

Relationship of basal metabolism and life history attributes in Neotomine–Peromyscine rodents (Cricetidae: Neotominae)

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Abstract:

With the exception of a positive relationship between energy expenditure and number of offspring per litter, few links have been made between energy expenditure and life history attributes in mammals. The purpose of this study was to examine relationships between basal metabolic rate (BMR) and life history attributes among 26 species within the Neotomine–Peromyscine rodents. Specifically, I used independent contrasts to determine whether variation in BMR is related to variation in life history attributes that represent reproductive effort and maturation, and I determined if there is an offspring size *versus* offspring number trade-off. My results demonstrate that within the Neotomine–Peromyscine rodents, 1) there exists an offspring number *versus* offspring size trade-off whereby taxa that have a large residual number of offspring per litter have a small residual neonate mass, 2) BMR is related to this trade-off whereby taxa that have large residual BMR have small residual neonate mass and a trend towards a large number of offspring per litter, and 3) BMR is not related to total reproductive effort as represented by total litter mass, total weanling mass, or total growth rate of the litter from birth to weaning. My results suggest that high BMR facilitates a large number of small offspring per reproductive event. A large number of small offspring may confer a fitness advantage for taxa with compensatory growth mechanisms for weaned young that minimize fecundity trade-offs with small offspring size.

À l'exception de la relation positive entre la dépense énergétique et le nombre de jeunes par portée, peu de liens ont été faits entre la dépense énergétique et les traits d'histoire de vie chez les mammifères. Le but de cette étude était d'examiner chez 26 espèces de rongeurs de la sous-famille Neotominae, les relations entre le métabolisme de base et les traits d'histoire de vie. Spécifiquement, j'ai utilisé des contrastes indépendants pour déterminer si la variation du métabolisme de base était reliée aux traits d'histoire de vie associés à l'effort reproducteur et à la maturation et j'ai déterminé s'il y avait un compromis entre la taille des jeunes et leur nombre. Mes résultats démontrent que chez les rongeurs de la sous-famille Neotinae : 1) il existe un compromis entre le nombre et la taille des jeunes de sorte que les taxons qui ont un nombre résiduel élevé de jeunes par portée ont une plus faible masse résiduelle à la naissance, 2) le métabolisme de base est relié à ce compromis ce qui fait que les taxons qui ont un métabolisme de base résiduel élevé ont une faible masse résiduelle à la naissance et ont tendance à avoir un grand nombre de jeunes par portée et 3) le métabolisme de base n'est pas relié à l'effort reproducteur total tel que mesuré par la masse totale de la portée, la masse totale au sevrage ou le taux de croissance de la portée de la naissance au sevrage. Mes résultats suggèrent qu'un

métabolisme de base élevé favorise un grand nombre de jeunes de petite taille pour chaque événement reproductif. Avoir un grand nombre de jeunes de petite taille pourrait représenter un avantage au niveau de la valeur adaptative chez les taxons ayant des mécanismes de croissance compensatoires pour les jeunes sevrés qui minimiseraient les compromis au niveau de la fécondité associés à des jeunes de petite taille.

Keywords: basal metabolic rate (BMR), endothermy, independent contrasts, life history, litter size, offspring number, offspring size, reproductive effort, contrastes indépendants, effort reproducteur, endothermie, histoire de vie, métabolisme de base, nombre de jeunes, taille de la portée, taille des jeunes

Article:

Introduction

Energy is limited either extrinsically or intrinsically (reviewed in Speakman, 2000). Female mammals incur relatively high energetic costs (*e.g.*, Millar, 1978; Kenagy, Sharbaugh & Nagy, 1989; Webb, Speakman & Racey, 1992; Poppitt, Speakman & Racey, 1993; Speakman & McQueenie, 1996; Kuenkele & Trillmich, 1997) and costs of reproduction (*e.g.*, Charnov, 1991) during offspring production. Energy use influences life history attributes related to reproductive effort because females have trade-offs regarding their use of limited energy resources (Stearns, 1992; Roff, 2003). Life history characters, in turn, can influence a suite of behavioural and ecological attributes of a female mammal's life.

A link between life history, ecology, and breeding behaviours has been recently made for a large clade of North American sigmodontine rodents, the Neotomine–Peromyscine rodents (Kalcounis-Rueppell & Ribble, 2007). In Neotomine–Peromyscine rodents, variation in social behaviour during the breeding season in species with solitary females compared with species with non-solitary females can be explained by species-level variation in basal metabolic rate (BMR). Species with females that live solitarily in the wild have higher BMR than species with females that do not live solitarily in the wild. Whether solitary living by a female is enabled by high BMR or forces a high BMR (Johnson, Thomson & Speakman, 2001; Speakman *et al.*, 2003) is not clear; however, the relationship exists (Kalcounis-Rueppell & Ribble, 2007).

Although energy is implicated in life history evolution (Stearns, 1992, discussed in Speakman, 2000), there have been relatively few examples where BMR has been shown to be related to life history attributes in eutherian mammals (*e.g.*, Johnson, Thomson & Speakman, 2001; White & Seymour, 2004). Where a relationship has been found, the relationship has been between BMR and an attribute related to reproductive effort (number of offspring per litter) as opposed to attributes describing longevity and/or maturation (Glazier, 1985a; Genoud, 1988, Read & Harvey, 1989; Harvey, Pagel & Rees, 1991; Stephenson & Racey, 1995). No correlation has been shown between BMR and life history attributes within a species (discussed in Johnson, Thomson & Speakman, 2001; White & Seymour, 2004), possibly reflecting the flexibility of BMR (or resting metabolic rate) in individuals within a species between non-reproductive and reproductive stages (Speakman & McQueenie, 1996; Johnson, Thomson & Speakman, 2001; Speakman, Krol & Johnson, 2004).

Evidence for a link between BMR and life history attributes reflecting reproductive effort (as opposed to attributes describing longevity and/or maturation) has implications for models that have been put forth to explain the evolution of endothermy in birds and mammals based on selection for high sustained levels of parental care (Farmer, 2000; Koteja, 2000). Although these models differ with respect to whether selection is acting on incubation (high growth rates and developmental stability of young: Farmer, 2000) or food provisioning (high growth rates and reduced predation of young: Koteja, 2000), both suggest that the evolution of high BMR was due to selection for traits relating to decreased mortality of young (see Figure 1 of Koteja, 2004). Support for both of these models requires a correlation between BMR and life history attributes that reflect total reproductive effort toward survival of young such as growth rate of litter from birth to weaning.

