

Habitat use and morphological adaptations of endemic rodents (Muroidea: Nesomyinae) of East Madagascar

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Zusammenfassung

Die endemischen Nagetiere Madagaskars haben sich in einer adaptiven Radiation an die verschiedensten Lebensräume angepasst. Im Rahmen der vorliegenden Doktorarbeit wurden ökologische und morphologische Aspekte der vielfach sympatrisch vorkommenden Nesomyinen von Ostmadagaskar bearbeitet. Im ersten Teil der Studie wurden für die ökologischen Fragestellungen Vegetationsanalysen im Zusammenhang mit dem Vorkommen der verschiedenen Arten modellhaft in einem Regenwaldgebiet im Osten von Madagaskar durchgeführt. Die Ergebnisse stellen eine erste ökologische Einteilung der Lebensweise und Habitatnutzung von Nesomyinen dar. Für den zweiten Teil der Studie wurde erstmalig die Morphologie der Hände und Füße (Chiridia) mit der Lebensweise und Habitatnutzung in Beziehung gesetzt. Adaptive Differenzierungen der Chiridia geben Hinweise auf die ökologische Einnischung einer Art. Bestimmte Strukturen des volaren Integuments, epidermale Bildungen sowie Längen- und Flächenverhältnisse lassen Rückschlüsse auf die funktionelle und ökologische Anpassung zu.

Sieben endemische Nagerarten (*Eliurus grandidieri*, *E. minor*, *E. tanala*, *E. webbi*, *Nesomys rufus*, *Gymnuromys roberti*, *Brachytarsomys albicauda*) wurden mit Hilfe von Lebendfallen in unterschiedlichen Mikrohabitaten gefangen. Ökologische Daten sowie Habitatstrukturen wurden entlang dieser 1 km langen Trails erfasst. Ganz unterschiedliche Nischen konnten für die spezialisierten Nager dokumentiert werden: manche bevorzugten die höchsten Bäume oder Lianen, andere wiederum wurden im Unterholz, Wurzelwerk oder Todholz gefangen. Manche Arten kamen in der Nähe von Flüssen und Bächen vor, andere in feuchten Tälern, auf trockeneren Hängen oder in der feucht-nebeligen Gipfelregion, bis zu 1200 m NN. Es wurden Mikrohabitatanalysen durchgeführt und die Trails, auf welchen Arten signifikant häufiger vorkamen mit anderen Trails verglichen. Es konnte herausgefunden werden, dass das Vorkommen der Arten stark von der Waldstruktur, der Beschaffenheit und der Dichte der Vegetation abhängt. Abgeholzte und degradierte Flächen waren dagegen sehr artenarm. Für die morphologischen Untersuchungen wurden detaillierte mikroskopische Zeichnungen speziell der Hände und Füße anhand von Belegexemplaren angefertigt und zwischen den Arten verglichen.

Die morphologischen Differenzierungen der Hände und Füße variierten signifikant zwischen den sieben untersuchten Arten. Bodenbewohner mit überwiegend terrestrischer Lokomotion, weisen oft schmale Hinterfüße mit deutlich

kleineren Thenarballen auf. Kletternde Arten besitzen große, prominente Ballen, welche eine viel größere Fläche der Fußsohle bedecken. Arten, welche an Bäumen klettern besitzen deutlich größere Ballen, als Arten, welche überwiegend an Halmen und Zweigen klettern. Diese Baumkletterer konnten als „Haftkletterer“ identifiziert werden. Halm- und Zweigkletterer dagegen weisen relativ lange Füße mit längeren Zehen auf und wurden als „Greifkletterer“ eingestuft. Um auf hohen Bäumen mit großem Stammdurchmesser zu Klettern, und nicht ab zu rutschen, bedarf es eine gute Haftung. Im Gegensatz dazu kommt es beim Klettern auf dünnen Zweigen und Halmen auf die bessere Greiffunktion an. Letztlich kann zusammengefasst werden, dass die Ausprägung von speziellen Merkmalen auf Händen und Füßen mit einer bestimmten Lebensweise und Fortbewegungsart einhergeht. Diese funktionalen Anpassungen sind besonders wichtig um ein genaues Bild der ökologischen Einnischung von verschiedenen Arten zu erhalten, welche sympatrisch im gleichen Gebiet vorkommen. So konnten verschiedene Habitatpräferenzen und besondere Lebensraumansprüche der endemischen Nesomyinen von Ost-Madagaskar erstmalig im Detail analysiert werden. Im Rahmen der vorliegenden Arbeit konnte durch die Kombination dieser ökologischen und morphologischen Ergebnisse erstmals gezeigt werden, dass mittels Fußballen-Morphologie die ökologische Einnischung madagassischer Nager-Arten bestimmt werden kann.

Summary

In an adaptive radiation, Madagascar's endemic rodents colonised a variety of different habitats. In this thesis, ecological and morphological aspects of the frequently sympatric nesomyines of East Madagascar were analysed. In the first part of the study, vegetation analyses were conducted in a model rainforest in East Madagascar and compared with species distribution to describe the species' ecology. The results represent a preliminary ecological classification of the habitat use of nesomyines. In the second part of the study, the morphology of the hands and feet (chiridia) was correlated with ecological parameters and habitat use for the first time. Adaptive differentiations of the chiridia give evidence of a species' ecological niche. Certain patterns of the volar integument, epidermal structures as well as length and area ratios are discussed in respect of their functional and ecological adaptive value.

Seven endemic rodent species (*Eliurus grandidieri*, *E. minor*, *E. tanala*, *E. webbi*, *Nesomys rufus*, *Gymnuromys roberti*, *Brachytarsomys albicauda*) were trapped with live traps in different microhabitats. Ecological data and information on habitat structures were collected along five 1 km long trails. The specialised rodents were found in different ecological niches: on trees, lianas, underneath wood and thick roots, in dead wood or rotten logs. Some were found close to small rivers, some in humid valleys, whereas others seemed to prefer the higher mountain slopes or misty ridges, up to 1200 m a.s.l. Microhabitat analyses were conducted and trails where a species was significantly more abundant were compared with those where it was rare. The presence of an endemic rodent species was strongly connected with forest type, forest structure and vegetation density. In contrast, the deforested and cleared areas were species-poor. For the morphological studies, detailed microscopic drawings of the hands and feet were prepared of voucher specimens to be compared between the species. The chiridian structures differed clearly between the seven species. Slender hind feet with small thenar pads were significantly correlated with a terrestrial locomotion and a ground-dwelling ecology. Species with a predominantly arboreal locomotion exhibit large and prominent pads, covering a great area of the chiridian surface. Large-tree-climbers have larger pads in relation to foot size than bamboo-grass and small-branch-climbers which possess relatively longer feet with longer toes. Climbing on large trees needs good adhesive properties and climbing on grass or thin branches needs good grasping abilities. In conclusion, certain morphological structures

of the rodents' chiridia are evidence of a special way of life and foot-pad morphology in particular mirrors special adaptations to a species' habitat. These adaptations are regarded as important to understand niche occupation, certain ecological aspects and locomotion forms of sympatric species. Thus, habitat preferences and special habitat requirements of the endemic nesomyines of East Madagascar could be analysed in details. In this thesis, it could be documented for the first time by the combination of these ecological and morphological results that the chiridian morphology allows to differentiate nesomyine taxa on ecological level.

1. Chapter - General introduction

1.1. Biological background

1.1.1 Madagascar - A hotspot of biodiversity and endemism

Madagascar is one of the most species-rich islands on earth and harbours a high number of endemics which are found nowhere else on the planet. Most of Madagascar's plant and animal species have evolved in long isolation. The mammal fauna of the island is very remarkable compared to mainland Africa. For instance, on Madagascar there are none of the large herbivores that so dominate the plains of the African continent; carnivores, such as wild cats, dogs and members of the weasel family as well as monkeys and apes and other smaller forms like lagomorphs are absent (Garbutt 1999, Meier 1992). In fact, only five mammal orders are found on Madagascar today which are not introduced: the bats (Chiroptera), tenrecs (Insectivora, family Tenrecidae), the rats and mice (Rodentia, family Nesomyidae), the carnivores (Carnivora, family Viverridae and Herpestidae) and the lemurs (Primates, infraorder Lemuriformes) (Wilson & Reeder 2005). It is still an open question whether the Bush Pig is introduced (Artiodactyla). In total, more than 90 % of species within these groups are endemic to Madagascar.

Because of its high degree of endemism, the island was placed into the highest protection category as a "mega diversity area" by the International Union for Conservation of Nature (IUCN). Madagascar is listed among the 25 worldwide hotspots, characterised by endemism, species diversity and the degree of threat (Mittermeier et al. 1999). Some others of these 25 earth's biologically richest and most endangered terrestrial eco-regions listed in Mittermeier et al. 1999 are the Tropical Andes, the Galapagos Islands, Southwest Australia, New Zealand, the Philippines, Guinean Forests of West Africa, Chile, Brazil, Caribbean. The highest protection category for Madagascar is to preserve a biocenosis, whose original habitats - mainly primary forests - have been destroyed through massive deforestation. Today, less than 10 % of the original forest cover remains and forest areas are often fragmented (Achard et al. 2002).

In Madagascar, little is known about biodiversity, taxonomy and ecology of the species communities in the remaining forest fragments, especially when compared to the state of research in Europe. Among the five orders of mammals endemic to Madagascar in particular lemurs have been studied so far (Ganzhorn & Bittner 1992, Ganzhorn & Kappeler 1993, Goodman et al. 1993, Mittermeier et al. 1994, Yoder 1996, Zimmermann et al. 1998, Garbutt 1999, Godfrey et al. 1999, Yoder et al. 2000, Thalmann 2000, Rasoloarison et al. 2000, Radespiel & Raveloson 2001, Goodman & Benstead 2003, Olivieri et al. 2007, Braune et al. 2008, Radespiel et al. 2009, Randrianambinina et al. 2010, Kappel et al. 2011).

The taxonomy and ecology of Madagascar's small mammals - mainly insectivores and rodents - has only been intensively studied for about a decade (Ellerman 1949, Petter 1972, Goodman & Benstead 2003, Goodman & Soarimalala 2005). This, however, has already yielded some amazing results regarding differentiation and morphology (Carleton & Schmidt 1990, Carleton 1994, Carleton & Goodman 1996, 1998, 2001, 2007, Goodman et al. 2009). Our study will give a first impression about the ecology and morphology of the endemic rodents which are strongly adapted to primary forest.

1.1.2 Logging - the human impact

In Madagascar, more than 90 % of the original habitat has been destroyed by massive deforestation. The extraordinary biodiversity of the island is highly threatened. Deforestation activities started right after human settlement about 2000 years ago when the first colonists from Africa and later on from Asia arrived (Bittner 1992, Burney 1997).

Only five million hectares of the primary vegetation still exist; 58 million hectares have already been destroyed. Former primary forests have been replaced by secondary vegetation and a species-poor fauna (Rauh 1992). The high plateau in the centre of the island is completely deforested. Madagascar is one of the poorest countries in the world. Between 2000 and 2005, the human population showed an annual growth of 2.8 % (UNFPA 2005). The rapidly increasing human population with a high need for natural resources for agriculture has led to exponentially increasing habitat loss and forest fragmentation (Lowry 1997). The high rate of poverty results in logging and deforestation of increasingly remote and pristine areas. The annual bush fires ("tavy") are one of the biggest problems on the island (Jenkins 1990). For new

grazing and agriculture, the people light thousands of hectares every year (Rauh 1992, Jenkins & Carleton 2005). After at best 3 years the fruitful land is leached out and new areas have to be burned resulting in erosion, floods and landslides.

In the remaining and often fragmented forest in the humid east, selective logging is another common practice (Ganzhorn et al. 1990). These traditional tree felling activities are concentrated on special species, large size and diameter. When falling down, large trees form a gap similar to natural tree fall, but usually several trees are felled close together which leads to larger unnatural gaps. The pathways that lead to these trees for harvesting the wood are often used afterwards which results in a high rate of disturbance, especially for mammalian species. If these practices continue, the last forest areas will be lost within the next 20 years. Politicians on Madagascar are nowadays aware that the biodiversity of the island is an irreplaceable heritage and resource (i.e. for ecotourism) and that the increasing human population is its main threat. Over the last years, a large number of governmental and non-governmental conservation projects have been initiated. To triple the surface of protected areas was one aim of the last government. However, in many countries the international know-how and aid in cooperation with local groups is still the key for the establishment and maintenance of newly protected areas. But for such plans, a stable government is necessary. The protection of existing primary forest and the reforestation of corridors between already protected sites are one of the most important aims for the survival of the large number of Madagascar's endemic species.

1.1.3 The insular history and mammalian migrations

Madagascar is the fourth largest island in the world, encompassing an area over 587,000 km². The island is 1600 km long and 580 km wide at its broadest extent. Separated by the Mozambique Channel, Madagascar is located only about 400 km east of the African mainland, along the Somalian, Kenyan and Tanzanian coast. Because of the early isolation about 165 million years ago, the island harbours a remarkable fauna and flora (Lowry 1997, Krause et al. 1997). For the last 120-130 million years, Madagascar has been in its present position relative to Africa, located south of the equator (Rabinowitz & Woods 2006). There is no doubt that Madagascar was joined to the continent of Africa at one time and has been separated by volcanic activity since. However, Madagascar was also once connected to the Asian continent

and part of the giant supercontinent known as Gondwana. Raval & Veeraswamy (2003) suggested that Madagascar was part of the mobile belt network of India and that the India-Madagascar break-up would have taken place along a relatively mobile corridor. Fossil records of Madagascar are known from the Pleistocene (1.8 million years), but it is even impossible to say with certainty if and when the various stocks of mammals crossed from Africa to Madagascar (Woods & Eisenberg 1989).

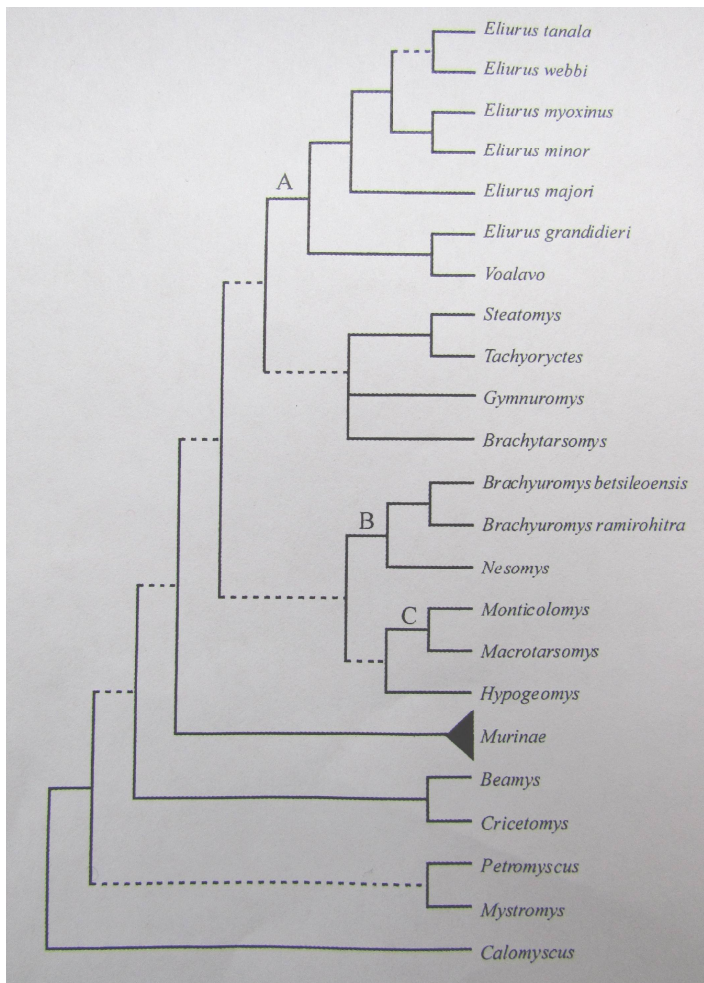
The first terrestrial mammals must have colonised the island during the Palaeocene about 65 million years ago, probably at irregular intervals and temporally separated by tens of millions of years (Yoder et al. 2003). The consensus opinion is that insectivores and primates arrived first by rafting on vegetation mats over the Mozambique Channel, which was during this time more than 400 km wide. There is no indication that stepping stones in form of small islands existed in the channel during the time interval of the terrestrial mammalian colonisations (Rabinowitz & Woods 2006). The colonisation of bats (Chiroptera), most of them derived from African relatives, also took place at several different times, but being volant, they have a more powerful colonising ability than terrestrial mammals (Woods & Eisenberg 1989). Primates and insectivores arrived first, followed by carnivores at a later date (primates, between 60-50 million years ago (Mya) (Poux et al. 2005, Martin 1993), insectivores between 50-20 Mya ago (Poux et al. 2005, Eisenberg 1981), carnivores between 26-19 Mya ago (Poux et al. 2005, McCall 1997). Recent studies conclude that primates on Madagascar are monophyletic (Yoder et al. 1996) and that all Malagasy lemurs are the product of a single colonisation event by an African ancestor. The same process is assumed for the Malagasy carnivores, the civets and mongooses (Yoder et al. 2003). For the rodents, it is still debated whether they belong to a monophyletic group. Some authors assume that they were relatively late immigrants to the island, between 24-15 Mya ago (Poux et al. 2005, Eisenberg 1981, Catzeflis et al. 1993), because they do not exhibit the diversity of forms displayed by rodents in continental areas and that primates have filled many of the rodent-like niches at an earlier date (Woods & Eisenberg 1989). Recent phylogenetic studies (Jansa et al. 1999) are contradictory to the theory of a monophyletic colonisation by rodents only from Africa. Instead, they point at a paraphyletic colonisation from Africa or Asia, resulting up to now, in an adaptive radiation of different rodent species.

1.1.4 *Nesomyinae - the biodiversity of Madagascar's rodents*

The Rodentia are by far the largest order of living mammals, encompassing 2277 species, or approximately 42 % of the worldwide mammalian biodiversity (Wilson and Reeder 2005). When compared to other island radiations of rodents, Madagascar has been characterised initially as a region relatively poor in rodent species, (Carleton and Goodman 1998). However, the increasing number of small-mammal field surveys over the past decade and detailed studies of the resulting collections have immensely augmented the number of new rodent species - resulting in a rich rodent fauna for Madagascar, divided into native and introduced species.

