

Relative medullary thickness of shrews from arid environments: Intraspecific spatial analysis, and comparison to arctic shrews and tropical tenrecs

Juha Laakkonen

Section of Ecology, Behavior and Evolution, Division of Biology, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0116, USA (e-mail: juha@biomail.ucsd.edu)

Received 19 June 2001, accepted 22 August 2001

Laakkonen, J. 2002: Relative medullary thickness of shrews from arid environments: Intraspecific spatial analysis, and comparison to arctic shrews and tropical tenrecs. — *Ann. Zool. Fennici* 39: 249–255.

Spatial analysis on the relative medullary thickness (RMT) of sympatric shrews *Notiosorex crawfordi* and *Sorex ornatus* from different habitats in southern California showed no significant intraspecific differences between habitats but RMTs of *N. crawfordi* were significantly higher than those of *S. ornatus*. Interspecific comparison of RMTs of *Sorex* shrews from Alaska did not differ significantly from each other but they were significantly lower than those of both shrew species from southern California. RMTs of another group of insectivorous mammals, the *Microgale* shrew tenrecs from Madagascar, did not differ significantly between species, or from those of shrews from mesic habitats. The interspecific comparisons showed that RMT is an informative way to estimate the ability of an insectivorous species to occur in arid habitats, and to compare the RMTs of closely related sympatric mammals.

Introduction

A close correlation has been detected between renal medullary thickness (RMT) and ability to concentrate electrolytes in the urine in mammals (Schmidt-Nielsen & O'Dell 1961, Ross *et al.* 1995; *see* however Tisher *et al.* 1972, Brownfield & Wunder 1976, Munkácsi & Palkovits

1977). The medullary thickness and therefore the length of the loop of Henle, increases with body mass but the RMT declines with body size (Beuchat 1990). Regardless of body size, RMT is usually greater in desert mammals than in those inhabiting mesic environments (Schmidt-Nielsen & O'Dell 1961, Beuchat 1990). Because arid environments place their most severe demands

on the water economy of the smallest mammals (Schmidt-Nielsen & O'Dell 1961), RMTs can be predicted most clearly to reflect the availability of moisture in the habitat in small mammal species, such as *Sorex* shrews.

Insectivorous *Sorex* shrews are widely distributed and abundant in many parts of the Northern Hemisphere where shrew communities usually consist of morphologically similar species differing mainly in size. Several species, including some of the smallest ones, inhabit the arctic areas including Alaska and Siberia (Wolsan & Hutterer 1998). In contrast, only a few species occur in hot, arid areas (Wolsan & Hutterer 1998).

Owing to their high surface-to-mass ratios and high metabolism (Taylor 1998), *Sorex* shrews are poorly adapted to arid environments. The RMTs of *Sorex araneus* (Linnaeus 1758) and *Sorex minutus* (Linnaeus 1766) from mesic habitats in northern Europe are significantly lower (RMT = 5.7 and RMT = 4.9; Sperber 1944) than that (RMT = 8.6; Lindstedt 1980) of the closely related gray (desert) shrew, *Notiosorex crawfordi* (Coues 1877) inhabiting hot, arid environments in southwestern United States and northern Mexico. The RMTs of *Sorex* species from arid habitats have not been investigated.

Our previous study showed that *S. ornatus* (Merriam 1895) is not as widely distributed or abundant in southern California as is the *N. crawfordi* (Laakkonen *et al.* 2001). Since no apparent interspecific competition was found, and *S. ornatus* was shown to avoid hot temperatures (Laakkonen *et al.* 2001), interspecific differences in physiological adaptations to arid environments (*see above*, also Taylor 1998) were predicted to be reason for the ecological differences between these shrew species.

To test whether the urine concentration capability of *S. ornatus* is as low as in other *Sorex* shrews, I compared the RMTs of the ornate shrew, *Sorex ornatus*, to those of the sympatric *N. crawfordi* in southern California, and to those of *Sorex* shrews from Alaska. I predicted the RMTs of *S. ornatus* to be higher than those of *Sorex* from more mesic areas. Furthermore, I compared the RMT of *Sorex ornatus* and *N. crawfordi* in several sites consisting of different types of habitats in southern California to gain

insights into the spatial differences in RMTs of the two shrew species in the fragmented landscape of coastal southern California. My aim was to investigate whether any correlation exists between the RMT and habitat on a spatial scale in closely related sympatric species.

