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RESEARCH ARTICLE

On the role of phylogeny in determining activity patterns of rodents

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Abstract Evolutionary plasticity is limited, to a certain extent, by phylogenetic constraints. We asked whether the diel activity patterns of animals reflect their phylogenies by analyzing daily activity patterns in the order Rodentia. We carried out a literature survey of activity patterns of 700 species, placing each in an activity time category: diurnal, nocturnal, or active at both periods (a-rhythmic). The proportion of rodents active at these categories in the entire order, was compared to the activity patterns of species of different families for which we had data for over ten species each: Dipodidae, Echimyidae, Geomyidae, Heteromyidae, Muridae, and Sciuridae. Activity times of rodents from different habitat types were also compared to the ordinal activity time pattern. We also calculated the probability that two random species (from a particular subgroup: family, habitat, etc.) will be active in the same period of the day and compared it to this probability with species drawn from the entire order. Activity patterns at the family level were significantly different from the ordinal pattern, emphasizing the strong relationship between intra-family taxonomic affiliation and daily activity patterns. Large families (Muridae and Sciuridae) analyzed by subfamilies and tribes showed a similar but stronger pattern than that of the family level. Thus it is clear that phylogeny constrains the evolution of activity patterns in rodents, and may limit their ability to use the time niche axis for ecological separation. Rodents living in cold habitats differed significantly from the ordinal pattern, showing more diurnal and

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a-rhythmic activity patterns, possibly due to physiological constraints. Ground-dwelling rodents differed significantly, showing a high tendency towards a-rhythmic activity, perhaps reflecting their specialized habitat.

Keywords Activity patterns · Habitat · Phylogeny · Rodents · Shifts

Introduction

The traits and behaviours of living organisms are moulded by their phylogenetic histories and by evolutionary selective forces. Birds have feathers, butterflies pupate, angiosperms flower. However, various traits may exhibit evolutionary plasticity and thus differ significantly even between closely related organisms, reflecting the action of selective forces. Studying phylogenetic constraints is important if we are to understand these selective forces and to gain insight into the process of evolution (e.g. Gould and Lewontin 1979).

Activity patterns of animals are an important adaptation; they have evolved in response to the time structure of the environment, which changes with a 24 h periodicity, and allow an animal to anticipate the right time for a given behaviour or activity (Daan 1981; DeCoursey 2004). At a time where we have increased dramatically our understanding of the proximate mechanisms controlling activity patterns of animals (e.g. Antle and Silver 2005; Saper and Scammell 2005; Saper et al. 2005), we still have little understanding of the ecological forces driving the evolution of activity patterns. Insight into the evolutionary constraints involved in circadian rhythmicity of animal species is key to gaining this understanding. Here we ask whether the activity times of animals reflect a strong phylogenetic imprint; if they do, closely related taxa will tend to be active in the same part of the diel cycle (Daan 1981; DeCoursey 2004).

The environment of living organisms changes between day and night. Abiotic conditions (solar radiation, light levels, ambient temperatures, relative humidity, wind regimes and velocities, etc.), some of which are indisputably very strong selective pressures, differ between day and night, requiring different physiological and morphological adaptations. Biotic conditions also vary according to activity phase; a different suite of ecological interactions can be anticipated during the day and during the night. Specifically, ecological theory postulates that temporal partitioning is a viable mechanism for separation between competing species and between predators and their prey (Schoener 1974a; Wiens et al.1986; Richards 2002). Inter-specific competition and predation are both perceived as strong selective forces (e.g. Lack 1947; Lima and Dill 1990; Day et al. 2002; Young et al. 2004), so one would expect them to mould activity patterns of animal species, yet there is little evidence for this occurring in nature (Kronfeld-Schor and Dayan 2003).

The rarity of temporal partitioning as a mechanism mediating coexistence has been ascribed to both ecological and evolutionary constraints. At the ecological scale, Schoener (1974a) argued that, ''In deciding to omit certain time periods, the consumer is usually trading something—a lowered but positive yield in the time period frequented by the competitor—for nothing, no yield at all'' (p. 33). Schoener (1974b) developed a theoretical model that predicts that temporal resource partitioning at the diel scale should be relatively rare, requiring severe depletion of resources before it is no longer optimal to feed in a period frequented by competitors. At the evolutionary scale, Daan (1981) suggested that,

''Since major morphological, physiological and behavioural adaptations often accompanied the specialization in nocturnal and diurnal ways of life, one rarely finds narrowly related species groups comprising both types'' (p. 282). DeCoursey (2004) also claims that the behavioural differences between nocturnal and diurnal species depend on the basic underlying physiological rhythms.

