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Phylogenetic Analysis of the Socioecology of Neotomine-Peromyscine Rodents

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Chapter 6 A Phylogenetic Analysis of the Breeding Systems of Neotomine-Peromyscine Rodents

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A BREEDING SYSTEM describes who copulates with whom, who contribntes genes to the next generation, and is the result of the combination of female and male mating strategies, which are often conflicting (see Waterman chap. 3 and Solomon and Keane chap. 4 this volume). Under some conditions the conflict between the sexes is ultimately played out in terms of one gender monopolizing access to the other, otherwise known as polygamy (Emlen and Oring 1977). The environmental potential for polygamy (EPP) is dictated by ecological, physiological, and life-history characteristics that, in turn, have evolved within a particular phylogenetic framework (fig. 6.1). The environmental potential for polygamy depends on the degree to which multiple mates, or the resources necessary to gain multiple mates, are economically defendable (Emlen and Oring 1977). Ecological, physiological, and life-history characteristics either allow organisms to, or prevent organisms from, taking advantage of or utilizing this potential. In the case of mammals, lactation and gestation are solely the provenance of females. However, as originally indicated by Emlen and Oring (1977), emancipation from parental care duties need not necessarily lead to the evolution of polygamy. Furthermore, as pointed out in chapter 3 by Waterman and chapter 4 by Solomon and Keane, female strategies often prevent males from monopolizing matings.

This chapter focuses on the breeding systems of Neotomine-Peromyscine rodents. There are three specific objectives to this chapter. First, we describe the patterns for major Neotomine-Peromyscine clades using data collected from the literature (table 6.1). Second, we examine data
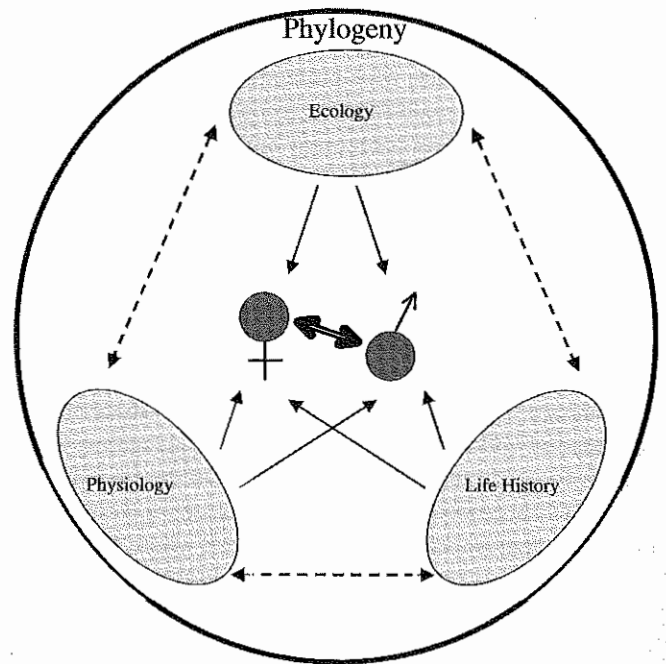
Figure 6.1 A general scenario for the determinants of breeding systems as indicated by Emlen and Oring (1977) and expanded to incorporate phylogenetic influences on ecology, physiology, and life history of the mating individuals. The breeding system (double solid line) is dictated by the influence of ecological, physiological, and life-history characteristics (single solid lines) on both males and females. In turn, ecological, physiological, and life-history characteristics are interrelated (dashed line) and have evolved within a particular phylogenetic framework.

Table 6.1 Breeding behaviors of Neotomine-Peromyscine rodent species

Taxon	Female spacing	Male spacing	Space size	Paternal care	Dispersal	References
Onychomys torridus	Solitary	Roving	M > F	Y		McCarty 1975; Horner 1961; Chew and Chew 1970; Blair 1943
Onychomys leucogaster	Solitary	Roving	M > F	N		Horner and Taylor 1968; Frank and Heske 1992; Stapp 1999
Baiomys taylori	Extensive overlap	Roving	Equitable	Y		Morrison et al 1977; Eshelman and Cameron 1987; Hudson 1974; Packard 1960; Blair 1941; Raun and Wilks 1964
Reithrodontomys humulis	Little overlap	Roving	Equitable	N		Dunaway 1968; Stalling 1997; Cawthorne and Rose 1989; Chandler 1984
Reithrodontomys fulvescens	Little overlap	Roving	M > F		Equal	Cameron and Kincaid 1982; Spencer and Cameron 1982; Packard 1968
Reithrodontomys megalotis		Polygynous	Equitable			Blaustein and Rothstein 1978; Webster and Knox Jones, Jr. 1982; Fisler 1963; Fitch 1958
P. crinitus	Solitary			N		Eisenberg 1963a
P. boylii	Solitary	Roving/polygynous	M > F	N		Ribble and Stanley 1998; Kalcounis-Rüppell and Spoon (submitted) and references therein
P. eremicus	Solitary			Y		Hatton and Meyer 1973; Lewis 1972; Eisenberg 1968
P. californicus	Solitary	Monogamous	M > F	Y	Females	Ribble 2003 and references therein
P. melanocarpus				Y		Rickart 1977; Rickart and Robertson 1985
P. attwateri			M > F			Schmidly 1974; Brown 1964
P. gossypinus	Solitary	Roving				Pournelle 1952; Wolfe and Linzey 1977; Pearson 1953
P. mexicanus	Solitary			Y		Rickart 1977; Duquette and Millar 1995a, 1995b, 1998
P. truei	Solitary	Roving	M > F	N		Hall and Morrison 1997; Ribble and Stanley 1998
P. leucopus	Solitary and gregarious	Roving/polygynous	M > F	N	Males	Wolff 1989; Wolff and Cicirello 1989, 1991; Schug et al. 1992; Xia and Millar 1988; Xia and Millar 1989
P. polionotus	Solitary	Monogamous	M > F	Y	Equal	Blair 1951; Smith 1966; Foltz 1981
P. maniculatus	Solitary	Roving/polygynous	M > F	N	Males	Horner 1947; Howard 1949; Ribble and Millar 1996; Wolff 1989; Wolff and Cicirello 1989, 1991
Neotomodon alstoni		Monogamous		Y		Luis et al. 2000, 2004
Neotoma albigula	Little overlap	Monogamous	Equitable	N		Boggs 1974; Batemen 1967; Macêdo and Mares 1988
Neotoma floridana	Little overlap	Monogamous	M > F	N		Rainey 1956; Fitch and Rainey 1956; Wiley 1980
Neotoma micropus	Little overlap	Roving	M > F	N	Males	Davis 1966; Wiley 1972; Raun 1966; Braun and Mares 1989
Neotoma stephensi	Solitary	Roving				Jones and Hildreth 1989; Ward 1984; Conditt and Ribble 1997
Neotoma cinerea	Little overlap	Roving	M > F		Males	Topping and Millar 1996a, 1996b, 1998
Neotoma macrotis	Solitary	Roving	M > F		Males	Matocq and Lacey 2004; Kelly 1989
Sigmodon	Solitary	Roving	M > F	N	Males	Cameron and Spencer 1985, 1981; Doonan and Slade 1995; Diffendorfer and Slade 2002
Akodon	Solitary	Roving	M > F	N	Males	Gentile et al. 1997; Suarez and Kravetz 2001; Steinmann et al. 1997; Citadino et al, 2002, 1998

NOTE: *Sigmodon* and *Akodon* are included as outgroups for comparative purposes.

from the literature on the following breeding behaviors: male spacing, female spacing, relative intersexual home range/territory size, paternal care, and juvenile dispersal patterns. We examine breeding behavior data in a phylogenetic framework to test if any phylogenetic patterns emerge in the observed variation in these breeding behaviors and if relationships occur among these behaviors. Third, we examine in a phylogenetic framework whether dietary, physiological, or life-history characteristics of the taxa are able to explain the observed variation in these breeding behaviors.

We explicitly focus on data from natural populations, although much of the information that we have on Neotomine-Peromyscine breeding systems and social behavior comes from the lab or seminatural situations. One of us recently published a phylogenetic review of monogamy and paternal care in *Peromyscus* (Ribble 2003). The current study is expanded to encompass the entire lineage of North American rats and mice within the rodent family Muridae, and includes mating strategies and taxa for which we have data from the field. Our taxonomy and phylogenetic topologies in this study reflect recent systematic work on the relationships among the genera *Peromyscus*, *Baiomys*, *Neotoma*, *Onychomys*, and *Reithrodontomys* (Edwards and Bradley 2002; Arellano et al. 2003; Bradley et al. 2004).

Descriptions of Breeding Systems

Peromyscini

The genus *Peromyscus* (> 50 species) has a large distribution in the Nearctic and northern Neotropics. An overview of *Peromyscus* social behavior was provided by Wolff (1989), with the majority of information coming from the deer mouse (*P. maniculatus*) and the white-footed mouse (*P. leucopus;* for discussion of the bias toward these two species see Wolff 1989). The societal structure of the deer mouse and the white-footed mouse is similar despite their varied habitats, resources, and widespread distributions. The following is from radiotelemetry studies. Males and females occupy home ranges, and in some cases home ranges are defended against conspecifics, thereby becoming territories. Maintenance of territories may be density dependent. In the wild, males and females do not nest together except in nest-boxes. Males occupy home ranges and/or defend territories to provide access to resources including food and reproductive females, whereas females occupy home ranges and/or defend territories to provide access to resources including food and space for raising their young and to pro-

tect their young from infanticide (Wolff 1993b). The pattern of overlap in home range/territories for males and females differs. In general, one male overlaps home ranges/territories of more than one female, whereas the females have home ranges or territories that are exclusive of other females. Using a polymorphic Esterase-1 locus, in a study of *P. leucopus,* Xia and Millar (1991) found that in two separate years 1 of 29 and 6 of 32 litters contained more than 2 paternal alleles, providing direct evidence that females and males were engaging in multiple mating, and they estimated that over 68% of females were involved in multiple mating. Similarly, in a study of *P. maniculatus,* Ribble and Millar (1996) found that male home ranges were significantly larger than female home ranges, and male home ranges overlapped multiple female and male home ranges. Using DNA fingerprinting they found 1 of 11 litters to be sired by two males, one of which also successfully sired litters of two more females. Additionally, 2 to 3 of 7 litters were likely sired by multiple males, based on band sharing values lower than observed among full-siblings (Ribble and Millar 1996). This frequency of multiple inseminations was similar to that found for *P. maniculatus* by using protein electrophoresis (Birdsall and Nash 1973).