Finally, I compared RMTs of shrews to those of several species of shrew tenrecs of the genus *Microgale*. These members of the family Tenrecidae are endemic to Madagascar, and only distantly related to shrews (Stanhope *et al.* 1998). The metabolic rate of tenrecs is lower than that of *Sorex* shrews (McNab 1983, *see also* Stephenson & Racey 1993). Tenrecs represent a speciose group (about 28 species) of insectivorous mammals, which similarly to shrews, show a remarkable degree of morphological diversification in body size (Goodman *et al.* 1996). Several species are larger than *Sorex* shrews (Goodman *et al.* 1996) but they resemble shrews in general appearance. The ecology of tenrecs is poorly known but many species are threatened by habitat destruction (Goodman & Rakotondravony 2000). Since previous studies (*see above*) have shown that availability of water in the environment is more important in determining the RMT of a species than body size or taxonomy, I predicted the RMTs of shrew tenrecs to be similar to those of shrews from mesic environments. The comparison of morphologically similar but only distantly related species will provide insights to the effect of phylogeny on the RMT in insectivorous mammals.

Material and methods

Study sites of shrews and tenrecs

The *N. crawfordi* and *S. ornatus* material (Table 1) was collected with pitfalls at four study sites in the San Diego and Riverside counties in southern California during February and March in 1998 and 1999. The Wild Animal Park (33.09°N, 117.01°W) study site is within a large inland landscape (397 km²) area of coastal sage scrub and grassland habitats. Both shrew species are relatively common in the area. The St. Margarita Reserve (33.46°N, 117.16°W) is a rela-

tively large inland site (42 km²) of coastal sage scrub and oak woodland habitats. Both shrew species are common at this site. The Point Loma Reserve (32.67°N, 117.23°W) is a small coastal site (5.5 km²) of maritime succulent scrub and coastal sage scrub habitats. Only one of the shrew species, the *N. crawfordi*, occurs at this site. The Torrey Pines State Park (32.92°N, 117.24°W) is a small coastal site (1.5 km²) where *S. ornatus* is much more abundant than *N. crawfordi*. Coastal sage scrub, thick chaparral and Torrey Pine forests are the main habitat types. All study sites are within 80 kilometers of each other (for details of the study sites see Laakkonen *et al.* 2001). The *N. crawfordi* examined in this study belong to the *Notiosorex crawfordi crawfordi* (Carraway & Timm 2000, and the *Sorex ornatus* to the *Sorex ornatus ornatus* (Maldonado *et al.* 2001).

The masked shrews, *Sorex cinereus* (Kerr 1792) and pygmy shrews, *Sorex hoyi* (Baird 1857) were captured with pitfalls at Tanana Valley near Fairbanks, Alaska (64°42'N, 148°16'W, altitude 130 m) along a coniferous forest edge bordering a bog in August 2000 (Table 2). The tundra shrews, *Sorex tundrensis* (Merriam 1900) and montane shrews, *Sorex monticolus* (Merriam 1890) were caught with pitfalls around the Toolik lake (68°38'N, 149°36'W, altitude 720 m) in the arctic tundra of Alaska in August 2000 (Table 2).

Because of the seasonal mass recession (the Dehnel effect) of soricine shrews documented also from a site without severe winters (Hays & Lidicker 2000), all shrew material consisted of immature animals caught during months when immature shrews were abundant in that particular area.

Microgale dobsoni (Thomas 1884), *M. longicaudata* (Thomas 1882), *M. parvula* (G. Grandidier 1934), and *M. soricoides* (Jenkins 1993) were caught with pitfalls in Madagascar (Table 2) during October and November in 1999, at the commencement of the rainy season. The kidney material came from several sites where animals could be obtained from ongoing taxonomical, ecological and parasitological studies. The sites were Forêt de Betaolana (14°36.6'S, 49°25.5'E; altitude 1200 m; Province d'Antsiranana), Forêt de Manambolo (22°9.8'S, 47°2.5'E; altitude 1600 m; Province de Fianarantsoa), Forêt de Ravaro (22°12.7'S, 46°50.7'E; altitude 1500 m; Province de Fianarantsoa), and western slopes of the Anjanaharibe-Sud Massif (14°47'S, 49°26.5'E; altitude 1200 m; Province de Mahajanga).

