Estonian Journal of Ecology, 2009, **58**, 1, 60–71 doi: 10.3176/eco.2009.1.07

Substrate utilization and feeding strategies of mammals: description and classification

Andrei Miljutin

Zoological Museum, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia; amiljutin@hot.ee

Received 17 December 2008, revised 3 February 2009

Abstract. Describing species' ecological strategies enables us to condense ecological information and to express it in evolutionary terms. However, the process of categorizing species is hampered by methodological difficulties and insufficient development of the typology and nomenclature of different strategies. In this article an approach for overcoming these difficulties is proposed. For a precise description of mammalian substrate utilization, it is better to combine two characteristics rather than use only one. The categorization should reflect: (1) the media or substrates primarily used for foraging; and (2) the media or substrates primarily used for sleeping. The numerous substrate utilization strategies of mammals fall into five broad groups: (1) aquatic and semiaquatic; (2) subterranean; (3) terrestrial and subterranean–terrestrial; (4) arboreal and semiarboreal; and (5) aerial and semiaerial. Three main mammalian feeding strategies are proposed: animalivorous, frugivorous, and herbivorous. An example of ecological classification of mammals in terms of substrate utilization and feeding strategy is provided.

Key words: mammals, ecological strategies, ecological classification.

INTRODUCTION

It is sometimes the case that the more details of a species' natural history we accumulate, the harder it is to define the ecological essence of that particular species and how it differs from others. For example, the lists of plant species eaten by the common vole (*Microtus arvalis*) and the striped field mouse (*Apodemus agrarius*) show considerable overlap, and the more comprehensive these respective lists are, the more similar they become, with both eventually approaching the entire flora of the relevant area. In such a situation the differences between the feeding habits of the two species become unclear. In fact, the two rodents used in this example are very different in their feeding habits, with each tending to consume different parts (either leaf or seeds) of the same plant species. Rather than make a fruitless comparison of food plants, it is perhaps preferable to simply categorize the vole as a herbivore and the field mouse as a granivore. In this way we concisely indicate the feeding strategies of the species concerned. Determination of species' ecological strategies thus enables us to condense ecological information and to express it in evolutionary terms. Indeed, it is nonsense to study evolution from eating plant species A to eating plant species B, while the study of evolution from granivory to herbivory is a meaningful task.

By *ecological strategy*, a mode of species adaptations to environmental factors (e.g. climatic factors, circadian rhythm, substrate, food, and predators) is meant. The number of strategies used by one species corresponds to the number of environmental factors with which it interacts. The concept of an ecological strategy is largely equivalent to that of specialization, but has a broader meaning. Namely, specialization is the mode by which a species utilizes resources, whereas not all environmental factors that determine ecological strategies are resources; for example, climatic factors or predators.

The names of ecological strategies such as aquatic, terrestrial, arboreal, herbivorous, etc., have been widely used in the zoological literature for a long time (e.g. Osborn, 1902; Eisenberg, 1981; Samuels & Van Valkenburgh, 2008). The most comprehensive treatment of mammalian ecological strategies was provided by John F. Eisenberg (1981), and some further developments were proposed in my earlier works (Miljutin, 1997, 1998). Unfortunately, the process of determining species' ecological strategies is still hampered by methodological difficulties and insufficient development of appropriate typology and nomenclature.

Firstly, there is no stable terminology. Thus, different terms are used for one and the same ecological strategy; for example, 'arboreal' (Eisenberg, 1981) and 'dendrobiont' (Vepsäläinen et al., 2008); 'animalivore' (Castro-Luna et al., 2007) and 'faunivore' (Heesy, 2008). Moreover, different meanings are provided to one and the same term. For example, a carnivore is considered as (1) a meat-eater (eating the meat of mammals and birds, e.g. Eisenberg, 1981) or (2) an animal-eater, whose food includes fishes, insects etc. (e.g. 'carnivorous plants' in Juniper et al., 1989). Secondly, the typology of ecological strategies used is frequently logically incorrect. Thus, sometimes a mixture of essentially different terms is used, like 'aquatic and fossorial' (Eisenberg, 1981), instead of 'aquatic and subterranean' (habitat) or 'notatorial and fossorial' (locomotion). Furthermore, the terms used are sometimes superfluous. For example, expressions like 'Frugivores/Omnivores, Frugivores/Granivores, Frugivores/Herbivores' (Eisenberg, 1981) indicate on concealed hierarchy: Frugivores (Omnivores, Granivores, Herbivores). Finally, there are no clear criteria for the determination of the ecological strategy of particular species. In other words, it is still unclear how to decide whether an animal is arboreal or not.