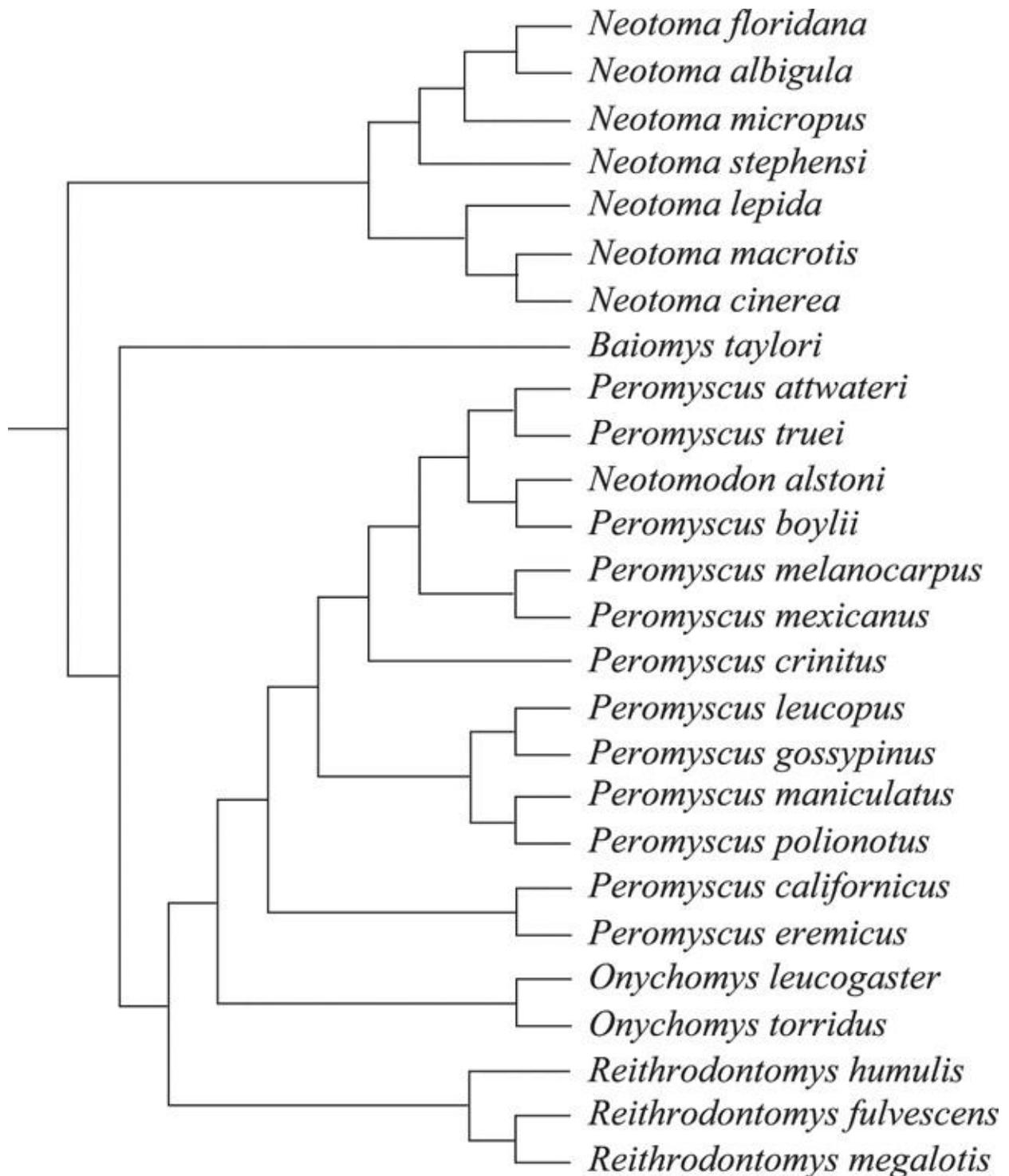


Figure 1. Phylogenetic tree topology used for the independent contrasts analysis (all species present).

The main life history attribute reflecting reproductive effort that has been linked to BMR is number of offspring per litter. This attribute is paramount to the offspring size *versus* offspring number trade-off (Smith & Fretwell, 1974). Over a wide variety of taxa, including mammals

(Charnov & Ernest, 2006), offspring size is a proxy for reproductive investment, and the number of offspring that an individual can produce is inversely proportional to the investment per offspring (Smith & Fretwell, 1974, reviewed in Roff, 1992; Stearns, 1992; Charnov, 2003; Roff, 2003). It follows that if BMR is positively related to number of offspring per litter within a clade of mammals and there is a trade-off between offspring size and offspring number, there should be a corollary negative relationship between BMR and offspring size.

The aim of this study was to examine relationships between BMR and life history characters among 26 species within the clade of Neotomine–Peromyscine rodents to determine whether BMR is correlated with life history attributes. I also examined whether there is an offspring size *versus* offspring number trade-off within this group. I predicted that as with other interspecific comparisons in general (Genoud, 1985; Harvey, Pagel & Rees, 1991; Stephenson & Racey, 1995) and Glazier's (1985a) study of 5 *Peromyscus* species in particular, I would find a positive relationship between BMR and number of offspring per litter. Following from the Smith–Fretwell offspring size *versus* offspring number trade-off, I predicted a negative relationship between number of offspring per litter and offspring size, and a corollary negative relationship between BMR and offspring size (Smith & Fretwell, 1974; Stearns, 1992; Roff, 2003).

Examining these relationships within the Neotomine–Peromyscine clade of rodents is particularly insightful because 1) the phylogeny of this clade is generally resolved (Reeder *et al.*, 2006); 2) this clade varies in ecological, behavioural, and physiological attributes, so fine-scale interspecific patterns of BMR and life history can be examined over a diverse array of taxa; and 3) despite the varied ecology, behaviour, and physiology within this clade, taxa all occur in the nearctic realm, thereby minimizing zoo-geographic effects on underlying patterns of metabolism (Lovegrove, 2000; but see Mueller & Diamond, 2001).

Specifically, I used a phylogenetic- and body-size-corrected comparative analysis (Felsenstein, 1985; Garland, Harvey & Ives, 1992; Felsenstein, 2003) to examine whether the observed variation in BMR ($\text{mLO}_2 \cdot \text{h}^{-2}$) of the Neotomine–Peromyscine taxa could explain the observed variation in life history characteristics of the taxa. BMR was used as a measure of metabolism because field metabolic rates (FMR) are not available for the majority of Neotomine–Peromyscine taxa (see Speakman, 2000) and because BMR is correlated with FMR and maximum metabolic rate (MMR) in eutherian mammals in general and rodents in particular (Koteja, 1991; White & Seymour, 2004). Furthermore, BMR is correlated with energy expenditure during lactation within 5 species of Neotomine–Peromyscine rodents (Glazier, 1985b). The life history attributes I used reflect reproductive effort and age at maturation and include neonate mass at birth, weanling mass, number of offspring per litter at birth (litter size), number of litters during breeding season (per season or per year depending on seasonality of breeding), inter birth interval, gestation length (with or without concurrent lactation), lactation length (with or without concurrent pregnancy), male age at maturity (age when testes are scrotal), and female age at maturity (age of first oestrus, mating, or pregnancy). Using the neonate mass, weanling mass, and litter size data I also calculated 3 additional life history attributes related to total reproductive effort. Total litter size at birth was calculated as neonate mass \times litter size. Total litter size at weaning was calculated as weanling mass \times litter size. Rate of total litter mass increase from birth to weaning was calculated as $[(\text{weanling mass})(\text{litter size})-$

(neonate mass)(litter size)]/days of lactation.