All shrews examined in this study were found dead in traps. Most shrew tenrecs were sacrificed. Animals were taken to the laboratory (or field laboratory) for measurements and dissection. All animals examined were normal on gross pathologic examination with no signifi-

Table 1. Body mass, kidney size and relative medullary thickness (RMT) of shrews *Notiosorex crawfordi* and *Sorex ornatus* from four study sites in southern California.

Site	N	Body mass (g)		Kidney size (mm ³)		RMT			
		Mean	SD	Mean	SD	Mean	SD	Max	Min
<i>Notiosorex crawfordi</i>									
Wild Animal Park	5	3.4	0.89	44.50	9.72	8.33	0.58	9.27	7.84
St. Margarita Reserve	6	3.3	0.29	40.67	7.43	8.02	0.13	8.20	7.81
Point Loma Reserve	4	3.0	0.40	43.47	8.18	7.96	0.14	8.04	7.74
Torrey Pines State Park	2	3.3	0.14	42.01	6.12	8.13	0.27	8.33	7.94
<i>Sorex ornatus</i>									
Wild Animal Park	5	4.86	0.88	42.83	9.14	6.46	0.31	6.80	6.13
St. Margarita Reserve	4	4.58	0.82	37.50	10.6	6.02	0.31	6.30	5.61
Torrey Pines State Park	4	4.50	0.91	37.69	16.9	6.07	0.35	6.50	5.75

Only *N. crawfordi* occurs in Point Loma. Torrey Pines (altitude 11–71 meters above sea level) and Point Loma (22–113 m) are coastal sites. Wild Animal Park (141–255 m) and St. Margarita (243–265m) are inland sites.

cant decomposition of tissue other than the intestines.

Kidney measurements and comparative analyses

The weight of the animals was determined with spring scales (Pesola). The right kidney of each animal was removed, cleaned of surrounding fat, fixed and preserved in 90% ethanol. The size of the preserved kidneys was determined by measuring the length, width and depth with ruler (± 0.5 mm). Preserved kidneys were blotted dry, mid-sagittally halved with a razor blade, bisecting the papilla. The medullary thickness was measured as the longest straight-line distance from the cortico-medullary boundary to the area cribrosa (± 0.01 mm) using a dissecting microscope with an ocular micrometer. The morphology of the kidneys was similar in all species (see Sperber 1944). The relative medullary thickness (RMT) was calculated as defined by Sperber (1944):

$$RMT = 10(\text{medullary thickness})/\text{kidney size}^{1/3}.$$

Kruskal-Wallis one-way nonparametric analysis of variance test (Statistix® Analytical Software, Tallahassee, FL, USA) was used to compare

the RMTs of different species, and RMTs of individuals of the same species from different sites.

Results

No intraspecific differences in RMT were found in shrews from different sites in southern California (Table 1, $P = 0.16$ for *S. ornatus* and $P = 0.91$ for *N. crawfordi*). In the pooled data from all sites, the RMT of *S. ornatus* was significantly lower than that of *N. crawfordi* ($P < 0.001$), and comparison of mean ranks showed that all two means were significantly different from another. The RMTs of shrews from Alaska did not significantly differ from each other (Table 2, $P = 0.75$), nor did the RMTs of tenrecs in comparison between tenrec species (Table 2, $P = 0.37$). Comparison of all species of this study showed significant differences in the RMT between species ($P < 0.001$). The comparison of mean ranks demonstrated that *N. crawfordi* differed significantly from all other species, and *S. ornatus* differed significantly from all shrews from Alaska and from *M. parvula*.

In shrews, the RMT did not correlate with the body mass of the animal (Fig. 1). In tenrecs, the RMT increased with increasing body mass

Table 2. Body mass, kidney size and relative medullary thickness (RMT) of shrews of the genus *Sorex* and of shrew tenrecs of the genus *Microgale*.