In this article I attempt to overcome difficulties described above. I restrict myself here to only two groups of ecological strategies: substrate utilization (substrate) strategy and feeding strategy. These ecological strategies are of particular interest from an ecomorphological point of view because of their considerable impact on the gross morphology of animals' bodies.

The goals of this article are to provide the main substrate and feeding strategies with a consistent nomenclature and clear definitions, and develop a method of the assessment of species' ecological strategies. For the reason of theoretical nature of this work and because the methods proposed here constitute its results, the article lacks a chapter 'Materials and methods'. The content of the tables is based just on my own knowledge, not on special research or particular

publications. That is why it should be considered just as an illustration of the text with no pretence to comprehensiveness or even ultimate correctness.

RESULTS AND DISCUSSION

Substrate utilization strategies of mammals

The number of different media or substrates in or upon which animals exist is diverse but not unlimited. The number is further limited when considering mammals alone; for example, no benthic forms or internal parasites exist among mammals. There are only two media inside which mammals may exist: water and air. Mammals may move through or along five different media or substrates: water, air, ground, the ground surface, and plant surface. According to their predominant use of particular media or substrates for locomotion, mammals can be divided into five categories: aquatic (Aq), subterranean (S), terrestrial (T), arboreal (Ar), and aerial (Ae) (Miljutin, 1997).

These substrate utilization strategies are not equivalent to and should not be confused with the more restricted locomotor characteristics: natatorial, fossorial, cursorial, scansorial, and volant. For example, not all terrestrial species are cursorial (i.e. adapted to running) and not all subterranean species have fossorial habits. Similarly, substrate strategies are not equivalent to life forms (ecomorphs), since the latter reflect body construction, not modes of substrate utilization (Aleyev, 1986; Miljutin, 1992).

The terminology for the different substrate strategies described above has been present in the zoological literature for a long time (e.g. Osborn, 1902; Eisenberg, 1981; Samuels & Van Valkenburgh, 2008). However, the exact criteria for inclusion of a species into one or another category are still unclear. It is very difficult, for example, to decide whether the bobac marmot (*Marmota bobac*), which forages on the ground but spends the majority of its life in a burrow, is terrestrial or subterranean. It is even more difficult to describe using a single term the substrate strategy of the yellow-necked field mouse (*Apodemus flavicollis*), which forages both on the ground and in trees, and nests both in tree hollows and burrows.

It is possible to overcome these difficulties using three procedures: (1) estimate the utilization of substrate separately for active and passive periods; (2) characterize for each period only the predominant behaviour; (3) describe only the predominantly used media and substrates. The *active period* represents the time an animal spends moving; this could include foraging, seeking for a mate, territory defense, playing, etc. The *passive period* represents the time spent in non-locomotor behaviour, i.e., resting, sleeping, grooming, rearing young, etc. If we consider the time spent in each of these states for any species, *the predominant type of behaviour* during active periods is generally foraging, while for passive periods it would be sleeping. *Predominantly used media and substrates* are those that are usually used by a particular species. At this point it is necessary to define

'usual'; here it is used to categorize a medium or substrate that is utilized for foraging or sleeping in more than 10% of cases.

Thus, in order to describe the substrate utilization strategy of a species it is necessary to determine the media and substrates predominantly used by this species (1) for foraging and (2) for sleeping (both the position of the shelter and the way of entering into it are important). In other words, one should determine their *foraging* and *sheltering strategies*. Using such an approach the bobac marmot may be described as a terrestrial/subterranean species (T/S), and the yellow-necked mouse as a terrestrial-arboreal/subterranean-arboreal species (TAr/SAr). The latter designation is admittedly rather long, but it is nonetheless more precise and operational than an oversimplified label of 'terrestrial' or 'arboreal'. To avoid confusion in interspecific comparisons, the symbols in each half of the strategy formula should always be written in an unbroken string and with a consistent order. Here an intuitively 'upward' order is proposed: Aq–S–T–Ar–Ae (from water through soil, ground, and trees to air).