A strong phylogenetic imprint would imply limited use of the time niche axis among ecologically interacting species. More particularly, it would greatly diminish the use of time at the diel scale in ecological separation between closely related species, in which inter-specific competition is thought to be greatest (Darwin 1859; Losos et al. 2003), and thus explain the relative rarity of temporal partitioning in ecological communities (Kronfeld-Schor et al. 2001a, b; Kronfeld-Schor and Dayan 2003).

However, this notion has never been tested; the role of phylogeny in determining activity patterns of animal species has never been analyzed. We studied temporal activity patterns in the order Rodentia (class: Mammalia). Using taxonomy as a surrogate for phylogenetic relationships, we asked whether at the family, subfamily, and tribe levels activity patterns are a random subset of the ordinal activity pattern, or whether they differ significantly. Furthermore, we analyzed rodents' activity time patterns with regard to the habitats they occupy.

Methods

In all, our rodent database included about 1150 species, using only literature sources that provided data at the species level. For each species we noted the taxonomic status, activity time (observed in the field), and preferred habitat type as stated in the original literature. We used only those sources that provided activity time patterns, when literature sources differed regarding a species; we omitted it from our analysis.

Rodents were characterized as ''nocturnal'', ''diurnal'', or ''both'' [active both day and night, referred to sometimes as cathemeral (Tattersall 1988) or arrhythmic (Jacobs 1993)]. Very few rodents in our database (ten species) were referred to as ''crepuscular'' in the literature, so we omitted this category in order to simplify statistical analyses. Animals tend to refrain from the coldest and warmest parts of the day, and thus often tend to be crepuscular in activity (Morris 1965). Nevertheless, many of these crepuscular species posses either diurnal or nocturnal circadian rhythms. Consequently these species are categorized as either nocturnal or diurnal in the literature, and we used the categories provided by the available scientific literature as they appear.

Species that change their activity time patterns between seasons were also omitted from our analysis. All in all, for our analysis 700 species of rodents were used (see appendix 1 for species list and appendix 2 for reference used to build the database).

We used Wilson and Reeder (1993) as our taxonomic baseline and listed species by family, and where possible by subfamily (for Sciuridae and Muridae) and tribe (for Sigmodontinae). We used an evolutionary tree based on molecular data from Huchon et al. (2002) to determine the phylogenetic relations between the different rodent families.

Each species was placed in one of eight habitat categories: cold, aquatic, mixed, temperate forest, evergreen forest, grassland, desert/arid, or subterranean.

We conducted two separate tests to check whether the activity patterns of rodents of a certain group (be it a taxonomic group or a specific habitat type) differ significantly from the pattern shown by the rodents not included in that group.

We calculated for each of the three time phases (diurnal, nocturnal, and both) the probability that two random rodents have the same time phase (the squared value of the proportion of this time phase out of all of the rodents in this group). Then we added these values for the three time phases to arrive at the probability, for that group, that two randomly chosen rodents have the same time phase. The same procedure was done for the rodents from the entire order minus the group in question. In order to see if the group is significantly different from the rest of the rodents, we built a 2*2 table based on the calculated proportions (and their complementary values) and analyzed it using a χ^2-test. This test enabled us to see whether the group in question was more homogeneous in its patterns than the rest of the rodents (from here on we use the term ''homogeneous'' to describe those groups that are significantly different from the rest, using this test).

Furthermore, we wanted to see if the pattern of activity of the rodents from a certain group (be it homogeneous or heterogeneous) differs from that of the rest. To do this we conducted a goodness of fit (χ^2) test to compare the activity patterns of the rodents from a certain group to that of the entire order (minus that group). Our χ^2 values and their appropriate significance levels are for each comparison between one group (a specific family, subfamily, tribe or habitat type) and the entire order minus the group being compared.