Species	N	Body mass (g)		Kidney size (mm³)		RMT			
		Mean	SD	Mean	SD	Mean	SD	Max	Min
Shrews, Alaska									
<i>Sorex tundrensis</i>	3	6.66	1.61	78.75	22.88	5.00	0.30	5.34	4.77
<i>Sorex monticolus</i>	2	6.25	0.35	52.50	10.60	4.66	0.63	5.11	4.21
<i>Sorex cinereus</i>	5	3.00	0.00	37.04	4.77	4.76	0.38	5.15	4.27
<i>Sorex hoyi</i>	5	2.94	0.13	26.40	3.28	4.75	0.31	5.21	4.34
Shrews tenrecs, Madagascar									
<i>Microgale dobsoni</i>	5	30.70	3.05	242.60	33.71	5.54	0.26	5.90	5.23
<i>Microgale soricoides</i>	4	18.00	3.87	142.20	13.19	5.35	0.13	5.52	5.18
<i>Microgale longicaudata</i>	2	5.65	0.63	64.88	10.08	5.29	0.16	5.40	5.17
<i>Microgale parvula</i>	4	2.52	0.05	34.60	7.54	4.59	0.92	5.42	3.73

Sorex cinereus and *Sorex hoyi* are from Fairbanks, and *Sorex tundrensis* and *Sorex monticolus* from Toolik Lake, Alaska. The shrew tenrecs are from several localities in the eastern tropical rain forests of Madagascar.

but differences in RMTs were small compared to the differences in body mass (Fig. 1). Also, in *M. parvula* the standard deviation of RMT was high (Table 2).

Discussion

The significantly higher RMT of *S. ornatus* compared to those of *Sorex* shrews from moist areas (Tables 1 and 2; Sperber 1944) indicates that the theoretical maximum potential of *S. ornatus* to concentrate urine is greater than those of other *Sorex* species examined. *Sorex ornatus* has other adaptations, such as a lower metabolic rate than other *Sorex* species of similar body mass, and torpor-like behavior (Newmann & Rudd 1978), which enable it to occupy drier habitats than other *Sorex* shrews.

The RMT value of *N. crawfordi*, however, is similar to desert rodents (Beuchat 1990). The high RMT (Lindstedt 1980; Table 1), the relatively low metabolic rate, and the ability of *N. crawfordi* to enter torpor (Taylor 1998) most likely explain its larger distribution area in southern California as compared with that of *S. ornatus*.

It is not known whether the significant difference in RMTs of the southern California shrew species reflects any differences in prey items of these insectivores or differences in behavior (burrowing). The desert wood rat, *Neotoma lepida* (Thomas 1893) which is sympatric with *S. ornatus* and *N. crawfordi* in many areas in southern California, has adapted to the arid environment by diurnal residence within a stick nest and selection of moist vegetation (Lee 1963).

Blake (1967 cited in Lindstedt 1980) and Heisinger *et al.* (1973) showed that even within the same mammal species RMTs differ according to availability of water in their habitat. Although the RMTs of *S. ornatus* from the more arid inland site (Wild Animal Park) were higher than those measured from the coastal sites, no significant spatial differences in RMTs of either of the southern California shrew species from different habitats were found. This can at least partly be explained by the microhabitat choice of shrews in our study areas. Both shrew species occurred only in some parts of the study sites

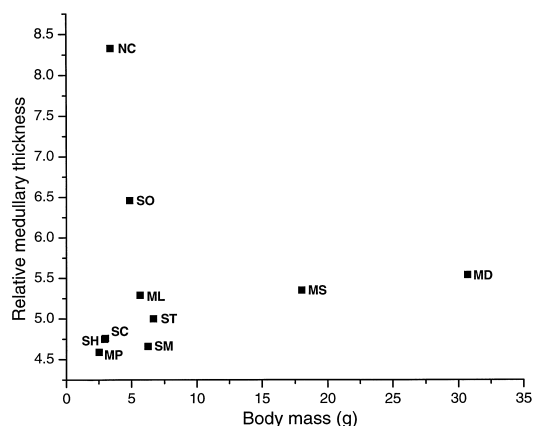


Fig. 1. The correlation between the mean relative medullary thickness and the mean body mass of shrews and of shrew tenrecs examined for this study. Note that not all species occurred in the same sites or habitats. NC = *Notiosorex crawfordi*, SO = *Sorex ornatus*, SH = *Sorex hoyi*, SC = *Sorex cinereus*, SM = *Sorex monticolus*, ST = *Sorex tundrensis*, MP = *Microgale parvula*, ML = *Microgale longicaudata*, MS = *Microgale soricoides*, MD = *Microgale dobsoni*.