Methods

Phylogenetic tree

The subfamily Neotominae are the North American rats and mice in the rodent family Cricetidae (Steppan, Adkins & Anderson, 2004; Musser & Carleton, 2005). Within the Neotominae there are major clades that include the Neotomini (woodrats), Peromyscini (deer mice), Reithrodontomyini (harvest mice), Bayomyini (singing mice), and Onychomyini (grasshopper mice; Musser & Carleton, 2005). This subfamily has also been referred to as Neotomine–Peromyscine rodents (Bradley *et al.*, 2004; Reeder *et al.*, 2006). Herein, I also refer to this group as the Neotomine–Peromyscine for consistency and to best reflect the 26 species included in my analysis.

The phylogeny I used (Figure 1) is primarily based on a study that used 2 nuclear and 1 mitochondrial gene to differentiate the Baiomyini, Neotomini, and Peromyscini within the Neotomine–Peromyscine complex (see Figures 2 and 4 of Reeder *et al.*, 2006). Not all species of interest in this study were included in Reeder *et al.*, 2006. I followed Matocq *et al.* (2007) for relationships among *Neotoma* and Arellano, Rogers, and Cervantes (2003) for relationships among *Reithrodontomys*. Within the Peromyscini, several species of *Peromyscus* were not part of the phylogeny published by Bradley *et al.* (2004) or Reeder *et al.* (2006), so I followed the topology from Kalcounis-Rueppell and Ribble (2007).

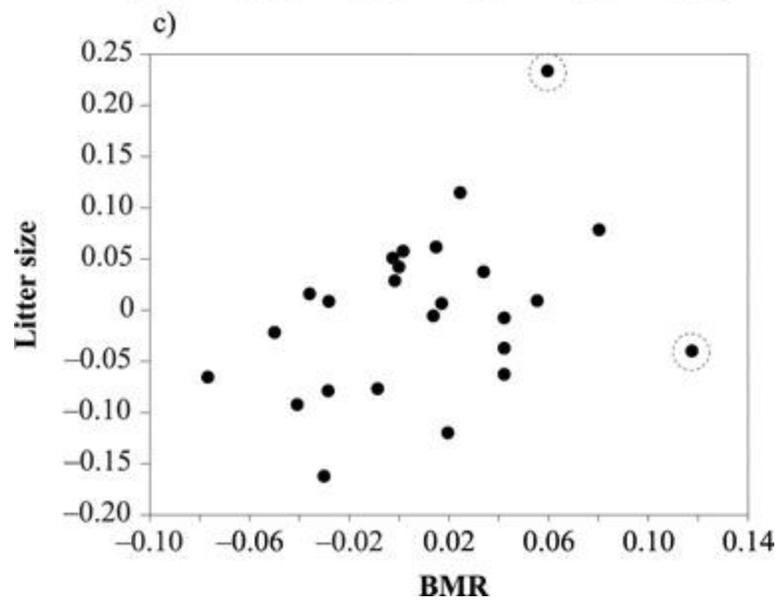
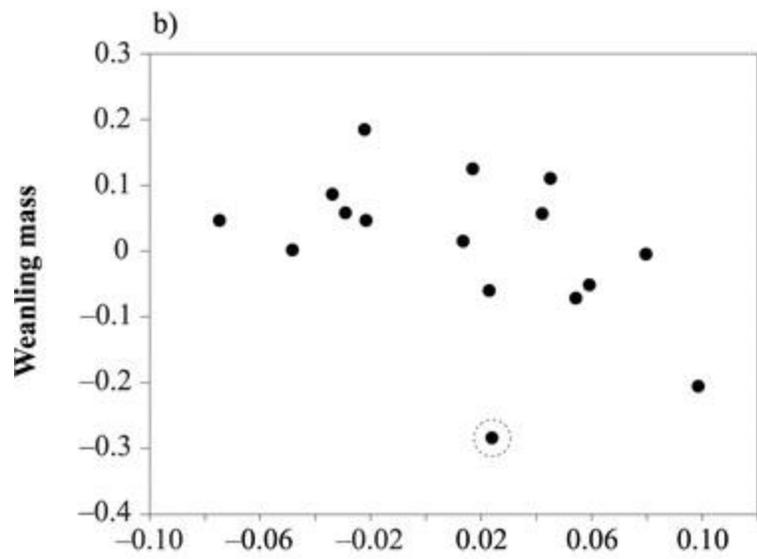
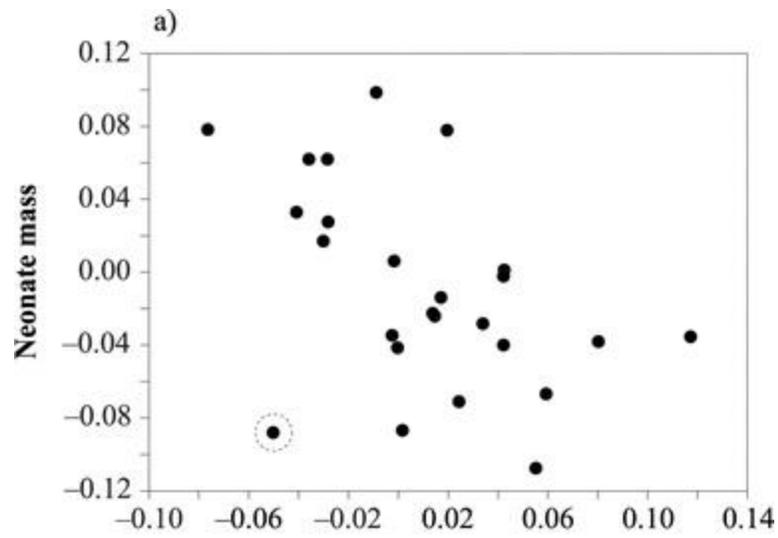


Figure 2. Plots of residual standardized independent contrast values of \log_{10} BMR and residual standardized independent contrast values of \log_{10} a) neonate mass, b) weanling mass, and c) litter size. These correlations are significant or show trends towards significance (see text). Outliers described in text are highlighted by a stippled circle.