The introduced rodents, all belonging to the family Muridae, the subfamily Murinae within the superfamily of Muroidea (Wilson and Reeder 2005), may have accompanied the first human settlers about 2000 years ago on their ships and boats along trade routes over sea. Three different introduced rodent species are documented for Madagascar: the House Mouse *Mus musculus* and the Brown Rat *Rattus norvegicus*, mainly documented from cities and larger towns, i.e. on rubbish dumps. The Black Rat *Rattus rattus* which is widespread on Madagascar, lives as human commensal in homes and fields as well as in the countryside. The fleas of the Black Rat have been documented as a reservoir for the plague, which has been present in Madagascar for at least a century (Duplantier et al. 2003, Laakkonen et al. 2003) (last recorded evidence of plague in 2000, in Anevoka, a village near the study site, personal record of a villager). Not only homes and fields are colonised by the Black Rats, along paths used by humans and pigs they have also penetrated deep into many pristine native forest areas up to an altitude of over 2500 m. Interaction and competition between the introduced and native nesomyine rodents is still poorly documented. Furthermore, it is unknown if any of the introduced rodent species spread diseases to native ones and if these are also able to transmit the plague. At some sites, when *Rattus rattus* colonise a forest, there is a decline in the number of native small mammals, particularly rodents (Goodman & Carleton 1996). Feral rats are good climbers and well able to adapt to new conditions, i.e. in rainforest areas far away from human habitation. They have been regarded as *Rattus rattus* var. *frugivorus* by some authors (described as *Mus flavigaster* by Heuglin 1861), according to the variability in belly colour and ecology. Most of the “forest-living” Black Rats are white-bellied.

The Malagasy native rodents have all been placed in a single endemic subfamily - the Nesomyinae within the superfamily of Muroidea (Wilson and Reeder 2005). Over the last decades, a variety of field and museum studies about nesomyine taxa have been published by Ellerman (1949), Petter (1972, 1959), Carleton (1994, 2003), Carleton & Goodman (1996, 1998, 2001, 2007), Goodman & Benstead (2003), Goodman & Soarimalala (2002, 2005) and Goodman et al. (2009). The number of these autochthonous rodent species - the Malagasy Rats - has meanwhile stepped up to nine genera comprising 27 species: **Brachytarsomys** Günther, 1875 (2) *albicauda*, *villosa*, **Brachyuromys** Major, 1896 (2) *betsileoensis*, *ramirohitra*, **Eliurus** Milne-Edwards, 1885 (12) *antsingy*, *carletoni*, *danieli*, *ellermani*, *grandidieri*, *majori*, *minor*, *myoxinus*, *penicillatus*, *petteri*, *tanala*, *webbi*, **Gymnuromys** Major, 1896 (1) *roberti*, **Hypogeomys** A. Grandidier 1869 (1) *antimena*, **Macrotarsomys** Milne-Edwards & G. Grandidier, 1898 (3) *bastardi*, *ingens*, *petteri*, **Monticolomys** Carleton & Goodman, 1996 (1) *koopmani*, **Nesomys** Peters, 1870 (3) *audeberti*, *lambertoni*, *rufus*, **Voalavo** Carleton & Goodman, 1998 (2) *gymnocaudus*, *antsahabensis*.



In the recent phylogenetic study (on the left), Jansa et al. 1999 employed the complete nucleotide sequence from the mitochondrial cytochrome *b* gene. Their study included all nesomyine genera and most species, along with several Asian and African taxa implicated as relatives. Cladistic analysis of these data suggest that Madagascar's rodents include a african dendromurine (*Steatomys*) and a afro-asian rhizomyine (*Tachyoryctes*) and point so at a paraphyletic origin, with three stable clades A, B, C (Jansa et al. 1999).

During the last 20 years, nine new species of nesomyines have been described, including one new genus which is named *Voalavo*, *E. petteri* and *E. ellermani* (Carleton 1994), *E. grandidieri*, *V. gymnocaudus* (Carleton & Goodman 1998), *E. antsingy* (Carleton & Goodman 2001), *M. petteri* (Goodman & Soarimalala 2005), *E. danieli* (Carleton & Goodman 2007) and *V. antsahabensis* (Goodman et al. 2005) and *E. carletoni* (Goodman et al. 2009). New genetic and morphological studies have boosted the number of recognised species within a very short time period and several new species will be described in the future.

All over Madagascar, nesomyines populate a wide variety of habitats, from arid savannahs, spiny forests and limestone regions in the dry lowlands (the Tsingys) to humid tropical rainforests. Almost every habitat harbours a particular species community that is adapted to certain environmental conditions. The most species-rich genus is *Eliurus*, which comprises the Tuft-Tailed Rats that are characterised by a densely haired tail that terminates in a tuft. Eight of the twelve currently known *Eliurus* species occur in the rainforests of eastern Madagascar. The knowledge about their elevational range, their distribution, their ways of life and niche occupations is scarce. Data on the number of embryos, for instance, allows inferences about reproductive rates (Goodman & Benstead 2003). But it is still unknown where the respective species raise their young and build their nests, which areas and structures in the rainforest they use and how sympatric species avoid competition. The knowledge about the morphological variation of nesomyines is only at the beginning and how morphological traits may influence their habitat choice and behaviour is still to be discovered.

This present thesis is conducted in two different parts **(1)** the microhabitat preference of seven Malagasy rodent species and **(2)** the morphological adaptations of hand and foot-prints of seven Malagasy rodents in relation to the local vegetation structures. **Chapter 1** focuses on all general information, the biological background and the general methods of the study. Starting from the wider picture of niche occupation in different habitats, this study goes further into detail: from habitat use via locomotion and distribution **in Chapter 2** to the morphological adaptations of the hands and feet **in Chapter 3**. It is my aim to obtain a complete picture of the examined taxa by documenting, analysing and finally, conclude with outlooks the interconnections of ecology and morphology **in the last Chapter 4**.

1.2. General methods

1.2.1 The study area - the rainforest of Maromizaha

Field work was conducted in a rainforest in Eastern Madagascar. During four years, field work was carried out for two months a year: 2003, 2004, 2005 and 2006 (15.9.-20.10.2003 / 20.9.-22.10.2004 / 2.11.-16.12.2005 / 20.11.2006-15.1.2007).

The rainforest of Maromizaha is a protected area near Andasibe (150 km east of Antananarivo, south east of Andasibe, 6.5 km away from the “Réserve Spéciale d'Analamazaotra”). It is part of the administrative region of Alaotra-Mangoro, rural district office at Moramanga, province of Toamasina. The region of Andasibe is quite populated and comprises six rural districts. To the north the border of Maromizaha is formed by the main road leading from Antananarivo to Toamasina (RN-2). The main entrance to the reserve is located south of the village of Anevoka and can be accessed from the main road (RN-2). The second entrance can be reached by passing the quarry of Amboasary (18°57.69'S, 48°27.14'E). To the south and the east large rivers form the natural border of the reserve.

The reserve comprises about 1600 hectares, with extraordinary species diversity and characteristic dragon trees (*Dracaena reflexa* and *Dracaena spec.*). It has been designated as a private protected area by the NGO (non-governmental organisation) NAT ("Natur- und Artenschutz in den Tropen e. V., Foundation for Tropical Nature and Species Conservation") in 2002. In 2008, the Malagasy NGO GERP (Groupe d'Étude et de Recherche sur les Primates de Madagascar) took over the management of Maromizaha from NAT. The aims remain the same: to protect the biodiversity of Maromizaha, to prevent further deforestation, to limit agricultural exploration and to give local people an alternative income in the form of ecotourism and reforestation. It is planned to allow guided tourism in the area along the main path, other parts are closed to public access. The north-western part of the reserve shows signs of former logging activities as well as burned trees and agriculture. The south-eastern part is much more intact and directly adjacent to the large intact rainforest area Vohidrazana, a "sacred" forest, where deforestation is prohibited for local people by a “fady”, a form of taboo, but there is deforestation by non-local employers. In the north, the National Park Mantadia and the Torotorofotsy marsh are adjacent to the large rainforest area Forêt Sianaka. Maromizaha connects these northern forest areas to Vohidrazana in the south. By reforesting corridors at

Maromizaha, full connectivity of large areas of rainforest north and south of Maromizaha could be achieved (see Fig. 1).

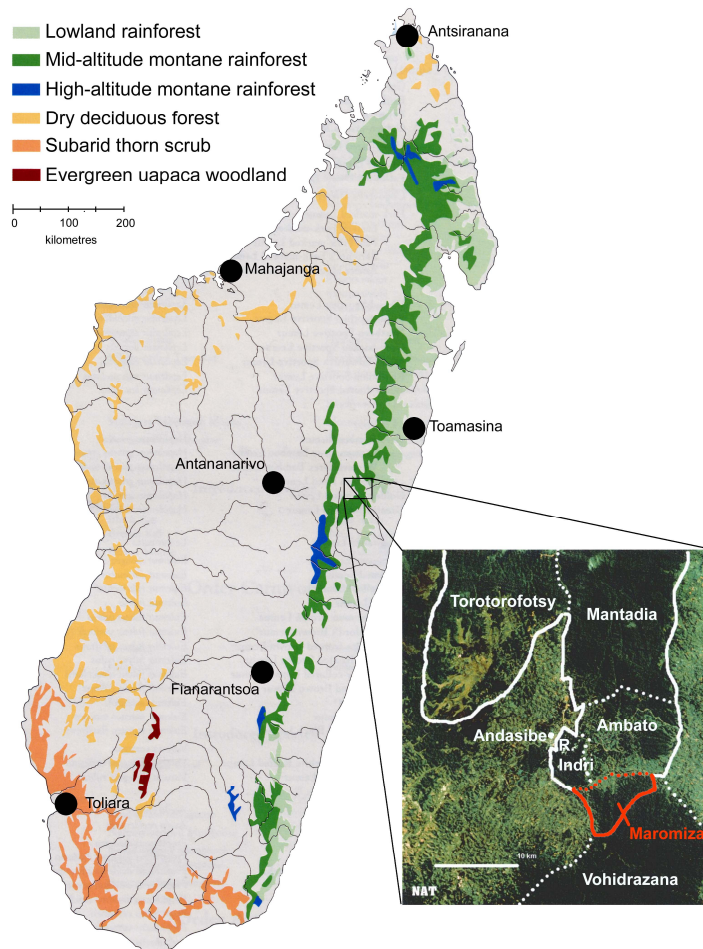


Fig. 1: The study site: Satellite image/aerial view of the region around the Maromizaha protected area.

Situated at altitudes between 800 and 1200 m, the primary forest of Maromizaha harbours a unique community of highland and lowland species. During our last survey, 33 mammal species could be detected: eleven lemurs, ten insectivores, three bats and nine rodents (one species was excluded from all investigations, because of the uncertain taxonomic status), see Tab. 1. In the same area 88 bird species (Woog 2006), 60 amphibian and 20 reptilian species (Zimmermann 2001) have been discovered so far. Our main rodent surveys were restricted to primary forest. During initial surveys of adjacent deforested agricultural land and disturbed primary and secondary forest, near burned areas, mainly the introduced feral Black Rat (*Rattus rattus*) was found.

Tab. 1: The inventory of mammal species of the study area Maromizaha (after Marquart 2004 and Marquart & Harisoa 2006)

ORDER	species	e= endemic Red List categories & criteria: EN: Endangered, LC = Least Concern, NT = Near Threatened, VU = Vulnerable (IUCN 2007 and 2008);	C = capture O = observation
RODENTIA			
9 species	<i>Nesomys rufus</i>	e, LC	C, O
	<i>Eliurus tanala</i>	e, LC	C, O
	<i>Eliurus tanala</i> spp.	e, not investigated	C
	<i>Eliurus minor</i>	e, LC	C
	<i>Eliurus webbi</i>	e, NT	C
	<i>Eliurus grandidieri</i>	e, LC	C
	<i>Gymnuromys roberti</i>	e, VU	C
	<i>Brachytarsomys albicauda</i>	e, LC	C
	<i>Rattus rattus</i>		C
INSECTIVORA			
10 species	<i>Microgale longicaudata</i>	e, EN	C
	<i>Microgale talazaci</i>	E	C
	<i>Microgale taiva</i>	e, first capture for study site	C
	<i>Microgale cowani</i>	E	C
	<i>Microgale thomasi</i>	E	C
	<i>Microgale parvula</i>	E	C
	<i>Oryzorictes hova</i>	e, EN	C
	<i>Hemicentetes semispinosus</i>	E	C
	<i>Sertifer setosus</i>	E	C
	<i>Tenrek ecaudatus</i>	E	C
LEMURIFORMES			
11 species	<i>Microcebus lehilahytsara</i>	e, EN	O, C
	<i>Allocebus trichotis</i>	e, EN, first capture for study site	O, C
	<i>Cheirogaleus major</i>	e, EN	O, C
	<i>Lepilemur microdon</i>	e, EN	O
	<i>Hapalemur griseus</i>	e, EN	O
	<i>Eulemur rubiventer</i>	e, EN	O
	<i>Eulemur fulvus</i>	e, EN	O
	<i>Varecia variegata</i>	e, EN	O
	<i>Avahi laniger</i>	e, EN	O
	<i>Propithecus diadema</i>	e, EN	O
	<i>Indri indri</i>	e, EN	O
CHIROPTERA			
3 species	<i>Rousettus madagascarie.</i>	e, EN	O
	<i>Mormopterus jungularis</i>	e, EN	O, C
	<i>Eptesicus matroka</i>		O, C
Total : 33			

1.2.2 Climate of the study area

Madagascar's climate is tropical, with the exception of the southern tip. A wide range of microclimates can be found and can be explained by the complex topography of the island and its geographical situation. The centre of the island is formed by a high plateau that runs from the north to the south. It rises from the east coast from a narrow costal plain up to 1500 m in elevation. This high mountain range divides the island into two major floral zones, a dry western and a humid eastern region. The western region is dominated by dry deciduous forests; the southern region is much more arid. The eastern region of Andasibe, with the rainforest of Maromizaha, is a tropical evergreen rainforest region, influenced by mountain ridges and dominated by high rainfall. Between December and April, cyclones are frequent. Average temperatures are strongly affected by elevation and precipitation. We documented the average precipitation and temperature at 985 m a.s.l. (main camp side) during the studies between Sep.-Feb. (see Fig. 2).

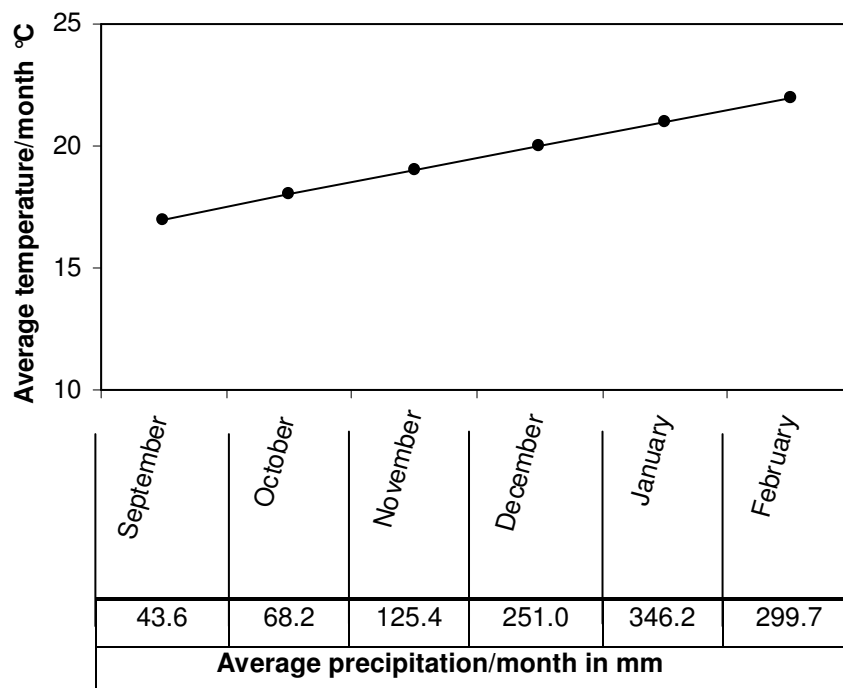


Fig. 2: Average temperature and precipitation at main camp side in Maromizaha, at 985 m a.s.l. between Sep.-Feb. 2005 and 2006 collected: Michael R. Manesimana.

The highest average rainfall (346-299 mm per month) was recorded in the warmest average period in Jan. and Feb. The lowest rainfall was recorded in the colder period in Sep. and Oct. The relative humidity in Maromizaha is correlated to rainy periods and can approach saturation at night between 80-90 % humidity when it rains.

Thesis outline / aim of study

This present doctoral thesis is divided into two different parts:

In the **first part of the study**, the different microhabitat preferences of each of the nesomyine rodents within the study area were examined, including a characterisation of the different forest types. The aim was to analyse the ecology and niche occupation of seven endemic species.

(1.) In this context my first hypothesis was that the different species occur in various microhabitats within the rainforest area of Maromizaha.

(2.) Secondly, these microhabitats are characterized by different vegetation structures, vegetation density, cover and different canopy openness.

In the **second part of the study**, the morphological adaptations and the characterisation of the morphology of the Chiridia (the hand and foot-prints) among these seven species of Nesomyinae were examined. In this context, I assumed the following hypotheses:

(1.) Sympatric species are characterised by specific adaptations to different living conditions and a special way of life.

(2.) Each organism is adapted to its environment.

(3.) All of the examined seven species show morphological differences in their chiridian structure and size.

The thesis is divided in 4 chapters: **Chapter 1** focuses on general information, the biological background and the general methods, **chapter 2** contains the first part of the study and **chapter 3** contains the second part of the study. In the final **chapter 4** the most important results of this thesis are summarized and discussed together. Moreover, as this conclusion, this chapter outlines potential prospects for a better conservation management of the endemic rodents from East Madagascar.

2. Chapter - First part of the study (Ecology)

Forest type characterisation and microhabitat preferences of endemic rodents (Nesomyinae) in the rainforest of Maromizaha, Eastern Madagascar

Abstract

The goal of this comparative study was to investigate the ecology and niche occupation of the endemic rodent species of eastern Madagascar. These rodents form their own subfamily Nesomyinae and are restricted to the threatened evergreen and humid forests. Over four years, we carried out surveys for small mammals in a rainforest area called “Maromizaha”, near Andasibe, east of Antananarivo. Using live traps (Sherman), in total seven endemic rodents were trapped: six endemic rodent species were recorded for different microhabitats (*Eliurus grandidieri*, *E. minor*, *E. tanala*, *E. webbi*, *Gymnuromys roberti*, *Brachytarsomys albicauda*), only one endemic species, *Nesomys rufus* occurred throughout the whole study area. For the first time, species composition in relation to the various microhabitats within the forest of Maromizaha was studied. Ecological data and information on habitat structures along 1 km trails were collected. The specialised rodents were found in different ecological niches: in trees, lianas, underneath wood and thick roots, in dead wood or rotten logs and on the ground. Some were found close to small rivers, some in humid valleys, whereas others seemed to prefer the higher mountain slopes or misty ridges, rich in moss and lichen, up to 1200 m. Microhabitat analyses were conducted and trails where a species was significantly more abundant were compared with those where it was rare. The presence of an endemic rodent species was strongly connected with forest type, forest structure and vegetation density. In contrast, the deforested and cleared areas were species-poor.