When describing foraging strategies, it is important to consider the medium or substrate used by animals for locomotion when foraging, rather than the location of the food item (though these may often be the same). For example, the wild boar (*Sus scrofa*) obtains a great deal of its food from the soil but it moves on the soil surface, not underground. For this reason the wild boar should be classified as a terrestrial rather than a subterranean forager. When evaluating sheltering strategies, one should consider not only the location of the shelter but also the medium or substrate used to build the shelter and the way of entering. For example, the Russian desman (*Desmana moschata*) uses underground burrows with entrances submerged below the surface of ponds or streams. Thus, while the animal sleeps underground, the excavation of the burrow and entrance into it require aquatic as well as subterranean locomotion. Hence, the substrate strategy of the wild boar would be T/T, and that of the desman – Aq/AqS.

The merging of foraging and sheltering strategies creates numerous combinations; however, not all possible combinations are used by mammals. Unused combinations are usually simply impractical. For example, for an animal which forages underground, it would be disadvantageous to sleep in trees. Firstly, a subterranean shelter is likely to represent a safer option than an arboreal one. Secondly, climbing requires certain morphological adaptations that are usually incompatible with a fossorial way of life.

Theoretically, each half of the substrate strategy formula may include up to five components (Aq, S, T, Ar, Ae). However, it seems that in reality each half does not include more than two media or substrates. The following nine foraging strategies are used or appear likely to be used by mammals (the exact number is so far unknown): Aq, AqT, S, ST, T, TAr, Ar, Ae, TAe. The same set of media and substrates is also used for sheltering, with the exception of TAe and the addition of AqS and SAr, giving a total of ten sheltering strategies. The matrix composed of these nine foraging and ten sheltering strategies provides 90 combinations, of which 32 are used or appear likely to be used by mammals (Table 1).

Table 1. Combinations of foraging and sheltering strategies of mammals. Aq – aquatic (foragers/dwellers), S – subterranean, T – terrestrial, Ar – arboreal, Ae – aerial. The plus (+) sign designates combinations used or likely to be used and the minus (–) sign combinations unlikely to be used

Foraging	Sheltering									
	Aq	AqS	AqT	S	ST	SAr	T	TAr	Ar	Ae
Aq	+	+	+	+	+	–	+	–	–	–
AqT	+	+	+	+	+	–	+	–	–	–
S	–	–	–	+	–	–	–	–	–	–
ST	–	–	–	+	+	–	–	–	–	–
T	+	–	+	+	+	+	+	+	+	–
TAr	–	–	–	+	+	+	+	+	+	–
Ar	–	–	–	–	–	–	–	–	+	–
Ae	–	–	–	–	–	–	–	–	–	+
TAe	–	–	–	–	–	–	–	–	–	+

The typology of substrate utilization strategies given in Table 1 obviously does not adequately reflect the ecological diversity of flying mammals (i.e., bats, Chiroptera). They obtain their food not only from the air but also from the ground, water, and trees. They sleep in caves, tree hollows, or hanging from tree branches. Nevertheless, bats usually collect their food in flight and do not generally use terrestrial or arboreal locomotion for entering caves or trees. There are no specialized aquatic or arboreal bats analogous to penguins or woodpeckers among birds. That is why in the common matrix with non-flying mammals it is more reasonable to regard them as using predominantly one medium (Ae/Ae), with a possible exception of bats belonging to the genus *Mystacina*, found in New Zealand, which forage both in flight and while crawling on the ground (TAe/Ae) (Nowak, 1991).

The data in Table 1 demonstrate that approximately 32 substrate utilization strategies may be concealed within the five that are traditionally recognized. If it is necessary to further simplify this list of strategies to create groups of ecologically similar species, it may be done by grouping them according to the presence of a given medium/substrate in the formulae, whether it is used for foraging or sheltering (Table 2).