In his chapter on *Peromyscus* social behavior Wolff (1989) suggested that the species diversity, habitat, and geographical variation in this genus provide a great opportunity for comparisons of social behavior. There are contrasts to the patterns of social organization in *P. maniculatus* and *P. leucopus,* and since that review, we have gained insight into the social behavior of some other *Peromyscus* species.

Relatively little is known about the behavior or ecology of the Canyon mouse (*P. crinitus*) because, as its common name implies, it inhabits rock outcrops at high elevations in western North America. Through intensive trapping and genotyping at microsatellite loci it was found that in two Utah populations of *P. crinitus* a minimum of 3 of 10 litters were multiply sired (Shurtliff et al. 2005). By genotyping all captured individuals in the population, including the potential sires, it was shown that although there is multiple mating by females, there was no instance where a male mated with more than one female (within or between litters), suggesting genetic polyandry in addition to genetic monogamy for this species. Behavioral studies were not conducted in these populations and it is not clear whether there was any nest sharing among mates; however, males assigned with high confidence of paternity were always trapped near their female mates (relative to males who did not have a high confidence of paternity; Shurtliff et al. 2005). These results suggest that home ranges of these males likely overlapped with females.

The brush mouse (*P. boylii*) is found in canyon bottoms and, in California populations, are associated with oak trees and the acorns (mast) they produce (Kalcounis-Rüppell and Millar 2002). During a two-year study when the population density was high (40–70 mice/ha), males and females did not differ in home range size, but inter- and intrasexual home-range overlap was higher during a high population density year. Males and females did not share nests and did not maintain long-term pair bonds. Although multiple mating appeared infrequent, based on behavioral observations (transfer of fluorescent powder), microsatellite analyses showed that 1 of 7 litters was sired by more than one male (Kalcounis-Rüppell 2000). At high population densities neither males nor females defended territories (Kalcounis-Rüppell 2000). These results differ from a comparable study on a *P. boylii* population at a relatively low population density in New Mexico (highest minimum number known alive: 30/2.7 ha; Ribble and Stanley 1998); where home range size was inversely related to conspecific density, females did not overlap with each other, and males had home ranges that overlapped with multiple females. Furthermore, there was a difference in home range size between the sexes, with male home ranges being almost twice as large as female home ranges. These results show population variation in social structure and highlight the importance of resource availability and population density. Indeed, during low mast years (and subsequent low population densities), *P. boylii* in California appears to have a social structure similar to that of low population density *P. boylii* in New Mexico (Kalcounis-Rüppell and Spoon [manuscript submitted for publication]).

In some species of *Peromyscus*, pairs of males and females have exclusive territories and exclusive genetic contributions to their litters, and are thus considered to be monogamous from a behavioral and a genetic standpoint. Oldfield mice (*P. polionotus*) nest in burrows that can house males, females, and offspring (50.5% of burrows contain an adult male and female; Foltz 1981). Using starch-gel electrophoresis of 5 polymorphic proteins, it was demonstrated that the males who were nesting with females were the sole sires of the litters, and when a female had at least 2 consecutive litters, the same male sired both of the litters (Foltz 1981). Home range size and dispersal distance is equal for males and females (Swilling and Wooten 2002). The California mouse (*P. californicus*) is exclusively monogamous, with DNA fingerprinting confirming that in 28 of 28 litters examined, the behavioral pairs from the field were the parents of litters (Ribble 1991). Males and females nest together during breeding and nonbreeding seasons, and maintain a pair bond permanently unless one mate dies or disappears from the grid (Ribble and Salvioni 1990).

Mean home range size is 1161 m², and does not differ between males and females (Ribble and Salvioni 1990). Dispersal is female biased (Ribble 1992). Male removal in the field has a negative effect on reproductive success, as a result of the absence of direct care of young rather than protection against infanticidal intruders (Gubernick and Teferi 2000).

The volcano mouse (*Neotomodon alstoni*) is a species that has long been taxonomically associated with *Peromyscus* (Carleton 1989), but little is known about its mating system in natural populations. In the laboratory, however, much is known about male and female parental behaviors (Luis et al. 2000; Luis et al. 2004). In captivity, males actually spend more time than females huddling, grooming, and retrieving young (Luis et al. 2000).

Lastly, the genus *Reithrodontomys* is also included in the Peromyscini clade (Bradley et al. 2004), and most of the published information from this genus is from *R. megalotis*, *R. fulvescens*, and *R. humulis*. Based on multiple captures in the same trap, *R. megalotis* is reported to be the most social of these species (Blaustein and Rothstein 1978; Cawthorn and Rose 1989), but male and female home ranges are reported to be similar in size (Fitch 1958). For *R. humulis*, there is no evidence of male care (Kaye 1961), and home ranges of males and females are similar in size and overlap extensively (Chandler 1984; Dunaway 1968; Cawthorn and Rose 1989). Male home ranges are larger than those of females in *R. fulvescens* (Packard 1968; Cameron and Kincaid 1982), but there is little evidence of territorial behavior in either sex (Packard 1968).

Neotomini

The Neotomini clade includes the genera *Neotoma* and *Onychomys* (Bradley et al. 2004). The genus *Neotoma* (approx. 20 species) is distributed from Canada to Central America. Two of these species have been studied over the long term and provide a basic understanding of their social structure in the wild. The bushy-tailed woodrat (*Neotoma cinerea*) is distributed through much of northwestern North America. Its local distribution is limited by the availability of rock outcrops for suitable nest sites (Hickling 1987), which can be up to 470 m away from foraging sites (Topping and Millar 1996a), resulting in a clumped distribution of females (Hickling 1987). Matrilineal females tend to be more closely associated in space than nonmatrilineal females, and there are fitness advantages associated with mothers and daughters coexisting in space (Moses and Millar 1994). Juvenile females were more likely to survive if they stayed on the outcrop with their mothers, and they suffered fewer reproductive failures when breeding as year-

lings if their mothers were present (Moses and Millar 1994). Radiotelemetry revealed that in addition to the clumped distribution of females on rocky outcrops, females and resident males had considerable overlap of home ranges on the outcrops (Topping and Millar 1996b). DNA fingerprinting demonstrated that despite high levels of inter- and intraspecific overlap of home ranges on outcrops, 35 of 35 litters were sired by a single male; no male fathered more than one litter from a given female within or between years, resulting in low variation in reproductive success of males and females (Topping and Millar 1998).

The big-eared woodrat (*Neotoma macrotis* [formerly *N. fuscipes*, but now recognized as distinct]; Matocq 2002) occupies stick 'houses' (Linsdale and Tevis 1951) along canyon bottoms of oak woodland habitat. In a population of *N. macrotis* that has been studied for over 50 years, individuals are found in the long (580 m) and relatively narrow (26 m) riparian buffer (Matocq and Lacey 2004). Livetrapping and radiotelemetry data on this population show similar female group structure as in *N. cinerea*, with high levels of female philopatry and male-biased dispersal (Kelly 1989), suggesting matrilineal kin groups. However, using microsatellite genotyping, it was found that these were not matrilineal kin groups, because females that were grouped in space were no more related to each other than to other females in the population, and no more successful, with respect to number of pups weaned, when living in close proximity to first-order relatives (Matocq and Lacey 2004). Thus for *N. macrotis* female philopatry is not the only factor contributing to population genetic structure; factors such as habitat quality and interactions with conspecifics may be important (Matocq and Lacey 2004). Similar to *N. cinerea*, however, variation in reproductive success for males and females was low and equitable despite the occurrence of males and females having multiple partners across litters and some litters being multiply sired (Matocq 2004).

Although less intensively studied than *N. cinerea* and *N. macrotis*, the social biology of the desert woodrat *N. lepida* and the southern plains woodrat (*N. micropus*) has received some attention. The Danzante woodrat (*N. lepida latirostra*) is larger bodied than its continental counterparts, and it has larger home ranges that are more exclusive within both sexes than is displayed in continental *N. lepida* and other *Neotoma* species (Vaughan and Schwartz 1980). From trapping data, the mean home range size of *N. l. latirostra* is 0.33 ha and 0.11 ha for males and females, respectively (Vaughan and Schwartz 1980); these home ranges are larger than for populations in a Californian coastal sage (mean male home range 0.04 ha; Bleich and Schwartz 1975) and the San Gabriel Mountains (mean male home range 0.19 ha; MacMillen 1964). Home range esti-

mates from radiotelemetry in a Texas population of *N. micropus* show that like *N. lepida*, home ranges are exclusive within sexes, with males (0.19 ha) having larger home ranges than females (0.02 ha); however, there was more overlap of female home ranges by male home ranges than male home ranges overlapped by female home ranges (Conditt and Ribble 1997). Additionally, there was no nest sharing among *N. micropus*, and the majority of observations of this species were of solitary animals at the nest, suggesting that *N. micropus* is relatively asocial (Conditt and Ribble 1997).

Onychomyini

The two species in the genus *Onychomys* were traditionally considered monogamous (see review in Frank and Heske 1992), but radiotelemetry studies indicate otherwise. Radiotelemetry of *O. torridus* (Frank 1989; Frank and Heske 1992) and *O. leucogaster* (Stapp 1999) indicate that males have larger ranges than females, which overlap with multiple females during the breeding season, consistent with a promiscuous mating system. No genetic studies of paternity have been conducted in either species.

Baiomyini

This monophyletic group includes *Baiomys* and *Scotinomys*, of which there is only information on *Baiomys taylori*. Early studies under laboratory conditions by Blair (1941) and Packard (1960) indicated that males will care for the young. In the field, males and females have similar size ranges, with considerable overlap within and among both sexes (Raun and Wilks 1964). No genetic paternity information is available for either species in natural populations.

Phylogenetic Analyses

Relationships among breeding behaviors

We conducted a phylogenetic comparative analysis to reconstruct ancestral character states of breeding behaviors and to test if any of these behaviors appear in the phylogeny at similar times. Furthermore, we wanted to test if there were any correlations in the appearance of these behaviors, and if the presence of one behavior influenced the appearance of others, taking into account their evolutionary history (Felsenstein 1985; Maddison 2000). Sufficient data are available (see table 6.1) for the Neotomine-Peromyscine rodents to critically evaluate mating system hypotheses. For example, various hypotheses predict that male spacing be-

havior will be dependent on female spacing behavior (Emlen and Oring 1977; Ostfeld 1990), or that parental care would be dependent on monogamous spacing in males (Brotherton and Komers 2003). Specifically, we examined data on male spacing, female spacing, relative intersexual home-range/territory size, paternal care, and juvenile dispersal patterns to test for phylogenetic patterns in the observed variation in these breeding behaviors and to determine if any relationships occur among these behaviors. We coded all traits as indicated in table 6.1. Female spacing patterns were scored as solitary (no overlap between home ranges), little overlap, extensive overlap, or gregarious (largely overlapping home ranges, usually accompanied with nest-sharing), based on spatial overlap during the breeding season. Species with both solitary and gregarious female spacing were scored as gregarious. Male spacing patterns were scored as monogamous, roving, polygynous, or variable if populations exhibited multiple patterns. No species has been documented to be solely polygynous; those species with polygyny have also been documented as roving. Space size was recorded as equitable or male range size being greater than female (M > F in table 6.1). If a species has been observed to exhibit male care in the laboratory, but not in the field, then they were considered nonpaternal. If a species has exhibited paternal behavior in the lab, has other life-history traits consistent with paternal care (e.g., Dewsbury 1981), and there was no conflicting information from the field, they were considered paternal (table 6.1). Where there was conflicting information from the field, we used the best evidence from the field studies to determine paternal care (e.g., we characterized *P. leucopus* as not having paternal care despite the results of Schug et al. 1992, table 6.1). Finally, dispersal of juveniles was coded as being equitable, female biased, or male biased.