Keywords: rodents, Nesomyinae: *Brachytarsomys*, *Eliurus*, *Gymnuromys*, *Nesomys*, eastern rainforest, ecology, habitat structures, vegetation density, deforestation.

2.1. Introduction

Madagascar is one of the most species-rich islands on earth and the home of many endemic taxa. As a "mega diversity area" it has been placed in the highest conservation category by the IUCN. Deforestation started with the colonisation by humans about 2000 years ago. Since then, more than 90 % of all primary forests have already disappeared. The remaining forests are becoming more and more fragmented. The establishment and management of national parks and other protected areas is an important part of conservation efforts, but the fragile corridors between already protected sites play a very special role in the network of the remaining primary rainforests. The investigation, assessment and monitoring of populations is very important for effective protection plans in such areas. It seems that some small mammals use cultivated plants and introduced plantation trees as an additional food source (Marquart 2001). But their long-term behavioural responses to reforestation with endemic and non-endemic plants remain unknown.

2.1.1 *Nesomyinae* - the endemic rodents of the eastern region

Little is known about the taxonomy and ecology of the rodent subfamily Nesomyinae - the Malagasy Rats - endemic to Madagascar. It is still contended whether they belong to a monophyletic group. Recent phylogenetic studies (Jansa et al. 1999) are contradictory to the theory of monophyletic colonisation from Africa. Instead, they point at a paraphyletic colonisation from Africa and Asia and a subsequent adaptive radiation resulting in, up to now, nine genera and 27 species (Garbutt 1999, Carleton & Goodman 2007): Muroidea - Nesomyidae - Nesomyinae: *Monticolomys* (1 species), *Hypogeomys* (1), *Nesomys* (3), *Macrotarsomys* (3), *Voalavo* (2), *Brachytarsomys* (2), *Eliurus* (12), *Brachyuromys* (2), *Gymnuromys* (1).

The most species-rich genus is that of the tuft-tailed rats (*Eliurus*), characterised by a densely haired tail ending in a conspicuous terminal tuft or pencil. During the last 16 years, four new species of *Eliurus* were recognised: *E. grandidieri* (Carleton & Goodman 1998), *E. antsingy* (Carleton & Goodman 2001), *E. danieli* (Carleton & Goodman 2007) and *E. carletoni* (Goodman et al. 2009). The greatest species diversity of this genus occurs within the humid evergreen forests in the east (eight of the twelve species); one *Eliurus* species is confined to the dry deciduous forest and scrub vegetation in the west and south (*E. myoxinus*), one occurs in dry

deciduous lowland forest associated with limestone karst formations in northern and western Madagascar (*E. antsingy*, Carleton & Goodman 2001), one *Eliurus* species was described from the Parc Nationale de Isalo, in south-central Madagascar (*E. danieli*, Carleton & Goodman 2007) and the most recently described form which is closely related to *E. antsingy* was described from the extreme north of the island, the Ankarana region (*E. carletoni*, Goodman et al. 2009). So far, with the increasing number of species and newly recognised species-associations (five larger groups are now identified by Carleton & Goodman 2007), almost nothing is known about their life history, ecology and habitat preferences.

In this study, capture and recapture investigations and vegetation analyses for habitat use yielded very interesting results. The goal of this research was to map the distribution of rodent species in a protected area and to examine habitat preferences. This included a comparison with one area cleared for agriculture. One of the main questions was: how do the species differ in microhabitat preference and niche occupation?

2.2. Material and methods

2.2.1 Study site

The rainforest of Maromizaha is a 1600 hectare area in the humid east of Madagascar, near Andasibe, 150 km east of Antananarivo. This area is an important link between the last remaining rainforests and connects the strongly degraded forest of Ambato in the north with the primary forest of Vohidrazana in the south, the latter being disturbed only to a minor extent because of a “fady”.

The biodiversity in the region of Andasibe is very rich as at an altitude between 800-1200 m species typical for higher elevations mix with those found at lower elevations. But these unique habitats are already heavily fragmented and those that remain are further threatened by illegal logging and deforestation for agriculture. The forest of Maromizaha was put under protection in 2001 and deforestation was stopped. At the edges of the forest, however, trees are still exploited for charcoal production and construction. The forest of Maromizaha is a primary forest, with characteristic dragon trees along valleys and montane vegetation on dryer slopes. The study area harbours a unique community of animals, 11 lemur species, 10 insectivores, 3 bats (Marquart 2004, Marquart & Harisoa 2006, Woog et al. 2006), 88 bird species (Woog 2006), 60 amphibian and 20 reptilian species (Zimmermann 2001) have been discovered so far. We carried out annual surveys for four years (in 2003, 2004, 2005 and 2006) and each time spent an investigation period of two months between Sep.-Feb. During this study period the average monthly precipitation (main camp site at 985 m a.s.l.) was for Sep. 45 mm / Oct. 63 mm / Nov. 118 mm / Dec. 251 mm / Jan. 343 mm / Feb. 297 mm; the wettest time was in January and February. The average coldest time was in Sep. / Oct. (16 °C / 18 °C); the average warmest time was in Jan. / Feb. (21 °C / 22 °C). The average temperature for Nov. / Dec. was 19 °C / 20 °C (T°min: 16 °C / T°max 27 °C).

2.2.2 Description of trap-lines

The rodent communities were surveyed along an elevational gradient of five different trails (see Fig. 3). The trap-lines covered representative vegetation formations at different altitudes. The rodents were caught in 50 baited live traps (Sherman, 23.5 cm x 8 cm x 9 cm). These were set up in the late afternoon, baited with pieces of banana and checked for animals between five and six o'clock the next morning. In each year, we trapped animals during three nights per trail (in total 600 traps were installed per trail over the study time of four years, for all trails together 3000 traps). The traps were positioned on three different levels: 1. on the ground or on wood lying on the ground up to 40 cm (under roots, wood, vegetation); 2. on vegetation from 1.30 m up to 1.70 m (we called this level “breast height till head”), on small branches, bushes and in thickets; 3. on vegetation from 2.60 m up to 3 m in height, on lianas, big tree branches and vegetation, if existent. To position the traps on level 3, trees were climbed with a top rope and climbing harness. The top rope was installed with an arrow around a big branch up in the treetop. Along 1-2 km transects the positions of the 50 traps (in a 20 m spacing), were marked with plastic ribbons on each of five different trails (Trails: TI, TII, TIII, TIV, and TV; see Fig. 3 and Tab. 2).

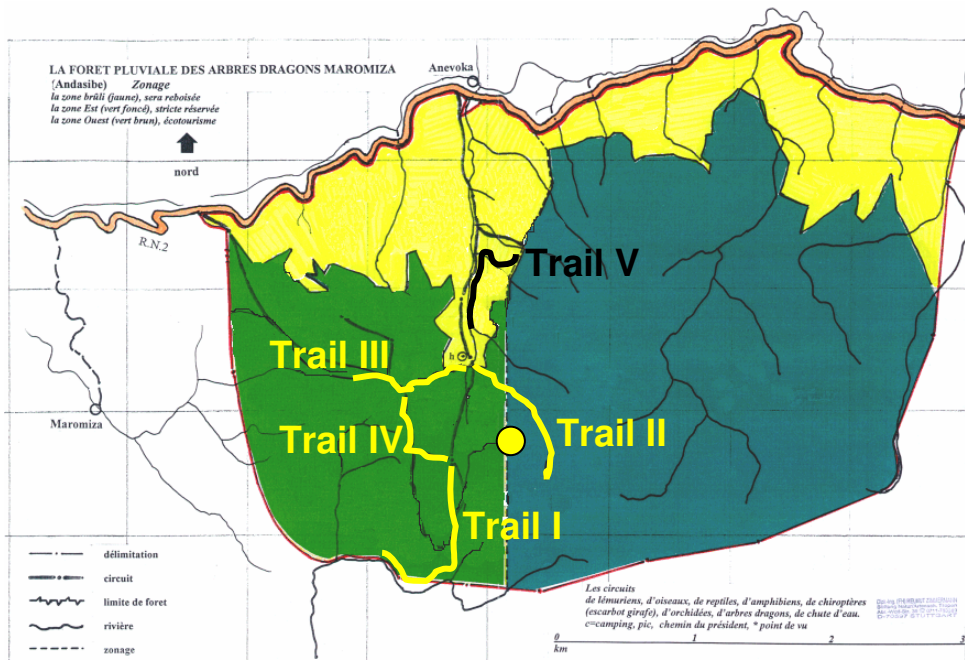


Fig. 3: The study site Maromizaha with five different trails along an elevational gradient. (O: camp site, yellow: cultivated areas, green: primary rainforest area at middle altitude, blue: primary forest passing into high-altitude misty montane forest).

Tab. 2: Transects trails at Maromizaha

Trail/Place	ASL	Habitat
Trail I	800-1000	primary forest, low elevation, humid area along watercourses with tree ferns, lianas and dragon trees
Trail II	1200	primary forest, highest region, very humid, misty mountain region with low bushes, mosses, lichens and epiphytes
Trail III	1100	primary forest, often bamboo thickets, little understory, high canopy, on mountain ridge, some open spaces in canopy vegetation
Trail IV	1100	primary forest, often bamboo thickets, on mountain ridges, lianas, closed understory and little fern
Trail V	800	disturbed primary/secondary forest, near strongly degraded areas with agriculture, burned areas, exploitation, human presence and habitations

ASL: metres above sea level

Directly after capture, the following data were recorded for each individual: date and time, trap-line, trap-point, trap-level, species, sexual condition (as size of testes, lactation or pregnancy), body weight to the nearest gram (using a spring balance: Pesola, measuring range 0-300 g), tail, body, head, ear and hind-foot length to the nearest mm were measured for taxonomy (using callipers: Sylvac, measuring range 0-10 cm) (Wilson et al. 1996). Special attention was given to tail morphology, which differs between the species. Some individuals were photographed. Ectoparasites, little pieces of ear tissue and two samples of hairs were collected of each species, which were then conserved in 70 % pure alcohol for further studies e.g. genetics. All animals were released directly at their place of capture.

2.2.3 Habitat and vegetation analyses

Habitat preferences were inferred from the respective trapping localities. For each of the five 1 km trails, 11 points (in 100 m spacing) were selected for analysis.

Points have to be understood as well as “used” trap positions. For classification, the PCQ method (**P**oint-**C**entered-**Q**uarter-method) of Mueller-Dombois & Ellenberg (1974), cf. Mühlenberg (1989) was used. For this, plots of radius 10 m were divided into quarters around each point. Then the presence and quantity of different vegetation (such as trees with lianas or large trees) were noted. Afterwards the densities of certain tree categories were calculated for each Trail over all of the 11 measured plots, using the PCQ formula (Mühlenberg, 1989):

$$\check{D} \text{ (abs. density)} = \text{plot area} / \text{mean distance of selected category squared}$$

For this, trees were classified according to their diameter at breast height (DBH) and presence or absence of lianas. Trees were divided into six categories: 1. trees with many (more than two) lianas; 2. trees without lianas; 3. trees with Ø 2-4.9 cm; 4. trees with Ø 5-10 cm; 5. trees with Ø > 10 cm, 6. shrubs with Ø > 100 cm). From the central point of each plot, we then measured the distance to the nearest tree of every category for every quarter of that plot (see Fig. 4).

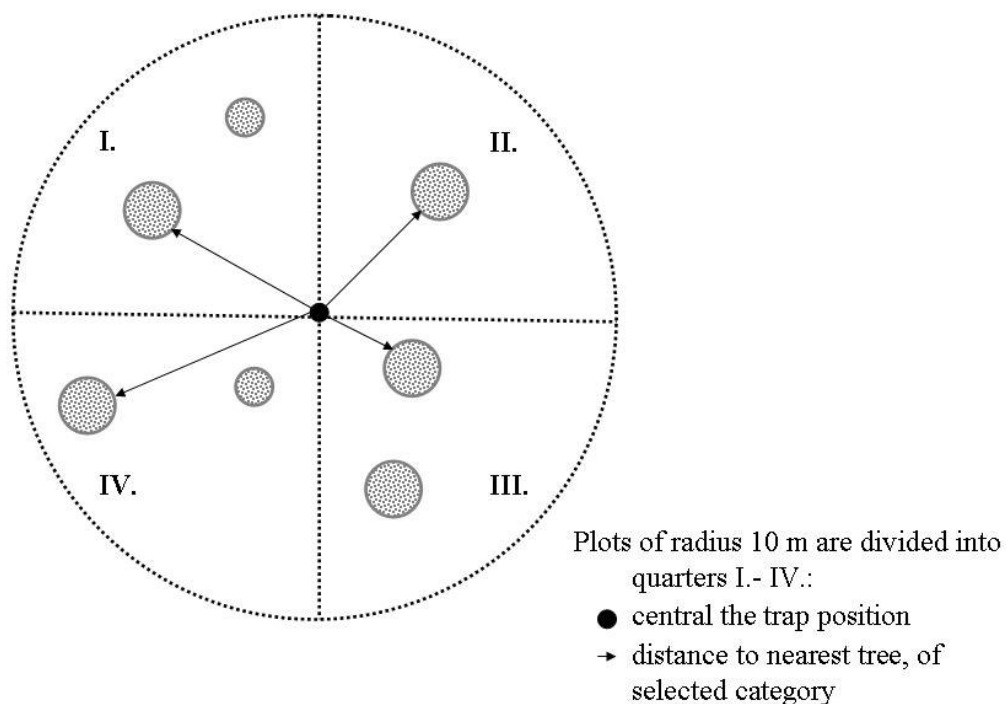


Fig. 4: Habitat parameters according to the PCQ-method.

Furthermore, we estimated for each plot the upper canopy height and the percentage of the vegetation cover (estimated in 5 % intervals). For the vegetation cover, five different strata were selected: 1. ground cover: classified as 0-0.5 m above ground, this grouped Bamboo- grass, ferns, moos and other soil cover plants; 2. shrub cover: classified as 0.5-1.50 m above ground, this grouped shrubs and tree ferns; 3. lower canopy cover: classified as 1.50-5 m in height; 4. middle canopy cover: classified as 5-10 m in height and 5. upper canopy cover: classified as > 10 m in height (Kramer 1987, Krebs 1989). Vegetation cover was assessed for each of the eleven selected plots. Assuming a total vegetation of 100 % the relative percentage of cover was determined for each of the five strata.

2.2.4 Hemispherical photography

For analysing the openness of canopy structure in primary forest and the logging effects in one area adjacent to the side, hemispherical photography was used. Hemispherical canopy photography is a technique that is typically applied to characterise plant canopies using an extreme wide-angle lens (fish-eye), which has a 180° view producing a circular projection of the sky's hemisphere (Anderson 1964, Rich 1990, Steege 1997). Hemiphots were taken with a Nikon Coolpix 990 digital card camera and a Sigma 8 mm, f/4.0 D hemispherical lens. The photos were taken looking up to the canopy from each survey-point (Whitmore 1998, Whitmore et al. 1993). For all records on the trails, the camera was mounted horizontally on a tripod, fixed at 1.5 m above ground and orientated with always the same side facing the true north. To take the photos, the examiner always lay down on the ground to stay below the visual field of the lens. Hemiphots were taken during periods without rain but with cloud cover when the sun was low. Care was taken to avoid sky illumination and reflections from shiny wet leaves. Hemispherical photography was used to assess the canopy openness by analysing the gap size for the eleven chosen plots. At total all 55 Hemiphots were taken on the same way, exactly noted the trap-line and trap-point number (see Fig. 5).

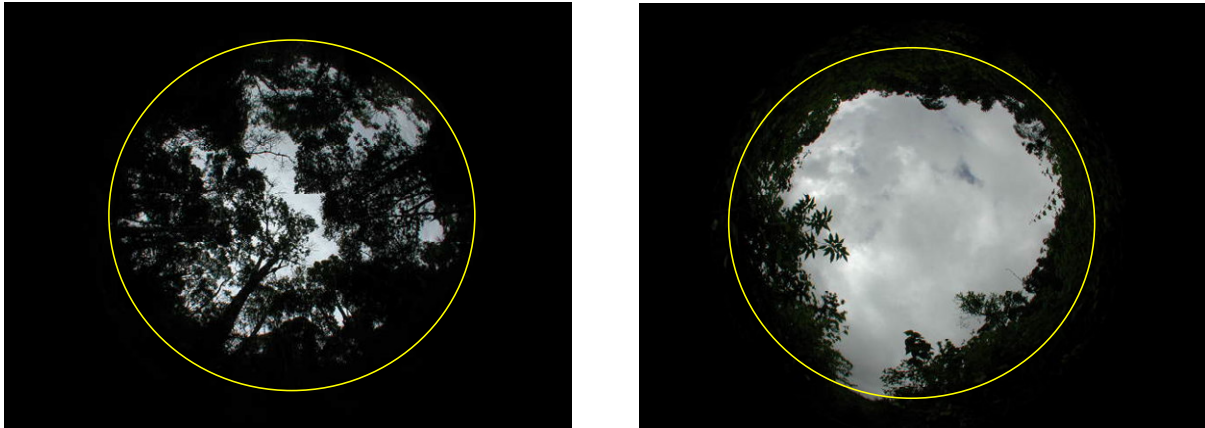


Fig. 5: Hemiphotos: producing a circular projection of the sky's hemisphere.

2.2.5 Data analysis

Statistical evaluation of the ecological data was carried out using Statistica 5.0 (Weiß 2007). To compare the different trails and the vegetation data (densities of all six categories of trees) a Mann-Whitney-U-test (MWU-test) for independent samples was used (Siegel 1997). For all statistics we chose a maximum likelihood ratio of $p = 0.05$ as level of significance. Hemiphotos were downloaded onto the computer, digitised and canopy openness was then calculated using Winphot 5.0 (Steege 1997), to analyse vegetation indices, light and light quality as well as the density value (openness) of the vegetation in relation to the amount of sky visible.

