

Probability of competition between introduced and native rodents in Madagascar: An estimation based on morphological traits

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Received 17 December 2007, in revised form 22 April 2008

Abstract. An ecomorphological approach was used to estimate the probability of interspecific competition between introduced and native rodents in Madagascar. Comparison of body size, body construction, and craniodental characters leads to the conclusion that there is a high probability of competition between introduced *Rattus rattus* and the following native taxa: all species of *Nesomys*, larger semiarboreal *Eliurus* species (e.g. *E. tanala*, *E. webbi*), and especially *Gymnuromys roberti*. The competitive relationships between introduced rodents and the remaining species of the Nesomyinae have a low probability or are improbable, except possibly for *Mus musculus* and the so far poorly studied *Monticolomys koopmani* and *Voalavo* species.

Key words: competition, ecomorphology, Madagascar, Nesomyinae, *Rattus rattus*, alien species.

INTRODUCTION

To avoid competition, coexisting species use various resources that usually require different morphological adaptations (reviewed by Begon et al., 1990; Dayan & Simberloff, 1998; Moulton et al., 2001). For example, arboreal mammals need curved and sharp claws, while fossorial mammals require claws that are straight and blunt. Two animal species with a similar body form but different body sizes may avoid competition by using food items (Gittleman, 1985; Dayan & Simberloff, 1994) and shelters (burrows, rock crevices, tree hollows etc.) of different dimensions.

Several authors (Grant, 1972; Strong et al., 1979; Simberloff & Boecklen, 1981; Duncan & Blackburn, 2002) criticized the importance of interspecific competition. Begon et al. (1990, p. 738) concluded that even when interspecific competition is important, it affects only interactions between members of the same guild and even within a guild only those species closest together are likely to compete. Therefore, it is not always certain that the morphological overlap between two coexisting species leads to interspecific competition, but we can assume that morphologically

different species are very unlikely to compete. These considerations were taken into account here to estimate the probability of interspecific competition between introduced and native rodents in Madagascar.

There are 9 genera and 24 species of native rodents in Madagascar (Goodman & Soarimalala, 2005; Goodman et al., 2005; Musser & Carleton, 2005), all belonging to the same endemic subfamily of murid rodents: the Nesomyinae. Their monophyletic origin, however, is a matter for discussion and was neither clearly confirmed nor rejected (Jansa et al., 1999; Jansa & Carleton, 2003a; Musser & Carleton, 2005).

The number of introduced species of rodents in Madagascar is three: the black rat *Rattus rattus*, the brown rat *R. norvegicus*, and the house mouse *Mus musculus* (Garbutt, 1999); all three are synanthropic species with worldwide distribution. The brown rat in Madagascar is restricted to urban environments, while the black rat is found throughout the island, occupying a variety of habitats from human dwellings to pristine rainforests (Goodman, 1995). However, the abundance of *R. rattus* increases with the level of habitat disturbance (Lehtonen et al., 2001). The oldest record of *R. rattus* in Madagascar is from an 11th–14th century Islamic archaeological site in the northern part of the island (Rakotozafy, 1996; Radimilahy, 1997). An allozymic study demonstrated that specimens of *R. rattus* collected in different habitats and altitudes in Madagascar all belong to the same species and present the same diploid number ($2n = 38$) (Duplantier et al., 2003).

The house mouse is found in houses, rice fields, savannas, and marshes, but never in closed forests (Langrand & Goodman, 1997; Rakotondravony & Randrianjafy, 1998; Lehtonen et al., 2001). A mitochondrial study showed that the house mouse in Madagascar originated from the Arabian Peninsula in a single colonization (Duplantier et al., 2002).

The introduction of alien rodents may threaten native rodent species of Madagascar (Goodman, 1995). The more so as in certain intact areas of primary forest 96% of the rodents captured were *R. rattus* (Goodman et al., 1997). It was suggested that *R. rattus* competes with nesomyine rodents as a result of overlap in their food preferences (Goodman & Sterling, 1996). However, more detailed field studies are needed to clear up this competition hypothesis. Steps in this direction were taken by Ramanamanjato & Ganzhorn (2001) and Ganzhorn (2003). Ganzhorn (2003) stated that for the time being it is impossible to evaluate the effects of introduced rats on the native mammal fauna of Madagascar.

The main goal of this work is to provide a preliminary estimation of the potential for interspecific competition between introduced and native rodents in Madagascar. Regarding the scarcity of data on the ecology of Nesomyinae, this estimation would hardly be done on the basis of ecological data. Thus, we use the degree of ecomorphological similarity between introduced and native Malagasy rodents as a measure of the probability of competition between them. In doing so, we proceeded from the suggestion that the more similar these species are, the more strongly they may compete for living resources.

MATERIAL AND METHODS

Specimens examined

A total of 87 introduced and 62 nesomyine rodent specimens were measured, including representatives of all genera of the Nesomyinae except *Hypogeomys*, *Monticolomys*, and *Voalavo* (Tables I–III of the Appendix). In total, data on 11 species of native Malagasy rodents are used here. Other nesomyine species were excluded because of insufficiency of data (*Monticolomys*, *Voalavo*, *Brachytarsomys villosa*, *Brachyuromys ramirohitra*, *Macrotarsomys petteri*, *Nesomys lambertoni*, *Hypogeomys antimena*, and some *Eliurus* species). However, data on the length of the head and body (HB) for most of these excluded species were obtained from the literature and used for comparison of size.

Specimens of *R. rattus* were collected by J. T. Lehtonen in Ranomafana National Park in the eastern humid forest of Madagascar between September and November 2000. Unfortunately, we did not have access to any Madagascar specimens of *R. norvegicus* and *M. musculus*, that is why our data on these species belong to the European specimens collected from Estonia. We assumed that the external and cranial proportions did not differ significantly between European and Malagasy populations of the same species.

The deficiency of the available material and our intention to use samples that were as homogeneous as possible (in terms of sex, age, and geography) resulted in a small sample size for some species. We believe that these small homogeneous samples reveal general tendencies better than large but heterogeneous ones. The results may be verified later using more representative data.

The specimens of Nesomyinae used in this study are from the collections of the Museum of Natural History, London; Muséum National d'Histoire Naturelle, Paris; and the Finnish Museum of Natural History, Helsinki (collected by J. T. Lehtonen). The specimens of *R. norvegicus* and *M. musculus* are from the Zoological Museum of the University of Tartu, Estonia.

Measurements, abbreviations, and estimation of qualitative characters

A total of 19 measurements were used in this study: 8 external, 4 skeletal, and 7 craniodental. All characters used are ecology-dependent. They were selected from a larger number of characters in the course of a previous study by comparison of morphological traits and ecology in different species of rodents (see Miljutin, 1997, 1999 for details). These characters, as well as certain qualitative characters, may serve as morphological indicators of ecological strategies. The measurements were taken using a ruler and dial callipers graduated to tenths of millimetres through a lens. The angles were measured with a protractor. Standard external measurements (W, HB, T, E, and HF) were mostly obtained from specimen labels. The symbols of measurements and their meanings are explained below.

External measurements:

W – weight

HB – head and body length: the distance from the tip of the nose to the base of the tail

T – length of tail: the distance from the base of the tail to its tip without terminal hairs

E – ear length: the distance from the basal notch to the tip without terminal hairs (standard measurement)

HF – length of hind foot: the distance from the heel to the tip of the longest digit without claw (standard measurement)

FF – length of forefoot: the distance from the notch between the radius and carpus to the tip of the longest digit without claw. The notch may be located in dead animals or study skins by touching the area with a finger. In the birch mice it more or less coincides with the most proximal end of the inner metacarpal pad

Vib – length of vibrissae: the length of the longest vibrissa from base to tip in natural position

UM – length of forefoot claw: the distance from the base of the longest claw at its inferior surface to the tip.

Skeletal measurements:

Fe – length of femur: the distance from the most proximal surface of the caput to the distal surfaces of the condylae, parallel to the femur's axis

Ti – length of tibia: the greatest length of the tibia parallel to its axis

Hu – length of humerus: the greatest length of the humerus parallel to its axis

Ra – length of radius: the greatest length of the radius without the styloid process.

Craniodental measurements:

CBL – condylo-basal length: the distance from the border between the anterior surface of the upper incisors and intermaxilla to the posterior surfaces of the occipital condyles measured parallel to the cranial axis

LR – length of rostrum: the distance from the tip of the nasal bones to the anterior edge of the zygomatic arch, measured level with the nasals and parallel to the cranial axis

ZB – zygomatic breadth: the greatest breadth across the zygomatic arches

BIT – breadth across incisor tips: the distance across the tips of the incisors

LMT – alveolar length of maxillary toothrow: the distance from the anterior edge of the alveolus of the maxillary toothrow's first tooth to the posterior edge of the alveolus of the third molar

HMd – height of mandibular corpus: measured perpendicular to the masticatory surface of the mandibular toothrow from the antero-dorsal part of the first molar to the ventral surface of the mandibular corpus

ACP – angle of condylar process: the angle between the tangent to the ventral surface of the mandibular corpus parallel to the masticatory surface of the

mandibular toothrow and the line connecting the tangent's contact point with the axis of the mandibular condyle.

One qualitative feature was used in this work: the development degree of the tail cover. The different states of this character were provided with the following values: 0 = tapering tail without elongated hairs; 2 = tail with terminal tuft of elongated hairs, and 4 = bushy tail (not found in Malagasy rodents). We estimated the development of the tail cover in species of *Eliurus* and *Macrotarsomys* as 2. In all other Malagasy rodents it is 0.

Data processing

Conversion of raw data to ratios

To enable comparisons of species of different size, absolute values were converted to ratios. For this the absolute value of each external and skeletal character was divided by HB and the absolute value of the craniodental character was divided by CBL. The result was multiplied by 100 to express it as a percentage. To distinguish an absolute value from its ratio, an apostrophe (') was used for the ratio. For example, E is the absolute length of the ear in millimetres, while E' is its percentage of the length of the head and body (HB).

Estimation of similarity

For the estimation of similarity between species we used cluster analysis (described in Sneath & Sokal (1973) and statistical manuals). Two procedures were made: (1) ranging of character values and (2) calculation of the distances between species. Ranging is necessary for equalizing the raw data in gross size and variability. Otherwise characters with larger size and higher variability (e.g. length of tail) would obtain a greater statistical weight than the smaller and less variable characters (e.g. length of ear). For ranging, the ratios from Tables I–III were processed using the formula: $X_r = [(X' - X'_{\min}) / (X'_{\max} - X'_{\min})] \times 4$, where X' is the ratio and X_r its ranged value. This formula differs from those usually used (Sneath & Sokal, 1973) having two peculiarities. Firstly, the maximum and minimum values here are not those of the sample but of the majority of rodents (Table 1). Namely, the minimum values are for rodents in general, and the maximum values reflect a specialized condition of characters. As a specialized condition of a character we accepted the value about 75% of its actual maximum in rodents. The value 75% was arbitrarily selected, just because it is exactly between 50% (medial development of a character) and 100% (maximal development of a character). The actual maximum values are the means for species, not individual records. They were obtained from our data base on rodent morphology. Secondly, the results of ranging division were multiplied not by 100 as usual, but by 4, which is why the results normally range from 0 to 4 (or may exceed 4 in the case of an extraordinarily large value of a character) (Table 2). The first modification makes the results more meaningful in an ecological sense and comparable with data

Table 1. Limits of quantitative character variability (in the majority of rodents) used for data ranging (in % except for ACP)

Character	Limits of variability	
	Minimum	Maximum
Tail length (T')	0	150
Ear length (E')	0	35
Vibrissae length (Vib')	5	60
Forefoot claw length (UM')	0	5
Hind foot length (HF')	10	40
Forefoot length (FF')	5	20
Rostrum length (LR')	15	40
Zigomatic breadth (ZB')	40	70
Breadth across incisor tips (BIT')	3	10
Length of maxillary tooththrow (LMT')	5	25
Height of mandibular corpus (HMD')	10	25
Angle of condylar process (ACP, °)	10	60

Table 2. Ranged data matrix (based on data from Tables I–III of the Appendix). The abbreviations for the measurements are explained in Table 1

Species	T'	E'	Vib'	UM'	HF'	Tuft	LR'	ZB'	BIT'	LMT'	HMD'	ACP'
<i>Rattus rattus</i>	3.0	1.5	2.1	0.6	1.3	0	1.8	1.5	1.4	2.7	2.2	1.5
<i>R. norvegicus</i>	2.1	1.0	1.4	0.6	1.2	0	2.0	1.5	2.1	2.1	2.4	1.5
<i>Mus musculus</i>	2.3	1.8	1.6	0.7	1.3	0	1.6	2.1	2.0	2.3	1.8	1.6
<i>Brachytarsomys albicauda</i>	2.8	0.9	1.8	0.6	0.7	0	0.9	2.8	2.6	2.8	2.9	2.0
<i>Brachyuromys betsileoensis</i>	1.4	1.5	0.9	1.2	1.1	0	1.4	3.0	3.4	3.1	2.6	2.2
<i>Eliurus minor</i>	2.7	1.9	3.0	0.7	1.5	2	2.2	2.1	1.8	2.1	2.0	1.8
<i>E. myoxinus</i>	2.9	1.8	2.8	0.6	1.3	2	2.0	1.7	1.7	1.9	1.9	1.7
<i>E. tanala</i>	3.5	1.7	2.9	0.8	1.6	2	2.5	1.4	1.7	2.0	1.9	1.7
<i>E. webbi</i>	3.6	1.7	2.8	0.8	1.7	2	2.8	1.8	1.5	2.0	1.8	1.7
<i>Gymnuromys roberti</i>	2.9	1.6	2.4	0.6	1.7	0	2.6	2.0	1.8	2.2	2.1	1.8
<i>Macrotarsomys bastardi</i>	3.9	2.8	3.3	1.0	2.6	2	2.8	2.0	1.5	2.1	1.8	1.7
<i>M. ingens</i>	4.2	2.1	2.8	0.8	2.3	2	3.5	2.1	1.7	1.8	2.2	1.8
<i>Nesomys audeberti</i>	2.5	1.4	1.8	1.0	2.1	0	3.2	2.4	1.7	2.4	2.0	1.5
<i>N. rufus</i>	2.5	1.5	1.6	1.0	2.0	0	3.0	2.5	1.5	2.5	1.9	1.6

on other rodents. Indeed, if we considered the values of a few species with extreme morphology as maximum, we would conceal the important differences between hundreds of rodent species and might draw wrong ecological conclusions. For example, the ecological differences between animals with the relative tail length

equal to 150% and 200% (both are highly specialized) are very small if any, while animals with the tails 50% and 100% have a completely different ecology. In both cases the tail length difference is 50%. If we take 200% as a maximum value, then the medial or unspecialized condition would be 100%. It is a completely wrong interpretation, because the rodents with such a long tail are certainly specialized. If we take 150% (75% of 200) as a maximum value, then the medial (unspecialized) condition would be 75% – the value we find in the brown rat, a classical example of an unspecialized rodent. The second modification, multiplying by 4, enables using both quantitative and coded qualitative data in the common data matrix. In the case of qualitative traits, it is usually easy to estimate the minimal (0), medial (2), and maximal (4) condition of the trait. We may use 1 when we hesitate between 0 and 2, and 3 when we hesitate between 2 and 4. To represent quantitative data in comparable size we should consider their maximal values as equal to 4.

The Manhattan (city-block) distances between species were calculated using unweighted pair-group average linkage (UPGA) (Sneath & Sokal, 1973). For this, the ranged values of 12 morphological characters: 6 external and 6 craniodental ones (from Table 2) were used. The forefoot length and the skeletal measurements were omitted from calculations because of insufficiency of data. The distances were calculated separately for external characters and for craniodental ones. Because the value of Manhattan distances depends on the number of characters concerned, the distances are expressed here in a more comparable way – as a percentage of the maximally possible distance. Since the maximum possible distance for a single character is equal to 4, the maximum possible distance for all characters used is obtained by multiplying the number of characters by 4. In our case it is 24 ($6 \times 4 = 24$) both for external and craniodental characters. For a verbal interpretation of distances we recognized five degrees of similarity (external or craniodental): (1) no similarity (dissimilarity is 50% or more – species are more dissimilar than similar), (2) very low similarity (49.9–37.5%), (3) moderately low similarity (37.4–25.0%), (4) moderately high similarity (24.9–12.5%), and (5) very high similarity (12.4–0%). The number of similarity degrees is just arbitrary, and the interval between them (12.5%) is dictated by the number of degrees ($50\% : 4 = 12.5\%$).

RESULTS AND DISCUSSION

The initial data are presented in Tables I–III of the Appendix, ranged data in Table 2, the size differences in Table 3, and dissimilarity distances in Table 4. Ecological interpretations of morphological characters are based on the ecological meaning of characters used (see Miljutin, 1997 for details). Ecological data are from Garbutt (1999), if not indicated otherwise.

Table 3. Mean body length of Malagasy rodents and their length differences

Species	Mean head and body length, mm	Head and body length differences, % [(X _{max} - X _{min})/X _{min}] × 100		
		<i>Rattus rattus</i>	<i>Rattus norvegicus</i>	<i>Mus musculus</i>
<i>Rattus rattus</i>	170.9	0	34	119
<i>R. norvegicus</i>	229.2	34	0	193
<i>Mus musculus</i>	78.1 ^a	119	193	0
<i>Brachytarsomys albicauda</i>	221.6	30	3	184
<i>B. villosa</i>	228 ^b	33	1	192
<i>Brachyuromys betsileoensis</i>	157.5	9	46	107
<i>B. ramirohitra</i>	155.0 ^c	10	48	98
<i>Eliurus ellermani</i>	152.0 ^d	12	51	95
<i>E. grandidieri</i>	127.3 ^d	34	80	63
<i>E. majori</i>	157.9 ^c	8	45	102
<i>E. minor</i>	102.6	67	123	31
<i>E. myoxinus</i>	140.0	22	64	79
<i>E. petteri</i>	133.0 ^d	28	72	70
<i>E. tanala</i>	146.2	17	57	87
<i>E. webbi</i>	137.3	24	67	76
<i>Gymnuromys roberti</i>	161.0	6	42	106
<i>Hypogeomys antimena</i>	332.1	94	45	325
<i>Macrotarsomys bastardi</i>	91.8	86	150	18
<i>M. ingens</i>	136.5	25	68	75
<i>Monticolomys koopmani</i>	95.7 ^e	79	139	23
<i>Nesomys audeberti</i>	199.0	16	15	155
<i>N. lambertoni</i>	200 ^f	17	15	156
<i>N. rufus</i>	179.0	5	28	129
<i>Voalavo gymnocaudatus</i>	87.7 ^d	95	161	12

^a Duplantier et al., 2002.^b Carleton & Goodman, 2003.^c Goodman & Carleton, 1996.^d Carleton & Goodman, 1998.^e Carleton & Goodman, 1996.^f Goodman & Schütz, 2003.

Table 4. Distances between introduced and native species of Malagasy rodents: E – based on the external characters, C – based on the craniodental characters (in % of the maximum possible difference)

Species	<i>Rattus rattus</i>		<i>Rattus norvegicus</i>		<i>Mus musculus</i>	
	E	C	E	C	E	C
<i>Rattus rattus</i>	0	0	9	7	7	10
<i>R. norvegicus</i>	9	7	0	0	6	8
<i>Mus musculus</i>	7	10	6	8	0	0
<i>Brachytarsomys albicauda</i>	7	20	7	19	10	17
<i>Brachyuromys betsileoensis</i>	15	22	10	22	11	20
<i>Eliurus minor</i>	16	10	23	8	17	6
<i>E. myoxinus</i>	13	8	21	6	16	7
<i>E. tanala</i>	17	10	26	8	21	10
<i>E. webbi</i>	17	11	26	11	21	10
<i>Gymnuromys roberti</i>	4	11	12	9	9	8
<i>Macrotarsomys bastardi</i>	30	12	39	11	33	9
<i>M. ingens</i>	24	16	33	14	27	14
<i>Nesomys audeberti</i>	9	13	10	13	8	11
<i>N. rufus</i>	9	12	10	15	6	11

Potential competitors with introduced rodents

Hutchinson (1959) stated that in order to coexist, two species need a minimum size ratio of approximately 1.3 in the linear dimension. Bowers & Brown (1982) in their study of interspecific competition in desert rodents regarded species as being of similar size if their body mass ratios were less than 1.5. We used here the length of the head and body for comparison of size, because it has smaller intraspecific variability than mass. We did not use the criterion of Hutchinson because (1) it is not universal (Ganeshiah, 1999) and (2) we do not have empirical data, and so is safer to use an arbitrary criterion than an empirical one based on completely different taxa.

Based on the size differences (Table 3) and distances (external and craniodental) between species (Table 4), we compiled preliminary lists of potential competitors by selecting pairs of species with the degree of similarity more than very low (with at least one distance or size difference less than 37.5%). Doing so we obtained the following groups of species for further comparison:

- (1) ***Rattus rattus*** – *R. norvegicus*, *Brachytarsomys albicauda*, *B. villosa*, *Brachyuromys betsileoensis*, *B. ramirohitra*, *Eliurus ellermani*, *E. grandidieri*, *E. majori*, *E. myoxinus*, *E. petteri*, *E. tanala*, *E. webbi*, *Gymnuromys roberti*, *Macrotarsomys ingens*, *Nesomys audeberti*, *N. lambertoni*, *N. rufus*
- (2) ***Rattus norvegicus*** – *R. rattus*, *Brachytarsomys albicauda*, *B. villosa*, *Nesomys audeberti*, *N. lambertoni*, *N. rufus*
- (3) ***Mus musculus*** – *Eliurus minor*, *Macrotarsomys bastardi*, *Monticolomys koopmani*, *Voalavo gymnocaudatus*.

***Rattus rattus* as a potential competitor with other Malagasy rodents**

Rattus rattus and *R. norvegicus*

Comparison. *Rattus norvegicus* (European) averages about 34% larger than *R. rattus*. In Europe, however, this difference is smaller (19% in Estonia). The degree of external and craniodental similarity is very high.

Discussion. The competition between synanthropic rats is outside the scope of this study, but the morphological differences between them may serve as a scale for comparison of other species. Laboratory experiments and field observations of synanthropic populations demonstrated that these two species compete for territory and that *R. norvegicus*, which is on average larger, is competitively dominant over the smaller *R. rattus* (Barnett, 1958; Miljutin et al., 1991). In addition, these species successfully coexist under natural conditions due to spatial niche segregation, e.g. in the Transcaucasus (Bernstein, 1959; Kalinin, 1995) and in Australia (Williams et al., 2003). Therefore, the differences in ecology, behaviour, and morphology between these two species of synanthropic rats allow them to avoid competition under normal conditions but to switch a mechanism of competition in particular situations.

Rattus rattus and *Brachytarsomys* species

Size and body form. *Brachytarsomys* species are about 30% larger than *R. rattus*. The degree of external similarity is very high. *Brachytarsomys albicauda* differs from *R. rattus* in having a broader head, shorter ears, and shorter hind feet. Both the forefeet and hind feet of *B. albicauda* are very broad and they are supplied with large pads. The functional digits terminate in curved claws that are strong and sharp. All these characters indicate a high degree of specialization for arboreal life that parallels the way it nests in tree holes. The feet of *R. rattus* are slenderer with smaller pads and weaker claws. Both species exhibit specialization for arboreal locomotion, but *B. albicauda* is more specialized than *R. rattus*.

Craniodental characters. The degree of craniodental similarity is moderately high. The skull construction of *B. albicauda* betrays its specialization for a herbivorous (folivorous) diet. It has a short rostrum, broad zygomatic arches, relatively wide incisors, and a long row of molars that have ridged masticatory surfaces with an arvicolinelike enamel pattern. The skull of *R. rattus* has, in contrast, an elongated shape and bunodont molars. Both features are typical of frugivorous (granivorous) rodents.

Concluding remarks. The craniodental features described above enable us to conclude that *Rattus rattus* and *Brachytarsomys* species have rather different diets. The degree of their external similarity suggests that spatial niches of these species may overlap somewhat, but due to larger sizes and higher levels of specialization *Brachytarsomys* species are probably not threatened by *R. rattus*.

Rattus rattus and *Brachyuromys* species

Size and body form. *Brachyuromys betsileoensis* and *B. ramirohitra* average about 9% and 10% smaller than *R. rattus*. The degree of external similarity is moderately high. The two *Brachyuromys* species are very similar and differ from

R. rattus in having a shorter tail, shorter vibrissae, and longer forefoot claws. The proportions of limb segments in *B. betsileoensis* are similar to those of *R. rattus*. The forefoot of *Brachyuromys*, compared with that of *R. rattus*, is shorter and broader with smaller interdigital pads. The claws are longer and less curved. The relative length and width of the hind foot of *Brachyuromys* are more or less equal to those of *R. rattus*, but in *Brachyuromys* the two proximal interdigital pads and the thenar pad are smaller. The peculiarities of *Brachyuromys* external morphology reveal its moderate specialization for subterranean (fossorial) life, while *R. rattus* is a semiarboreal species. As far as we know, *Brachyuromys* species have never been captured above ground.

Craniodental characters. The degree of craniodental similarity is moderately high. The craniodental characters of *B. betsileoensis* are more dissimilar to those of *R. rattus* than to those of any other native Malagasy rodent. The skull and dentition of *B. betsileoensis* differ from those of *R. rattus* in having a short rostrum, broad zygomatic arches, a more vertical condylar process, wide incisors, and long molar rows. The molars have rather high crowns and their masticatory surface is flat with oblique ridges.

Concluding remarks. The morphology of *Brachyuromys* demonstrates specialization for a herbivorous diet and a semifossorial locomotion, while *R. rattus* is a semiarboreal frugivore. Thus, *R. rattus* and *Brachyuromys* species show differing ecological specialization, which makes competition between them unlikely. Nevertheless, J. Ryan (unpublished data, cited in Jansa & Carleton, 2003b) suggested that *R. rattus* may displace *B. betsileoensis* in rice fields.

Rattus rattus and *Eliurus* species

Size and body form. All *Eliurus* species average 8–64% smaller than *R. rattus*. The degree of external similarity is moderately high in all four species studied. *Eliurus* species differ from *R. rattus* in having a tufted tail, longer ears, longer vibrissae, and longer limb segments. *Eliurus webbi* and *E. tanala* also have tails that are much longer than those in *R. rattus*. The forefoot of *Eliurus*, compared with that of *R. rattus*, is broader and the forefoot claws are stronger (larger and with a wider base). The forefoot interdigital pads are relatively larger than in *R. rattus* (*E. majori*) or about the same size (*E. tanala* and *E. webbi*). The hind foot of *E. myoxinus* (and small *E. minor*) is broad with large plantar pads, while *E. tanala* and *E. webbi* have hind feet that resemble the hind feet of *R. rattus* and are slenderer than those of *E. myoxinus* and with smaller pads. Both *R. rattus* and *Eliurus* species demonstrate specialization for arboreal locomotion, but *Eliurus* species are more specialized. It should be noted that *Eliurus* species vary in their level of specialization. Among the species studied, the morphological characters of *E. tanala* and *E. webbi* indicate that they are more terrestrial than the others.

Craniodental characters. The degree of craniodental similarity is very high. Based on their ecology-dependent craniodental characters, *Eliurus* species differ from *R. rattus* most significantly in their dentition. *Eliurus* species have short molar rows with low-crowned lophodont teeth. This unusual combination of traits suggests a predominantly frugivorous diet.

Concluding remarks. Both *R. rattus* and *Eliurus* species are semiarboreal or arboreal frugivores (in the broad sense) but the latter appear less granivorous and are more specialized for arboreal life. In addition, some *Eliurus* species are apparently more terrestrial than others. It is likely that the trophic and spatial niches of *R. rattus* and the larger *Eliurus* species (especially *E. tanala* and *E. webbi*) may overlap, which may lead to interspecific competition.

Rattus rattus and *Gymnuromys roberti*

Size and body form. *Gymnuromys roberti* averages only 6% smaller than *R. rattus*. The degree of external similarity is especially high. The difference in size and external dissimilarity between *R. rattus* and *G. roberti* are less than those between *R. rattus* and any other Malagasy rodents including *R. norvegicus*. *Gymnuromys roberti* differs from *R. rattus* in having relatively longer hind feet, while the differences in the other external characters studied are insignificant. The forefoot of *G. roberti* is similar in proportion to that of *R. rattus*, but the claws are less curved and the palmar pads are smaller. The hind feet of these two species are similar in relative broadness, but *G. roberti* has smaller pads and a slightly shorter fifth digit. These peculiarities of the foot structure of *G. roberti* indicate that it is more terrestrial than *R. rattus*. It was suggested that *G. roberti* do not climb trees (Goodman & Carleton, 1996, 1998; Carleton & Goodman, 2000).

Craniodental characters. The degree of craniodental similarity is very high. The skull of *G. roberti* has a longer rostrum, while the differences in other proportions are insignificant. Its relatively short molar rows consist of low-crowned molars with a plane masticatory surface and numerous perpendicular ridges. The molars may functionally correspond to the molar teeth of *Eliurus* and the Myoxidae, thus connecting them with a frugivorous diet.

Concluding remarks. The close morphological resemblance between the generalist frugivore *G. roberti* and the semiarboreal frugivore *R. rattus* indicates a close ecological resemblance between them. This makes competition between the two species highly probable, the more so as they are more or less equal in size.

Rattus rattus and *Macrotarsomys ingens*

Size and body form. *Macrotarsomys ingens* is about 25% smaller than *R. rattus*. The degree of external similarity is moderately high. The external dissimilarity between *R. rattus* and *M. ingens* is greater than that between *R. rattus* and any other Malagasy rodent, except *M. bastardi*. *Macrotarsomys ingens* differs from *R. rattus* in having a longer tail, ears, vibrissae, and all limb segments, especially those of the hind limbs. The relative length of the forelimb is 34.6% in *R. rattus* and 40.2% in *M. ingens*. The relative length of the hind limb is 57.6% and 72.9%, respectively. The tail of *M. ingens* has a tuft of elongated hairs on its distal part. The forefeet of *M. ingens* have relatively longer digits and smaller pads than those of *R. rattus*. The hind feet of *M. ingens* are significantly elongated and have small pads. These peculiarities of the foot structure of *M. ingens* indicate its terrestrial habits and saltatorial locomotion. In addition, the long forefoot digits enable the animal to climb bushes and grasses.

Craniodental characters. The degree of craniodental similarity is moderately high. The skull of *M. ingens* has a longer rostrum and wider zygomatic arches than in *R. rattus*. The molar rows of *M. ingens* are quite short and consist of low-crowned bunodont molars, which are generally connected with a predominantly granivorous diet.

Concluding remarks. The body structure of *M. ingens* indicates a high level of specialization for terrestrial locomotion. Despite the possibility of partial overlap of the trophic niches of *M. ingens* and the black rat, the obvious differences in their locomotor specialization and size make competition between these two species unlikely.

Rattus rattus and *Nesomys* species

Size and body form. *Nesomys* species average 5–17% larger than *R. rattus*. The degree of external similarity is very high. *Nesomys* species differ from *R. rattus* in having a slightly shorter tail, longer forefoot claws, and greater length of all limb segments. The last difference is especially striking. The relative lengths of the forelimb and hind limb in *N. audeberti* are 41% and 73.3%, respectively. Thus, the proportion of limb segments of *Nesomys* is comparable to that of *Macrotarsomys*. The feet of *Nesomys* are slenderer than those of *R. rattus*. The claws are longer and straighter, the pads are smaller, and the fifth digit is relatively shorter than in *R. rattus*. These peculiarities of the foot structure of *Nesomys* testify to a greater degree of terrestriality than in *R. rattus* and even *G. roberti*. The radiotracking study of Ryan et al. (1993) showed that the *Nesomys* species are strictly terrestrial and only rarely move along the tops of fallen logs. In our preliminary cage experiment (Lehtonen et al., unpublished) *N. audeberti* and *N. rufus* regularly but awkwardly climbed a metal net wall and a trunk at an angle of 45 degrees, but we have never captured them in trees.

Craniodental characters. The degree of craniodental similarity is very high or moderately high. The skull of *Nesomys* has a remarkably long rostrum and slightly broader zygomatic arches than *R. rattus*. The molar rows are of medium length and the molars are brachyobunodont. Thus, the dentition of *Nesomys* probably is functionally equivalent to that of *R. rattus*.

Concluding remarks. The close morphological similarity in size and body proportions between *Nesomys* species and *R. rattus* suggests that interspecific competition between them is highly probable, despite the greater terrestriality of *Nesomys*.

***Rattus norvegicus* and *Mus musculus* as potential competitors with other Malagasy rodents**

The size of *R. norvegicus* may make it a potential competitor for *R. rattus* and *Brachytarsomys* and *Nesomys* species. Its relationships with *R. rattus* were discussed above. Competition with such specialized arboreal rodents as *Brachytarsomys*, despite their superficial resemblance to the brown rat (external dissimilarity is 7%), is highly improbable. Encounters of *R. norvegicus* with the

forest-dwelling *Nesomys* are also improbable. Thus, *R. rattus* is apparently the only rodent that may be threatened by *R. norvegicus* in Madagascar.

Mus musculus is one of the smallest rodents in Madagascar. The probability of its competition with such highly specialized native small rodents as *E. minor* and *M. bastardi* is low. Attention should be focused on its relationships with the relatively recently described *M. koopmani* and *Voalavo* species. It is noteworthy that *M. musculus* in Madagascar averages 7.4 mm shorter (HB) and 4.0 g lighter (Duplantier et al., 2002) than our specimens from Estonia used in this study.

CONCLUSIONS

The ecomorphological comparison given above supports the probability of interspecific competition between introduced and native rodents in Madagascar. The black rat is not only the most widespread introduced rodent on the island but also the most universally potential competitor.

Based on the degree of dimensional and ecomorphological similarity, we estimate the probability of interspecific competition as (1) very high between *R. rattus* and *G. roberti*, (2) high between *R. rattus* and *Nesomys* species and between *R. rattus* and the larger semiarboreal species of *Eliurus* (*E. tanala*, *E. webbi*), (3) moderately low between *R. rattus* and *Brachytarsomys* species and between *R. rattus* and the larger arboreal species of *Eliurus* (e.g. *E. myoxinus*), and (4) low between *R. rattus* and *Brachyuromys* species and between *R. rattus* and *M. ingens*.

Interspecific competition between *R. rattus* and native Malagasy rodents other than those mentioned above is unlikely. Interspecific competition of *R. norvegicus* and *M. musculus* with native Malagasy rodents is also improbable, except possibly for *M. musculus* and the recently described *Monticolomys koopmani* and *Voalavo* species.

Rattus rattus may not be the stronger competitor with all native rodent species. Among the potential competitors with *R. rattus*, four species – *B. albicauda*, *B. villosa*, *N. audeberti*, and *N. lambertoni* – are on average larger than the black rat, which may help them to predominate over *R. rattus*. All other potential competitors with *R. rattus* have smaller or equal sizes and may be threatened by the black rat.

We recommend that in further studies special attention be directed to the relationships between *R. rattus* and two Malagasy rodents: *G. roberti* and *N. rufus*. Especially because in Madagascar *R. rattus* is largely terrestrial and uses the same burrow types as *G. roberti* and *N. rufus* (Laakkonen et al., 2003).

ACKNOWLEDGEMENTS

We express our deepest gratitude to the staff of the Laboratoire de Zoologie, Mammifères et Oiseaux, Muséum National d'Histoire Naturelle in Paris, and to the staff of the Vertebrate Department of the British Museum (Natural History) in

London for allowing us to study their collections and for the sincere help we received there. Volatiana Rasataharilala and François Zakamanana assisted in the field and Jari Niemelä provided constructive advice on drafts of this article. The Association National pour la Gestion des Aires Protégées (ANGAP) allowed J.T.L. to work in Madagascar and the Madagascar Institut pour la Conservation des Environnements Tropicaux (MICET) helped with the logistics. A.M.'s visit to the British Museum in 1994 was made possible with the support of the George Soros Foundation. The Finnish Cultural Foundation granted support to J.T.L.'s work in Madagascar. All the above-mentioned persons and organizations are highly appreciated.

APPENDIX

Table I. Body weight (W), head and body length (HB), relative length of the tail (T'), ear (E'), vibrissae (Vib'), and forefoot claw (UM') of rodents (in % of HB except W and HB) (mean, standard deviation, and number and sex of specimens: m – males, f – females, ? – sex unknown)

Species	W, g	HB, mm	T'	E'	Vib'	UM'
<i>Rattus rattus</i>	119.0±19.1 (9 m)	170.9±9.2 (9 m)	113.9±3.3 (8 m)	13.0±0.6 (9 m)	33.5±2.6 (9 m)	0.8±0.1 (9 m)
<i>R. norvegicus</i>	343.0±52.2 (5 m)	229.2±13.8 (57 m)	77.8±4.1 (57 m)	8.9±0.6 (57 m)	24.0±2.2 (8 m)	0.8±0.1 (8 m)
<i>Mus musculus</i>	16.9±2.9 (16 m)	85.5±4.7 (21 m)	85.6±6.8 (21 m)	15.6±0.9 (21 m)	26.6±2.8 (21 m)	0.9±0.1 (21 m)
<i>Brachytarsomys albicauda</i>	–	221.6±20.3 (5 mf)	103.8±10.1 (5 mf)	7.8±0.8 (5 mf)	30.4±2.5 (5 mf)	0.8±0.04 (5 mf)
<i>Brachyuromys betsileoensis</i>	–	157.5±6.1 (6 mf)	52.9±4.2 (5 mf)	12.7±0.8 (6 mf)	17.2±2.1 (6 mf)	1.8±0.2 (6 mf)
<i>Eliurus minor</i>	–	102.6±4.3 (7 mf)	103.0±10.2 (5 mf)	16.4±1.1 (6 mf)	46.8±3.0 (7 mf)	0.9±0.1 (7 mf)
<i>E. myoxinus</i>	–	140.0±5.0 (3 mf)	109.2±13.1 (2 mf)	16.0±0.4 (3 mf)	43.8±2.7 (3 mf)	0.7±0.0 (2 m)
<i>E. tanala</i>	104.8±15.2 (4 mf)	146.2±10.2 (6 mf)	132.8±7.6 (4 mf)	14.7±1.2 (6 mf)	45.3±4.4 (6 mf)	1.0±0.2 (6 mf)
<i>E. webbi</i>	–	137.3±2.5 (3 f?)	136.0±6.9 (3 f?)	14.8±1.4 (3 f?)	43.7±0.1 (3 f?)	1.0±0.2 (3 f?)
<i>Gymnuromys roberti</i>	–	161.0 (1 f)	108.7 (1 f)	13.7 (1 f)	37.9 (1 f)	0.7 (1 f)
<i>Macrotarsomys bastardi</i>	–	91.8±4.4 (14 m)	145.0±8.8 (14 m)	24.8±1.4 (14 m)	47.2±6.2 (14 m)	1.3±0.3 (14 m)
<i>M. ingens</i>	60.0 (1 m)	136.5±19.1 (2 mf)	158.4±2.2 (2 mf)	18.0±1.0 (2 mf)	43.8±2.5 (2 mf)	1.0±0.3 (2 mf)
<i>Nesomys audeberti</i>	216.0 (1 m)	199.0±11.2 (11 mf)	94.6±6.7 (11 mf)	12.5±0.9 (11 mf)	30.4±2.0 (10 mf)	1.3±0.2 (11 mf)
<i>N. rufus</i>	174.0 (1 m)	179.0±8.6 (4 mf)	93.3±3.9 (4 mf)	12.8±0.8 (4 mf)	27.5±2.3 (4 mf)	1.2±0.0 (4 mf)

– No data.

Table II. Relative length of the limb segments of rodents (in % of HB) (mean, standard deviation, and number and sex of specimens: m – males, f – females, ? – sex unknown)

Species	Femur (Fe')	Tibia (Ti')	Hind foot (HF')	Humerus (Hu')	Radius (Ra')	Forefoot (FF')
<i>Rattus rattus</i>	17.5±0.5 (7 m)	20.3±0.6 (8 m)	19.8±0.9 (9 m)	12.8±0.5 (8 m)	12.3±0.5 (8 m)	9.5±0.5 (9 m)
<i>R. norvegicus</i>	15.0±0.9 (8 m)	17.7±0.6 (7 m)	18.7±1.2 (57 m)	12.3±0.6 (6 m)	10.7±0.4 (6 m)	9.0±0.6 (5 m)
<i>Mus musculus</i>	16.0 (1 m)	18.9 (1 m)	19.7±0.8 (21 m)	12.7 (1 m)	12.0 (1 m)	8.7±0.7 (7 m)
<i>Brachytarsomys albicauda</i>	–	–	14.9±0.9 (5 mf)	–	–	–
<i>Brachyuromys betsileoensis</i>	16.5±0.7 (5 mf)	19.2±1.0 (5 mf)	18.5±0.7 (6 mf)	12.9±0.7 (5 mf)	12.2±0.6 (3 m)	8.4±0.6 (2 mf)
<i>Eliurus minor</i>	18.4 (1 f)	21.7 (1 f)	21.0±0.9 (7 mf)	14.6 (1 f)	15.0 (1 f)	10.8±0.2 (5 mf)
<i>E. myoxinus</i>	18.3±0.7 (3 mf)	20.3±0.3 (3 mf)	20.0±1.3 (3 mf)	14.4±0.7 (3 mf)	13.7±0.6 (3 mf)	–
<i>E. tanala</i>	20.0±2.4 (4 mf)	23.6±2.1 (4 mf)	22.0±1.7 (6 mf)	15.6±1.8 (4 mf)	15.3±1.7 (4 mf)	9.8±0.6 (4 mf)
<i>E. webbi</i>	20.0±0.0 (2 f?)	23.3±0.6 (2 f?)	22.6±0.5 (3 f?)	15.1±0.7 (2 f?)	15.3±0.4 (2 f?)	10.5±0.1 (2 f?)
<i>Gymnuromys roberti</i>	–	–	22.4 (1 f)	–	–	–
<i>Macrotarsomys bastardi</i>	21.1±1.2 (5 m)	27.0±1.3 (5 m)	29.3±1.8 (14 m)	13.9±1.0 (5 m)	14.9±0.6 (5 m)	10.6±0.5 (2 m)
<i>M. ingens</i>	20.8±1.1 (2 mf)	25.2±1.2 (2 mf)	26.9±2.3 (2 mf)	14.8±0.8 (2 mf)	14.8±0.8 (2 mf)	10.6±0.9 (2 mf)
<i>Nesomys audeberti</i>	21.4±1.3 (2 f)	26.0±0.4 (2 f)	25.9±1.6 (11 mf)	15.8±1.2 (2 f)	14.9±0.7 (2 f)	10.3±0.4 (7 mf)
<i>N. rufus</i>	19.6±1.1 (3 mf)	24.6±1.9 (3 mf)	25.2±1.9 (4 mf)	14.7±1.0 (3 mf)	14.5±1.0 (3 mf)	9.6±0.3 (2 mf)

– No data.

Table III. Cranial size and proportions of rodents (in % of CBL, except CBL and ACP) (mean, standard deviation, and number and sex of specimens: m – males, f – females, ? – sex unknown). Abbreviations of measurements are explained in Table 1 and Material and Methods

Species	CBL (mm)	LR'	ZB'	BIT'	LMT'	HMd'	ACP, °
<i>Rattus rattus</i>	38.1±1.0 (8 m)	31.6±0.8 (8 m)	51.2±1.0 (8 m)	5.5±0.4 (8 m)	18.7±0.4 (8 m)	18.4±0.3 (8 m)	29.2±1.8 (8 m)
<i>R. norvegicus</i>	46.3±2.8 (20 m)	32.4±0.7 (20 m)	51.2±2.0 (19 m)	6.6±0.4 (20 m)	15.5±0.8 (20 m)	19.0±1.0 (20 m)	29.3±3.0 (20 m)
<i>Mus musculus</i>	20.3±0.5 (10 m)	29.9±1.4 (10 m)	55.5±1.4 (10 m)	6.5±0.5 (10 m)	16.5±0.5 (10 m)	17.0±0.7 (10 m)	30.1±1.8 (10 m)

Probability of competition between rodents in Madagascar

Table III. Continued

Species	CBL (mm)	LR'	ZB'	BIT'	LMT'	HMd'	ACP, °
<i>Brachytarsomys albicauda</i>	43.4±1.5 (5 mf)	25.9±0.6 (5 mf)	61.2±2.6 (5 mf)	7.6±0.3 (5 mf)	19.2±1.3 (5 mf)	20.8±0.9 (5 mf)	34.5±1.3 (5 mf)
<i>Brachyuromys betsileoensis</i>	34.3±1.0 (6 mf)	28.9±1.0 (6 mf)	62.4±1.4 (6 mf)	8.9±0.3 (5 mf)	20.5±1.2 (6 mf)	19.7±0.7 (6 mf)	37.0±1.9 (6 mf)
<i>Eliurus minor</i>	27.3±0.9 (6 mf)	33.7±1.6 (6 mf)	55.9±2.6 (4 mf)	6.1±0.2 (6 mf)	15.3±0.7 (6 mf)	17.6±0.7 (6 mf)	32.0±2.4 (6 mf)
<i>E. myoxinus</i>	34.5±1.1 (3 mf)	32.2±1.1 (3 mf)	53.0±1.1 (3 mf)	5.9±0.0 (2 m)	14.5±0.4 (3 mf)	17.3±0.8 (3 mf)	30.7±1.2 (3 mf)
<i>E. tanala</i>	38.8±0.7 (3 mf)	35.9±0.8 (3 mf)	50.6±1.1 (3 mf)	5.9±0.3 (3 mf)	14.9±0.7 (3 mf)	17.3±0.3 (3 mf)	31.0±1.0 (3 mf)
<i>E. webbi</i>	35.6±1.0 (3 f?)	37.5±1.9 (3 f?)	53.6 (1 f)	5.6±0.2 (3 f?)	14.8±0.3 (3 f?)	16.6±0.7 (3 f?)	30.7±1.2 (3 f?)
<i>Gymnuromys roberti</i>	36.4±1.9 (5 m?)	36.1±1.8 (5 m?)	55.3±3.8 (4 m?)	6.2±0.3 (4 m?)	15.8±1.0 (5 m?)	17.7±0.7 (5 m?)	32.0±1.4 (5 m?)
<i>Macrotarsomys bastardi</i>	26.4±0.7 (12 m)	37.7±2.1 (12 m)	55.3±1.0 (10 m)	5.6±0.5 (11 m)	15.7±0.4 (11 m)	16.7±0.4 (12 m)	30.7±2.0 (11 m)
<i>M. ingens</i>	35.4±1.7 (2 mf)	41.6±0.6 (2 mf)	56.1±0.8 (2 mf)	5.9±0.1 (2 mf)	14.2±1.1 (2 mf)	18.2±1.9 (2 mf)	32.5±0.7 (2 mf)
<i>Nesomys audeberti</i>	43.4±0.9 (5 mf)	40.2±1.6 (5 mf)	57.9±1.1 (4 mf)	5.9±0.4 (5 mf)	17.0±0.7 (5 mf)	17.5±0.5 (5 mf)	29.0±1.7 (5 f)
<i>N. rufus</i>	39.9±0.7 (8 mf)	38.6±0.9 (8 mf)	58.8±1.3 (8 mf)	5.6±0.4 (7 mf)	17.7±0.5 (8 mf)	17.2±0.4 (8 mf)	30.0±2.5 (8 mf)

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Sissetoodud ja aborigeensete näriliste vahelise konkurentsivõime tõenäolisus Madagaskaril: morfoloogilistel tunnustel põhinev hinnang

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Sissetoodud (kodurott, rändrott ja koduhiir) ning aborigeensete näriliste (Nesomyinae) vahelise konkurentsivõime hindamiseks Madagaskaril on kasutatud ökomorfoloogilist lähenemist. Keha suuruse ja keha ning kolju ehituse võrdlus on tuvastanud kõrge konkurentsivõime saarele sissetoodud koduroti (*Rattus rattus*) ja järgmiste kohalike liikide vahel: kõik liigid perekonnast *Nesomys*, suuremad ronivad liigid perekonnast *Eliurus* (*E. tanala*, *E. webbi* jt) ning eriti *Gymnuromys roberti*. Konkurentsivõime sissetoodud näriliste ja ülejäänud aborigeensete näriliste vahel (välja arvatud võib-olla vähe uuritud *Monticolomys koopmani* ning liigid perekonnast *Voalavo*) on aga vähe tõenäoline või ebatõenäoline.