Relationships between behaviors and diet, physiological, and life-history characteristics

We conducted a phylogenetic comparative analysis to test for relationships between mapped character states of breeding behaviors and ecological, physiological, or life-history characteristics, taking into account their evolutionary history (Felsenstein 1985; Maddison 2000). Specifically, we examined whether diet, physiological, or life-history characteristics of the taxa could explain the observed variation in breeding behaviors. The ecological, physiological, and life-history characters we used are shown in table 6.2. For empty cells for continuous variables (basic metabolic rate [BMR] and relative litter weight) the mean value for the genus was assumed (table 6.2).

A significant association exists between energy expenditure and diet in the wild in small mammals. Small mammals that exploit high-energy foods (vertebrates and insects) are able to spend more energy per unit mass relative to resting metabolic rates than small mammals that exploit energy-poor foods (seeds and grasses; Speakman 2000). Because Neotomine-Peromyscine rodents span this range of diets, and different costs and benefits are associated with different food resources, we hypothesized a relationship between diet and breeding behaviors. Kalcounis-Rüppell et al. (2002) demonstrate a higher energetic cost associated with mating for promiscuous males (*Peromyscus boylii*) than monogamous males (*P. californicus*), but no difference between females. Thus we predicted that roving males would have higher energy diets than solitary males, and that there would be no relationship between diet and female spacing. To test this hypothesis, we coded diet as carnivorous, insectivorous, omnivorous, granivorous, or herbivorous (table 6.2).

Ribble (2003) suggested that relative neonate and litter weight (relative to adult weight) might be correlated with mating strategies in *Peromyscus* because of the energetic cost of lactation and consequent maternal investment, which varies with offspring size and number. We hypothesized a relationship within the Neotomine-Peromyscine rodents between relative litter weight and breeding behaviors. We predicted that solitary females would have higher relative litter weights (Ribble 2003). The majority of data required to calculate relative litter weight (litter size, neonate weight (g) at birth, relative neonate weight) were from Millar (1989), with some data from Hayssen et al. (1993). Relative litter weights were calculated by dividing litter weights by adult weights (table 6.2). For the outgroups *Sigmodon* and *Akodon,* we took the average of all the species values for each genus for all variables used to calculate relative litter weights (table 6.2).

The size of the distributional range of a taxon correlates with both the ecological conditions of the range (Glazier 1980) and species life-history patterns (Glazier 1980, Brown 1995). For example, in an analysis of *Peromyscus,* Glazier (1980) found a positive correlation between geographical range and litter size, and he argued that larger geographic ranges were found in species with larger litter sizes, short life spans, and smaller body size. Since these species-level traits likely affect the distribution of organisms (Brown 1995), we wanted to test if the distribution was correlated with the behaviors we measured. To determine the species distribution area we recorded the size (km²) of the geographic ranges of all species, using the digital distribution maps of mammals of the western hemisphere (Patterson et al. 2003). To calculate species distribution areas we used the XTools extension in ArcView 3.2 (ESRI, Redlands,

Table 6.2 Ecological, physiological, and life-history characteristics of Neotomine-Peromyscine rodent species

Taxon	Species distribution area (km^2)	Relative litter weight	BMR (mlO$_2$/g/minute)	Residual BMR (mlO$_2$/g/minute)	Feeding habit	References[a]
O. torridus	3907553.78	0.30	1.55	−0.01	Carnivorous	McCarty 1975 and references therein; Chew and Chew 1970
O. leucogaster	3907553.78	0.29	1.55*	−0.10	Carnivorous	McCarty 1978 and references therein
Baiomys taylori	1164795.22	0.45	1.95	0.01	Omnivorous	Eshelman and Cameron 1987 and references therein
R. humulis	1596620.06	0.38	2.46*	0.01	Omnivorous	Stalling 1997 and references therein
R. fulvescens	2640627.61	0.27	2.46*	0.10	Insectivorous	Spencer and Cameron 1982 and references therein
R. megalotis	5303556.43	0.44	2.46	0.07	Granivorous	Webster and Knox Jones, Jr. 1982 and references therein
P. crinitus	930352.55	0.45	1.33	−0.18	Omnivorous	Johnson and Armstrong 1987 and references therein
P. boylii	2680094.46	0.31*	2.34	0.14	Omnivorous	Kalcounis-Rüppell and Spoon (ms. submitted) and references therein
P. eremicus	1387374.30	0.29	1.47	−0.10	Omnivorous	Veal and Caire 1979 and references therein
P. californicus	158389.58	0.25	1.37	−0.04	Omnivorous	Merritt 1978 and references therein
P. melanocarpus	9334.39	0.18	1.67*	0.11		
P. attwateri	490547.28	0.31*	1.67*	0.01	Herbivorous	Brown 1964
P. gossypinus	1401995.07	0.24	1.72	0.03	Omnivorous	Wolfe and Linzey 1977 and references therein
P. mexicanus	512873.21	0.20	1.67*	0.10		
P. truei	2184728.43	0.27	1.71	0.01	Omnivorous	Hoffmeister 1981 and references therein
P. leucopus	6593854.13	0.38	1.66	−0.03	Omnivorous	Lackey et al. 1985 and references therein
P. polionotus	478832.59	0.44	1.79	−0.06	Herbivorous	Gentry and Smith 1968
P. maniculatus	14104524.90	0.40	1.74	−0.01	Omnivorous	Baker 1983
Neotomodon alstoni	51636.24	0.16	1.67*	0.09	Insectivorous	Glendinning and Brower 1990
N. albigula	1952915.28	0.13	0.74	−0.08	Herbivorous	Mačedo and Mares 1988 and references therein
N. floridana	2172842.61	0.19	0.72*	−0.06	Herbivorous	Rainey 1956; Wiley 1980 and references therein
N. micropus	1121208.66	0.13	0.72*	−0.06	Herbivorous	Braun and Mares 1989 and references therein
N. stephensi	228873.06	0.11	0.72*	−0.12		
N. cinerea	3636547.44	0.17	0.73	−0.03	Herbivorous	Smith 1997 and references therein
N. macrotis	327006.17	0.12	0.79	0.01	Herbivorous	Carraway and Verts 1991 and references therein
Sigmodon	937034.08	0.32	1.48	0.18	Omnivorous	Cameron and Spenser 1981 and references therein
Akodon	556064.75	0.49	1.70	0.02	Omnivorous	Dalby 1975

NOTES: *Sigmodon* and *Akodon* are included as outgroups for comparative purposes. Average values for genus, where specific value was not available is denoted by an asterisk (*).
[a] For feeding habit only; see text for other sources of data in this table.

CA). For outgroups *Sigmodon* and *Akodon*, we took the average of all the species for each genus as the geographic range for that genus (table 6.2).

All of our hypotheses about whether ecological, physiological, or life-history characteristics of the taxa are able to explain the observed variation in these breeding behaviors are largely based on energetic reasoning. Thus we also include basal metabolic rate (BMR) as an independent variable (table 6.2). The data on metabolic rates were from McMillan and Garland (1989). We used mass independent data in our analyses by using residual values from the predicted values from the significant relationship of body mass and mass-specific BMR for all Neotomine-Peromyscine rodents included in our analysis ($F_{1,25} = 81.18$, $P < 0.001$, $R^2 = 0.76$; logBMR $= -0.32$ log Body Mass $+ 0.67$).

Phylogenetic methods

The phylogeny we used is based on the study of Bradley et al. (2004), which differentiated the Baiomyini, Neotomini, Onychomyini, and Peromyscini groups with *Sigmodon* and *Akodon* as outgroups. Not all species of interest in this study were included by Bradley et al. (2004), so we followed Edwards and Bradley (2002) for relationships among *Neotoma* and Arellano et al. (2003) for relationships among *Reithrodontomys*. Within the Peromyscini, several species of *Peromyscus* were not part of the phylogeny published by Bradley et al. (2004), so we relied on information from Stangl and Baker (1984) and Bradley (unpublished data) when necessary. We use two tree topologies that differ primarily in the placement of the Onychomyini. In the first,
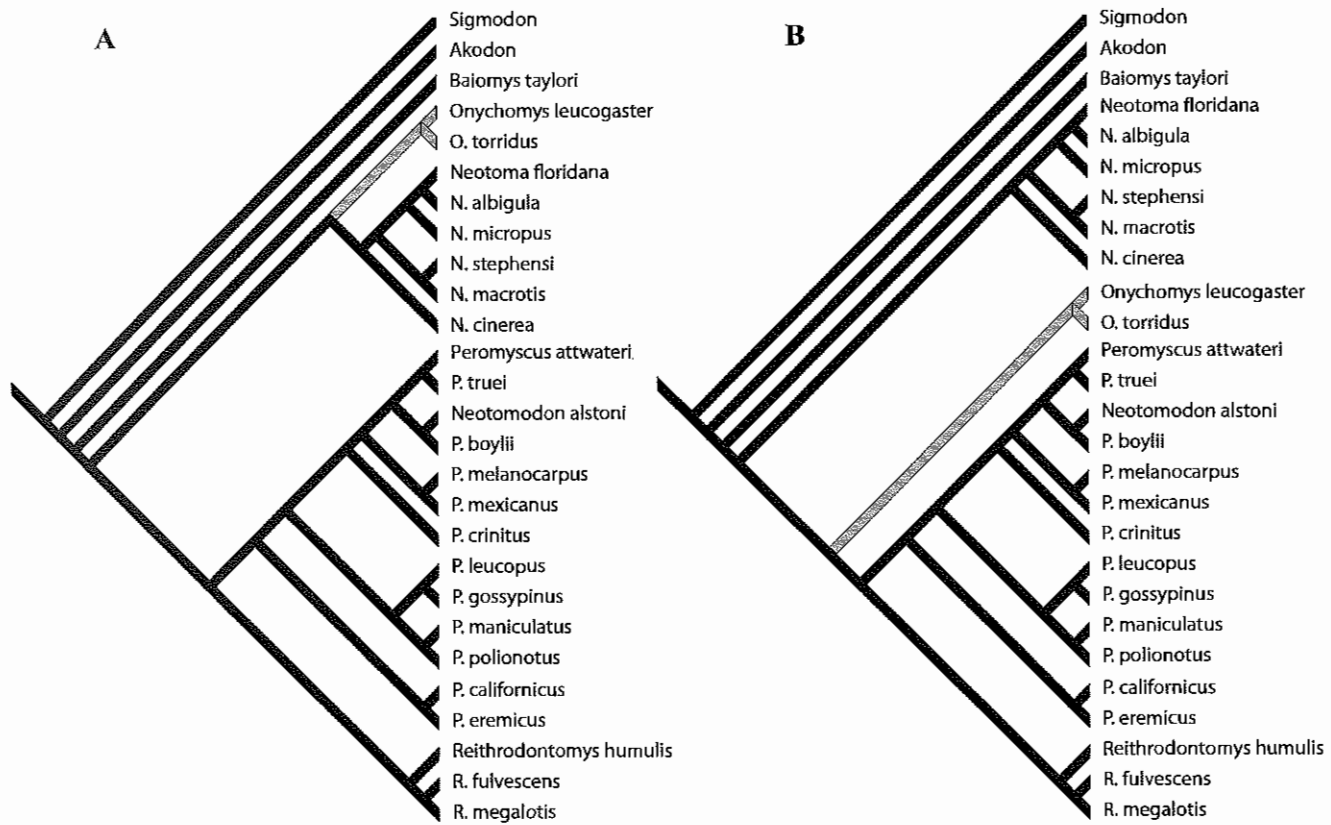
Figure 6.2 The two phylogenies used in our comparative analyses that reflect the two current hypotheses of the evolutionary relationship among the Neotomine-Peromyscine rodents. The differences are highlighted in gray. In topology A *Onychomys* is a sister taxon to Neotoma. In topology B, *Onychomys* is basal to *Peromyscus*.