2.3. Results

2.3.1 Species assemblages

Seven endemic rodent species from four genera and one non-endemic species were trapped over the four years of sampling (2003-2006), in total $n = 336$. Over all trap-lines a total of 3000 traps were installed, resulting in a capture rate of 11.2 %. In detail we caught in the year 2003: 71; in 2004: 82; in 2005: 90; and in 2006: 93 individuals. Animals caught and trapping success varied between the different years and trapping sites.

Four species of tuft-tailed rat: Grandidier's Tuft-tailed Rat (*Eliurus grandidieri* Carleton & Goodman 1998), Lesser Tuft-tailed Rat (*Eliurus minor* Major 1896), Tanala Tuft-tailed Rat (*Eliurus tanala* Major 1896) and Webb's Tuft-tailed Rat (*Eliurus webbi* Ellerman 1949) as well as the Eastern Red Forest Rat (*Nesomys rufus* Peters 1870), the rare Voalavoanala (*Gymnuromys roberti* Major 1896) and the White-tailed Tree Rat (*Brachytarsomys albicauda* Günther 1875) were recorded at the study site. These species are strongly adapted to primary forest. Morphological differences such as body weight, tail and foot length clearly separate the species. There were no significant differences in body mass and size between males and females within the same species. In some species, however, males seem to be bigger than females (*N. rufus*) compared to other species, where females seem to be bigger than males (*E. tanala*). Furthermore, only one introduced and non-endemic species was recorded at the study site, the Black Rat (*Rattus rattus* Fischer 1803).

E. grandidieri is very similar to *E. minor* regarding body weight and size, but there are significant differences in tail colour and tail length. Typical for this species is a less developed tuft with short white hairs. The tail is two-coloured, dark above and whitish below. Furthermore, the proximal end of the tail is spotted dark ventrally over 1-2 cm. Body coloration is more greyish than brownish, ventrally dark and dorsally white with grey underwool. *E. minor* is one of the smallest species in this genus with a well developed dense and uni-coloured brown tail tuft. In contrast, the much larger *E. tanala* is a species with very conspicuous bright white hairs at the end of the tail. The hairs of the tuft are very long. The body colour is grey dorsally and more whitish ventrally. *E. webbi* is more brownish with white underparts; the tail is uni-coloured brown, also with a well developed tail tuft. The tuft hairs which cover the distal 2/5

end of the tail are also entirely dark. *N. rufus* can be clearly distinguished from all others by its reddish colour and shorter, untufted tail. The tail is covered with short hairs and occasionally ends in a white tip. *G. roberti* shares similarities with the introduced Black Rat. Typical for this species is the silver grey shiny pelage, dark above and white below. Its eyes are small and the tail seems naked, exhibiting only some short, hardly visible fluff. The tail is bicoloured, dark grey above and pale below. The terminal part of the tail is often speckled white; the tip is frequently completely white. *B. albicauda* can also be clearly separated from all others by its large size (weight up to 250 g), its dense and quite woolly fur, the greyish brown upperparts and the off-white underparts. The tail is dark towards its base but white over most of its length and is sparsely haired. The introduced Black Rat (*R. rattus*) is widely distributed throughout Madagascar. The feral form of *R. rattus* (as *R. rattus* var. *frugivorus* named by some authors) is generally associated with rural villages, degraded areas and secondary forests but also has penetrated deep into many pristine native forest areas. *R. rattus* can also be clearly separated from the endemic rodents by its longer tail, more conspicuous hairless ears and the shaggy pelage due to the long dark guard hairs and the short grey undercoat. The upperparts vary from dark grey, brown to black while the underparts and throat are for the feral form in most cases pale white with a dusty yellow appearance. The tail is quite long (up to 115 % of head/body length), thin and without any hairs (see Tab. 3).

Tab. 3: Morphological differences of the Nesomyinae from Maromizaha

Species	HBL (mm)	TL (mm)	LHF (mm)	EL (mm)	Weight (g)	Tuft L (mm)	Tail Morphology
<i>Eliurus grandidieri</i> (n=19)	105 95-120	147.5 140- 160	28 26.5- 28.3	17 14.4- 19.2	49 27-78	16 1.9-40	tail: dark above, white below. tuft: white tuft hairs: less developed, short
<i>Eliurus minor</i> (n=69)	96 74.3- 193.2	121 110- 140	21 18.8-23	14 10.3- 18.5	38 21.5-80	13.5 11.2- 15.2	tail and tuft: brown tuft hairs: long, very dense
<i>Eliurus tanala</i> (n=74)	135 107- 158	181 122- 210	33 30.7- 37.3	18 14.7- 24.5	109 60-168	42 10-89	tail: brown tuft: bright white tuft hairs: long, dense
<i>Eliurus webbi</i> (n=5)	99 98.6- 98.7	162.5 160- 165	25 24.5- 24.9	-	45 40-50	57 48.2- 67.0	tail and tuft: dark brown tuft hairs: long, very dense
<i>Nesomys rufus</i> (n=116)	153 125.8- 188.9	149 110- 170	44 42.3- 47.4	20 14.8- 25.3	151 34-230	no tuft	tail: brown, completely covered with hairs, some ending in a white tip
<i>Gymnuromys roberti</i> (n=10)	143 113.4- 160	163 150- 170	36 35.3- 36.5	18 14.2- 20	104 90-138	no tuft	tail: dark grey above and pale below, the tip is often completely white
<i>Brachytarsomys albicauda</i> (n=1)*	250	255	40	16	209	no tuft	tail: white over most of its length, dark towards its base, sparsely haired
<i>Rattus rattus</i> (n=42)	138 124.9- 165	187 145- 210	33 29.6- 34.9	21 16.8- 25	121 90-174	no tuft	tail: grey to black, thin without any hairs

Only adult specimens were measured. Mean and min.-max. values are given. HBL: Head-body-length, TL: Tail-length, LHF: Length of hind-foot with claw, EL: Ear-length, Tuft L: Length of tail tuft, * For *B. albicauda* no statistic data are available; only one single specimen could be captured in a tree hole in December 2005.

2.3.2 Species distribution and habitat preference

The number of captured individuals varied widely between the species and trails. For each trail a characteristic species community could be detected (see Fig. 6). Some species were trapped only on the ground, others exclusively on vegetation. Each trail or trail section represented different vegetation characteristics thus allowing the determination of habitat preferences of the nesomyines.

For *B. albicauda*, we only captured one single specimen in December 2005 on trail IV, 1100 m a.s.l. on a mountain ridge. There is no more information about the distribution of this species at the study site. The specimen was captured near a hole in a large tree which was 15 m in height and 42 cm in diameter. The nesting hole was more than 8 m above ground and the hole-entrance measured 4.5 cm in diameter and 25 cm in depth.

E. webbi was trapped (five individuals) only on trail I, at low elevations between 800-1000 m a.s.l., mostly in the vicinity of water courses and large trees. This species was trapped exclusively on tall trees with a large trunk diameter. It could never be observed or caught on the ground or on lower bushes and lianas.

G. roberti was trapped (10 individuals) on all four different trails I-IV in the primary forest. The species occurred predominantly on different mountain ridges where the ground cover of vegetation and the understory was dry and dense but was also found on trail I (5 % of total captures), nearby the riverside in an area with dry bamboo grass. *G. roberti* was caught at ground level as well as on lower vegetation (within the ground level).

E. grandidieri was also trapped (19 individuals) on all four trails I-IV in the primary forest, but occurred predominantly in the humid misty mountain region of trail IV (14 % of total captures) at 1100-1200 m a.s.l. *E. grandidieri* occupied traps on the ground, on finely ramified vegetation as well as on large tree trunks.

E. minor was trapped (69 individuals) on all four trails I-IV in the primary forest, even along watercourses, in swamps or on slopes up to 1100 m a.s.l. Most of the individuals of this species were trapped on trail II (31 % of total captures). This species was mostly caught in traps on finely branching vegetation.

E. tanala was also trapped (74 individuals) on all four trails within the primary forest, but this species showed a significant preference for areas along watercourses, where ground and vegetation were more humid. *E. tanala* was therefore predominantly trapped on trail I (54 % of total captures). *E. tanala* was the only

endemic species which was trapped three times on trail V in secondary vegetation. *E. tanala* predominantly occupied traps on large vegetation with a wide trunk diameter.

N. rufus was the most common species and was trapped on all of the four trails in the primary forest (116 individuals). It was most frequently captured on trail II and III (55 % and 52 %, respectively). This species was mostly caught in traps on the ground or, on rare occasions, also on broad, large trunks close to the ground (see Fig. 6: for habitat preferences).

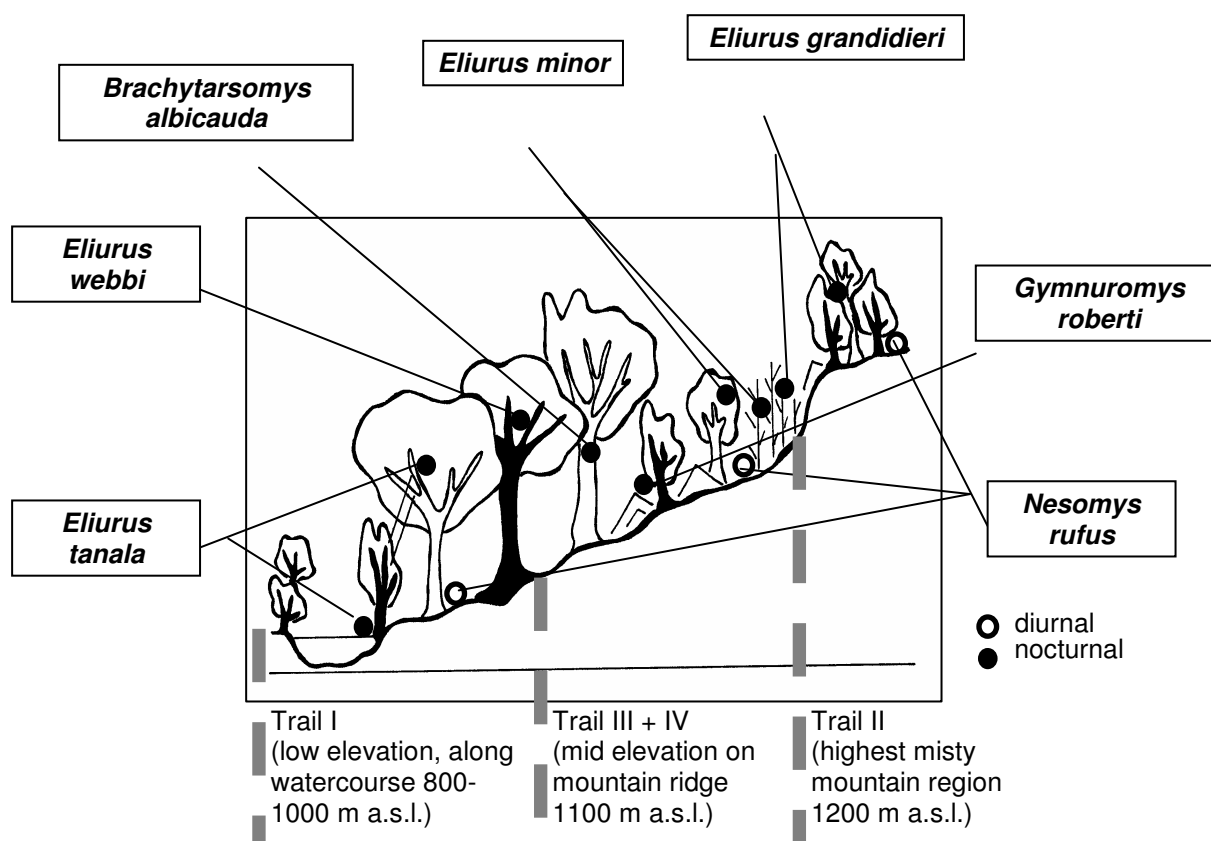


Fig. 6: Habitat preferences of endemic rodent species in the primary forest of Maromizaha.

The introduced *R. rattus* (42 individuals) was sporadically trapped on all trails, but occurred mostly on trail V along strongly degraded secondary vegetation, at altitudes of 800 m a.s.l. (89 % of total captures). *R. rattus* was caught in traps at ground level as well as on vegetation (see Fig. 7: for the number of captured individuals per species).

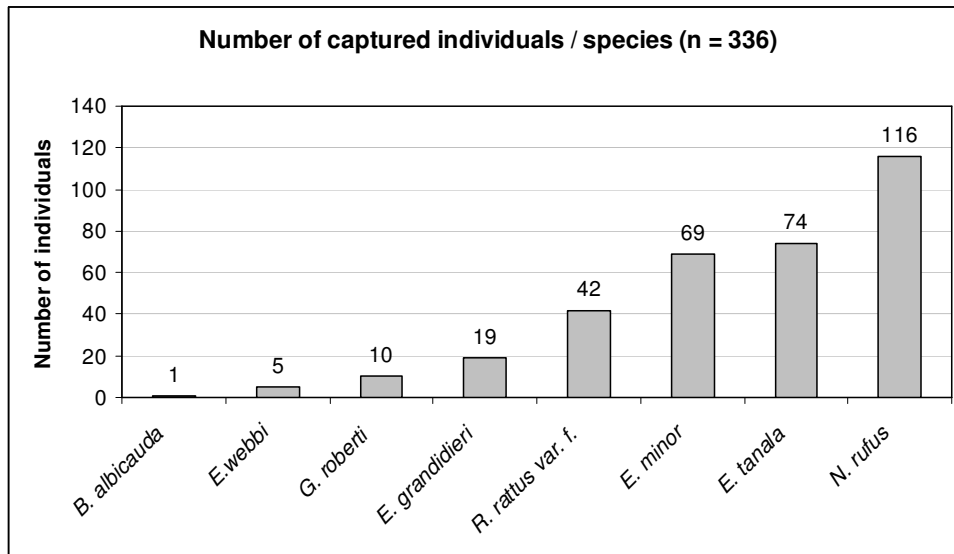


Fig. 7: Number of captured individuals / species, in total 336.

See Tab. 4: for the number of captured individuals per trail and see Fig. 8: species communities per trail in %).

Tab. 4: Number of captured individuals / trail (maximum data *)

	trail I	trail II	trail III	trail IV	trail V
<i>B. albicauda</i>	-	-	-	1*	-
<i>E. webbi</i>	5*	-	-	-	-
<i>G. roberti</i>	4*	3	2	1	-
<i>E. grandidieri</i>	2	3	2	12*	-
<i>R. rattus</i>	6	2	8	2	24*
<i>E. minor</i>	6	31*	11	21	-
<i>E. tanala</i>	40*	6	1	24	3
<i>N. rufus</i>	11	56*	27	22	-

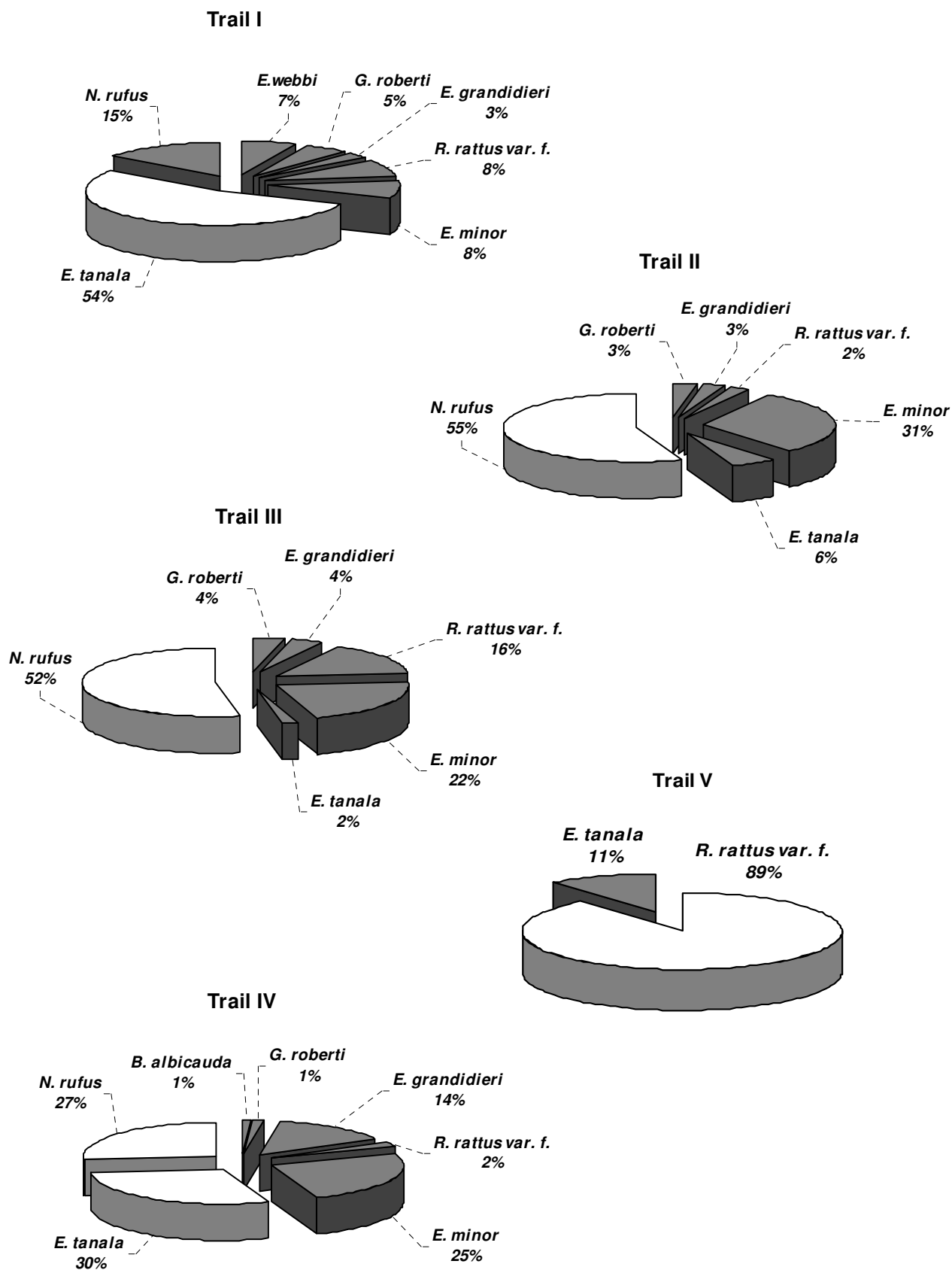


Fig. 8: Rodent species communities per trail in % (Trail I-IV), total number of captured individuals: 336.

2.3.3 Site description – habitat structure along trap-lines

Trail I ran alongside several watercourses, at elevations of 800-1000 m a.s.l. Compared to the vegetation density of the other trails I-IV inside the primary forest trail I was characterised by the second highest density ($\bar{D} = 17.4$) of massive trees with a trunk diameter larger than 10 cm (average per plot). Massive trees stood significantly denser on trail I than trail II (Mann-Whitney U test; $P < 0.05$). In contrast, trees with lianas ($\bar{D} = 31.3$) as well as bushes ($\bar{D} = 115.4$) were scarcest on trail I compared with the other three primary forest trails. The low density of trees with lianas and the low density of bushes was significant in comparison with trail II (Mann-Whitney U test; $P < 0.05$). Some trapping sites along the trail were situated in boggy areas resulting from flooding by the numerous brooks and rivers. The tall massive trees such as the dragon trees (*Dracaena spec.*) characteristic for this forest as well as its situation in a valley made this trail an especially boggy, damp and shady habitat. Bamboo lianas and tree ferns as well as a water growing species of pandanus were quite common there.

Trail II led to the highest, often misty elevation of the study area, at altitudes of up to 1200 m a.s.l. Compared to all other trails, this one showed the highest density of trees with lianas ($\bar{D} = 96.9$). Compared with trails I and IV trees with lianas stood significantly closer here (Mann-Whitney U test; $P < 0.05$). Slender trees with a trunk diameter of 2-4.9 cm ($\bar{D} = 139.5$) also occurred at a high density (significant in comparison with trail III; Mann-Whitney U Test; $P < 0.05$). In comparison, trail II showed a significantly higher density of bushes than all other trails (Mann-Whitney U test; $P < 0.05$). This trail was characterised by especially low and closed vegetation in the peak region. Mist and high amounts of precipitation as well as markedly lower temperatures during the day made this region a wet, cold and extremely windy habitat. Low vegetation, mosses and lichens abounded there.

Trail III ran along a mountain ridge at mid elevations (1100 m a.s.l.). Compared to the other trails in the primary forest the lowest density of trees without lianas ($\bar{D} = 37.3$), the lowest density of slender trees with a trunk diameter of 2-4.9 cm ($\bar{D} = 46.8$) and the lowest density of trees with a trunk diameter of 5-10 cm ($\bar{D} = 34.8$) were found. The low density of slender trees on trail III was significant compared to trail II and trail IV (Mann-Whitney U test; $P < 0.05$). This trail was characterised by its drier slopes. Typical for this habitat was the thick undergrowth

consisting, for instance, of bamboo grass, with exposed roots forming a maze among dead wood, leaf litter and a springy humus layer.

Trail IV also ran along a mountain ridge at mid elevations (1100 m a.s.l.), similar to trail III. Here, however, the highest density of tree without lianas could be recorded ($\check{D} = 139.5$ / significant in comparison with trail I; Mann-Whitney U test; $P < 0.05$), as well as the highest density of slender trees with a trunk diameter of 2-4.9 cm ($\check{D} = 139.5$ / significant in comparison with III; Mann-Whitney U test; $P < 0.05$) and the highest density of trees with a trunk diameter of 5-10 cm ($\check{D} = 86.98$ / significant in comparison with trails I and III; Mann-Whitney U test; $P < 0.05$). Tall, massive trees with a trunk diameter of > 10 cm reached their highest density on trail IV ($\check{D} = 20.76$). This habitat can be described as a particularly tree-rich region; slender, thin saplings as well as massive trunks stand closely together, forming a maze of twigs and roots. Noticeable features of this habitat are the pandanus trees with their broad crowns (different from those standing in water).

Trail V was situated on a degraded agricultural site outside the primary forest, at an altitude of 800 m a.s.l. This habitat was dominated by numerous non-endemic plant species such as *Clidemia hirta* (Melastomataceae), *Solanum mauritianum* (Solanaceae), *Lantana camara* (Verbenaceae) and *Passiflora edulis* (Passifloraceae); furthermore, several non-endemic crops were cultivated there, among these: eucalyptus (for charcoal production), banana and plantain, manioc, sweet potato, corn, beans and taro (*Colocasia esculenta*). The area was cut-and-burned every year (this kind of fire clearance is called "tavy" in Malagasy) to create new open spaces for agriculture. Trail V was located on more or less open agricultural land dotted with bushes and a few trees. A small brook coming from the primary forest ran across the study site to the valley, flanked by grasses and bushes. The vegetation along trail V merged with a thick, almost impenetrable vegetation belt consisting of *Rubus moluccanus*. This introduced species of Rosaceae is a strongly dominant plant which quickly overgrows all other vegetation at heights between 1-1.50 m. Adjacent to these bushy thickets around trail V the vegetation gave way to a more open secondary forest partly consisting of non-endemic eucalyptus and native tree species. This secondary forest was directly connected with the primary forest. Except few tall endemic dragon trees (*Dracaena spec.*) were able to withstand the annual fire, no other endemic plant species could be found on the agricultural land. Because of the scarcity of data only the trees (or non-endemic vegetation of

equivalent height, respectively) without lianas with a trunk diameter of 2-4.9 cm and the density of bushes could be compared statistically with the other trails in the primary forest. All three vegetation categories were present with the significantly lowest density on the agricultural area (Mann-Whitney U test; $P < 0.05$), see Fig 9: for density of vegetation and see Tab. 5: for density of vegetation categories).

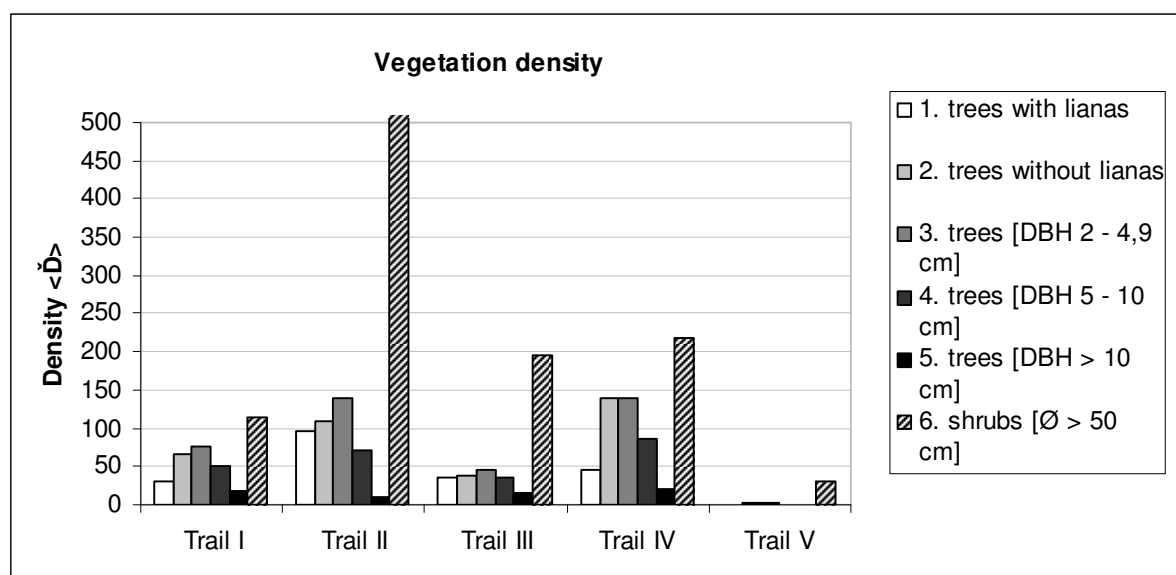


Fig. 9: Density [\check{D}] of vegetation recorded at the sample trails.

Tab. 5: Density of vegetation categories 1-6

Statistics	trail I (n=11) 800-1000 a.s.l.	trail II (n=11) 1200 a.s.l.	trail III (n=11) 1100 a.s.l.	trail IV (n=11) 1100 a.s.l.	trail V (n=11) 800 a.s.l.
1. Density <D> of trees with lianas	31.65	96.9*	34.8	46.44	0
Range trees/plot	1-10	0.5-10	0.5-10	1-10	0
mean	3.15	1.8	3	2.6	0
2. Density <D> of trees without lianas	64.87	108.6	37.3	139.55*	3.8
Range trees/plot	0.2-5	0.5-4	1-10	0.5-3.5	8-10
mean	2.20	1.7	2.9	1.5	9
3. Density <D> of trees DBH 2- 4.9 cm	75.48	139.5*	46.8	139.55*	3.8
Range trees/plot	0.2-7	0.1-3	0.5-10	0.5-4	9
mean	2.04	1.5	3	1.5	9
4. Density <D> of trees DBH 5-10 cm	50.24	71.2	34.8	86.98*	0
Range trees/plot	0.5-6	0.2-10	0.5-10	0.5-4	0
mean	2.50	2.1	3	1.9	0
5. Density <D> of trees DBH > 10 cm	17.44	9	15.5	20.76*	0
Range trees/plot	1-10	0.5-105	0.5-10	1-10	0
mean	4.25	5.9	4.5	3.9	0
6. Density <D> of shrubs Ø > 50 cm	115.44	872.2*	196.2	218	30.7
Range trees/plot	0.5-7	0.5-1	0.3-5	1-2	1-7
mean	1.65	0.61	1.3	1.2	3.2

DBH: diameter at breast height, *: highest density of vegetation in this category

2.3.4 Vegetation cover along trap-lines

In overall comparison of the trails in the primary forest, trail II and trail III show a high similarity regarding vegetation cover. At herbal and shrub layer vegetation cover averaged 20-25 %; for lower, middle and upper canopy similar values could be determined. The upper canopy layer showed a relatively low percentage (10 %) of cover. Regarding cover at herb and shrub layer, trail I and trail IV were very similar (5-10 %); the same held true for the upper canopy, which showed a relatively high percentage of cover amounting to 35-40 %. For trail V on the degraded agricultural site a high percentage of ground vegetation could be determined. There was virtually no middle or upper canopy layer on trail V (see Fig. 10).

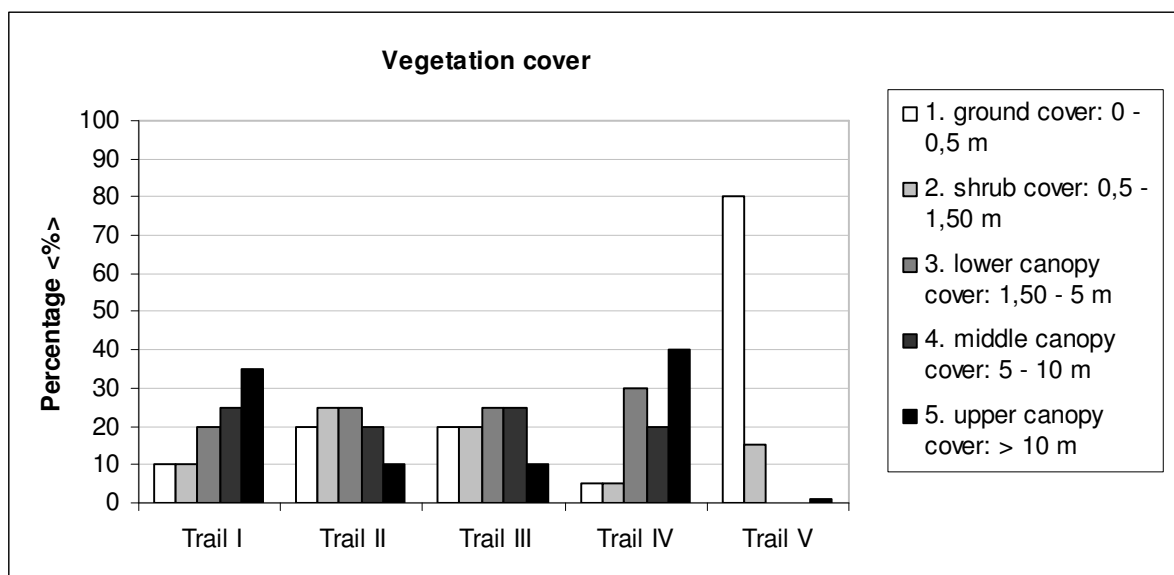


Fig. 10: Vegetation cover on trails I-V.

2.3.5 Canopy openness along trap-lines

A significant difference in canopy openness was only found between trail V, the degraded area, and all other trails in primary forest (Mann-Whitney U test; $P < 0.05$). We discovered a significant difference of 32 % in openness resulting from the impact of logging and bush fires. No significant differences in openness could be detected between the four trails in the primary forest but there were differences in gap size and canopy height between the different trails, so we used these two parameters to estimate the canopy cover and structure characteristics. We found a significant difference of 28 % in gap size between trail I (≈ 79 m) at lower elevation and trail II (≈ 22 m) at the highest elevation (Mann-Whitney U test; $P < 0.05$). A significant difference in gap size was also detected between all other trails in the primary forest and trail V in the degraded area (Mann-Whitney U Test; $P < 0.05$). Also, canopy height differed significantly between trail III along a mountain ridge and all other trails in the primary forest (Mann-Whitney U test; $P < 0.05$); canopy height on trail III was significantly lower. As was to be expected, we also found a significantly lower canopy height for trail V, the degraded area, compared to the trails in primary forest (Mann-Whitney U Test; $P < 0.05$, except trail III). The average canopy height for trail I was 13 m, with a minimum of 10 m and a maximum of 18 m; the average canopy height for trail II was 11 m, with a minimum of 11 m and a maximum of 13 m; the average canopy height

for trail III was 8 m, with a minimum of 6 m and a maximum of 10 m; the average canopy height for trail IV was 11 m, with a minimum of 9 m and a maximum of 16 m; and finally the average height of some single trees on the degraded area of trail V was 6 m, with a minimum of 2 m and a maximum of 10 m. The highest trees therefore were recorded on trail I, in the valley and along the water courses (see Tab. 6).

Tab. 6: Canopy openness, gap size and canopy height of trails I-V

Statistics	trail I (n=11) 800-1000 a.s.l.	trail II (n=11) 1200 a.s.l.	trail III (n=11) 1100 a.s.l.	trail IV (n=11) 1100 a.s.l.	trail V (n=11) 800 a.s.l.
Openness mean <%>	10.9	9.9	10.1	10.6	31.2*
Range	7.7 – 18.7	7.4 – 13.5	7.9 – 12.3	8.1 – 16.4	21.5 – 47.9
Std. dev.	2.90038	1.67571	1.46412	2.41446	9.57801
Gap size mean <m>	79.0	22.1	77.3	27.8	1229.9*
Range	22 – 217	6 – 46	3.6 – 270	6 – 63	408 – 4846
Std. dev.	53.30291	12.30004	80.78823	18.40980	1271.6604
Upper canopy high mean <m>	13.2*	11.5	8.1	11.3	6.6
Range	10 - 18	11 - 13	6 - 10	9 - 16	2 – 10
Std. dev.	2.53341	0.68755	1.64040	1.91168	3.23335

* highest value in this category

2.4. Discussion

2.4.1 Species distribution

By trapping the nesomyines at Maromizaha it could be shown that these endemic rodents form different species assemblages. Some species were very common, for instance *E. minor*, *E. tanala* and *N. rufus*. Other species occurred more rarely, such as *B. albicauda*, *E. webbi*, *G. roberti* and *E. grandidieri*. The presence and abundance of a species in a habitat can be influenced by several factors. The following aspects might provide an explanation: 1.) Similar habitat and food preferences of sympatric species may lead to interspecific competition, influencing in turn the density of the respective taxa. 2.) The species prefer different habitat structures and adapt to their environment. Some species may be more flexible in their habitat requirements and thus may be able to adapt more easily. 3.) It can further be assumed that certain species have to be regarded as generalists, others as specialists, concerning their use of food resources; their frequency therefore depends on the availability of food.

If species co-exist in the same habitat, especially if they belong to the same genus, a divergence as to vital resources is to be expected. To be able to exploit the different resources of a forest in an optimal way and to be protected from predators at the same time morphological adaptation is necessary. The morphological adaptations of hand and feet of the nesomyines were investigated in the second part of this doctoral thesis. Furthermore, factors such as the presence of species-specific roosting sites as well as anthropogenic influences play an important role. It was found for hole-dwelling mouse lemurs (*Microcebus murinus*), for instance, that "their density depended on the availability of suitable tree holes for raising their young" (Radespiel et al. 1998, Rendigs 1999). The supply of large potential nesting trees, however, is frequently shortened by human activities. My study showed that the endemic rodents have only a low tolerance against anthropogenic influences. Only *E. tanala*, a species primarily found along brooks and rivers, could also be detected at the anthropogenically influenced site. Possibly, *E. tanala* can survive in the degraded area only because of the relatively intact riverine habitat. The brook running from the primary forest down to the valley may constitute a special food source for this species. *N. rufus* was the most common species at Maromizaha and also that with the highest density. As a diurnal and special ground-dweller *N. rufus* could be

observed gathering fruits (e.g. of *Olea madagascariensis*, *Ocotea cymosa*) and taking cover in burrows and among roots and dead wood. During the early rainy season (November/December), plenty of fruit can be found on the ground at the study site making it easy for a mobile diurnal species to find food at this time of year which might be a reason for the frequent occurrence of this species at the time of study. This species could not be recorded in the degraded area, possibly due to the lack of endemic food plants.

Furthermore, the trapping frequency of a species can also depend on the trapping technique used: Sherman traps are not equally suitable for all taxa. Observations have shown that the diurnal and terrestrial *N. rufus* exhibited little shyness towards the traps: it was not uncommon that a newly set trap was immediately occupied again by *N. rufus*. Some animals could be seen during daytime foraging on the ground in the immediate vicinity. As *N. rufus* travels long distances the trapping probability for this species is increased. In comparison, all *Eliurus* species were very shy and cryptic. Even during observations in the forest at night, this genus could be observed only very rarely and from a large distance. Other species such as *B. albicauda* were only caught occasionally. The latter species possibly has only a very small home-range and a very high site fidelity which reduces the likelihood of being caught during a sampling period. For this reason, estimates of population densities were not the aim of this study; my results rather serve as a first estimate of species distribution and document the occurrence as well as the ecology of the species.

2.4.2 Site descriptions in relation to vegetation parameters

Habitat selection of the species could best be described by the following parameters: 1.) trunk diameter of trees, 2.) presence of lianas, 3.) presence of bushes, 4.) coverage at the lower herb and shrub layer, and 5.) degree of coverage at the upper canopy level. Furthermore, habitat choice also correlated with the detected light transmission of the canopy as well as with canopy openness (gap size) and height, respectively. In combination with the altitudinal range of the trails from 800-1200 m a.s.l. distinctive microhabitats could be characterised for each species, in particular when vegetation, habitat structure and substrate showed marked individual differences between trapping sites.

Hemispherical photography is an established method for documenting the formation and closure of larger vegetation gaps; in my case, however, it could be not used to assess logging effects in the primary forest, because the gaps in Maromizaha, caused by selective logging are too small for detection with this method. Gap size is influenced by several factors, for example, the composition of tree species, leaf distribution on branches (Küppers 1989), the crown shape (Terborgh 1985) and, consequentially, the transmission of light through the canopy (Küppers 1989). The four trails in the primary forest represented different forest structures which were among other things influenced by gap size. Larger canopy gaps can also be caused by watercourses and streams; accordingly, I detected a higher level of openness along Trail I near the river side than in the dense forest. Selective logging usually causes larger canopy gaps than those detected in the study area. At the study site selective logging is now on a very low level and the last logging inside the protected area occurred more than 15 years ago; time enough for large gaps to have been closed by dense young vegetation - but in some places there is still a lack of large trees. The highest level of openness (significant to primary forest) was found on the degraded area, clearly resulting from the annual bushfires.

2.4.3 Microhabitat preferences and niche occupation of rodents at the study site

B. albicauda was detected in a region with a dense undergrowth of saplings and tree ferns. The large tree with the roosting cavity stood in close proximity of other tall, massive trees. Vegetation analyses showed that *B. albicauda* was trapped in a region at mid-elevations with an especially high density of trees from every category resulting in a comparatively closed upper canopy layer. Herb and shrub layer were only weakly developed. Many massive old trees were present. The first section of the trail on which *B. albicauda* was caught led across a watercourse with particularly conspicuous large dragon trees alongside its banks. In this region the occurrence of these massive trees is always associated with the presence of a watercourse. Following the trail uphill there were also massive trees but of slightly lower height than in the valley. *B. albicauda* is considered an exclusively nocturnal and arboreal species nesting in tree cavities above 2.50 m above ground level and in tree holes close to dense tangles of lianas and vines allowing easy access to the canopy (Carleton & Goodman 2003). My observations showed *B. albicauda* to be rather territorial with a relatively small home range. The species foraged in the canopy for

seeds and fruits. In my study, it preferred a microhabitat with dense vegetation and a close canopy offering better protection from predators. Filigree vegetation structures and thin lianas were not used for locomotion but served as cover instead. The presence of close standing tall, massive trees was more important, perhaps to allowing easy access between massive trees and to the canopy.

E. webbi could also be recorded in a region with very dense vegetation. Similar to the habitat of *B. albicauda* this region was characterised by a high density of trees with a trunk diameter > 10 cm. There were only a few bushes or trees with lianas. The densely clustered massive and very tall trees along the watercourse formed a closed canopy within this microhabitat. On the other hand, herb and shrub layer were only weakly developed. This species was also exclusively caught on massive trees with large trunk diameter. It was never observed or trapped on the ground or on low bushes and lianas. Carleton (2003) characterises *E. webbi* as an exclusively nocturnal and scansorial species, primarily occurring on lianas, lower branches and in ground burrows up to one meter in depth with chambers to store seeds. Goodman (1994) describes the behaviour of *E. webbi* as "probably nests and forages at different levels in the forest, recorded sharing the same burrow system as a nesting bird (Scaly Groundroller (Brachypteraciidae, *Brachypteracias squamiger*))". In the study area at Maromizaha, however, *E. webbi* could not be observed on the ground. Instead, this species occurred in an area with a particularly high density of massive trees. In contrast to *B. albicauda* a mixed mode of locomotion can therefore be assumed for *E. webbi*, this species using broad as well as filigree structures for climbing. If enough massive trees with cavities are available in a microhabitat these are possibly preferred by *E. webbi* during the rainy season.

G. roberti was very common in dry areas with a dense leaf-strewn ground layer. This microhabitat was particularly dominated by dense partly dead bamboo grass, dead wood as well as a loose soil structure of roots and burrows. *G. roberti* was trapped on the ground as well as on low vegetation. This species is considered to be "exclusively terrestrial and nocturnal, and lives in burrows up to one meter deep" (Carleton & Goodman 2003). But *G. roberti* could also be caught on lower vegetation occurring (but within the so called "level I" on the ground or on wood lying on the ground up to 40 cm), however, mostly on broad structures and horizontal dead wood. Observations showed that *G. roberti* took cover not only in cavities under roots but also on vegetation: in one case it was a fallen hollow tree trunk with a nesting

hole at approximately 1.50 m height lined with dry bamboo leaves and containing fresh fleshy and hard shelled fruits (Oleaceae: *Olea madagascariensis*, Lauraceae: *Ocotea cymosa*, Gentianaceae: *Anthocleista amplexicaulis*, (Marquart and Harisoa 2006)). As a good climber and runner *G. roberti* was observed foraging for seeds and fruits not only among leaf litter and bamboo grass but also climbed onto low trunks and rocks, which occurred mostly along the steep slopes. A dense ground vegetation of, for instance, bamboo grass appears to be important for the habitat choice of *G. roberti*, possibly for protection from predators or as nesting materials. Furthermore, this species was exclusively recorded in "dry regions at mid-elevation" in the study area this was mainly the case for steep slopes. In the valley, for example along the river, where *E. webbi* was caught the ground was markedly wetter, marshier and thus not suitable as a microhabitat for *G. roberti*. This species was also recorded at sites within the primary forest characterised by a well developed shrub layer, low trees and a slightly lower degree of coverage at canopy level.

E. grandidieri was most frequently caught in two climatically very similar microhabitats: 1.) in the misty and humid peak region, and 2.) on a rocky slope; at this elevated site the ground fell steeply towards the valley giving rise to ascending clouds and dense fog. These misty and humid habitats were dominated by low shrubs, mosses, lichens as well as numerous epiphytes on the trees. Here, tree height was low, slender trees and bushes were very common and significantly more often overgrown with lianas. *E. grandidieri* occupied traps on the ground as well as on filigree vegetation but also on broad logs. My investigations showed, however, that *E. grandidieri* can be found more often on vegetation than on the ground and I conclude so that this species can be considered as an exceptionally good climber on trees and bushes. Other authors report from the northern regions of Madagascar that *E. grandidieri* climbs only rarely but instead prefers to stay on the forest floor, around tree roots, fallen logs or rocks and was frequently trapped in front of hollows and tunnels suggesting it may occupy burrows (Carlton & Goodman 2000). At the study site Maromizaha the occurrence of *E. grandidieri* correlated with the presence of low vegetation and bushes, a dense ground cover, plenty of lianas and a misty and humid microclimate at exposed sites within the primary forest. The animals could often be clearly observed as they climbed swiftly along lianas and bamboo lianas to hide in the vegetation. *E. grandidieri* could never be observed inhabiting burrows in the ground. Possibly this difference in behaviour may be connected with foraging and

food availability as well as with the wet rainy time of year. I could observe *E. grandidieri* to take many insects as protein-rich food: large beetles, cockroaches, wood lice, larvae and moths were gleaned from the vegetation and then eaten aided by the free front paws. Furthermore, *E. grandidieri* was seen feeding on the sweet sticky fruits of a palm species (Arecaceae) only growing at higher altitudes in the study area. Unlike *G. roberti* this species was never recorded gathering hard shelled seeds and fruits. It can safely be assumed that *E. grandidieri* digs burrows in which to shelter during the colder season as the species could often be observed digging for food: large larvae were dexterously extracted from the loose soil with the front paws. During the study period we noticed nests of *E. grandidieri* woven from the lanceolate leaves of small dragon trees (*Dracaena* spec.) in the undergrowth or in tree crevices and cavities but always 1-2 m above ground. In these nests up to twelve animals could be found. Trapping results (this observation was not part of the Sherman trapping session, the nesting-group was captured with a net and released together) have shown that the groups consisted of 2-3 adult males, 5-6 adult females and 2-3 juveniles. *E. grandidieri* appears to live in social groups, especially during the breeding season. In how far this behaviour continues after the rainy season is currently still unknown.

E. minor was caught on all trails at all sorts of places: on lianas, small trees, in bamboo grass, on tree ferns as well as on dead wood. In contrast to *E. grandidieri* it is not possible to define a preferred microhabitat with certain climatic factors; instead, *E. minor* abounded on filigree structures, trees with a small trunk diameter or lianas on all trails within the primary forest. *E. minor* does not use tree cavities, however, but was observed retiring to rain-sheltered branches in the crowns of pandanus trees where it built nests from the lanceolate leaves e.g. of bamboo grass or dragon trees. This species can be considered as a very good shrub climber. In fact, I observed *E. minor* moving very nimbly along filigree vegetation, lianas and in dense filigree undergrowth. Other authors observed *E. minor* also climbing to heights of several meters (Goodman & Carleton 1996, Carleton & Goodman 1998). My own studies confirm that this species climbs up to the highest tree tops, possibly for foraging.

E. tanala was trapped along watercourses with the significantly highest frequency and also very often on high massive trees with an exceptionally large trunk diameter the characteristic dragon trees. The ground along the watercourse often was very damp and marshy. Tree ferns, broad lianas, dense bamboo lianas as well

as pandanus trees growing in the water abounded there. The presence of the dragon trees along the watercourses can be explained by their water demand - large trees need a lot of water - and the surface water from precipitation often does not suffice for an optimal growth of these giants which accordingly line the river edges at Maromizaha. Possibly, *E. tanala* uses the habitat along the watercourses for foraging and catching micro-organisms from the water or along the banks. Observations of this species in captivity (in a cage installed in the forest, which was one of my previous researcher project with Michael R. Manesimana, University of Antananarivo) have shown that the animals preferably fed on animal proteins such as insects and took less plant material and seeds. *E. tanala* was also observed soaking the hard and dead lanceolate leaves of a smaller dragon tree in water to use them as nesting material. Furthermore, *E. tanala* could be seen actively wading through running water to ford the river. Captures of the same marked individuals on both river banks confirmed this behaviour; if available, large logs were used as bridges across the water. The frequent occurrence of *E. tanala* along rivers has already been reported by other authors who observed that "this species used a variety of microhabitats including grassy glades, herbaceous growth, tangles of vines along watercourses" (Goodman & Carleton 1996, Goodman et al. 1999, Carleton & Goodman 2000). The massive dragon trees provide sufficient protection and roosting opportunities within this microhabitat: *E. tanala* was frequently caught right inside the spacious cavities of these trees. The trunk of a dragon tree occasionally can be completely hollow, thus accommodating several individuals - up to four different animals could be recorded at the same tree. In how far these live together as groups is not known. During the mating season, however, pairs could be observed together in the same hole. The presence of *E. tanala* as the only endemic species at the degraded site might possibly be explained by the brook bordering the agricultural field as a relatively intact habitat. Possibly *E. tanala* also used single dragon trees as a retreat in the otherwise species-poor degraded area.

N. rufus was the most common species throughout the study area and was trapped on all trails and at all elevations. This is confirmed by Goodman & Charleton (1996) who also observed this species over mid and high altitudes in rainforest regions. Yet, even for this diurnal and exclusively ground-dwelling species a preference for habitats characterised by a particularly high density of bushes and a low density of massive trees could be observed in the study area. This species was

also trapped more often on dry slopes with a dense undergrowth of bamboo grass, exposed roots, plenty of dead wood, leaf litter and a spongy humus layer. As far as coverage at different vegetation layers is concerned, the most frequent occurrence of *N. rufus* correlated with a high percentage of coverage at bush, shrub and middle layer and a low percentage of coverage at upper canopy level. *N. rufus* as a typical diurnal ground-dweller seems to prefer a higher degree of coverage at ground level, possibly for easier concealment from predators such as raptors. Observations of Goodman and Charlton (1996) and Ryan et al. (1993) showed that *N. rufus* travelled an average daily distance of 400 m, had home ranges of about 0.5 ha and foraged in dense vegetation, leaf-litter, around dead logs and in ground burrows with several entrances and chambers. According to my capture- recapture results, I also can confirm, that *N. rufus* is a very good long distance runner.

The non-endemic Black Rat was trapped most often near paddy fields, cassava (*Manihot esculenta*) crops and banana plantations. Inside the primary forest this species usually occurred in the vicinity of old or presently used campsites. The species was also frequently found near a man-made footpath running through the entire study area. *R. rattus* was caught in traps on the ground as well as on vegetation and proved to be an extremely good climber even reaching traps on very high vegetation. Although *R. rattus* is very well adapted to forest habitats, this species still appears to favour proximity to human settlements. With increasing density and nativeness of the forest and with growing distance from camp sites or footpaths Black Rats were trapped with significantly lower frequency. I can confirm the report of Goodman et al. (2003), that this species is mostly associated with rural villages, degraded areas and wherever native forest have been replaced by agriculture.

2.4.4 Effects of logging on the distribution of endemic rodents

All rodents endemic to the Maromizaha region are strongly adapted to primary forests where they can find a wide variety of food such as various types of fruit and seeds, leaves, plants and insects as well as large trees and dense vegetation for sleeping sites and cover. In contrast, the degraded forest parts and deforested agricultural areas turned out to be alarmingly species-poor. Close to human habitation and in cultivated areas only the introduced Black Rats were found. One reason for this “species poorness” could be the seasonal bush fires and high

exploitation rates. In the absence of dense vegetation, endemic arboreal species are unable to find suitable retreats. Reproduction in these species is seasonal, thus seasonal fires possibly disturb their offspring. Moreover, endemic rodents frequently depend on particular prey species that may be lacking in cultivated areas.

Previous research has shown that, for example, small mouse lemurs use cultivated plants and introduced plantation trees as additional food sources (Marquart 2001). Ganzhorn (1995) also found in his studies that lemurs occurred on plantations in higher numbers during harvest. For the endemic rodents at Maromizaha, however, such behavioural responses remain yet unknown. Furthermore, competition between endemic and introduced rodents has not yet been thoroughly investigated. The introduced Black Rat is perfectly adapted to human civilisation. The population densities of this species could rise drastically along with the demographic increase of humans resulting in landfills and open canalisation. Black Rats have offspring all year round and in high numbers so any seasonal disturbance will not have much effect on their reproduction rate. In our study, Black Rats occurred together with many different cultivated plants and plantation trees - all of them xenophytes. It is still unclear, however, in which way these rodents use particular plant communities as food resources and how this will have an effect on the seed dispersal of xenophytes in the primary forest.

Logging is not only a severe problem inside the primary forest of Maromizaha; additionally, fires getting out of control can also threaten adjacent forest areas. Cleared areas between separate forests are constantly growing leading to an increase in forest fragmentation and thereby to an isolation of populations. Isolated populations are more susceptible to possible environmental disturbance as a withdrawal to new retreats is no longer possible. Investigations of forest fragments in Amazonian Brazil showed a significant decrease in overall biodiversity in small forest fragments - the smaller the area the fewer species per ha (area effects; Laurance et al. 2001). Morphologically large mammals are more threatened in forest fragments and avoid forest edges. Animals adapted to open forest with a higher percentage of undergrowth increasingly occur at forest edges (edge effects). This disturbs the original biological balance; some species become extinct, others become dominant (Laurance et al. 2001). The study site at Maromizaha is an important link to other rainforest areas in the north and south. In spite of this, selective logging of large trees at the forest edge and sporadically in the forest interior has always been going on in

this primary forest. At present, burned areas are spreading into the forest from the valley. Selective logging of large trees reduces the degree of coverage at the upper canopy level leading to a higher amount of sunlight reaching the lower forest layers, thereby changing the original vegetation. These changes may trigger fluctuations in ambient temperature which may in turn influence the entire species diversity of flora and fauna and the rodents' communities. In how far this also affects the study area Maromizaha is difficult to judge. My studies have shown that rodents exclusively using tree holes could be detected more rarely in the study area. The occurrence of suitable tree cavities is linked with other parameters such as a large trunk diameter, the age of the tree, etc. Such trees are frequently removed by selective logging (Rendigs 1999). Species not strictly dependent on tree cavities were much more common. These results, however, have to be viewed not only in connection with logging but also in relation to other factors such as the availability of food and the ecological needs of each individual species.

3. Chapter - Second part of the study (Morphology)

Morphological adaptations of the chiridia in Malagasy rodents (Muroidea: Nesomyinae)

Abstract

This study, as part of a doctoral thesis, was carried out to illuminate and describe morphological differentiations of the chiridia (the hands and feet) in relation to functional and ecological adaptations. Therefore, seven endemic rodents from Madagascar of the subfamily Nesomyinae were studied. The study site Maromizaha was located close to Andasibe, Perinet, forming a part of the eastern rainforest area of the island. The goal of the study was (1) to inventory the rodent species at the study site, (2) to compare morphological differences of the chiridia between the rodents, and (3) to correlate the differentiations of foot and hand-prints with capture rates in different habitats. For the first time, certain dermal structures of the feet are used to assess ecological niche occupation for Malagasy rodents. For results: the chiridian structures differ clearly between the species. Slender hind feet with small thenar pads are significantly correlated with a ground-living ecology. In contrast, species with an arboreal locomotion evolve large pads, covering most of the chiridian surface area. Large-tree climbers possessing larger pads in relation to foot size can be differentiated from climbers of grass and small branches which possess relatively longer feet with longer toes. Capture rates on different vegetation levels show that rodent species inhabit different forest formations and microhabitat types of the study site. It can be concluded that certain morphological structures of the rodent chiridia give evidence of a specific way of life and that foot pad morphology in particular, mirrors special adaptations to a species' habitat. In this thesis, it could be clearly demonstrated how the combination of morphological characteristics allows inferences about a particular habitat use and locomotion type, and that chiridian morphology makes it possible to separate nesomyine taxa although at the ecological level.

Keywords: Malagasy rodents, Nesomyinae, morphological adaptations, chiridian morphology, palmar and plantar pads, species diversity, ecological niche occupation.

3.1. Introduction

Rodents are the largest order of living mammals worldwide. They have colonised a wide variety of habitats and play an important role in each ecological system (Dieterlen 1969, 1978, 1985, 1986, Kingdon 1974, Delany & Happold 1979, Happold 1987). The endemic rodents of Madagascar belong to their own subfamily - the Nesomyinae (Malagasy rats) - within the superfamily of Muroidea (Wilson & Reeder 2005). The evolution of the recent nesomyines, originated from some Palaeocene common ancestors, resulted in an adaptive radiation of nine genera and 27 species (Ellerman 1949, Petter 1972, Carleton 1994, Carleton & Goodman 1996, 1998, 2007, Carleton & Goodman 2001, Goodman & Benstead 2003, Goodman & Soarimalala 2005, Goodman et al. 2009). The most species-rich genus is that of the tuft-tailed rats (*Eliurus*), which species are very similar in overall appearance and diversity is only manifested in sometimes very small morphological differences (Carleton 1994, Carleton & Goodman 1998, Goodman & Benstead 2003). Within this morphological diversity of Madagascar's native rodents, their monophyletic origin is questioned. Former theories concerned a monophyletic colonisation from Africa, but recent studies point to a paraphyletic colonisation from Asia and Africa (Jansa et al. 1999).

In addition to the uncertainty about the monophyly of the nesomyines, other major gaps still exist in the biological and systematic knowledge. There is still little known about the ecology and niche separation of these specialised rodents. So for this study, the morphological adaptations of seven species of Nesomyinae within four genera from the eastern rainforest area were investigated. Beyond the morphological comparison of the foot and hand-prints, the aim of this study was to discover correlations between these chirodian structures and the occurrence in a certain microhabitat. The number and arrangement of the chirodian pads and their overall appearance were analysed. But the objective was not only to recognise the importance of specific structures, but also to understand the niche occupation of sympatric species. For the first time the "ecomorphology" of the Malagasy rodents - as a comparison of the chirodian structures and the ecology - were investigated.

3.1.1 Morphological differences and adaptive differentiation

Similar studies of the chiridia have been conducted on primates (Cartmill 1974, Niemitz 1990). Illustrations and descriptions of rodent feet in literature are rare (Tullberg 1899, Whipple 1904, Bohmann 1939, Mohr 1954), for the most part consisting of simple outlines. For a long time, rodents were thought to have very homogeneously designed hands and feet. In 2003, dermal structures of the limbs were studied and compared for the first time in African Muroidea. Hand and foot morphology was found to be correlated to the mode of locomotion, posture, feeding habits or grooming behaviour (Ziekur 2004, Ziekur 2006). In continental African muroids, species with predominantly terrestrial locomotion frequently reduce the number of palmar and plantar pads and species with a larger range of activity tend to reduce the lateral toes as well for faster running. Additionally, species with arboreal locomotion conserve the full number of pads and evolve large and prominent pads and longer toes for climbing (Ziekur 2004, Ziekur 2006). There is only little information on chiridia morphology for Malagasy rodents (Carleton 1994, Carleton & Goodman 1998) and so far these data have exclusively been used for the comparison of species but not for niche characterisation.

The ecological niche is defined as the functional position of an organism in its environment, comprising its habitat, its periods of activity there, and the resources it uses. The niche differential is often regarded as the basis for a coexistence of species. Estimates from competition theory and niche concepts lead to the prediction that potential competitors coexisting in a community should exhibit niche differentiation and that this niche differentiation will often be manifest as morphological differentiation. Thus, the external appearance is not the result of a random process but instead the result of an adaptation, clearly documented in "adaptive differentiations".

3.1.2 Morphology and locomotion

The morphology of the limbs is closely correlated to a species' mode of locomotion. The hind limbs are important for forward movement. For fast running and wide leaps long, powerful hind legs are needed. In climbing species the hind legs may also adopt an anchoring function (Cartmill 1974). The front paws of rodents are frequently used for gripping and holding. Digging, scratching and grubbing are more often done

by the front paws than the hind paws, the latter being frequently used to support the body during the motion sequence or for carry the occurring substrate away. Both hands and feet are used for grooming, the hands predominantly for the head and the feet for back, belly and flanks.

A hand with four fingers and a strongly regressed thumb can be postulated as plesiomorphic in rodents. The foot probably had five toes and was of moderate length (Tullberg 1899, Mohr 1954). Climbing rodent species frequently support their grip using fingers and toes by pressing them against each other, thereby obtaining a secure hold. The palmar (hand) and the plantar (foot) surfaces are endowed with pads of varying size that are sometimes strongly pronounced. Most rodents have numerous glands on these pads to apply scents to the substrate, e.g. additionally, certain hairs can often be found along the pad edges which are not evenly distributed but occur singly. A dense cover of hairs can serve the protection of an organism, single hairs, so-called mechanoreceptors, are frequently used to detect items and food (Campbell 1997). Furthermore, hairs can adopt a preening function and be used like a comb. Foot length as well as hand length varies with body size. It is known from other mammal orders that good, fast runners have a long, slender foot, whereas climbing species usually have smaller feet in relation to body size. This could also be shown to be the case in African rodents (Zieckur 2004). In how far these morphological parameters are also present in nesomyines is to be examined in the following pages.

3.2. Material and methods

3.2.1 *Study area*

Field work was conducted over four years (2003-2007) in Maromizaha, a rainforest area in East Madagascar located close to Andasibe (Perinet, 150 km east of Antananarivo, 6.5 km from the Réserve Spéciale d'Analamazaotra).

The site Maromizaha is part of the administrative region of Alaotra-Mangoro, rural district, office Moramanga, province of Toamasina. The site can be reached by the quarry of Amboasary on the west side (18°57'69" S, 48°27'14" E) or the village of Anevoka from the north side. All samples were collected during the beginning of the rainy season (Nov.-Dec.) in each year (average min/max temperature during study periods: 16-26 °C, with an average precipitation of 124-250 mm/month). Maromizaha is a biological reserve, designated by the nature conservation agency NAT (Foundation for Conservation in the Tropics) and since 2007 organised by GERP (Groupe d' Étude et de Recherche sur les Primates de Madagascar), a local organisation. These two non-governmental organisations have stopped deforestation and developed reforestation efforts, ecotourism and education for local guides.

In the past, Maromizaha has experienced deforestation for wood exploitation and agriculture. Today, the study site harbours an extraordinary species diversity of 33 mammal species: eleven lemurs, ten insectivores, three bats (Marquart 2004, Marquart & Harisoa 2006, Woog et al. 2006) and nine rodent species could be detected, 88 birds (Woog 2006), 60 amphibians and 20 reptilian species (Zimmermann 2001). Situated at altitudes between 800-1200 m above sea level, both lowland and highland species are represented. More than 1600 hectare in size, this area is an important link in the network of the forestry belt in the humid east. In south-western direction, Maromizaha is directly connected to the large rainforest area Vohidrazana and in the north adjacent to the National Park Mantadia. The vegetation of the study site is typical for a rainforest habitat: a mountainous terrain with tall trees in the valleys and lower dense vegetation on the ridges consisting of bamboo grass passing into high-altitude misty montane forest represented by lower vegetation covered with moss. There are many small streams in the area. Outside the primary rainforest, cultivated and burned areas occur (see Fig. 11: in the east of Madagascar the Maromizaha study site).

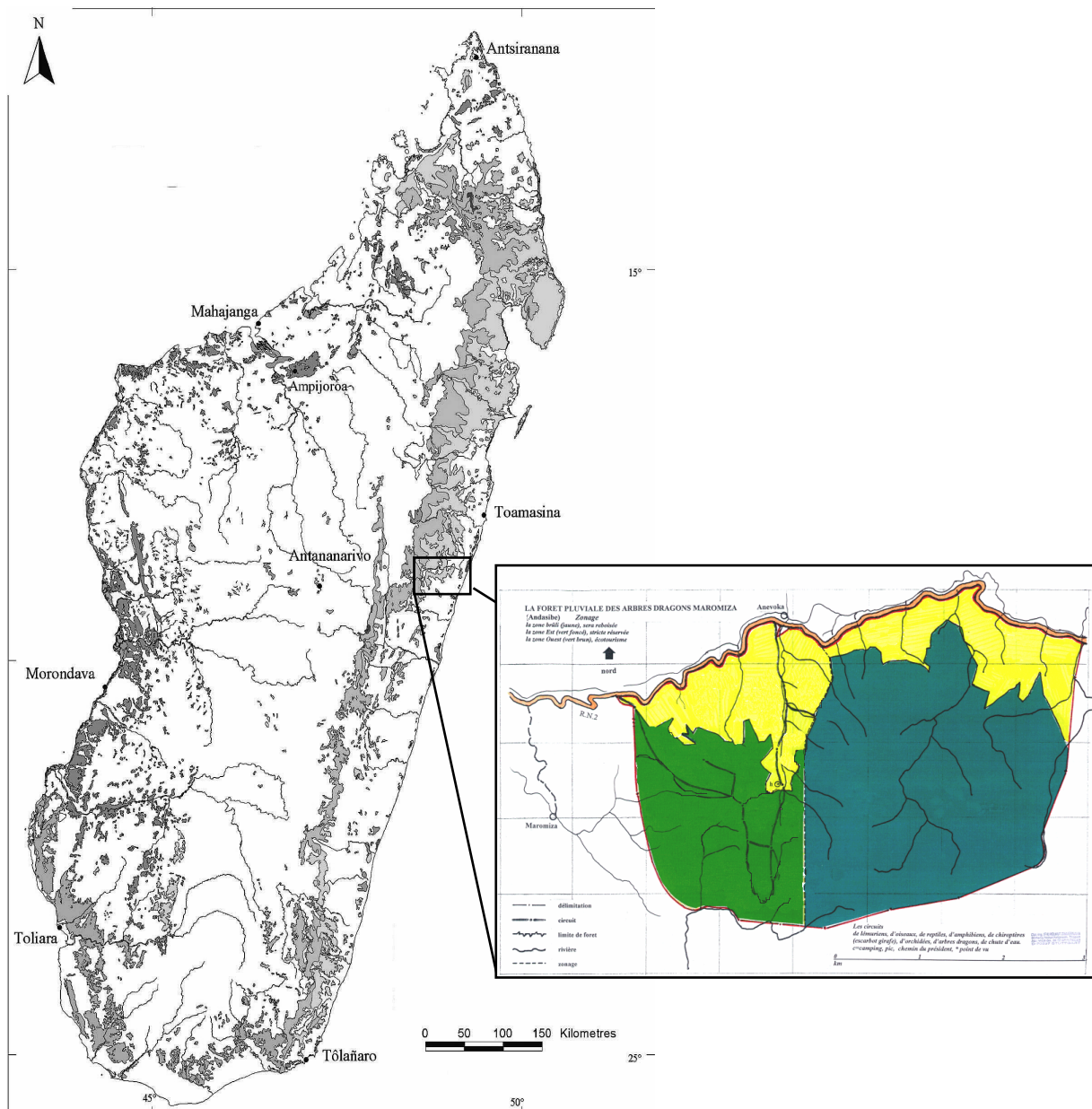


Fig. 11: Madagascar/ aerial view of the region around the Maromizaha protected area and study site Maromizaha, a rainforest area of eastern Madagascar (1600 hectare in size): yellow cultivated areas, green: primary rainforest area at middle altitude, blue: primary forest passing into high-altitude misty montane forest.

3.2.2 Capture / recapture

For data sampling, rodents were caught overnight in 50 baited live traps (Sherman, 23.5 cm x 8 cm x 9 cm), along 1-2 km transects. Along an elevational gradient of 800-1200 m above sea level, trap-lines were surveyed, each trap-line covering representative vegetation formations at different altitudes. The traps were prepared in the evening, baited with bananas and were examined the following morning. No traps

were set during daytime, because this proved to be unsuccessful, as even diurnal species were mainly active at dawn. The same trails and trapping positions were used over the four years of the study, with 50 trap-points for each live trap with 20 m spacing. Trap-points were marked with plastic flags on each of five different surveys. A detailed description of the respective trail characteristics regarding vegetation and altitude is given in the previous ecological study. For the correlation of the chiridian morphology with the vegetation preferences of each species, each of the five trails was sampled three times a year with special attention to the vegetation height and structure. Sampling along the transects resulted in a total of 3000 trapping activities over the four years of the study.

To analyse the habitat use of each species in detail, three different trap-levels per trap-line were examined.

1. Firstly, the traps were positioned on the ground, in leaf litter, grass bundles, under dead wood or tree trunks with or without cavities or holes or even upon wood lying on the ground, up to 0.4 m high.
2. Secondly, the traps were installed on vegetation approximately 1.3 m to 1.7 m high ("breast height till head of investigator") on small branches, bushes, thickets and on bamboo lianas.
3. For the last level, the traps were positioned on higher vegetation around 2.6 m to 3.0 m in height ("above head height of investigator") on lianas, big tree branches and foliage, sometimes covered with moss.

To position the traps on level III, trees had to be climbed with a top rope and climbing gear. All trapped animals were measured (body, head, tail and foot measurements) using callipers (Sylvac), weighed, sexed (reproductive condition: size of testes, lactation or pregnancy by body weight) and general appearance was noted. Rodents were handled in transparent net bags for measuring; for some animals before sampling and killing with chloroform, anaesthetic was injected into the hind foot muscle using a combination of ketamine (100 mg/kg weight) and xylazine (15 mg/kg weight). Two to four individuals per species were sampled and preserved in 70 % alcohol for the morphological analyses and are kept in the mammalian collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS). Rare represented species were not killed and collected. Specimens of these taxa were procured on loan from the collections of the Muséum National d'Histoire Naturelle de Paris (MNHN) and the

Field Museum of Natural History, Chicago (FMNH). All other animals were released at their place of capture.

3.2.3 Climbing structure and locomotion behaviour

To analyse habitat choice, not only the three capture levels were recorded for each species but according to the different vegetation types on which the climbing animals were caught they were assigned to three categories: L = large-tree-climber; S = small-branch-climber, B = bamboo-grass-climber.

Additionally, the locomotive behaviour of the animals after release from the traps was noted down. All captured individuals were released at the site of capture. It was interesting to observe their different ways of retreating into their habitat: some immediately climbed up the nearest vegetation; others ran away along the ground, dug holes in the earth, disappeared in burrows or even crossed watercourses by swimming or wading. The analyses of locomotive behaviour must be considered as first observations and general classifications. It is only possible to derive a first estimate from these records, not a complete description of all behaviour patterns. For this, the average percentages of vegetation use (use of different substrates) and the respective behaviour (locomotion mode) were determined and classified for each species as follows: + = 5-20 %, ++ = 25-60 %, +++ 65-90 % climbing behaviour or terrestrial running or digging or swimming/wading after release from captivity.

To observe special details such as resting, grooming and feeding behaviour (opening seeds, gripping vegetation etc.), some animals were kept for about 15 minutes in a plastic terrarium (30x20cm in size) or in a cage, before released at their place of capture.

3.2.4 Measurements and microscopic drawings

For comparison of the chiridian structure, hands and feet on the left side of each specimen were photographed. For this, the chiridia were preserved in alcohol, pinned to a polystyrene board with the volar side upwards and detailed photographs were taken using a tripod. To carry out detailed morphological analyses, anatomical drawings were set up under a binocular. The length of the foot and hand prints was taken from the photographs. The measurements were defined using a so called "reference line" which for the hand follows the flexor fold of the wrist. At a right angle

to this runs the longitudinal axis of the hand, through the centre of the palm and the middle finger. The "reference line" for the foot runs right behind the heel at a right angle to the longitudinal axis of the foot, through the heel and the middle toe. The measurements used were defined as follows:

Hand measurements

- Palm length: from the reference line at a right angle to the centre of the flexor fold of the middle finger
- Palm width: greatest width of the hand, below the root of the thumb, distance between outer and inner edge of palm, parallel to the reference line
- Track length of hand: distance between the outer edges of the proximal and the distal hand pad
- Track width of hand: distance between the outer edges of the medial and lateral hand pad
- Length of the third finger: from the centre of the flexion crease to the fingertip
- Claw length of the third finger: from the tip of the claw to the "nail bed"
- Claw width of the third finger: measured at the base, right above the "nail bed"

Foot measurements

- Sole length: from the reference line at a right angle to the centre of the flexor fold of the middle toe
- Sole width: greatest width of the foot, below the first toe, distance between outer and inner edge of the sole, parallel to the reference line
- Track length of foot: distance between the outer edges of the proximal and the distal foot pad
- Track width of foot: distance between the outer edges of the medial and lateral foot pad
- Length of the third toe: from the centre of the flexion crease to the tip of the toe
- Claw length of the third toe: from the tip of the claw to the "nail bed"
- Claw width of the third toe: measured at the base, right above the "nail bed"

From this, hand and foot surfaces (area ratio of the volar surface) as well as the pad areas (thenar pad area) can be calculated and their proportions given as percentages (%).

3.2.5 *Data analyses*

All measurements of the chiridia were taken by means of digital photos using the software Photoshop CS to provide for standardised measurements. An advantage of this method is that all distances can be read precisely and without handling errors at any time in a reproducible way. Lines of reference can be directly inserted into the digital pictures. For each species, one individual was exemplarily photographed and examined for the chiridia measurements. It has to be noted, however, that a morphologically typical specimen was chosen in each case. For each species, comparisons were made prior to the study, according to the amount of available collection material and animals in the field. Calculation of areas and statistical data analysis was carried out using the software Microsoft Office Excel 2003 and STATISTICA 5.0 (Weiß 2007). For all statistical tests, an error probability of $p = 0.05$ was used to check for significance (Siegel 1997).

Standard descriptive statistics (mean of body measurements) and analysed chiridian structure were derived only for adult specimens, recognised by the pelage colour (greyer for juveniles) and fully erupted third molars. For species identification, several basic studies on the systematics of all Malagasy rodents were conducted.

3.3. Results

3.3.1 Species inventory of the endemic rodents at the study site

Seven endemic rodent species from four genera were found and documented for the first time at the study site at Maromizaha. Four species of tuft-tailed rats, namely: Grandidier's Tuft-tailed Rat (*Eliurus grandidieri* Carleton & Goodman, 1998), Lesser Tuft-tailed Rat (*Eliurus minor* Major, 1896), Tanala Tuft-tailed Rat (*Eliurus tanala* Major, 1896) and Webb's Tuft-tailed Rat (*Eliurus webbi* Ellerman, 1949) as well as the Eastern Red Forest Rat (*Nesomys rufus* Peters, 1870), the rare Voalavoanala (*Gymnuromys roberti* Major, 1896) and the White-tailed Tree Rat (*Brachytarsomys albicauda* Günther, 1875) representing six species with a typically nocturnal way of life (*Eliurus* sp., *G. roberti* and *B. albicauda*) and one diurnal (*N. rufus*). The introduced *Rattus rattus*, which was also found at the study site, is excluded from this study, because my focus is on morphological adaptations of the chiroidea of endemic species. For species identification, average body length, hind foot length, ear length and tail length as well as weight were used (see Tab. 7).