Of these 12 groups, 5 represent specialists, which use only one medium or substrate for both foraging and sheltering (AqAq, SS, TT, ArAr, AeAe). They correspond to the traditional categories of aquatic, subterranean, terrestrial, arboreal, and aerial animals. The remaining groups representing species that use two or three media or substrates may be combined into four higher groups of 'semi-specialists': semiaquatic (AqS, AqT, AqST), subterranean–terrestrial (ST), semi-arboreal (TAr, STAr), and semiaerial (TAe). Theoretically, a generalist (AqSTAr) may also exist, but I am not aware of such a mammal. While a species like the racoon (*Procyon lotor*) forages in water, on the ground, and in trees, and sleeps both in trees and in a burrow, it does not normally obtain its food by swimming

Table 2. Groups of substrate utilization strategies (symbols are explained in Table 1)

No.	Name of group	Symbol of group	Number of strategies	Symbols of strategies (from Table 1)
1	Aquatic	AqAq	1	Aq/Aq
2	Aquatic–subterranean	AqS	2	Aq/AqS, Aq/S
3	Aquatic–terrestrial	AqT	7	Aq/AqT, Aq/T, AqT/Aq, AqT/AqT, AqT/T, T/Aq, T/AqT
4	Aquatic–subterranean–terrestrial	AqST	4	Aq/ST, AqT/AqS, AqT/S, AqT/ST
5	Subterranean	SS	1	S/S
6	Terrestrial	TT	1	T/T
7	Subterranean–terrestrial	ST	4	ST/S, ST/ST, T/S, T/ST
8	Arboreal	ArAr	1	Ar/Ar
9	Terrestrial–arboreal	TAr	5	T/TAr, T/Ar, TAr/T, TAr/TAr, TAr/Ar
10	Subterranean–terrestrial–arboreal	STAr	4	T/SAr, TAr/S, TAr/ST, TAr/SAr
11	Aerial	AeAe	1	Ae/Ae
12	Terrestrial–aerial	TAe	1	TAe/Ae

and diving. Thus, its correct substrate utilization strategy formula should be TAr/SAr (terrestrial–arboreal/subterranean–arboreal), placing it in the group STAr of semiarboreal mammals.

Since the prefix ‘semi-’ in the names of semi-specialist groups means ‘half’, it is appropriate to ask to what the other half refers. Examination of the symbols of these groups shows that here, as in other sources (e.g. Eisenberg, 1981), ground-connected strategies (subterranean and terrestrial) represent the other halves. Thus, a semiaquatic mammal is at the same time either ‘semiterrestrial’ or ‘semisubterranean’ or both. To avoid confusion with subterranean–terrestrial mammals, which are also ‘semiterrestrial’ or ‘semisubterranean’, the latter two terms are not used. For this reason, the strategy ST is named here subterranean–terrestrial.

If the semiaquatic, semiarboreal, and semiaerial groups may be further combined into higher categories with the aquatic, arboreal, and aerial groups respectively, the subterranean–terrestrial group may be joined either with the subterranean or with the terrestrial group. It is probably most reasonable to join it with the terrestrial group, because all subterranean–terrestrial mammals (e.g. rabbit) are terrestrial foragers and subterranean dwellers, not vice versa, and the foraging strategy probably has a greater impact on the animal’s overall morphology than the sheltering one.

By arranging the 32 substrate utilization strategies presented in Table 1 first into 12 groups (Table 2) and then these groups into the categories described above, we end up with five substrate utilization categories (Table 3) that are

Table 3. Higher categories of substrate utilization strategies (symbols are explained in Table 1)

No.	Category (name and symbol)	Subcategories (names and symbols) (groups of Table 2)
1	Aquatic and semiaquatic (Aq)	Aquatic (AqAq), aquatic–subterranean (AqS), aquatic–terrestrial (AqT), aquatic–subterranean–terrestrial (AqST)
2	Subterranean (S)	Subterranean (SS)
3	Terrestrial and subterranean–terrestrial (T)	Terrestrial (TT), subterranean–terrestrial (ST)
4	Arboreal and semiarboreal (Ar)	Arboreal (ArAr), terrestrial–arboreal (TAr), subterranean–terrestrial–arboreal (STAr)
5	Aerial and semiaerial (Ae)	Aerial (AeAe), terrestrial–aerial (TAe)

virtually the same as the traditional ones. This suggests that the traditional terms have biological sense and are suitable for coarse descriptions of substrate utilization strategies. Nonetheless, they should be considered as simplified categories reflecting a far more complex reality.

The practical benefit of such classification is that, when faced by questions such as whether the yellow-necked field mouse is arboreal or terrestrial, we no longer need to rely on subjective responses. The approach to resolving such questions described here is to compose substrate utilization formulae; in this case TAr/SAr, according to which the species may be placed in the subterranean–terrestrial–arboreal subcategory of semiarboreal mammals. The theoretical benefit of this approach is that it ultimately provides a more realistic portrayal of the diversity of substrate utilization strategies.

The typology of the mammalian substrate utilization strategies presented here nonetheless requires further development, specification, and amendment. Some strategies classified as likely to be used by mammals may in fact be unused. At the same time some apparently improbable strategies are used, for example that of hippopotamus *Hippopotamus amphibius* (T/Aq).

Feeding strategies of mammals

Despite the existence of a great variety of feeding strategies, these may be broadly grouped into a few major strategies. One example of such a division is the traditional categorization of animals as carnivorous, omnivorous, or herbivorous, where carnivorous describes animal-eaters, herbivorous describes plant-eaters, and omnivorous describes those species that eat both animals and plants. This classification is clear-cut, but it does not work. Closer examination reveals that almost all animals would be described as omnivores using this classification. Such a classification therefore does not adequately reflect the true diversity of feeding strategies.

Indeed, all mammals' diets consist of some animal, plant, and fungal material. However, mammals do not select particular food items based on their taxonomic positions; rather they choose their food according to two characteristics: its accessibility and its digestibility. So the pertinent question when considering the diet of mammals is: 'How accessible and digestible are animals, plants, and fungi for mammals?' To avoid confusion, let us replace in further discussion the term 'carnivore', which literally means 'flesh-eater', with a more precise term 'animalivore' (N.B. not 'faunivore', because animals eat other animals, but never faunas!).

The accessibility of a potential food item is determined by its mobility and any protective characteristics it may possess. While certain examples of animals, plants, and fungi all possess some similar protective characteristics (e.g., toxicity, spines, hard shell), the levels of mobility among these different taxa clearly differ. Plants, fungi, and attached animals are immobile, while other animals are mobile. This means that, in contrast to plants, most animal prey need to be caught first. Thus, as far as the accessibility of potential food items is concerned, the division of mammals into animal-eaters and plant-eaters seems to be biologically meaningful (with reservations concerning attached animals). However, in terms of digestibility, the border between major feeding strategies lies in a rather different place.

The traditional grouping of herbivores (in the broad sense of plant-eaters) in fact consists of two essentially different groups: (1) green matter eaters, which are able to break down the cellulose in plant cell walls with the aid of symbiotic microorganisms, and (2) others, which are unable to break down cellulose, and which consequently consume parts of plants containing little or no cellulose. Species belonging to the first group eat mainly vegetative parts of plants (leaves, stems, and roots), while for those in the second group predominant food items are plants' reproductive parts (fruit, seeds) and exudates (gum, nectar). For the first group the name 'herbivores' may be retained (as was done e.g. in Eisenberg, 1981 and Sues, 2000), while for the second group the name 'frugivores' may be used.

There are further fundamental differences between herbivores and frugivores. Species in the former group have almost entirely vegetarian diets, because the microorganisms in their digestive tracts require a more or less constant environment. Species in the latter group make use of both plant and animal foods to some extent. Considering that the majority of animalivorous species also occasionally, or even regularly, consume plant matter, the boundary between animalivores and frugivores becomes vague. Indeed, it does not exist in a meaningful way. A clearer boundary lies between herbivores and non-herbivores (or all other) species. Non-herbivores represent a continuum of strategies, which terminates with the transition to herbivory. For convenience, we may artificially divide the continuum into two stages, named here animalivory and frugivory.

Where do 'omnivores' fit into this classification? As noted above, almost all non-herbivores are omnivorous in the sense that they consume both plant and animal foods. However, traditionally the term 'omnivore' is used to describe

animals that consume these two categories of food in more or less equal proportions. In other words, omnivores are species that are difficult to categorize as either animalivores or frugivores. Thus, they represent a transitional stage between animalivority and frugivority rather than a separate group. An analogous transitional stage exists also between frugivores and herbivores, termed 'mixivores' by Shenbrot and coauthors (Shenbrot et al., 1999). This transitional stage, which is not less important than the omnivorous stage, remained unrecognized by the majority of scientists due to inadequate typology of feeding strategies.

If the preceding considerations are correct, it is reasonable to make the following changes to the traditional typology of mammalian feeding strategies: (1) substitute the term 'carnivore' with the term 'animalivore', (2) exclude the term 'omnivore', and (3) divide herbivores in the broad sense (plant-eaters) into two categories: frugivores (fruit, seed, and exudate eaters) and herbivores (green-matter eaters). As a result, we retain three major mammalian feeding strategies: animalivory, frugivory, and herbivory. The first two are closer to each other than they are to herbivory.