(referred to as topology A) *Onychomys* is sister to *Neotoma*, and in the second, *Onychomys* (referred to as topology B) is basal to *Peromyscus* (fig. 6.2). Both topologies were used, because they reflect two current hypotheses of the evolutionary relationship among the Neotomine-Peromyscine rodents; however, current multigene data support alignment of *Onychomys* with the Peromyscini (Reeder et al. 2006).

Character states from table 6.1 and table 6.2 were mapped on the phylogeny of Neotomine-Peromyscine rodents using Mesquite, Version 1.02 (Maddison and Maddison, 2004). We made no assumptions about the evolutionary sequence in which characters changed. Continuous characters, such as geographic range and litter size and weight characteristics, were compared using Felsenstein's method of independent contrasts (Felsenstein 1985). Correlations among categorical independent characters were examined using Maddison's pairwise comparisons (Maddison 2000). To facilitate pairwise comparisons with binary categorical independent variables, spacing variables were recoded for both sexes as female spacing: solitary or not solitary, and male spacing: monogamous or not mo-

nogamous. In all cases for pairwise comparisons, we ordered categorical variables according to determination of ancestral traits that we obtained from the character trace analysis in Mesquite.

Results

Ancestral states and relationships among breeding behaviors

For all results, we use topology A to discuss and graphically describe ancestral character states. For all analyses of interrelationships among breeding behaviors, there was congruence between topology A and topology B.

The relationships between male and female spacing are indicated in the mirror phylogenies of figure 6.3a. For most Neotomine-Peromyscine rodents examined, females are solitary and males are roving, and these traits are ancestral for the clade (fig. 6.3a). This pattern is consistent with Waterman's assertion that promiscuity is common in rodents (Waterman, chap. 3). Using pairwise comparisons,

A
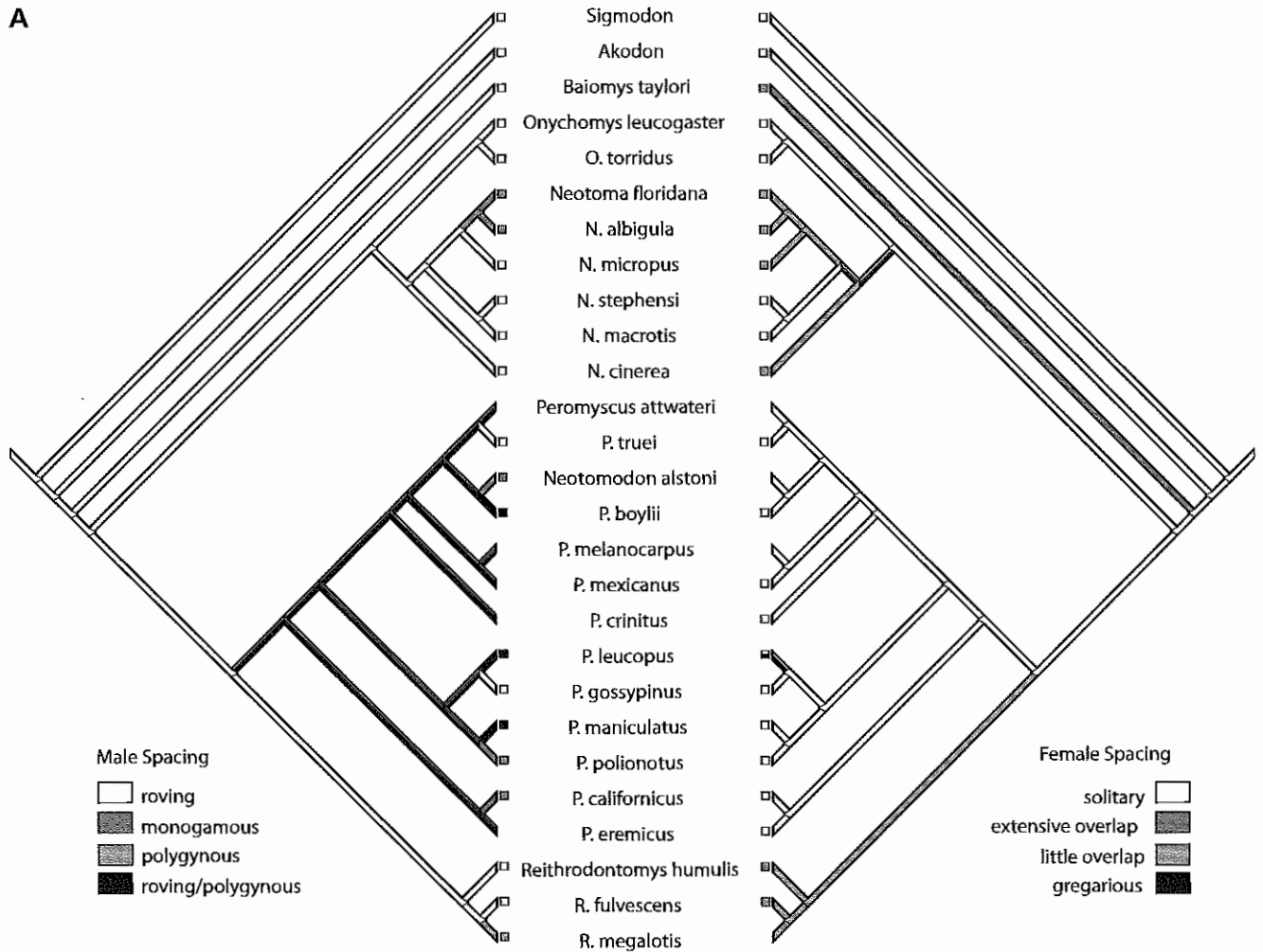
Figure 6.3 Mirror phylogenies showing the ancestral state reconstruction for (A) female and male spacing and (B) paternal care and male spacing in Neotomine-Peromyscine rodents. For this, and all phylogenies presented herein, the character state for each taxon is indicated in the block at the terminal end of the lineage and the origin of the character on the phylogeny is indicated by the shading. No block at the terminal end of a lineage indicates insufficient data for that particular character.

we found that male spacing behavior was independent of female spacing behavior (3,096 pairings of terminal taxa with 5 pairs contrasting female behavior, $P = 0.13-0.75$) and female spacing behavior was independent of male spacing behavior (4,416 pairings of terminal taxa with 4 pairs contrasting male behavior, $P = 0.5-1.0$). In general, female spacing appears most variable among lineages of the Neotomini, whereas male spacing is most variable among the clade of Peromyscini that includes *P. californicus, P. eremicus, P. leucopus, P. gossypinus, P. maniculatus,* and *P. polionotus.* What little information we have on *Baiomys* and *Reithrodontomys* suggests these lineages have different spacing strategies.

Paternal care appears to have evolved multiple times (fig. 6.3b), consistent with the conclusion of Ribble (2003)

for *Peromyscus.* We compared the evidence for paternal care to patterns of male spacing and found monogamous males provide paternal care (8,048 pairings of terminal taxa with 6 pairs contrasting paternal care behavior, $P = 0.03-0.75$; fig. 6.3b).