even when a site appeared to consist of entirely similar habitat (Laakkonen *et al.* 2001). Also, as for *N. crawfordi*, it is possible that the scale used in this study did not include sites (habitats) different enough in availability of moisture to show any spatial differences in RMT of this widespread species. The RMTs of *N. crawfordi* from Arizona (Lindstedt 1980) were higher (8.6; $N = 5$) than the means found in this study (Table 1). In contrast, Heisinger *et al.* (1973) did not find any significant differences in the medullary thickness of a vole species from two different geographic areas.

The RMTs of shrews from Alaska (Table 2) were similar to those found in *Sorex* shrews from northern Europe (Sperber 1944, see introduction). The RMTs of shrews from different habitats (bog vs. tundra) did not differ significantly (Table 2) indicating that water availability is not a limiting factor in the distribution of shrews in these areas.

Despite the contrasting habitats of *Sorex* shrews and *Microgale* shrew tenrecs, their RMTs were remarkably similar. The relatively low RMTs recorded in the suite of shrew tenrec species used in this study indicate that they are not adapted to arid habitats. This conclusion is supported by

ecological investigations of shrew tenrecs (e.g., Goodman *et al.* 1996). A recent field survey shows that several species of shrew tenrecs are able to maintain seemingly viable populations in fragmented and isolated forests but most species do not occur in non-forested habitats (Goodman & Rakotondravony 2000). Of the shrew tenrec species studied here, only *M. longicaudata* is known to occur also outside of forested zones (Goodman & Rakotondravony 2000).

In support of results of previous studies of RMT in *Sylvilagus* rabbits (Heisinger & Breitenbach 1969), *Tamias* chipmunks (Heller & Poulson 1972) and *Peromyscus* mice (Heisinger *et al.* 1973), results of this study showed that measurement of RMT is an informative way to estimate the ability of a species to occur in arid habitats also in insectivorous species. Unlike the previous studies, this study did not only compare closely related species but sympatric species sharing the same habitat fragments. While the results indicated that RMTs could be used to detect interspecific differences in adaptations to aridity, spatial intraspecific differences could not be demonstrated. Knowledge of other physiological adaptations to aridity, and of microhabitat choice of each species is needed to further study the adaptive differences between local populations, and to determine the potential distribution area of these species in detail. The rapid fragmentation of natural habitats around the world underlines the importance of such studies.

Acknowledgements

The Research Council for Biosciences and Environment of the Academy of Finland (#43542) funded this research. The work was carried out under the Californian Department of Fish and Game permit. I am grateful to Steven M. Goodman for providing the shrew tenrec material, and for critical comments on an earlier version of this paper. I thank Ted J. Case, Robert N. Fisher, Gordon H. Jarrell and Heikki Henttonen for providing, or sharing shrew material.