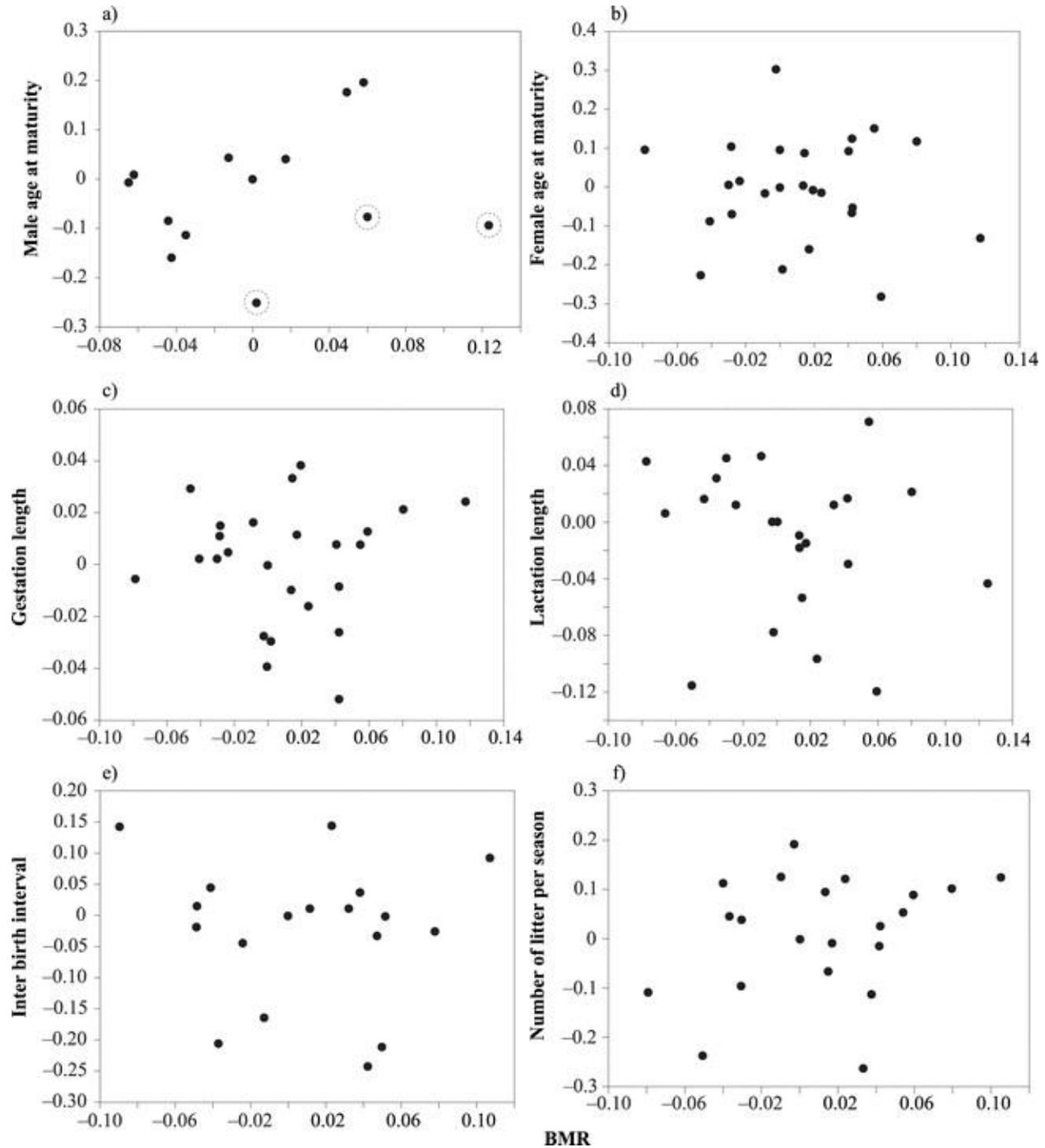


Figure 3. Plots of residual standardized independent contrast values of \log_{10} BMR and residual standardized independent contrast values of \log_{10} a) male age at maturity, b) female age at maturity, c) gestation length, d) lactation length, e) inter birth interval, and f) number of litters

per season. These correlations are not significant (see text). Outliers described in text are highlighted by a stippled circle.

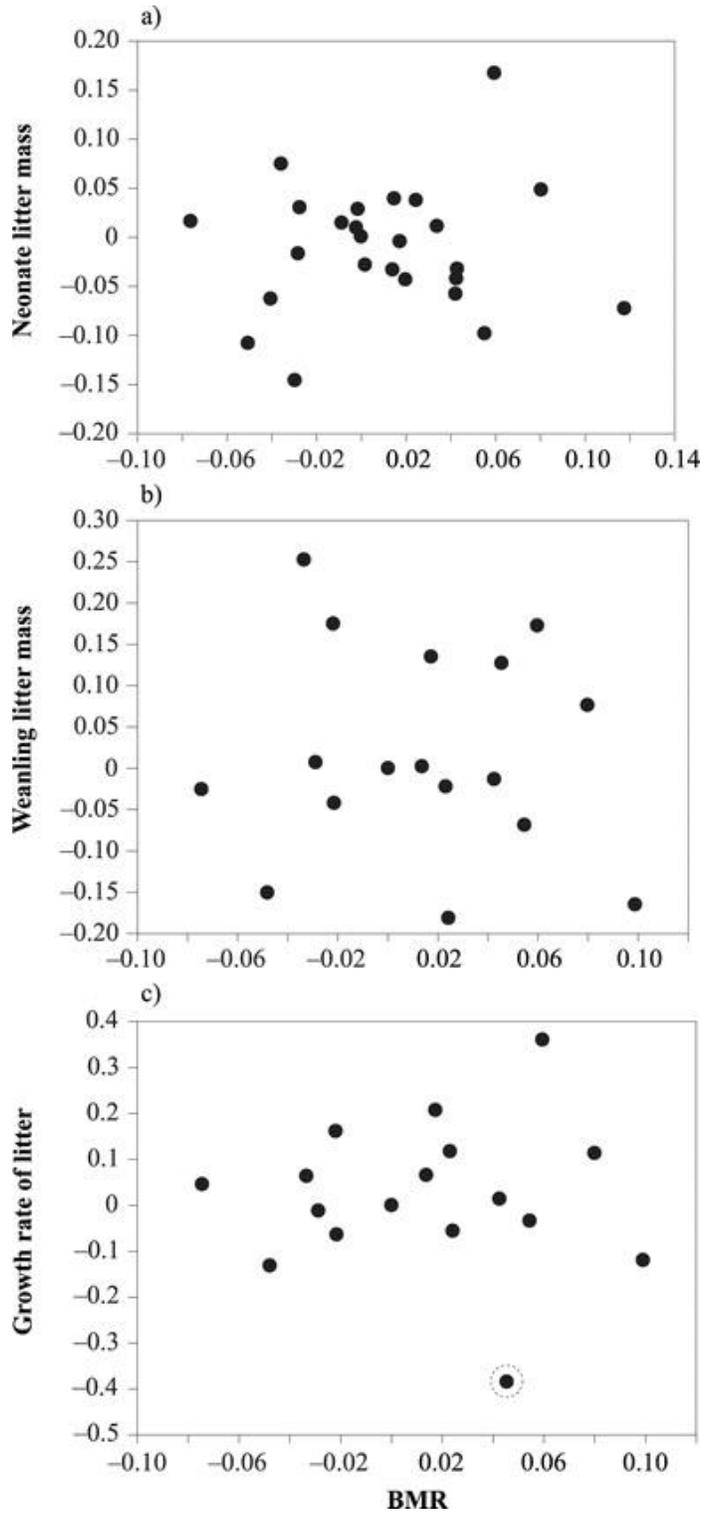


Figure 4. Plots of residual standardized independent contrast values of \log_{10} BMR and residual standardized independent contrast values of \log_{10} a) total litter mass at birth, b) total litter mass at weaning, and c) growth rate of litter from birth to weaning. These correlations are not significant (see text). Outliers described in text are highlighted by a stippled circle.

Phylogenetically based analyses

The data used for these analyses are in Table I (BMR and life history attributes) and Table II (BMR and calculated life history attributes from Table I). The data on mass and BMR were mainly from MacMillen and Garland (1989); however, some other sources were used (see footnotes to Table I). The life history data are mainly taken from Hayssen, van Tienhoven, and van Tienhoven (1993) and Ernest (2003). In my analyses I use an average of all mean data presented in Hayssen, van Tienhoven, and van Tienhoven (1993) or the average reported in Ernest (2003). For taxa with estimates of BMR, the associated mass value comes from the source of the BMR value. If a BMR value was not available for a particular species, an average value of the mass specific BMR ($\text{mLO}_2 \cdot \text{g}^{-2} \cdot \text{h}^{-2}$) for the genus was used to calculate whole animal BMR based on the mass value reported in Ernest (2003). If there were missing data for a life history variable for a particular species (Table I and Table II), that species was pruned from the phylogenetic tree topology for all related independent contrast analyses (Midford, Garland & Maddison, 2005). For example, all phylogenetic analyses concerning the relationship between BMR and gestation length would involve a phylogenetic tree topology (Figure 1) that would not include *Reithrodontomys fulvescens*.

	Mass [§] (g)	BMR* (mLO ₂ ·h ⁻²)	Neonate mass (g)	Weanling mass (g)	Litter size (number)	Male age at maturity (d)	Female age at maturity (d)	Gestation length (d)	Lactation length (d)	Inter birth interval (d)	Number of litters (per y)
<i>Baiomys taylori</i>	7.83	15.27	1.16	3.59	2.67	75.00	44.00	22.20	20.40	23.89	10.00
<i>Onychomys torridus</i>	19.00	29.45	2.32	9.35	3.58	45.50	45.50	29.10	20.70	29.50	2.60
<i>Onychomys leucogaster</i>	40.00	62.00**	2.65	13.20	3.63	124.00	95.00	32.40	27.30	31.50	2.50
<i>Reithrodontomys humulis</i>	10.30	22.71**	1.08		2.90		103.20	22.50	22.80	31.60	
<i>Reithrodontomys fulvescens</i>	12.50	24.38	1.08	3.25	3.10				14.40		2.00
<i>Reithrodontomys megalotis</i>	8.80	21.65	1.33		3.32	83.60	110.50	22.80	21.00	27.60	4.50
<i>Peromyscus crinitus</i>	16.80	24.53	2.20	13.87	3.08	70.00	70.00	24.60	26.10	26.00	2.05
<i>Peromyscus boylii</i>	23.20	54.29	2.20		3.19	60.00	50.93	24.60	26.40		
<i>Peromyscus eremicus</i>	20.10	29.55	2.33		2.63		39.21	25.50	24.60	38.50	3.50
<i>Peromyscus californicus</i>	45.50	54.15	4.46	18.65	2.02		44.10	29.10	29.40	24.00	4.56
<i>Peromyscus melanocarpus</i>	59.00	102.68**	4.50		1.90	124.40	79.30	33.60	21.90	37.10	
<i>Peromyscus atwateri</i>	30.00	52.20**	2.20		4.00	60.00	70.00	26.15			
<i>Peromyscus gossypinus</i>	21.50	36.98	2.20	13.69	3.60	45.00	43.00	24.90	24.30		4.00
<i>Peromyscus mexicanus</i>	60.50	105.27**	4.40		2.27	66.00	46.00	32.70			
<i>Peromyscus truei</i>	33.30	56.78	2.32	10.50	3.50		50.09	29.70	25.50	40.00	3.40
<i>Peromyscus leucopus</i>	23.60	45.55	1.89	9.58	4.42		46.70	24.90	23.10	25.69	3.90
<i>Peromyscus polionotus</i>	12.00	21.48	1.63	6.77	3.60		29.60	23.70	22.80	24.60	2.70
<i>Peromyscus maniculatus</i>	19.90	40.95	1.83	8.95	4.73	50.00	48.72	26.40	25.20	23.30	3.40
<i>Neotomodon alstoni</i>	50.00	87.00**	3.40		3.25		49.00	27.30			2.00
<i>Neotoma albigula</i>	185.00	127.19	11.35	78.15	2.15		83.50	35.70	28.80	49.00	2.00
<i>Neotoma floridana</i>	232.00	162.08**	13.28	50.45	3.10		98.50	36.00	21.90	83.00	2.50
<i>Neotoma micropus</i>	236.33	165.43**	11.70	35.60	2.51		155.00	34.20	26.10		2.40
<i>Neotoma stephensi</i>	180.00	108.00	10.60	35.00	1.08		294.00	30.90	39.30	130.00	1.95
<i>Neotoma cinerea</i>	262.60	191.17	13.50	107.30	3.08	547.00	547.00	29.40	27.00	30.00	2.00
<i>Neotoma macrotis</i>	186.70	147.49	12.10		2.65		180.00	30.60	26.40		1.17
<i>Neotoma lepida</i>	116.40	89.28	8.96	34.63	2.92	195.00	155.00	33.00	28.50	60.00	2.00

§Mass values reported are from BMR source where BMR source is available. Where BMR source is not available, mass values are from Ernest (2003). Mass values used to calculate residual values for life history variables are from Ernest (2003) and are not shown (except for those taxa where BMR is not available) but are available from Ernest (2003).