By far the most common and presumably ancestral state within the Neotomine-Peromyscine rodents is for males to have larger home ranges than females, with very few taxa demonstrating equitable range sizes and no taxa with female ranges larger than male ranges (fig. 6.4a). There are relatively few data on dispersal behavior within the Neotomine-Peromyscine rodents. However, available information indicates that the ancestral condition is for natal dispersal to be male biased (fig. 6.4b). Neither home range size nor natal dispersal were related to other breeding behaviors.
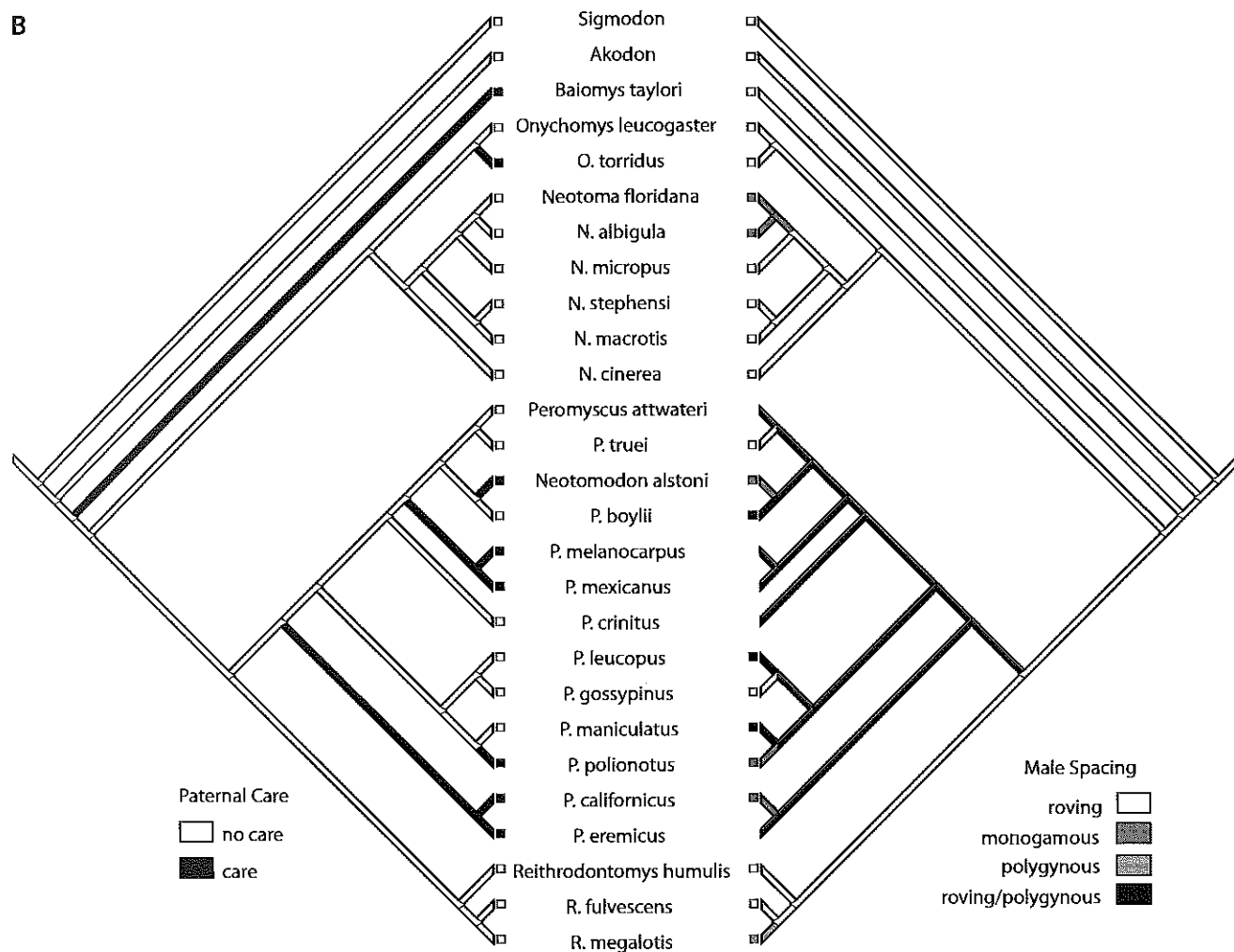
B

Sigmodon
Akodon
Baiomys taylori
Onychomys leucogaster
O. torridus
Neotoma floridana
N. albigula
N. micropus
N. stephensi
N. macrotis
N. cinerea
Peromyscus attwateri
P. truei
Neotomodon alstoni
P. boylii
P. melanocarpus
P. mexicanus
P. crinitus
P. leucopus
P. gossypinus
P. maniculatus
P. polionotus
P. californicus
P. eremicus
Reithrodontomys humulis
R. fulvescens
R. megalotis

Paternal Care
☐ no care
■ care

Male Spacing
roving ☐
monogamous ▨
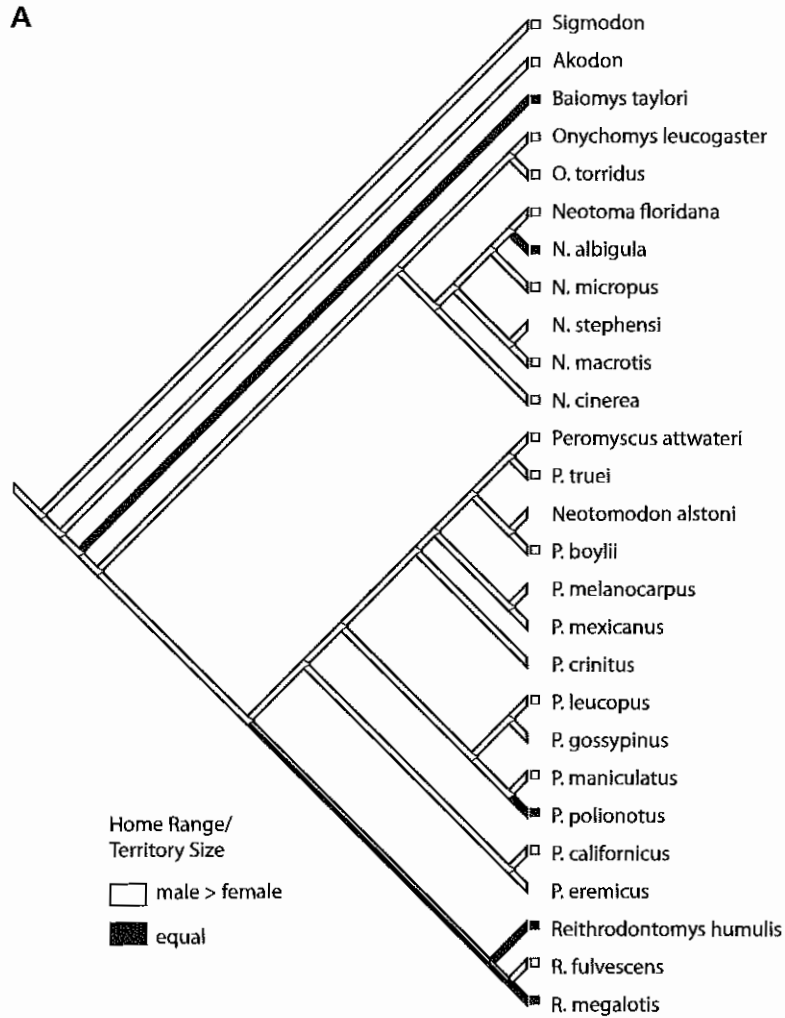polygynous ▦
roving/polygynous ■

Figure 6.3   (continued)

Relationships between behaviors and diet, physiological, and life-history characteristics

For all results, we use topology A to discuss and graphically describe ancestral character states. Although there was agreement between topology A and B in the analyses of the relationships between behaviors and diet, physiological, and life-history characteristics, the congruence was not perfect. Where the two topologies differed we present both results. We found significant relationships among breeding behaviors and physiological, life history, and diet characteristics as well as trends with P values of 0.06. We treat these trends as biologically meaningful.

Among the diet, physiological, and life-history characteristics for the Neotomine-Peromyscine rodents, we found a positive correlation between species distribution area and litter size (fig. 6.5). This relationship was also significant when placed in context of the phylogeny, using Felsenstein's method of independent contrasts (topology A: $r^2 = 0.15$, $F = 4.2$, df $= 25$, $P = 0.04$; topology B: $r^2 = 0.15$, $F = 4.6$, df $= 25$, $P = 0.04$).

Most Neotomine-Peromyscine rodents are omnivorous, but certain clades have evolved specific feeding adaptations (fig. 6.6a). For example, the *Onychomys-Neotoma* clade is derived, with *Onychomys* being carnivorous and *Neotoma* mostly herbivorons. There was a trend for male spacing behavior to be related to diet, with nonmonogamous males having a higher energy diet (i.e., carnivory and omnivory) than monogamous males (topology A: 4,416 pairings of terminal taxa with 4 pairs contrasting male spacing behavior, $P = 0.13-0.75$; topology B: 4,880 pairings of terminal taxa with 4 pairs contrasting male spacing behavior, $P = 0.06-0.75$; fig. 6.6a). There was also a trend for male spacing behavior to be related to BMR, with nonmonoga-

A

Home Range/
Territory Size

☐ male > female

■ equal

Sigmodon
Akodon
Baiomys taylori
Onychomys leucogaster
O. torridus
Neotoma floridana
N. albigula
N. micropus
N. stephensi
N. macrotis
N. cinerea
Peromyscus attwateri
P. truei
Neotomodon alstoni
P. boylii
P. melanocarpus
P. mexicanus
P. crinitus
P. leucopus
P. gossypinus
P. maniculatus
P. polionotus
P. californicus
P. eremicus
Reithrodontomys humulis
R. fulvescens
R. megalotis

Figure 6.4 Phylogeny depicting the ancestral state reconstruction of (A) home range size and (B) natal dispersal in Neotomine-Peromyscine rodents.

mous males having a higher BMR than monogamous males (4,416 pairings of terminal taxa with 4 pairs contrasting male spacing behavior, $P = 0.06-0.69$; fig. 6.6b). Female spacing behavior was not related to diet but was related to BMR, with solitary females having a higher BMR than nonsolitary females (3,096 pairings of terminal taxa with 5 pairs contrasting male spacing behavior, $P = 0.03-0.5$; fig. 6-6c). Paternal care was not related to diet or BMR.

There was a trend for relative litter weight to be related to male spacing, with monogamous males having smaller relative litter weights compared to nonmonogamous males (4,416 pairings of terminal taxa with 4 pairs contrasting male spacing behavior, $P = 0.06-0.69$; fig. 6.7). There was a trend for species distribution area to be related to male spacing, with monogamous males having a relatively small species distribution area compared to nonmonogamous

males (3,096 pairings of terminal taxa with 4 pairs contrasting male spacing behavior, $P = 0.06-0.69$; fig. 6.8). Female spacing behavior was not related to species distribution area or relative litter weight. Reflecting the relationship between male spacing behavior and paternal care (fig. 6.3b), paternal care was also related to species distribution, with males displaying paternal care tending to be from taxa with smaller species distributions (8,048 pairings of terminal taxa with 6 pairs contrasting paternal care behavior, $P = 0.03-0.65$).