In both tests we used only groups of rodents that had at least ten species. This included all of our habitat types and the rodents from the following families: Dipodidae, Echimyidae, Geomyidae, Heteromyidae, Muridae, and Sciuridae. Rodents from different subfamilies that have more than ten species included the two Sciuridae subfamilies (Petauristinae and Sciurinae) and four subfamilies of Muridae (Arvicolinae, Gerbillinae, Murinae, and Sigmodontinae). We also looked for this pattern in the various tribes of the Sigmodontinae (those that had more than ten species): Akodontini, Neotomini, Oryzomyini, Peromyscini, and Phyllotini.

We ascribed to each family one of the three activity time patterns described above, according to its mode of activity. Then, using the evolutionary tree in Huchon et al. (2002) and maximum parsimony, we asked how many times along the lineages of this tree, families of rodents switched their activity pattern. We chose a nocturnal ancestral state for the root of the tree because it is the ordinal mode, because the earliest mammals were probably nocturnal (Benton 2000), and because rodents appear to have independently evolved their diurnal patterns (Smale et al. 2003). We then asked what is the minimum number of changes, along the branches of the tree, that could produce the current family-level patterns.

Results

Rodent activity patterns are not distributed randomly throughout the order. The results of both tests for all taxonomic groups are given in Table 1. All families differ significantly from the entire order (minus that family) in both tests. There are four mainly nocturnal families (Dipodidae, Echimyidae, Heteromyidae and Muridae), one mainly diurnal family (Sciuridae) and one family whose members are active during both day and night (Geomyidae) (Fig. 1).

These non-random patterns persisted in lower taxonomic groups (Fig. 2). Within the family Sciuridae, both subfamilies have an activity pattern that differs significantly from that of the entire order (minus the subfamily being checked). The Sciurinae, which

Table 1 Significance levels of the homogeneity tests and the Goodness of fit tests, for rodents from the different taxonomic groups

Taxonomic group			Homogeneity test significance levels	Goodness of fit test significance levels
(Family)	(Subfamily)	(Tribe)		
Dipodidae			7.20E-04	0.022
Echimyidae			2.82E-08	2.74E-05
Geomyidae			0.0065	3.36E-32
Heteromyidae			3.42E-13	3.59E-08
Sciuridae			2.27E-05	2.09E-183
	Petauristinae		2.04E-05	0.0029
	Sciurinae		5.56E-18	8.98E-224
Muridae			3.36E-05	4.96E-48
	Arvicolinae		0.430[a]	6.49E-35
	Gerbillinae		0.0223	0.0471
	Murinae		4.05E-09	4.18E-09
	Sigmodontinae		1.58E-05	2.45E-08
		Akodontini	0.97[b]	4.98E-14
		Neotomini	3.95E-04	0.015
		Oryzomyini	8.52E-07	2.34E-04
		Peromyscini	4.85E-08	2.11E-05
		Phyllotini	0.107[c]	0.11[c]

[a] Rodents from the Arvicolinae subfamily do not differ significantly from the rest of the rodents in the homogeneity test

[b] Rodents from the Akodontini tribe do not differ significantly from the rest of the rodents in the homogeneity test

[c] Rodents from the Phyllotini tribe do not differ significantly from the rest of the rodents in both homogeneity and goodness of fit tests

includes the arboreal and terrestrial squirrels, is an entirely diurnal subfamily while members of the Petauristinae or the flying squirrels are all nocturnal. The subfamilies within the Muridae also have distinctive patterns of activity. The subfamilies Murinae, Sigmodontinae, and Gerbillinae are primarily nocturnal and differ significantly from the rest of the order (again each time minus the group being compared) by both tests. The Arvicolinae comprise mostly rodents active both day and night as well as nocturnal rodents. This subfamily differs significantly in its activity time pattern from that of the entire order by the goodness of fit test. However, it is not significantly different by the homogeneity test (Table 1).