*Values from MacMillen and Garland (1989) except *N. albigula* and *N. stephensi* from Sorensen, McLister, and Dearing (2005), *R. fulvescens* from Spencer and Cameron (1982), and *R. humulis* from Stalling (1995).

**Values calculated from average mass specific BMR (mLO₂·g⁻²·h⁻²) value of genus. For *Neotomodon*, average value of *Peromyscus* used.

Table I. BMR and life history attributes of Neotomine–Peromyscine rodent species used for the analyses.

	Mass§ (g)	BMR* (mL O ₂ ·h ⁻²)	Neonate litter mass (g)	Weanling litter mass (g)	Growth rate of litter (birth to weaning)
<i>Baiomys taylori</i>	7.83	15.27	3.10	9.59	0.32
<i>Onychomys torridus</i>	19.00	29.45	8.31	33.47	1.22
<i>Onychomys leucogaster</i>	40.00	62.00**	9.62	47.92	1.40
<i>Reithrodontomys humulis</i>	10.30	22.71**	3.13		
<i>Reithrodontomys fulvescens</i>	12.50	24.38	3.35	10.08	0.47
<i>Reithrodontomys megalotis</i>	8.80	21.65	4.42		
<i>Peromyscus crinitus</i>	16.80	24.53	6.78	42.72	1.38
<i>Peromyscus boylii</i>	23.20	54.29	7.02		
<i>Peromyscus eremicus</i>	20.10	29.55	6.13		
<i>Peromyscus californicus</i>	45.50	54.15	9.01	37.67	0.97
<i>Peromyscus melanocarpus</i>	59.00	102.68**	8.55		
<i>Peromyscus atwateri</i>	30.00	52.20**	8.80		
<i>Peromyscus gossypinus</i>	21.50	36.98	7.92	49.28	1.70
<i>Peromyscus mexicanus</i>	60.50	105.27**	9.99		
<i>Peromyscus truei</i>	33.30	56.78	8.12	36.75	1.12
<i>Peromyscus leucopus</i>	23.60	45.55	8.35	42.34	1.47
<i>Peromyscus polionotus</i>	12.00	21.48	5.87	24.37	0.81
<i>Peromyscus maniculatus</i>	19.90	40.95	8.66	42.33	1.34
<i>Neotomodon alstoni</i>	50.00	87.00**	11.05		
<i>Neotoma albigula</i>	185.00	127.19	24.40	168.02	4.99
<i>Neotoma floridana</i>	232.00	162.08**	41.17	156.40	5.26
<i>Neotoma micropus</i>	236.33	165.43**	29.37	89.36	2.30
<i>Neotoma stephensi</i>	180.00	108.00	11.45	37.80	0.67
<i>Neotoma cinerea</i>	262.60	191.17	41.58	330.48	10.70
<i>Neotoma macrotis</i>	186.70	147.49	32.07		
<i>Neotoma lepida</i>	116.40	89.28	26.16	101.12	2.63

Table II. BMR and life history attributes of Neotomine–Peromyscine rodent species used for the analyses. Footnotes as in Table I.

BMR and life history characters were compared using Felsenstein's method of independent contrasts (Felsenstein, 1985; 2003). I used independent contrasts because the probability of a phylogenetic signal in body size and life history characters in interspecific comparisons with more than 20 species is as high as 92% (Blomberg, Garland & Ives, 2003). Furthermore, there is a phylogenetic signal in body size among Neotomine–Peromyscine rodents, with the Neotomini being an order of magnitude larger than the Peromyscini.

All the life history characteristics I examined had the potential to be correlated with body size (Hayes, Garland & Dohm, 1992). I \log_{10} transformed all variables prior to analysis. For all variables, I examined allometric relationships and removed the effect of body size, as described in Garland, Harvey, and Ives (1992, p. 29). Briefly, this involves 1) computing standardized independent contrasts for BMR and all continuous life history variables, 2) regressing through the origin of independent contrasts, each variable on the positivized body mass independent contrasts, and 3) determining the residual independent variable values of the significant regressions (Garland, Harvey & Ives, 1992). Residual values of BMR were calculated based on the body mass value from the source of the BMR value, whereas residual values for all of the life history variables were calculated based on the body mass values of Ernest (2003). The residual independent contrast values were then used as body-mass– and phylogeny-corrected values in a product-moment correlation analysis.

I calculated all independent contrasts and residual values of independent contrasts in the PDAP:PDTREE 1.07 (Midford, Garland & Maddison, 2005) module of Mesquite, Version 1.06 (Maddison & Maddison, 2005). I assumed a model of evolution where all branch lengths were set to 1.0 (Maddison & Maddison, 2005) and verified adequate standardization of contrasts by examining plots and finding no relationships between the absolute value of each standardized independent contrast *versus* its standard deviation (Garland, Harvey & Ives, 1992). I performed all correlation analyses in Statistica Version 7.1 (StatSoft Inc., Tulsa, Oklahoma, USA). In all correlation analyses, residual independent contrast values were used even if a significant allometric relationship was not detected to ensure all data were uncorrelated with body size. For all correlation analyses, I examined outliers to determine what nodes they represented and if a particular lineage was consistently represented, indicating anomalous data for a particular species or a unique species with respect to life history attributes within the Neotomine–Peromyscine rodents.

Results

Relationships between body mass and life history variables

Taxa with large body mass had larger BMR relative to taxa with small body mass ($r = 0.96$, $n = 25$, $P < 0.001$). Taxa with large body mass had larger neonate ($r = 0.90$, $n = 25$, $P < 0.001$) and weanling masses ($r = 0.84$, $n = 16$, $P < 0.001$), longer gestation lengths ($r = 0.71$, $n = 24$, $P < 0.001$), and later female ($r = 0.43$, $n = 24$, $P < 0.05$) and male ages of maturity ($r = 0.70$, $n = 12$, $P < 0.01$) than taxa with small body mass. There was a trend for taxa with large body mass to have a higher rate of litter growth from birth to weaning ($r = 0.45$, $n = 16$, $P = 0.07$) and fewer litters per season ($r = -0.41$, $n = 20$, $P = 0.07$) than taxa with small body mass. There was no

relationship between body mass and number of offspring per litter ($r = -0.02$, $n = 25$, $P = 0.92$), lactation length ($r = 0.22$, $n = 22$, $P = 0.31$), or inter birth interval ($r = 0.19$, $n = 17$, $P = 0.45$).