Discussion

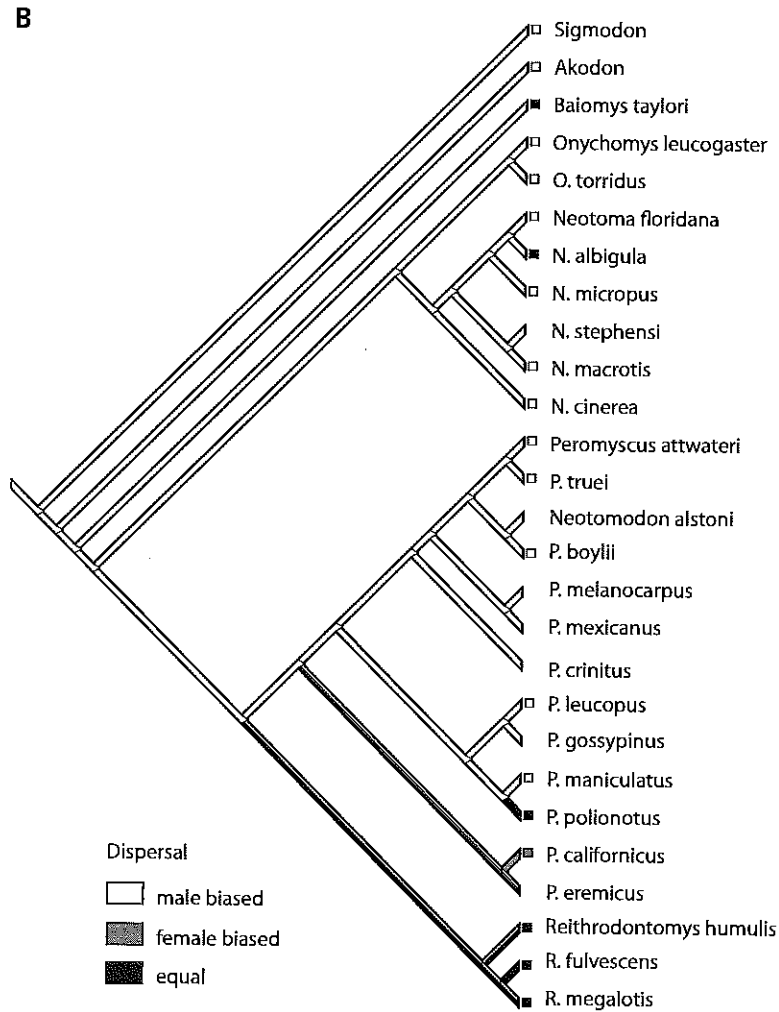For the majority of our analyses, there was strong congruence between topology A and topology B, suggesting that

B

Dispersal
- ☐ male biased
- ▨ female biased
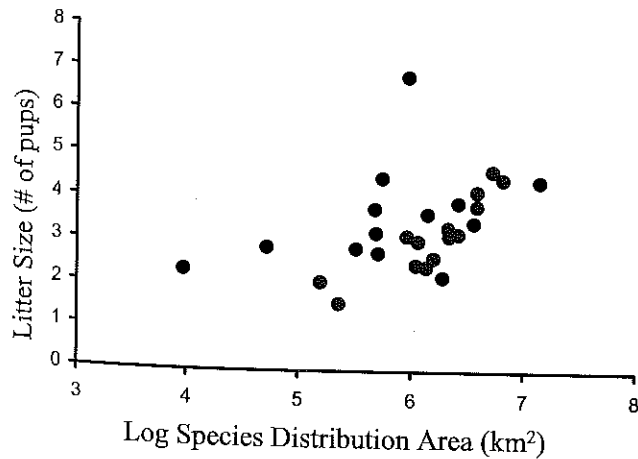- ■ equal

Figure 6.4 (continued)

Figure 6.5 Relationship between the logarithm of species distribution area (km²) and litter size for Neotomine-Peromyscine rodents, *Sigmodon* and *Akodon*.

the *Onychomys* clade does not differ substantially from the Neotomine-Peromyscine rodents with respect to the evolution of breeding behaviors and their correlates. In general, we found that females were solitary and males were not monogamous, and these traits are ancestral for the clade. Male spacing behavior was independent of female spacing behavior, and female spacing behavior was independent of male spacing behavior. Paternal care appeared to have evolved multiple times. Monogamous males tended to provide care to offspring. The ancestral state was for males to have larger home ranges than females, with very few taxa demonstrating equitable range sizes. The ancestral state was for natal dispersal to be male biased. We found a positive correlation between species distribution area and litter size. Nonmonogamous males had a higher-energy diet (i.e., carnivory and omnivory) and a higher BMR than monoga-

A
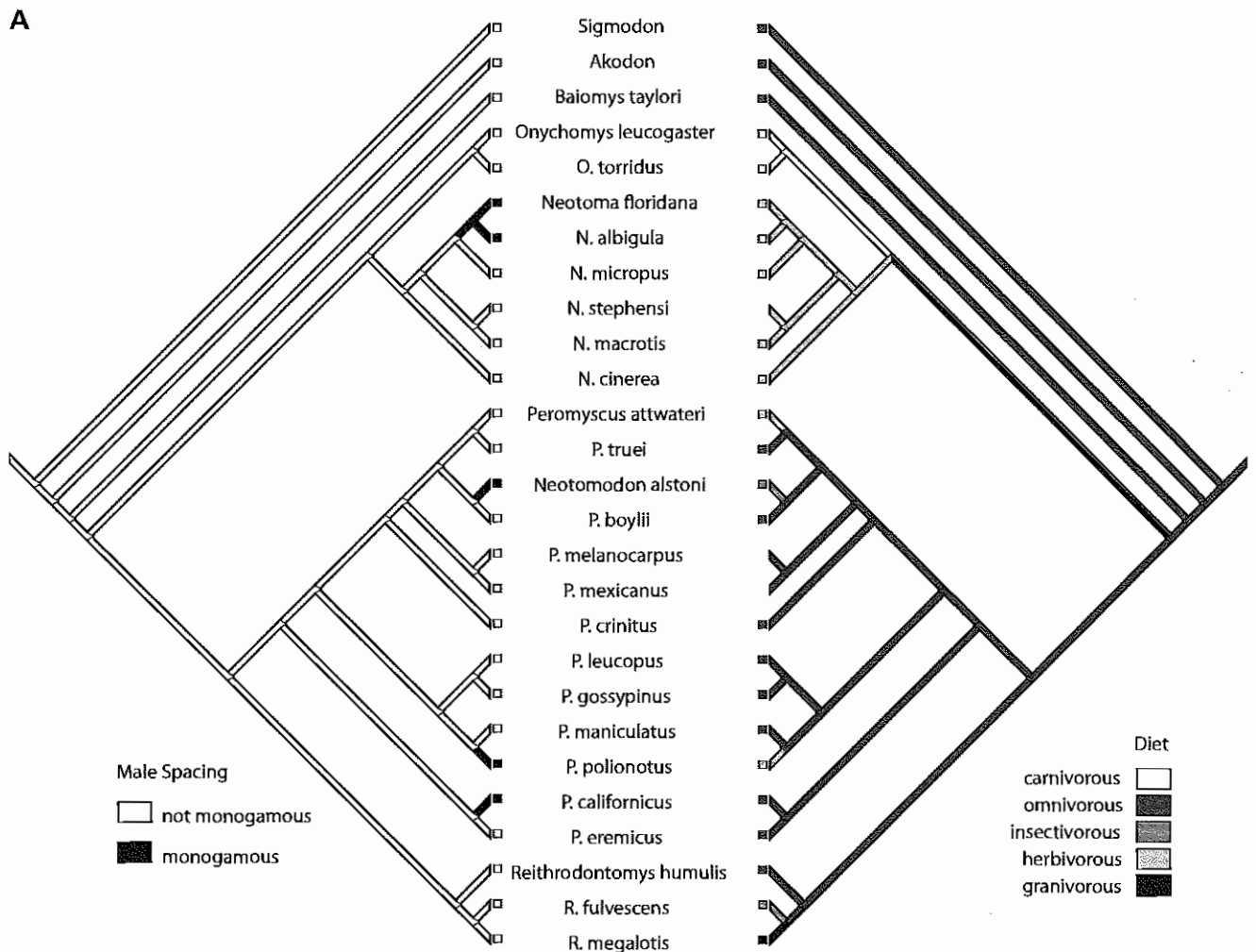
Figure 6.6 Mirror phylogenies of topology A, showing the ancestral state reconstruction for (A) male spacing and diet, (B) male spacing and BMR, and (C) female spacing and BMR in Neotomine-Peromyscine rodents. Although BMR is graphically presented as a binary variable, statistics were performed on continuous residual values.

mous males. Solitary females had a higher BMR than non-solitary females. Monogamous males had low relative litter weights and had smaller species distribution range sizes compared to males that were not monogamous. Males displaying paternal care tended to be from taxa with small species distributions.

Collectively, the influence and interrelationships of ecology, physiology, and life-history characters on the breeding behaviors of Neotomine-Peromyscine rodents from our analyses are summarized in figure 6.1 and are described as follows. We did not find significant relationships between the breeding behaviors of males and females. Males were influenced by ecological factors such as the species distribution area and feeding habits, as well as the life history characteristic of relative litter weight. Both male and female breeding behaviors were influenced by the physiological character of BMR. Aspects of ecology and life history were interrelated. Specifically, species distribution area was related to litter size.

Our determination of ancestral states for male and female breeding behaviors provided few surprises, given our knowledge of the energetic cost of lactation in mammals (e.g., Gittleman and Harvey 1982; Thompson 1992), the differential investment in offspring by males and females (Trivers 1972), and the theory of mating system evolution (Orians 1969; Arnold and Duval 1994). Overall, females tended to be solitary, whereas males tended to be non-monogamous or roving. Males had larger home ranges than females and dispersal tended to be male biased. These results are congruent with other reviews of Peromyscine social behavior (Wolff 1989; Ribble 2003). However, exceptions to these patterns exist and probably evolved, independently, several times within the Neotomine-Peromyscine rodents.
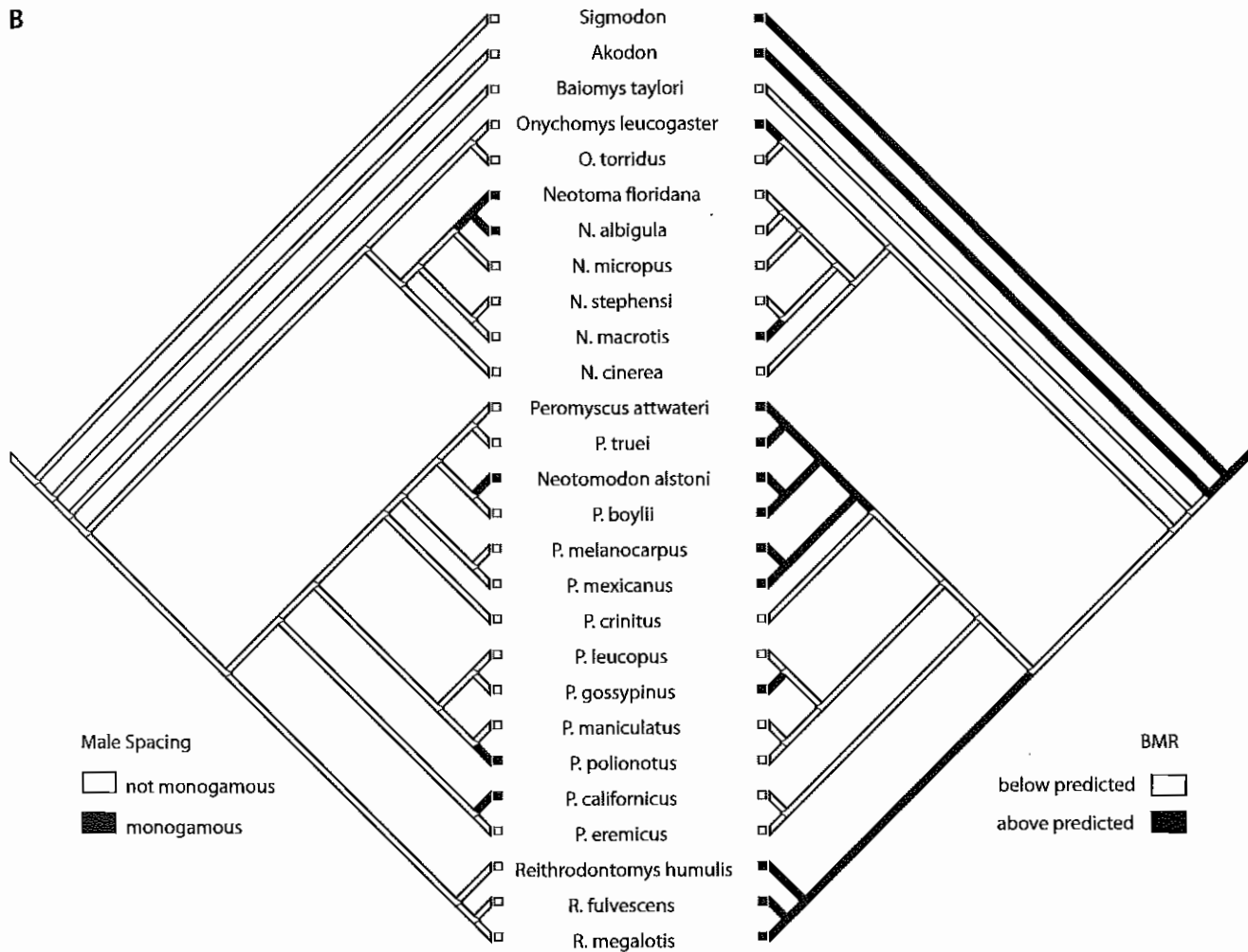
B

Male Spacing

☐ not monogamous

■ monogamous

BMR

below predicted ☐

above predicted ■

Sigmodon
Akodon
Baiomys taylori
Onychomys leucogaster
O. torridus
Neotoma floridana
N. albigula
N. micropus
N. stephensi
N. macrotis
N. cinerea
Peromyscus attwateri
P. truei
Neotomodon alstoni
P. boylii
P. melanocarpus
P. mexicanus
P. crinitus
P. leucopus
P. gossypinus
P. maniculatus
P. polionotus
P. californicus
P. eremicus
Reithrodontomys humulis
R. fulvescens
R. megalotis

Figure 6.6 (continued)

(*continued*)

Our results clearly show differences in male and female mating strategies. Furthermore, ecological, physiological, and life-history characteristics influence breeding behaviors differently for males and females. The discrepancy between ecological, physiological, and life-history influences on males and females supports the contention that the breeding system of a species does need to be defined specifically in terms of male and female mating strategies, because different selective pressures have been acting differentially on the sexes within species (Reynolds 1996).

That male spacing behavior appeared to be independent of female spacing behavior suggests that reproductive success of males is not limited only by the availability of females. This is counter to the paradigm in mammalian behavioral ecology—that the reproductive success of females is limited by their ability to secure energy resources for producing and raising offspring, whereas reproductive

success of males is limited by their ability to secure matings, and thus males are mainly responding to the distribution of females in space. Our results further suggest that male reproductive success is not limited by the availability of females because male spacing behavior appeared to be related to both diet and BMR, suggesting an energetic constraint to reproductive success. As expected, female spacing behavior was related to BMR, underscoring the influence that the high energetic demands of lactation impart on female breeding behavior (Thompson 1992). Although not identified by our analysis, there are other ecological factors that may affect breeding behaviors, such as pup-defense against infanticide (Wolff 1993b) and male-male competition (Bond and Wolff 1999).

Ribble (2003) suggested that relative litter weight might be correlated with the need for paternal care, and influence male mating strategies. This was not the case. There was
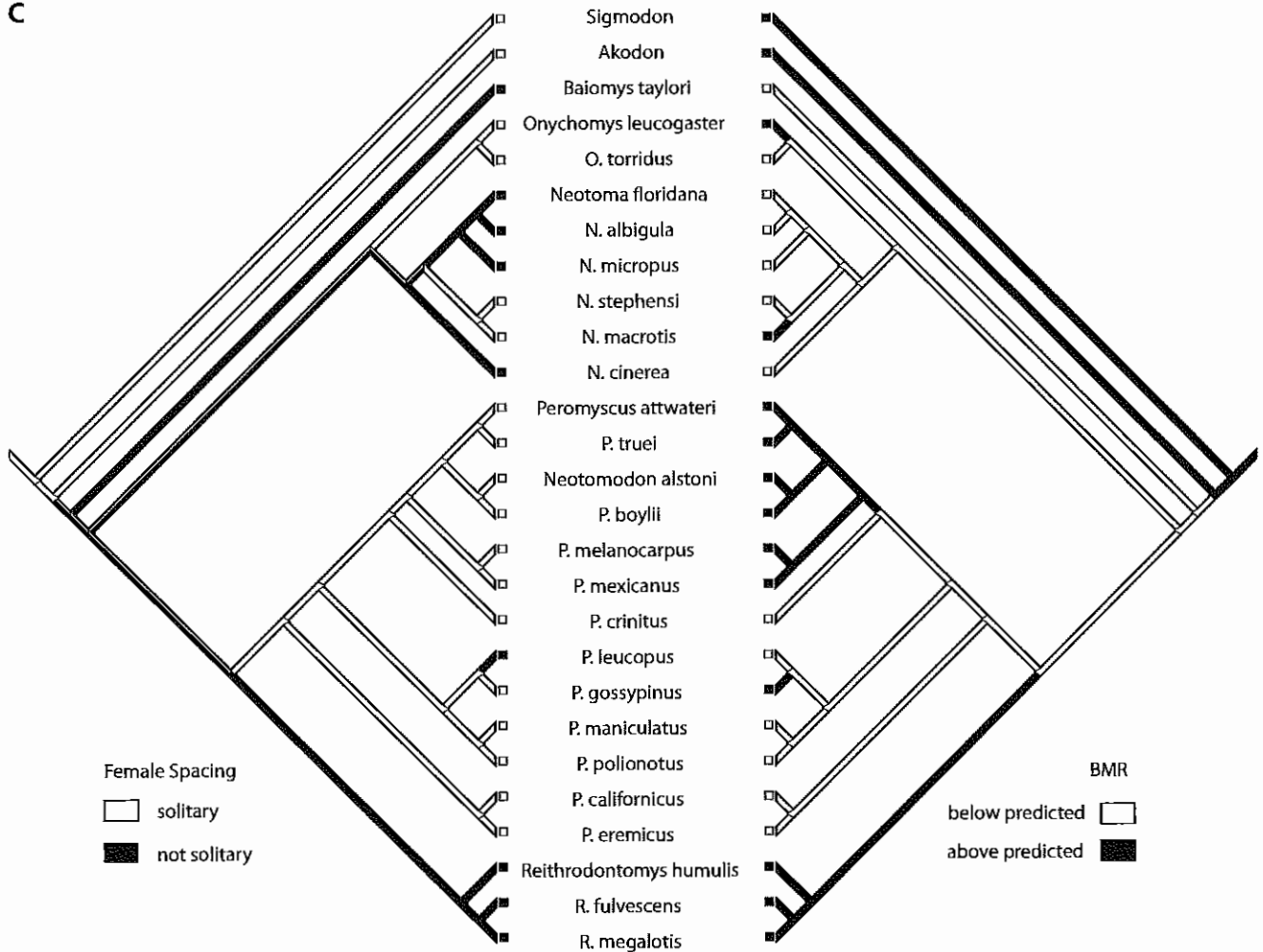
C

Figure 6.6 (continued)

no relationship between paternal care and relative litter weight. Although there was a relationship between male spacing behavior and relative litter weight, it was in the opposite direction to the prediction of Ribble (2003). Males of species with relatively low litter weights tended to be monogamous, suggesting that maternal investment in offspring (as measured by relative litter weight) may not necessitate male parental care.

Paternal care has evolved six times within the Neotomine-Peromyscine clade. This is consistent with the conclusions of Ribble (2003) that paternal care evolved more than once within *Peromyscus*. Comparing the evidence for male care to male spacing, we found a relationship between these two characters, with monogamously spaced males tending to provide paternal care. Thus across the entire clade, male care may be associated with monogamy, but there is little known about the social behavior of many species (e.g., *Neo-*

tomodon). These results suggest that male care may play a role in the evolution and maintenance of monogamy, and support the field experiments of Gubernick and Teferi (2000). These results are inconsistent with more global analyses (e.g., Komers and Brotherton 1997) that suggest that mammalian monogamy is not related to paternal care, but rather to female spacing and mate guarding. Whether the Neotomine-Peromyscine taxa are different from other mammals awaits more complete descriptions of social behavior from more taxa.

We found that the size of a species distributional range was related to breeding behavior and litter size. Consistent with findings of Glazier (1980), we found that litter size of Neotomine-Peromyscine rodents increased with the distributional range of a species. Furthermore, monogamous males and males that exhibited paternal care of offspring were from species with relatively small distribution ranges.
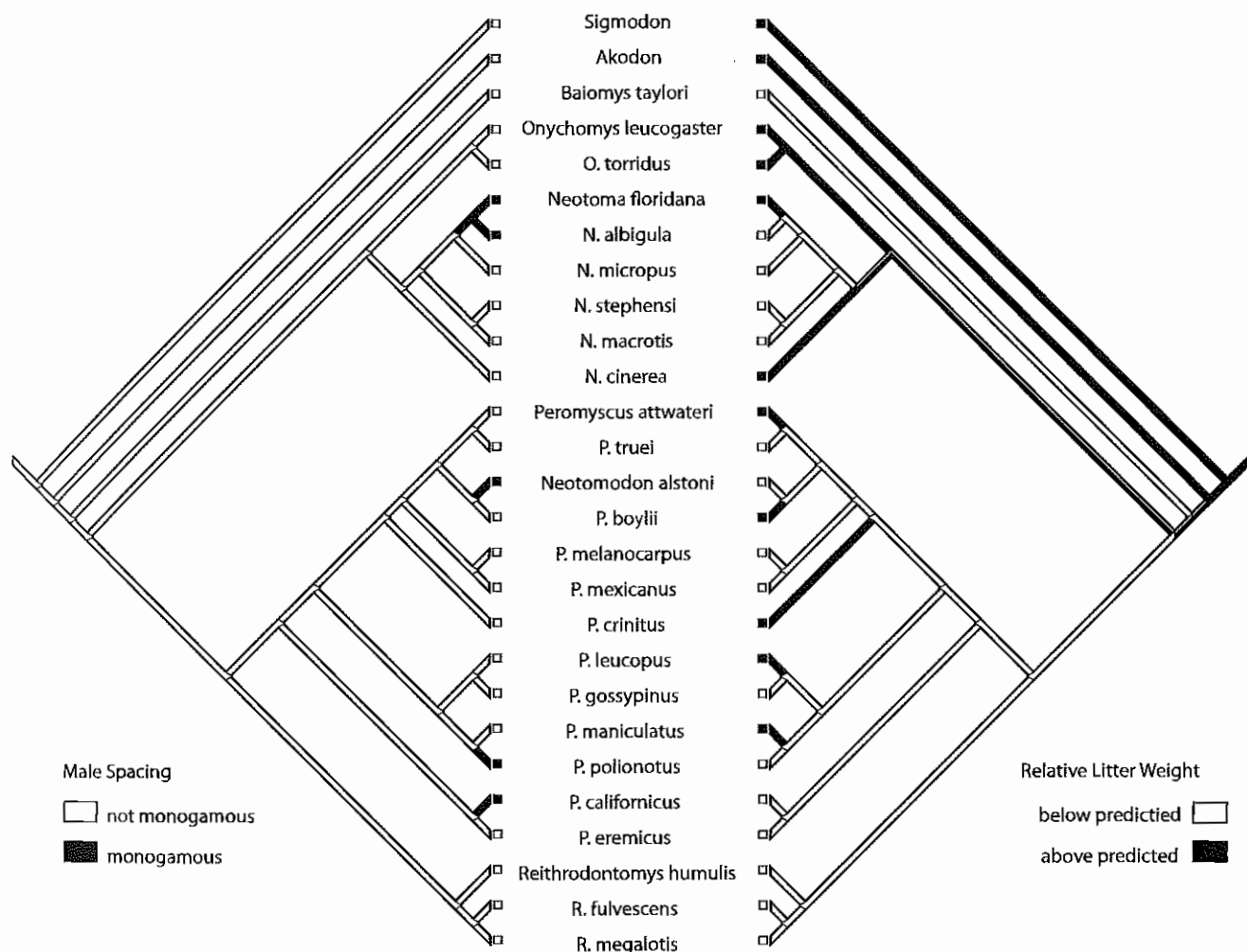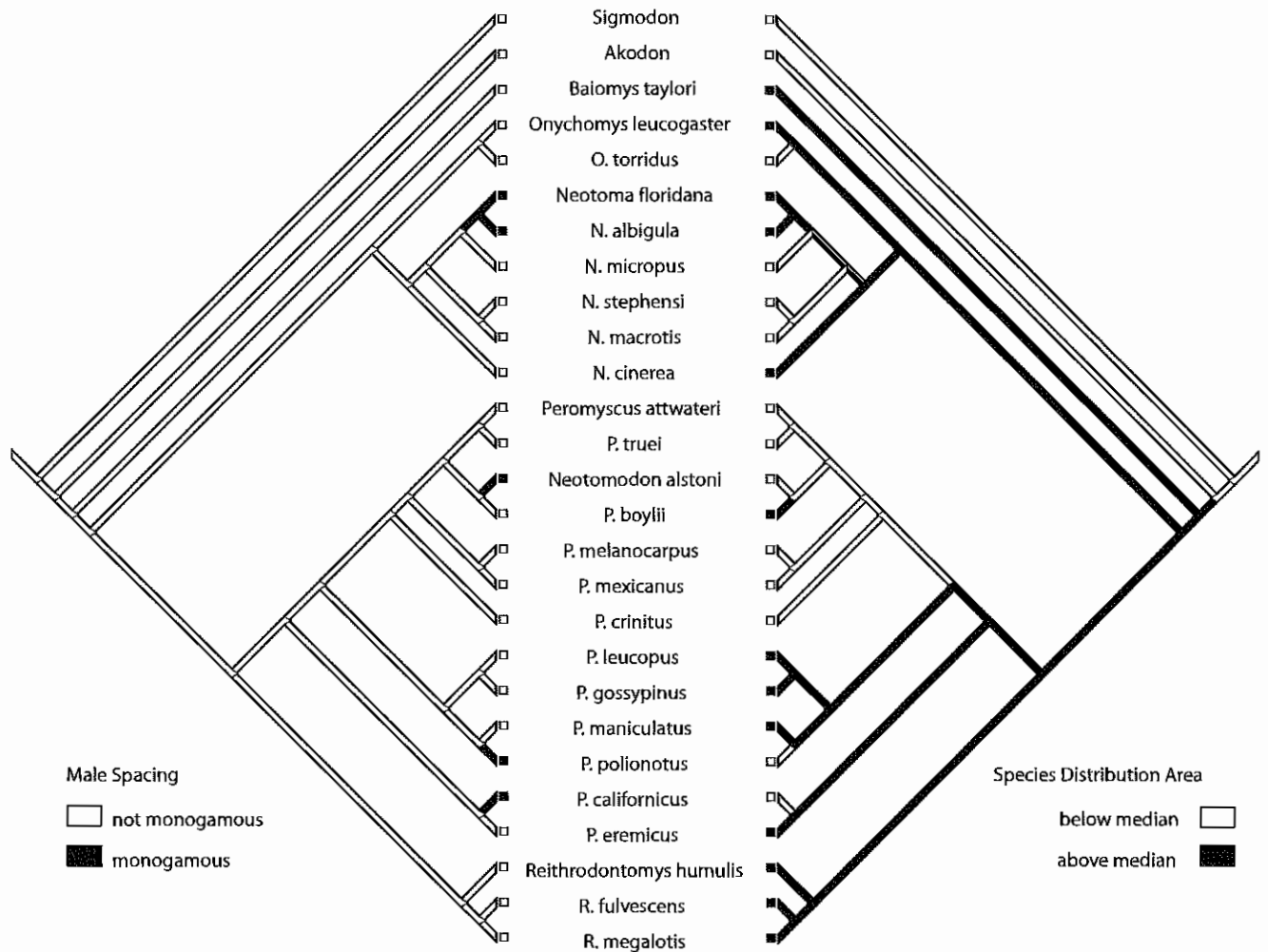
Figure 6.7 Mirror phylogenies showing the ancestral state reconstruction for male spacing and relative litter weight in Neotomine-Peromyscine rodents. Although average litter weight is graphically presented as a binary variable, statistics were performed on continuous data. Binary relative litter weight data are determined as weight being above or below the predicted values from the following significant regression line: Litter Mass = 0.14 Body Mass + 4.23 ($F_{1,23} = 103.64$, $P < 0.001$, $R^2 = 0.81$).

This may be because monogamy and paternal care are a relatively specialized set of behaviors that limits the distribution of taxa exhibiting these behaviors. Furthermore, species with large litter sizes could be widely distributed because they are more successful at dispersing and colonizing new areas than species with small litter sizes. These observations support Brown's (1995) view that dispersal and social behavior affect the geographic range of species.

Relative to other groups of rodents, there has been substantial research on wild populations of species in the *Neotoma-Peromyscus* clade. In spite of this work, however, our review and analysis highlights how little we know about the breeding systems of most species. For example, our knowledge of the genetic mating system, the patterns of juvenile dispersal and recruitment, and the extent of varia-tion among various breeding behaviors over different populations is minimal. The "molecular revolution" has largely passed by these field studies, most likely because of the difficulty in assessing behavioral interactions of nocturnal and secretive individuals in wild populations. Indeed, sampling individuals through trappiug is relatively easy in this group of rodents, so we tend to know more about spacing behaviors, which are certainly suggestive of behavioral interactions and subsequent genetic mating patterns. Regardless, more fieldwork with an aim of following individuals and assessing behavior would benefit our understanding of the evolution and maintenance of breeding patterns in Neotomine-Peromyscine rodents. Clearly, we need basic information from some of the lesser-known species. One of the most exciting areas of study in the future is to examine

Figure 6.8 Mirror phylogenies showing the ancestral state reconstruction for male spacing behavior and species distribution area in Neotomine-Peromyscine rodents. Although species distribution area is graphically presented as a binary variable, statistics were performed on continuous data. Binary species distribution area data are determined as being above or below the average value for all represented species.

intraspecific variation in these behaviors, within some of the well-characterized species.

Summary

The purpose of this chapter was to examine, in a phylogenetic context, components of the breeding system of Neotomine-Peromyscine rodents from wild populations. First, using a review of the literature, we describe the patterns in breeding systems within this clade. Second, we examine the following breeding behaviors to test if there are any phylogenetic patterns in the observed variation in these behaviors, and if relationships exist among them: male spacing, female spacing, relative intersexual home range/territory size, paternal care, and juvenile dispersal patterns. Third, we examine whether dietary, physiological, or life-history characteristics of the taxa explain the observed variation in these breeding behaviors. In general, we found that females are solitary and males are roving, and these traits are ancestral. Male spacing behavior is independent of female spacing behavior and female spacing behavior is independent of male spacing behavior. Paternal care has evolved multiple times, and there is a trend for monogamously spaced males to provide care. The ancestral state is for males to have larger home ranges than females, with very few taxa demonstrating equitable range sizes. Natal dispersal tends to be male biased. We found a positive correlation between species distribution area and litter size. There was a trend for nonmonogamous males to have a higher-energy diet and a higher BMR than monogamous males. Paternal care was not related to diet or BMR. Female spacing behavior was not related to diet but was related to BMR, with solitary females having a higher BMR than nonsolitary fe-

males. There was a trend for monogamous males to have smaller relative litter weights and species distribution areas compared with nonmonogamous males, and these relationships were absent in females. Our results not only demonstrate differences in male and female mating strategies, but also show that ecological, physiological, and life-history characteristics influence breeding behaviors differently for males and females. The independence of male and female spacing behaviors is counter to the paradigm in mammal-ian behavioral ecology that reproductive success of males is limited by their ability to secure matings and that males are mainly responding to the distribution of females in space. The independence of male and female spacing behavior, coupled with the relationships between male breeding behaviors and diet and BMR, suggests an energetic constraint to male reproductive success in Neotomine-Peromyscine rodents.