In the Sigmodontinae, a species-rich subfamily (of the Muridae family) with a fairly well understood taxonomy, we also analyzed activity patterns at the tribal level (Fig. 3). Of the five tribes with over ten species, four (Neotomini, Oryzomyini, Peromyscini, Phyllotini) are almost entirely nocturnal. The tribe Phyllotini does not differ significantly from the rest of the rodents in either test (Table 1), probably because of small sample size ($n = 17$), since almost all rodents from this tribe are nocturnal. The rodents from the Akodontini tribe are active during the day or during both day and night. This tribe differs significantly by the goodness of fit test but not by the homogeneity test (Table 1).

Because the evolutionary tree of the order Rodentia is not resolved yet, especially at the lower taxonomic levels (Hartenberger 1998; Huchon et al. 2002), we were able to see shifts in activity time only for the major families. Figure 4 shows an adaptation of the evolutionary tree by Huchon et al. (2002), each family with its mode of activity. According to this tree it would take at least seven shifts from one activity pattern to another to explain

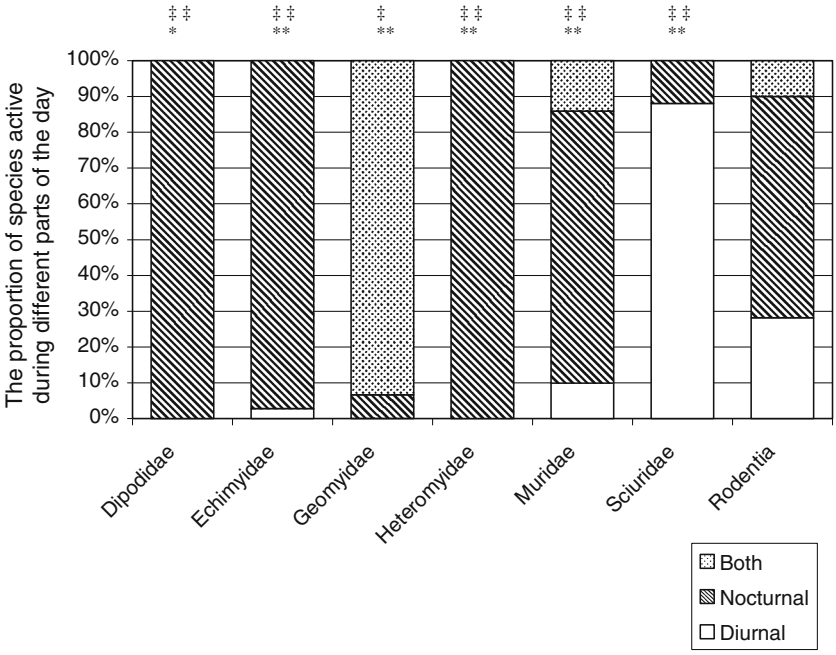

Fig. 1 Activity time patterns for rodent families (for which we had more than 10 species). The proportion of the three activity time categories is shown for each family and for the entire order. All families differ significantly in their activity time pattern from that of the entire order (minus the family being compared) by both tests—homogeneity ($^{\ddagger}P < 0.01$, $^{\ddagger\ddagger}P < 0.001$) and goodness of fit ($^{*}P < 0.05$, $^{**}P < 0.001$)

the family-level activity patterns. One of these most parsimonious ways to explain this pattern is shown in Fig. 4, but others are possible.

The activity patterns of rodents from all habitat types (but the grasslands) differ from those of the entire order (minus the habitat that is being compared), by the goodness of fit test (see Table 2). Rodents from two habitats—those living underground and those from cold habitats, proved to differ greatly in pattern from the rest of the order with a very high level of significance. Subterranean rodents are mostly active during both day and night, while rodents living in cold habitats are active mostly during the day. However, in the homogeneity test, only two habitat types (aquatic/semiaquatic, and mixed) differed significantly from the entire order (minus the habitat in comparison) (Table 2). Most rodents from these two habitats are active during the night. Figure 5 shows the proportion of species active during different parts of the day for the different habitat types.