Relationships between BMR and life history variables

Taxa that had large residual BMR had small residual neonate mass ($r = -0.47$, $n = 25$, $P = 0.02$) (Figure 2a). This relationship was reflected in the trend for taxa that had large residual BMR to have small residual weanling mass ($r = -0.46$, $n = 16$, $P = 0.07$), and with the single outlier removed this relationship was significant ($r = -0.55$, $n = 15$, $P = 0.03$) (Figure 2b). There was a trend for taxa that had large residual BMR to have a large residual number of offspring per litter ($r = 0.36$, $n = 25$, $P = 0.08$), and with the outliers removed this trend came closer to being significant ($r = 0.39$, $n = 23$, $P = 0.06$) (Figure 2c). Although this correlation was not significant, the trend is evident (Figure 2c) and I treat this relationship as biologically relevant.

There was no relationship between residual BMR and residual male age at maturity ($r = 0.23$, $n = 12$, $P = 0.48$; Figure 3a) or residual female age at maturity ($r = -0.05$, $n = 24$, $P = 0.82$; Figure 3b). However, when the outliers were removed for residual male age at maturity, the relationship became significant ($r = 0.80$, $n = 9$, $P = 0.009$; Figure 3a). There was no relationship between residual BMR and residual gestation length ($r = 0.04$, $n = 24$, $P = 0.84$; Figure 3c), residual lactation length ($r = -0.19$, $n = 22$, $P = 0.40$; Figure 3d), residual inter birth interval ($r = -0.08$, $n = 17$, $P = 0.75$; Figure 3e), or residual number of litters per season ($r = 0.29$, $n = 20$, $P = 0.22$; Figure 3f). There was no relationship between residual BMR and residual total litter mass at birth ($r = 0.08$, $n = 25$, $P = 0.71$; Figure 4a) or residual total litter mass at weaning ($r = -0.08$, $n = 16$, $P = 0.7$; Figure 4b). The residual rate of litter growth from birth to weaning ($r = -0.003$, $n = 16$, $P = 0.99$; Figure 4c) was not correlated with residual BMR, and removal of the outlier did change the non-significance of the relationship ($r = 0.14$, $n = 15$, $P = 0.61$; Figure 4c).

Relationships between offspring size and offspring number

There was a negative relationship between residual number of offspring per litter and residual neonate mass ($r = -0.61$, $n = 25$, $P = 0.001$). Removal of the outliers strengthened the correlation coefficient ($r = -0.65$, $n = 23$, $P = 0.001$). Taxa that had a large residual number of offspring per litter had small residual neonate mass (Figure 5).

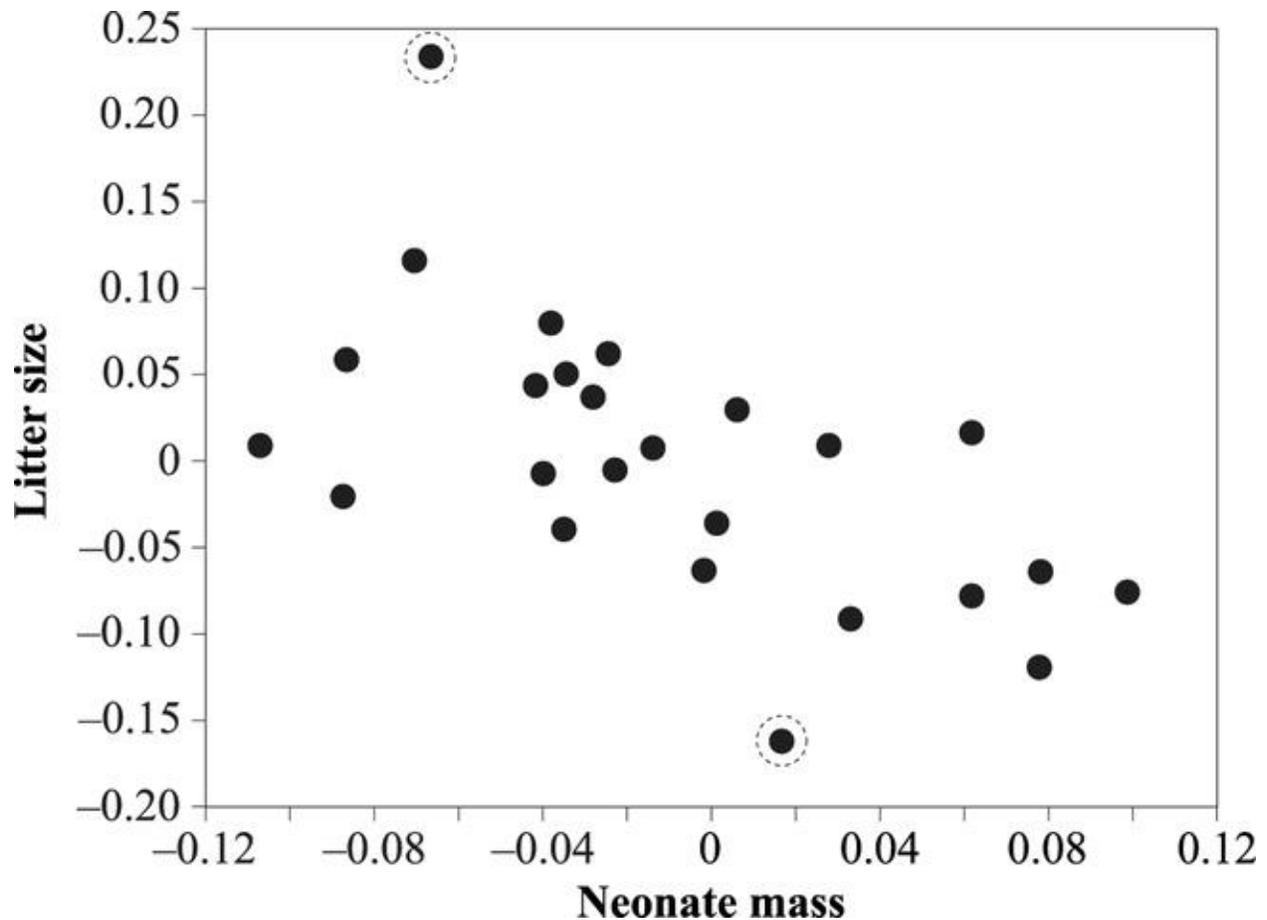


Figure 5. Plot of residual standardized independent contrast values of \log_{10} neonate mass and residual standardized independent contrast values of \log_{10} litter size. This correlation is significant (see text). Outliers described in text are highlighted by a stippled circle.

Outliers

Of the 10 identified outlier nodes (see figures), none appeared more than once as an outlier with the exception of the node between *N. stephensi* and the *floridana–albigula–micropus* clade that appeared twice (Figure 2c and Figure 5). Reasons for this node being an outlier are that there is a large residual independent contrast value for litter size between *N. stephensi* and the *floridana–albigula–micropus* clade and there is little support for placing *N. stephensi* in the basal position of this clade despite strong support for it belonging to this clade (Matocq *et al.*, 2007).