The main feeding strategies of mammals may be defined as follows. *Animalivores* are animals in which animal foods constitute more than 50% of their annual food intake. *Herbivores* are animals in which vegetative parts of plants (leaves, stems, and roots) constitute more than 50% of their annual food intake. *Frugivores* are animals which consume various kinds of food, but animal foods and vegetative parts of plants constitute less than 50% of their annual food intake. Representatives of these three groups not only use different food objects, but also display different foraging behaviour. In behavioural terms they are respectively hunters, grazers (browsers), and gatherers.

Within the main feeding strategies it is possible to describe a variety of narrower specializations. The 16 'feeding categories' described by Eisenberg (1981) are a good example of such subdivision. In Table 4 the correspondence between Eisenberg's categories and the three main feeding strategies proposed here is shown (N.B., three of Eisenberg's categories – Aerial Insectivores, Foliage-gleaning Insectivores, and Insectivores/Omnivores – are combined in Table 4 into one category: Insectivores).

Table 4. Correspondence of the three main feeding strategies proposed in this paper to the mammalian feeding categories described by Eisenberg (1981)

This paper	Eisenberg, 1981
Animalivores	Piscivores and Squid-Eaters, Carnivores, Crustacivores and Clam-Eaters, Myrmecophages, Insectivores, Planktonivores, Sanguivores
Frugivores	Frugivores/Omnivores, Frugivores/Granivores, Frugivores/Herbivores, Nectarivores, Gumivores
Herbivores	Herbivores/Browsers, Herbivores/Grazers

Ecological classification of mammals

Short descriptions of animals' ecological strategies may be used as the basis for an ecological classification. A simple example of such a classification is provided in Table 5. In this case only substrate and feeding strategies are considered, and consequently a two-dimensional matrix is obtained. This classification is combinative in form rather than hierarchical, as would be the case in a taxonomic classification. This is possible due to the almost complete independence of substrate and feeding strategies. This means that, with two exceptions, these groups of strategies may create all possible combinations. The two exceptions are aquatic frugivores and subterranean frugivores. These combinations are unused for obvious reasons: there are no fruit (seeds, nectar) in water or underground. This combinative type of ecological classification was recognized by Eisenberg, who provided a matrix of 'feeding and foraging categories' (Eisenberg, 1981: 248). The classification in Table 5 therefore represents a further development of Eisenberg's ideas. Such ecological classifications can indicate the position of species within the multidimensional continuum of adaptive evolution.

Table 5. An example of the ecological classification of mammals based on combinations of substrate utilization and feeding strategies. Each cell in the matrix contains one specialized substrate user (the first or the only one) and some of the cells contain also one semi-specialized (the second one) substrate user (genus or species)

	Animalivores (An)	Frugivores (F)	Herbivores (H)
Aquatic and semiaquatic (Aq)	Common dolphins (*Delphinus*), otters (*Lutra*)	–	Manatees (Trichechus), muskrat (*Ondatra zibethicus*)
Subterranean (S)	Moles (*Talpa*)	–	Blind mole rats (*Spalax*)
Terrestrial and subterranean–terrestrial (T)	Lion (*Panthera leo*), foxes (*Vulpes*)	Wild boar (*Sus scrofa*), ground squirrels (*Spermophilus*)	Deer (*Cervus*), marmots (*Marmota*)
Arboreal and semiarboreal (Ar)	Silky anteater (*Cyclopes didactylus*), martens (*Martes*)	Marmosets (*Callithrix*), chipmunks (*Tamias*)	Sloth (*Bradypus*), North American porcupine (*Erethizon dorsatum*)
Aerial and semiaerial (Ae)	Mouse-eared bats (*Myotis*), New Zealand short-tailed bats (*Mystacina*)	Flying foxes (*Pteropus*)	–

CONCLUSIONS

- For a precise description of mammalian substrate utilization it is better to combine two characteristics rather than use a single one. Categorization should reflect: (1) the main media or substrates used for foraging; and (2) the main media or substrates used for sleeping.
- The numerous substrate utilization strategies of mammals fall into five broad groups: (1) aquatic and semiaquatic, (2) subterranean, (3) terrestrial and subterranean–terrestrial, (4) arboreal and semiarboreal, and (5) aerial and semiaerial.
- Mammalian feeding strategies can be allocated into three main groups: animalivores (animal eaters), frugivores (fruit, seed, and plant exudate eaters), and herbivores (leaf, stem, and root eaters). These groups represent three major parts of a continuum of feeding strategies.
- Substrate utilization and feeding strategies are largely independent of one another and can be combined together to form a matrix of strategies that may serve as an ecological classification.

ACKNOWLEDGEMENTS

The author is very thankful to Dr John Davison for proofreading the first version of this article, and to him as well as to Dr Anne Kirk and especially to an anonymous reviewer for numerous valuable suggestions and corrections they made.

REFERENCES

Aleyev, Yu. G. 1986. *Ecomorphology*. Naukova Dumka, Kiev (in Russian).

Castro-Luna, A. A., Sosa, V. J. & Castillo-Campos, G. 2007. Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest. *Acta Chiropterol.*, **9**(1), 219–228.

Eisenberg, J. F. 1981. *The Mammalian Radiations*. University of Chicago Press, Chicago.

Heesy, Ch. P. 2008. Ecomorphology of orbit orientation and the adaptive significance of binocular vision in primates and other mammals. *Brain Behav. Evol.*, **71**, 54–67.

Juniper, B. E., Robins, R. J. & Joel, D. M. 1989. *The Carnivorous Plants*. Academic Press, San Diego.

Miljutin, A. 1992. Two approaches to the study of life forms in mammals. In *Proceedings of the I-st Baltic Theriological Conference*, pp. 7–16. Tartu (in Russian with English summary).

Miljutin, A. 1997. Ecomorphology of the Baltic rodents: body form, ecological strategies and adaptive evolution. *Folia Theriol. Est.*, 3.

Miljutin, A. 1998. Ecological strategies of the Baltic rodents. *Proc. Latvian Acad. Sci*., Section B, **52**(1/2), 20–30.

Osborn, H. F. 1902. The law of adaptive radiation. *Am. Naturalist*, 34, 353–363.

Nowak, R. M. 1991. *Walker's Mammals of the World*. 5th edn, Vol. 1. J. Hopkins University Press, Baltimore and London.

Samuels, J. X. & Van Valkenburgh, B. 2008. Skeletal indicators of locomotor adaptations in living and extinct rodents. *J. Morphol.*, **269**(11), 1387–1411.

Shenbrot, G., Krasnov, B. & Rogovin, K. 1999. *Spatial Ecology of Desert Rodent Communities*. SpringerVerlag, Berlin.

Sues, H.-D. 2000. Herbivority in terrestrial vertebrates: an introduction. In *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record* (Sues, H.-D., ed.), pp. 1–8. Cambridge University Press, Cambridge.

Vepsäläinen, K., Ikonen, H. & Koivula, M. J. 2008. The structure of ant assemblages in an urban area of Helsinki, southern Finland. *Ann. Zool. Fenn.*, **45**, 109–127.

Substraadi kasutamise ja toitumise strateegiad imetajatel: kirjeldamine ning klassifikatsioon

Andrei Miljutin

Liigi ökoloogilise strateegia kirjeldamine võimaldab ökoloogilise info kokkusurumist ja selle esitamist evolutsioonilistes terminites. Paraku on ökoloogiliste strateegiate kirjeldamine raskendatud nende tüpoloogia ja nomenklatuuri ebapiisava väljaarendamise tõttu. Artiklis on esitatud lähenemisviis, mis võimaldab nende raskuste ületamist. Imetajate substraadi kasutamise strateegiate analüüs näitas, et nad jaotuvad viide põhirühma: veelised ja poolveelised, pinnasesisesed (subterrestrilised), pinnasepealsed (terrestrilised) ning pinnasesisesed-pinnasepealsed, taimepealsed (arboreaalsed) ja pooltaimepealsed ning aeraalsed (“õhused”) ja poolaeraalsed. Liigi substraadi kasutamise strateegia kirjeldamisel on soovitatud anda topeltiseloomustus, mis kajastaks: 1) toidu otsimisel enim kasutatavaid keskkondi või pindu ja 2) magamiseks enim kasutatavaid keskkondi või pindu. Toitumisstrateegia järgi on imetajad jaotatud kolme põhirühma: loomtoidulised, viljatoidulised ja lehetoidulised. On esitatud imetajate ökoloogilise klassifikatsiooni näide.