Discussion

Our results clearly demonstrate a strong taxonomic imprint on the diel activity patterns of rodents, suggesting that diel activity patterns are phylogenetically constrained. The taxonomic status of a rodent at the family, subfamily, or tribal level determines in large measure its activity pattern. Our tests reveal high homogeneity within lineage in terms of activity patterns. This homogeneity may reflect evolutionary conservatism of this trait. Closely related species are those most likely to compete owing to their ecological overlap. These results suggest that temporal partitioning at the diel scale is an uncommon mech-

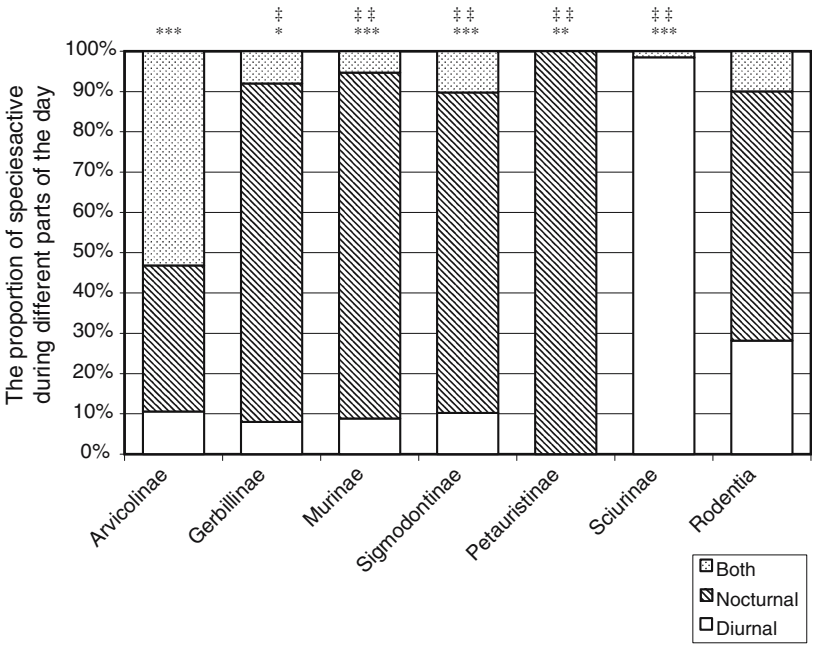

Fig. 2 Activity time patterns for subfamilies of the Muridae and Sciuridae (for which we had more than 10 species). The proportion of the three activity time categories is shown for each subfamily and for the entire order. All subfamilies but the Arvicolinae differ significantly in their activity time pattern from that of the entire order (minus the subfamily being compared) in the homogeneity test ($^{‡}P < 0.05$, $^{‡‡}P < 0.001$). All subfamilies differ significantly in the goodness of fit test ($^{*}P < 0.05$, $^{**}P < 0.005$, $^{***}P < 0.001$)

anism of coexistence among competitors because of phylogenetic constraints (Kronfeld-Schor et al. 2001). Closely related taxa tend to be active at the same part of the day.

This conservatism may reflect the role of circadian rhythmicity *per se* as an evolutionary constraint (see Kronfeld Schor et al. 2001a). However, alternatively, it may reflect other possible evolutionary constraints, such as morphological constraints related to eye structure (Kronferld-Schor et al.2001b), physiological constraints that relate to thermoregulatory adaptations (Kronfeld-Schor et al. 2000), or others. Kronfeld-Schor and Dayan (2003) pointed out to an inherent rigidity in mechanisms that are driven by photic cues, but qualitative morphological traits may be equally constrained.

Nevertheless, some inversions of activity patterns have occurred in evolutionary time; a minimum of seven such shifts produced the family-level activity patterns. Of course, many more shifts occurred to produce the species-level activity patterns. Shifts in activity patterns suggest that, under some (severe?) selection regimes, an inversion may occur. Because of multiple selective pressures and because of multiple possible constraints to activity rhythms, it seems impossible at this point to reconstruct the conditions that have enabled these activity shifts.