References

- Beuchat, C. A. 1990: Body size, medullary thickness, and urine concentrating ability in mammals. — *Amer. J. Physiol.* 258: R298–R308.
- Blake, B. H. 1967: *A comparative study of energy and water conservation throughout the annual cycle in ground-dwelling sciuridae*. — Ph.D. dissertation, Yale University.
- Brownfield, M. S. & Wunder, B. A. 1976: Relative medullary index: a new structural index for estimating urinary concentrating capacity of mammals. — *Comp. Biochem. Physiol.* 55A: 69–75.
- Carraway, L. N. & Timm, R. M. 2000: Revision of the extant taxa of the genus *Notiosorex* (Mammalia: Insectivora: Soricidae). — *Proc. Biol. Soc. Washington* 113: 302–318.
- Goodman S. M., Raxworthy, C. J. & Jenkins, P. D. 1996: Insectivore ecology in the Réserve Naturelle Intégrale d'Andringitra, Madagascar. — In: Goodman, S. M. (ed.), *A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation*. *Fieldiana Zoology* 85: 218–230.
- Goodman, S. M. & Rakotondravony, D. 2000: The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. — *J. Zool.* 250: 193–200.
- Hays, W. S. T. & Lidicker, W. Z. Jr. 2000: Winter aggregations, Dehnel effect, and habitat relations in the Suisun shrew *Sorex ornatus sinuosus*. — *Acta Theriol.* 45: 433–442.
- Heisinger, J. F. & Breitenbach, R. P. 1969: Renal structural characteristics as indexes of renal adaptation for water conservation in the genus *Sylvaticus*. — *Physiol. Zool.* 42: 160–172.
- Heisinger, J. F., King, T. S., Halling, H. W. & Fields, B. L. 1973: Renal adaptations to macro- and microhabitats in the family Cricetidae. — *Comp. Biochem. Physiol.* 44A: 767–774.
- Heller, H. C. & Poulson, T. 1972: Altitudinal zonation of chipmunks (*Eutamias*): adaptations to aridity and high temperature. — *Amer. Midl. Nat.* 87: 296–313.
- Laakkonen, J., Fisher, R. N. & Case, T. J. 2001: Effect of land cover, habitat fragmentation, and ant colonies on the distribution and abundance of shrews in southern California. — *Journal of Animal Ecology* 70: 776–788.
- Lee, A. K. 1963: The adaptations to arid environments in the wood rats of the genus *Neotoma*. — *Univ. Calif. Publ. Zool.* 64: 57–96.
- Lindstedt, S. L. 1980: Energetics and water economy of the smallest desert mammal. — *Physiol. Zool.* 53: 82–97.
- Maldonado, J. E., Vilà C. & Wayne, R. K. 2001: Tripartite genetic subdivisions in the ornate shrew (*Sorex ornatus*). — *Molec. Ecol.* 10: 127–147.
- McNab, B. K. 1983: Energetics, body size, and the limits to endothermy. — *J. Zool.* 199: 1–29.
- Munkácsi, I. & Palkovits, M. 1977: Measurements on the kidneys and vasa recta of various mammals in relation to urine concentrating capacity. — *Acta Anat.* 98: 456–468.
- Newman, J. R. & Rudd, R. L. 1978: Observations of

- torpor-like behavior in the shrew, *Sorex sinuosus*. — *Acta Theriol.* 23: 436–438.
- Ross, M. H., Romrell, L. J. & Kaye, G. I. 1995: *Histology. A textbook and atlas*. — Williams and Wilkins, Baltimore. 823 pp.
- Schmidt-Nielsen, B. & O'Dell, R. 1961: Structure and concentrating mechanism in the mammalian kidney. — *Amer. J. Physiol.* 200: 1119–1124.
- Sperber, I. 1944: Studies on the mammalian kidney. — *Zool. Bidrag från Uppsala* 22: 249–432.
- Stanhope, M. J., Waddell, V. G., Madsen, O., de Jong, W., Hedges, S. B., Cleven, G. C., Kao, D. & Springer, M. S. 1998: Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. — *Proc. Nat. Acad. Sci.* 95: 9967–9972.
- Stephenson, P. J. & Racey, P. A. 1993: Reproductive energetics of the Tenrecidae (Mammalia: Insectivora). II. The shrew-tenrecs, *Microgale* spp. — *Physiol. Zool.* 66: 664–685.
- Taylor, J. R. E. 1998: Evolution of energetic strategies in shrews. — In: Wójcik, J. M. & Wolsan, M. (eds.), *Evolution of shrews*: 309–346. Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland.
- Tisher, C. C., Schrier, R. W. & McNeil, J. S. 1972: Nature of urine concentrating mechanisms in the macaque monkey. — *Amer. J. Physiol.* 223: 1128–1137.
- Wolsan, M. & Hutterer, R. 1998: A list of the living species of shrews. — In: Wójcik, J. M. & Wolsan, M. (eds.), *Evolution of shrews*: 425–448. Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland.