fig. 2). The ancient split between the polyprotodont marsupials and the plant-eating order Diprotodontia ultimately led to life history diversification. Further changes have tended to occur at the family level, and little diversification of diet type has accompanied speciation within families (Fig. 2). This has led to conservation of life history traits within marsupial families.

Although most studies have failed to find robust ecological correlates of life history diversity in birds, mammals, and other taxa (Partridge and Harvey 1988, Harvey et al. 1989, Promislow and Harvey 1991), there are some exceptions. Owens and Bennett (1995) found that risk of predation is related to reproductive effort in birds, and Sæther (1994) found that energy availability (prey size) is correlated with clutch size in altricial birds. Diet is correlated with life history variation within some subgroups of eutherians. For in-

stance, Geffen et al. (1996) suggested that litter size is related to food availability in canids because of energetic constraints, and Sæther and Gordon (1994) showed that changes to browsing from grazing were accompanied by relative increases in litter size and decreases in neonate size in ungulates. Sæther and Gordon (1994) argued that this result could be seen as support for the age-specific mortality hypothesis, because browsers are more prone to population crashes and may have higher rates of juvenile mortality due to food shortage. Nevertheless, the lack of an overall correlation between life history variables and ecological factors in eutherians remains puzzling. Recently, Purvis and Harvey (1995) confirmed many predictions of Charnov's (1991, 1993) model, but could not identify a consistent ecological correlate of Charnov's key parameter, the ratio between weaning mass and maternal mass (δ). Only population density was weakly correlated with δ within four particular orders (Carnivora, Artiodactyla, Rodentia, and Lagomorpha). It remains to be seen whether quantitative application of Charnov's model to patterns of life history variation in marsupials will reveal any further ecological correlates.

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APPENDIX

A table providing the life history traits and associated ecological variables for species of marsupials used in these analyses is available in ESA's Electronic Data Archive: *Ecological Archives* E082-042.