Our results provide a direct quantitative test of a pattern that can be perceived qualitatively in many other taxa, allowing some broad generalizations. Namely, zoologists have previously observed that different animal taxa tend to be active during different parts of the diel cycle. Several arthropod groups show this pattern, bristletails (Thysanura), woodlice (Isopoda), wind scorpions (Galeodidae) and scorpions (Scorpiones) are all primarily nocturnal (Weinstein 2003). Among spiders (Araneae) several families are diurnal

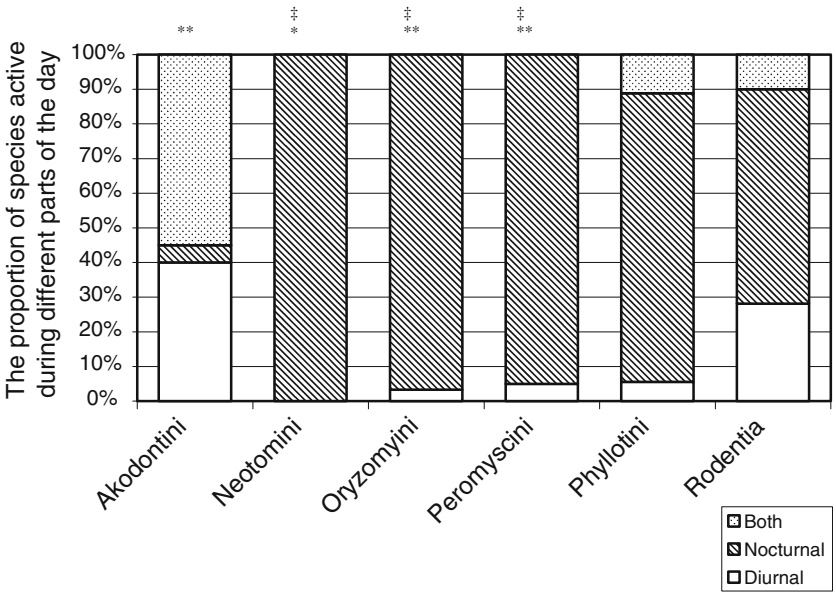

Fig. 3 Activity time patterns for tribes of the Sigmodontinae (for which we had more than 10 species). The proportion of the three activity time categories is shown for each tribe and for the entire order. All tribes but the Phyllotini and Akodontini differ significantly in their activity time pattern from that of the entire order (minus the tribe being compared) in the homogeneity test ($^{\ddagger}P < 0.001$). All tribes but the Phyllotini differ significantly in the goodness of fit test ($^{*}P < 0.05$, $^{**}P < 0.001$)

(Lycosidae, Salticidae) while others are predominantly nocturnal (Gnaphosidae) (Weinstein 2003). Many lizards are diurnal but there are mostly nocturnal groups such as the geckos (Geckkonidae) (Pianka and Vitt 2003). Birds, as a group, are predominantly diurnal but owls (Strigiformes) and night-jars (Caprimulgiformes) are nocturnal (Gill 1994). In placental mammals there are also orders that are predominantly diurnal (Hyracoidea, Scandentia), nocturnal (Insectivora, Chiroptera) and those with many species incorporating both activity time patterns (Carnivora, Artiodactyla) (Nowak 1999). These, of course, are broad generalizations that have been observed but never analyzed. Future investigation of this phenomenon in various taxa may contribute to our understanding of the specific conditions that have produced shifts in activity patterns.

While the occurrence of a phylogenetic imprint is clear, it is equally clear that environmental selective pressures strongly determine activity patterns of rodents. For all habitats but one, we found a significant difference between the activity patterns of rodents of a given habitat and rodents from the entire order (minus the habitat being tested). On the other hand, homogeneity tests revealed a significant difference (high homogeneity) only for two (of eight) habitats. The significant differences revealed by the goodness of fit tests suggest that selective pressures in different habitats resulted in activity patterns that differ from those of rodents in other habitats. Two particular habitats stand out in this respect. Subterranean species are generally both diurnal and nocturnal, an activity pattern that befits life in a fairly stable environment. In these habitats there is not an overwhelming advantage to diurnality or nocturnality, and light is not the most important cue for timing circadian rhythms (e.g. Goldman et al. 1997; Riccio and Goldman 2000; Oster et al. 2002). Indeed, we find rodents from different families and subfamilies that concur with this rule—for