Discussion

Within the Neotomine–Peromyscine rodents, larger species had larger BMR than smaller species. Species with large body mass had larger neonate and weanling masses, longer gestation lengths, and later ages of maturity than species with smaller body mass. Species that had large residual BMR had small residual neonate mass and tended towards smaller residual weanling mass and a large residual number of offspring per litter. Species that had a large residual number of offspring per litter had offspring of small residual neonate mass. There was no relationship between residual BMR and residual total reproductive effort as measured by residual total litter mass at birth, residual total litter mass at weaning, or the residual rate of growth of the litter from

birth to weaning. My results demonstrate that within the Neotomine–Peromyscine rodents, 1) there exists an offspring number *versus* offspring size trade-off, 2) BMR is related to this trade-off, but 3) BMR is not related to total reproductive effort.

Relationships between body mass and BMR (Elgar & Harvey, 1987; McNab, 1988) and body mass and life history attributes (Millar, 1977) were expected. However, specific relationships were different from those previously reported (*e.g.*, reviewed in Millar & Hickling, 1991). I found that species with large body mass had larger neonate and weanling masses, longer gestation lengths, and later maturation dates than species with smaller body mass as opposed to larger litters and earlier maturation dates (as in Millar & Hickling, 1991). The discrepancy between these 2 analyses supports independent selection on body size and life history attributes under different conditions (*e.g.*, artificial *versus* natural selection) as discussed in Millar and Hickling (1991).

Taxa that had a large residual litter size had small residual neonate mass, demonstrating the trade-off between number of offspring per litter and offspring size (Smith & Fretwell, 1974; see reviews in Roff, 1992; Stearns, 1992; Roff, 2003; Charnov & Ernest, 2006). If the number of offspring per litter and offspring size were perfect (slope of -1), for a given reproductive output (*i.e.*, total litter mass) female fecundity would be higher with larger litters. However, the fecundity reward for current reproduction by females associated with large litters is opposed by tradeoffs with maternal and offspring survival and fecundity. Within species, large litters may correlate with diminished survival and fecundity of mothers (Koivula *et al.*, 2003) and/or diminished survival (Millar, 1973; Hare & Murie, 1992; Koskela *et al.*, 1998; Humphries & Boutin, 2000) and fecundity (Mappes & Koskela, 2004) of female offspring. For example, in litter size manipulation studies of female bank voles (*Clethrionomys glareolus*), mothers with enlarged litters had low survival and lower litter size and litter mass in subsequent breeding attempts (Koivula *et al.*, 2003). Furthermore, small size at birth of female offspring was correlated to late maturation, low probability of breeding, and small size of first litter relative to females that have a large size at birth (Mappes & Koskela, 2004). However, trade-offs with fecundity rewards from large litters may be lessened if weaned young have compensatory mechanisms for growth (Sikes, 1998a; Oksanen, Koskela & Mappes, 2002). Within the Neotomine–Peromyscine rodents there should be an average optimal litter size that maximizes offspring survival and fecundity while minimizing the unit cost per offspring to the mother (Sikes, 1998b).

Interestingly, BMR was related to the offspring number *versus* offspring size trade-off in this group of rodents: taxa that had large residual BMR had a large residual number of offspring per litter with small residual offspring size. The pattern between BMR and number of offspring per litter agrees with the few studies that have found a positive relationship between number of offspring per litter and metabolism (either basal or during lactation: Glazier, 1985a; Genoud, 1988; Harvey, Pagel & Rees, 1991; Stephenson & Racey, 1995). The offspring number *versus* offspring size trade-off in mammals is common (Charnov & Ernest, 2006) and the positive relationship between offspring number and BMR in mammals has been demonstrated across a wide number of species (Harvey, Pagel & Rees, 1991). It follows, as I have demonstrated within the Neotomine–Peromyscine rodents, that there should be corollary negative relationship between offspring size and BMR. However, this negative relationship between offspring size and

BMR is rarely demonstrated. It is possible that the relationship between BMR and the offspring size *versus* offspring number trade-off may be obscured by comparing species within a taxonomic unit (*i.e.*, Family level or above) that cross zoogeographic realms (Lovegrove, 2000) using analyses that do not account for body size or phylogeny.

Nevertheless, the relationships between BMR and the offspring size *versus* offspring number trade-off exist in the Neotomine–Peromyscine rodents. Reproductive effort by the mother, as measured by BMR, increases with litter size in this group of rodents. Increase in maternal reproductive effort with litter size has been demonstrated within species for other muroid rodents (Millar, 1975; Fleming & Rauscher, 1978; Millar, 1978; König, Riester & Markl, 1988; Sikes, 1995) and between species of mammals (Millar, 1977). The efficiency with which a female mammal can use energy should be related to the amount of energy that she can spend during a reproductive event, and relatively high BMR within the Neotomine–Peromyscine rodents either facilitates large litter sizes because of a greater capacity for energy acquisition and use (Thompson, 1992) or is a result of large litter sizes causing higher energetic output by mothers (Johnson, Thomson & Speakman, 2001). The latter scenario was demonstrated for house mice (*Mus musculus*) when females with augmented litters increased their body mass more between pre-breeding and late lactation than females that had culled litters (Johnson, Thomson & Speakman, 2001). This distinction is important, especially when examining correlations between metabolism and life history attributes because it is not clear whether metabolism enables life history attributes, or life history attributes force metabolism (Speakman *et al.*, 2003).

Parental-care–based models of the evolution of endothermy (Farmer, 2000; Koteja, 2000) require a correlation between BMR and life history attributes that reflect total reproductive effort toward survival of young. I did not find evidence that BMR was related to the rate of growth of the litter from birth to weaning. This suggests that the evolution of high BMR was not due to selection for traits relating to accelerated growth of neonates (Koteja, 2004). However, I did find a relationship between BMR and the offspring size *versus* offspring number trade-off whereby taxa with high BMR had a large number of small offspring. A simple interpretation of my result is that high levels of BMR may have evolved to facilitate a large number of small offspring per reproductive event. A large number of small offspring would have been favoured if there were compensatory growth mechanisms for weaned young (Sikes, 1998a; Oksanen, Koskela & Mappes, 2002) that minimized fecundity trade-offs with small offspring size. This interpretation is supported by work that shows that the negative relationship between offspring number and offspring size (Charnov & Ernest, 2006) and the positive relationship between offspring number and metabolism (Glazier, 1985a; Genoud, 1988; Harvey, Pagel & Rees, 1991; Stephenson & Racey, 1995) are common among mammals.

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