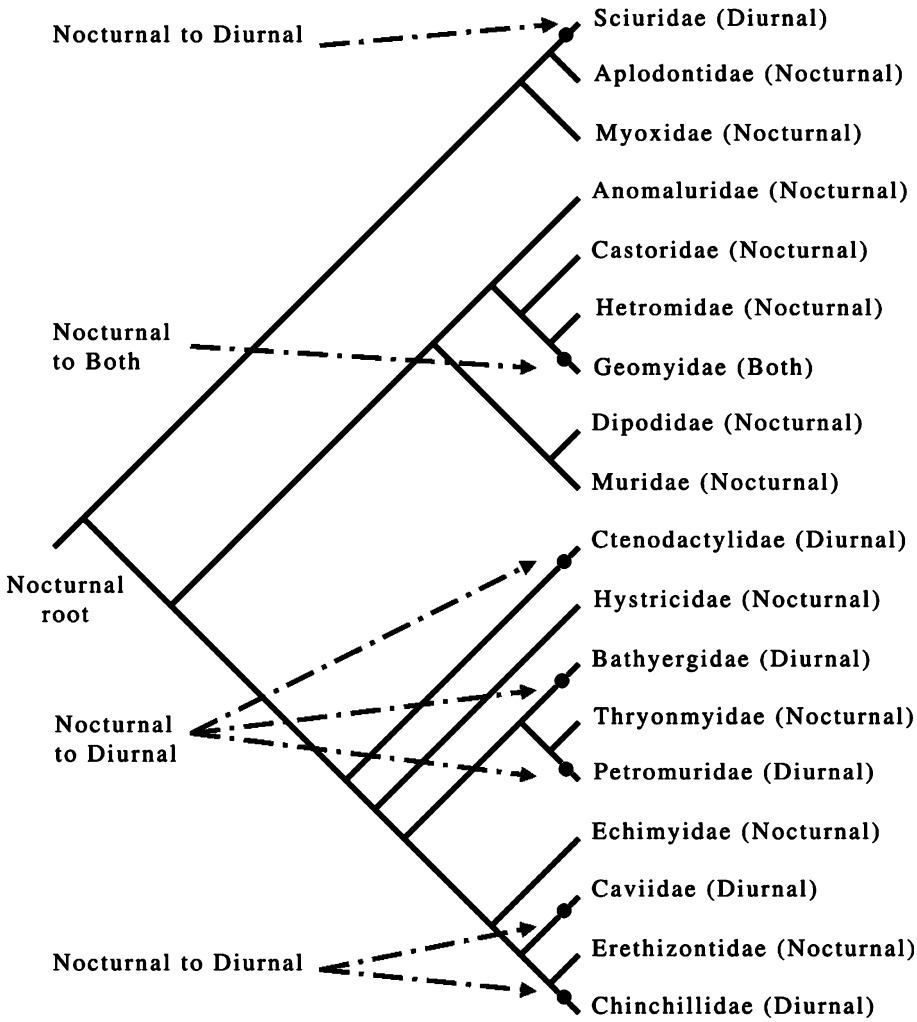

Fig. 4 The evolutionary tree for the various rodent families adopted from Huchon et al. (2002). Each family is given its mode of activity time. The tree illustrates a minimum of seven shifts of activity times from a nocturnal root in order to arrive to the final state at the family level

example, the families Bathyergidae, Ctenomyidae, Geomyidae and subfamilies: Arvicolinae and Spalacinae of the Muridae.

As a result of their large surface-area to volume ratio and their low thermal inertia, rodents have difficulties regulating their body temperatures in extreme conditions (Degen 1997). Rodents from cold environments are frequently diurnal, suggesting that they preferentially exploit the warmer hours of the diel cycle in these extreme environments (Willmer et al. 2000). Here too, this pattern is present in species from both the Sciuridae and the Muridae.

When one compares activity times of rodents from different habitats to those of the entire order, it is difficult to detach taxonomy from habitat type. Most squirrels are arboreal, while most gerbils live in sandy deserts. While both taxonomy and habitat affect activity patterns, it appears that phylogeny plays a more significant role. The significant homogeneity of activity patterns within lineage contrasts with the heterogeneity in activity

Table 2 Significance levels of the homogeneity tests and the Goodness of fit tests, for rodents from the different habitat types

Habitat type	Homogeneity test significance levels	Goodness of fit test significance levels
Cold habitats	0.798	1.01E-06[a]
Aquatic/Semi-aquatic	0.010[b]	0.017
Mixed habitat	0.047	0.043
Forest	0.145	6.68E-05
Evergreen forest	0.076	0.036
Grasslands	0.958	0.89
Arid/Desert	0.052	0.0058
Underground	0.243	1.15E-89[c]
Not known	0.919	0.0082

[a] Rodents from the cold habitats differ significantly from the pattern of the rest of the rodents with a high level of significance in the goodness of fit test

[b] Rodents from aquatic or semi-aquatic habitats differ significantly from the pattern of the rest of the rodents by homogeneity test

[c] Rodents from the underground habitats differ significantly from the rest of the rodents with a high level of significance in the goodness of fit test

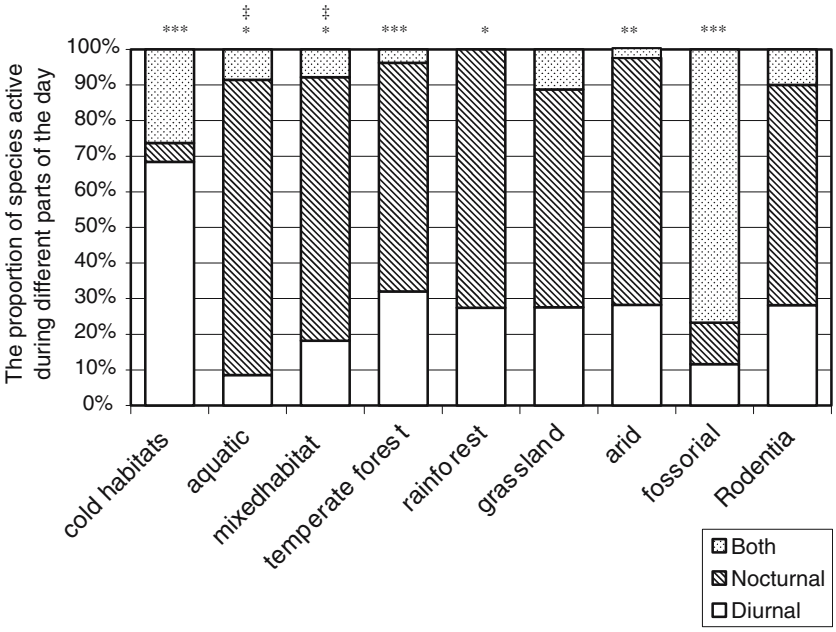

Fig. 5 Activity time patterns for the different habitat types. The proportion of the three activity time categories is shown for each habitat and for the entire order. Three habitats (aquatic, arid, and mixed) differ significantly in their activity time pattern from that of the entire order (minus the habitat being compared) in the homogeneity test ($^{\ddagger}P < 0.05$). All habitats but one (grasslands) differ significantly in the goodness of fit test ($^{*}P < 0.05$, $^{**}P < 0.005$, $^{***}P << 0.001$)

patterns within habitat type (including subterranean and cold climates). These results suggest that, while phylogenetic constraints strongly channel activity patterns within taxa, habitat-specific environmental selective forces do not have such strong effects. Indeed, the

two habitats that exhibit a significant degree of homogeneity comprise species mostly of a single family, the Muridae. Although activity patterns that have evolved within habitat differ from those of rodents of other habitats, activity patterns in most habitat types are not homogeneous. This pattern may reflect the fact that rodents from different lineages (that are homogeneous), occur in the same habitat. Thus the heterogeneity in the patterns of activity of rodents in each habitat may reflect the phylogenetic stamp of different taxa. A possible alternative hypothesis is that rodents respond to environmental conditions at a finer scale than that studied here, and that the inherent complexity of selective forces at different microhabitats confounds what could have been a clearer pattern. At present, the available data on specific species and their microhabitat requirements do not allow a test of this hypothesis.

Our results shed some light on how evolutionary constraints can shape ecological communities (see also Webb et al. 2002). Community ecology as a discipline comprises relatively few fuzzy generalizations rather than universal rules (Lawton 1999; Simberloff 2004). Here we point to what may be such a rule: closely related species tend to be active at the same part of the diel cycle, reflecting a phylogenetic constraint on activity patterns. This constraint limits the plasticity of species in the use of the diel niche axis and limits the use of temporal partitioning among competitors within ecological communities.

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