3.3.2 Capture rates at different trapping levels

Over four years of sampling a total of 336 rodent individuals were caught in 3000 traps (during different trapping-sessions) from all trap-lines. The average capture rate was 11.2 %. In 2003, 71 individuals were captured, in 2004: 82, in 2005: 90, and in 2006: 93, respectively. Numbers and trapping success changed only slightly from year to year but varied significantly between trapping sites. The species showed a distinct distribution over the different capture levels which could be confirmed during the years of the survey. For each species, clear preferences for one level could be determined and documented here in percent (%) (see Fig. 12).

Tab. 7: Species inventory: List of endemic Rodents, which were caught overnight in 50 baited live traps along 1-2 km transects, at the study area of Maromizaha.

Species	Specimen number	Lifestyle	HBL - TL - HFL - EL - WT mean of: head body length - tail length - hindfoot length – ear length (mm) – body weight (g)	IUCN status	Number of specimens investigated for chiridian morphology
<i>Eliurus grandidieri</i>	SMNS 50430 – 50431 FMNH 173269 - 173270	n	105 – 147 – 28 – 17 – 49	LC	4
<i>Eliurus minor</i>	SMNS 50432 - 50434, 50440	n	96 – 121 – 21 – 14 – 38	LC	4
<i>Eliurus tanala</i>	SMNS 50340 - 50342, 50435	n	135 – 181 – 33 – 18 – 109	LC	4
<i>Eliurus webbi</i>	FMNH 154251 - 154252	n	99 – 162 – 25 – / – 45	NT	2*
<i>Nesomys rufus</i>	SMNS 50338 - 50339, 50558 - 50559	d	153 – 149 – 44 – 20 – 151	LC	4
<i>Gymnuromys roberti</i>	SMNS 50336 - 50337	n / d	143 – 163 – 36 – 18 – 104	VU	2*
<i>Brachytarsomys albicauda</i>	MNHN 1992 / 1234	n	250 – 255 – 40 – 16 – 209	LC	1*

Red List categories & criteria: LC = Least Concern, NT = Near Threatened, VU = Vulnerable (IUCN 2007 and 2008); n = nocturnal, d = diurnal; SMNS: Staatliches Museum für Naturkunde, Stuttgart; *Rare or vulnerable species were not or only sparingly collected and instead obtained as loans from the collections of the FMNH: Field Museum of Natural History, Chicago, and MNHN: Muséum National d'Histoire Naturelle de Paris.

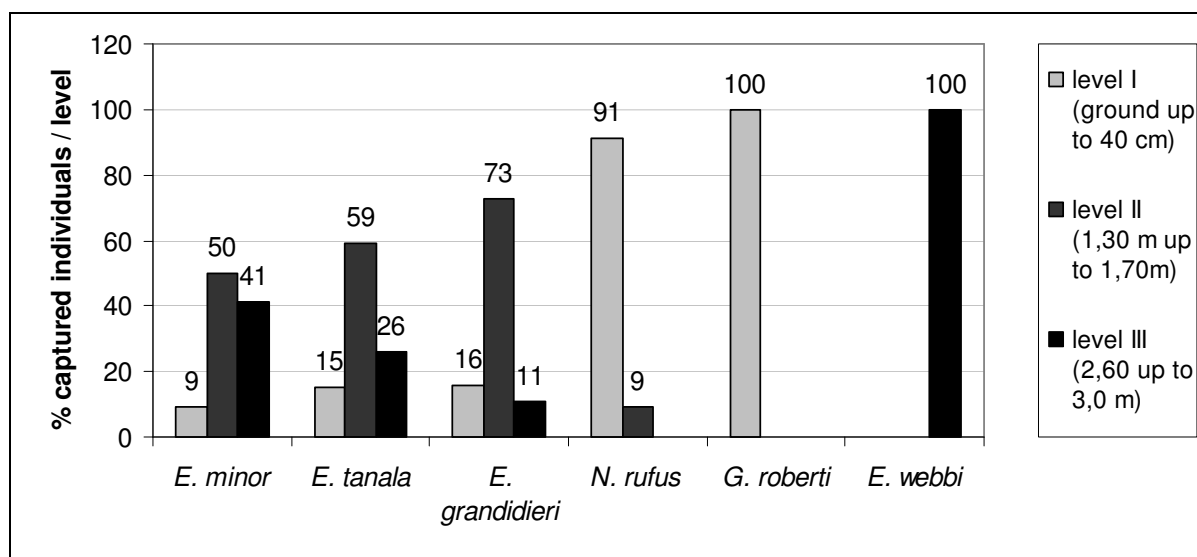


Fig. 12: Capture rates over three different trapping levels.

E. minor was caught in traps placed on the ground up to 0.4 m (level I) in 9 % of all captures. In 41 % of all cases this species was caught on high vegetation (level III: 2.6 m to 3.0 m) and was most frequently (50 %) trapped on vegetation of medium height (level II: 1.3 m to 1.7 m).

E. tanala was found in traps at ground level (level I) in 15 % of all captures. In 26 % of all cases this species was caught on high vegetation (level III) and was also most frequently (59 %) trapped on vegetation of medium height (level II).

E. grandidieri was found in traps on high vegetation (level III) in 11 % of all captures. In 16 % of all cases this species was caught on the ground (level I) and, as the two previous species, was most frequently (73 %) trapped on vegetation of medium height (level II).

N. rufus never occupied traps on high vegetation (level III). In only 9 % of all captures the species was caught in traps on vegetation of medium height (level II). Instead, it was most often (91 %) found in traps placed on the ground (level I).

G. roberti neither occupied traps on vegetation of medium height nor on the tallest trees (levels II and III) but was exclusively caught on the ground and up to 40 cm on vegetation (level I).

E. webbi, on the contrary, neither occupied traps on the ground nor on vegetation of medium height (levels I and II) but was exclusively trapped on the tallest trees (level III).

For *B. albicauda* only one single specimen could be captured within the study area on a single occasion in a separate trapping effort. After several periods of observation we installed a live trap directly in front of the sleeping hole, 10 m high in the roosting tree. We positioned the trap in the late afternoon and captured the animal the next morning. The sleeping hole of *B. albicauda* was located in a tree (diameter 42 cm, height 15 m) more than 8 m above ground. The hole entrance measured 4.5 cm in diameter, the hole depth was about 25 cm. The single record of *B. albicauda* therefore occurred on level III (not within the statistic figure).

The percentage calculated for each level resulted from the respective number of individuals of each species trapped and identified without doubt over the years of the study (see Tab. 8).

Tab. 8: Captured rodent individuals per level over four survey years.

	<i>E. minor</i>	<i>E. tanala</i>	<i>E. grandidieri</i>	<i>N. rufus</i>	<i>G. roberti</i>	<i>E. webbi</i>	<i>B. albicauda</i>
Level I	6	11	3	105	10	0	0
Level II	35	44	14	11	0	0	0
Level III	28	19	2	0	0	5	1*

*Because of the difficulties in capturing this species these data were excluded from the statistics.

3.3.3 Chiridian morphology

At first glance, the foot and hand morphology of the nesomyines appears to be very uniform. After analysing detailed measurements of the seven nesomyine rodents found at the study site, however, clear distinctions could be detected.

The **hands (palmae)** of all examined nesomyines have four fingers and a reduced thumb. All species studied show five main pads on their palms that can be clearly distinguished. Further pads and differences in size and shape will be presented below. Following the terminology established by Tullberg (1899), Winge (1941) and Kimura et al. (1994) for the palmar pads, these can be subdivided into "distal pads" (all pads located distal to the radio-ulnar transverse furrow) and "proximal pads" (all pads located proximal to the ulnar transverse furrow, also referred to as "carpal pads" due to their proximity to the wrist: *caruncula carpalis*). The distal pads lying between or below the fingers are denoted as "interdigital pads" (Debrunner 1955, Biegert 1961) and are numbered in the subsequent drawings with Roman numerals. The interdigital pad associated with the thumb is always the proximal one and is therefore called "proximal interdigital pad". The other proximal pads are denoted as "thenar pad" (on the radius side) and "hypothenar pad" (on the ulna side), respectively (Biegert 1961). In all examined nesomyines the thenar and the proximal interdigital pad are merged into a "pollical-thenar pad". The proximal hypothenar pad is always well pronounced. In some species it is subdivided into a distal and a proximal hypothenar pad.

All of the examined species show a prominent apical pad (terminology following Whipple 1904) on each of their finger tips. Furthermore, in all species studied the fingers show marked transverse furrows. At the level of the carpal joint all examined taxa show a carpal hillock called "*caruncula carpalis*" (Tullberg 1899, Ziekur 1999). There, the hair is shorter than on the upper sides of hands and arms, bristly and stiffly upright like a brush. All species also exhibit certain long vibrissae in this area (ulnocarpal vibrissae, Hershkovitz 1977) which insert proximal to the wrist and point distalwards. Number, arrangement (grouped or single) and length of these vibrissae differs among the studied species and are presented below. All of the following morphological expressions are referring to the research project of Ziekur 2004, on African rodents, which was generated as well with the help of Dr Fritz Dieterlen at the State Museum of Natural History in Stuttgart.

The **feet (plantae)** of all examined nesomyines always have five toes of different length. The soles always show at least six large pronounced pads which in the subsequent drawings are denoted as follows: "interdigital pads" (Debrunner 1955, Biegert 1961) lie distally between or below the toes and are numbered by Roman numerals. The interdigital pad associated with the hallux is always the proximal one and is therefore referred to as the "proximal interdigital pad". The other proximal pads are referred to as "thenar pad" (on the tibia side) and "hypothelar pad" (on the fibula side), respectively (Biegert 1961). Proximal thenar pad and proximal hypothelar pad are well pronounced in all of the examined nesomyines. In some species these pads can be divided into smaller distinguishable subunits such as "distal thenar pad" and "distal hypothelar pad". If these subunits are not discernible they may have become merged with other pads.

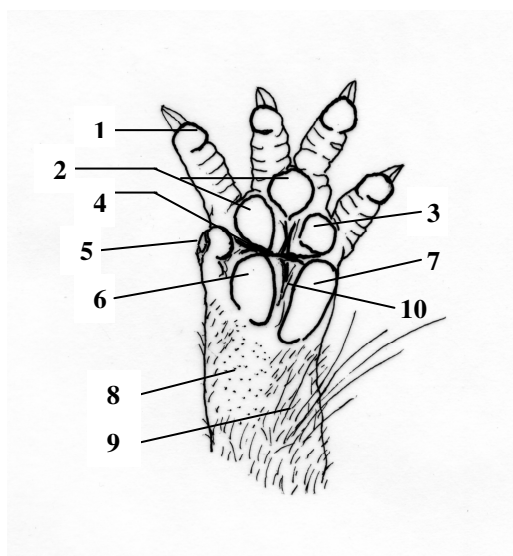
Like the fingers, the toes show prominent apical pads (terminology following Whipple 1904) and marked transverse furrows. Another characteristic could be established for all nesomyines: the fifth toe is always long with a large surface area and opposable against the hallux for gripping, can be spread apart. Furthermore, most of all examined taxa possess posterior vibrissae on their heels; number, length and arrangement (grouped or single) of these vibrissae vary among the species. All of the following expressions are referring to the research project of Zieck 2004, on African rodents.

Palma: The palms of *Eliurus grandidieri* possess five distinct pads. Proximal and distal halves of the hand are separated by a transverse furrow extending across the entire palm. A longitudinal furrow divides the right from the left half of the palm. Both furrows clearly intersect at the centre of the hand. The three distal pads (interdigital pads II-IV) are only marginally different in size; the two proximal pads (carpal pads) - thenar and hypothenar pad - are slightly larger than the distal pads. As in all examined species, the proximal interdigital pad I is merged with the thenar pad to form a "pollical-thenar pad". The carpal pads are noticeably more raised and stand out towards the transverse furrow. All other palmar pads of *E. grandidieri* are also raised and clearly stand out from the palm. There are no glands visible on the entire palm, on the pads or between them. The claws of the fingers are short, pointed and comparatively fine. The thumbnail is rather flat and broad and does not project beyond the tip of the thumb but ends with it or is even shorter. A bunch of on average six long ulnocarpal vibrissae grows on the carpal hillock (see Fig. 13, palma of *E. grandidieri*).

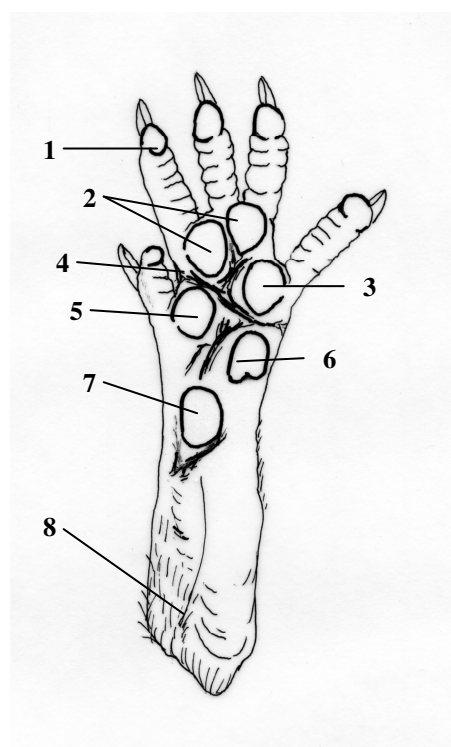
Planta: The soles of *E. grandidieri* possess six large prominent pads. A transverse furrow divides the sole into a distal and a proximal half. The proximal hypothenar pad is particularly raised with a slight notch and a little smaller than the distal interdigital pads II-IV. The proximal thenar pad is large and not as elongated as in the other *Eliurus* species. Smaller subunits such as distal thenar pad and distal hypothenar pad are not discernible. The large proximal interdigital pad I is apparently merged with the small distal thenar pad to a cup-shaped adhesive pad below the hallux. There are no glands on or between the pads. The claws of the toes are short, thin and pointed. In relation to the head-body-length the feet are long and slender. The five toes are of medium length compared to the long volar area of the sole. The fourth toe is the longest, followed by the third. The fifth toe is opposable against the hallux for gripping and can be spread wide apart. A cluster of several longish posterior vibrissae pointing inwards between the feet is situated near the heel on the inner side of the foot (see Fig. 14, planta of *E. grandidieri*).

Fig. 13: Palma of *Eliurus grandidieri*

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Thumb bearing a nail
6. Interdigital pad I +
thenar pad
7. Hypothenar pad
8. Carpal hillock
9. Ulnocarpal vibrissae
10. Longitudinal furrow

**Fig. 14: Planta of *Eliurus grandidieri***

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Interdigital pad I +
distal thenar pad
6. Proximal hypothenar
pad
7. Proximal thenar pad
8. Posterior vibrissa

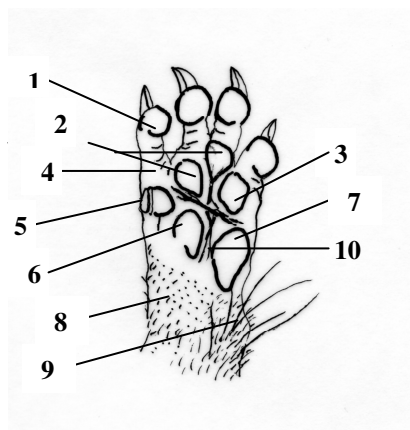


Palma: The palms of *Eliurus minor* possess five distinct pads. Proximal and distal halves of the palm are separated by a transverse furrow extending across the entire width of the palm. A slight longitudinal furrow divides the right half of the palm from the left. Both furrows clearly intersect at the centre of the palm. The three distal pads (interdigital pads II-IV) differ only slightly in size; the two proximal carpal pads are a little larger than the distal pads. The proximal hypothenar pad in particular is distinctly larger in relation to the interdigital pads. In *E. minor* the proximal interdigital pad I is merged with the thenar to form a "pollical-thenar pad". All palmar pads are equally raised and the carpal pads only stand out slightly towards the transverse furrow. There are no glands on the entire palm nor on or between the pads. The claws of the fingers are short, pointed and, compared with other *Eliurus* species, particularly fine. The flat and broad thumbnail does not project over the tip of the thumb but ends with it or is even shorter. A bunch of on average seven long ulnocarpal vibrissae inserts on the carpal hillock (see Fig. 15, palma of *E. minor*).

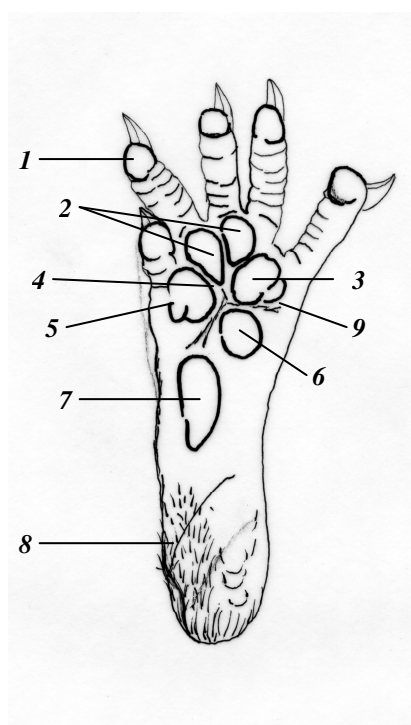
Planta: The soles of *E. minor* possess six large prominent pads. The distal and proximal halves of the foot are only slightly separated by a transverse furrow. The proximal hypothenar pad is particularly raised and equally large as the distal interdigital pads II-IV. The proximal thenar pad is large and noticeably elongated. The existence of smaller subunits such as distal thenar pad (below the hallux) and distal hypothenar pad (beneath the fifth toe) is of note. These two "secondary pads" are clearly visible and at the same time merged with the large interdigital pads I and IV to form a cup-shaped adhesive pad. There are no glands either on or between the pads. The claws of the toes are short, fine and pointed. The feet are slightly stocky and not as slender as, for instance, in *E. grandidieri* but can nevertheless be classified as being of medium length in relation to the head-body-length. All five toes are also of medium length in relation to the volar area of the soles, the fourth toe being the longest. The fifth toe is opposable against the hallux for gripping and can be spread wide apart. On the inner side of the foot, near the heel, there is a cluster of several posterior vibrissae of medium length which point inwards between the feet (see Fig. 16, planta of *E. minor*).

Fig. 15: Palma of *Eliurus minor*

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Thumbnail
6. Interdigital pad I +
thenar pad
7. Hypothenar pad
8. Carpal hillock
9. Ulnocarpal vibrissae
10. Longitudinal furrow

**Fig. 16: Planta of *Eliurus minor***

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Interdigital pad I +
distal thenar pad
6. Proximal hypothenar pad
7. Proximal thenar pad
8. Posterior vibrissa
9. Distal hypothenar pad

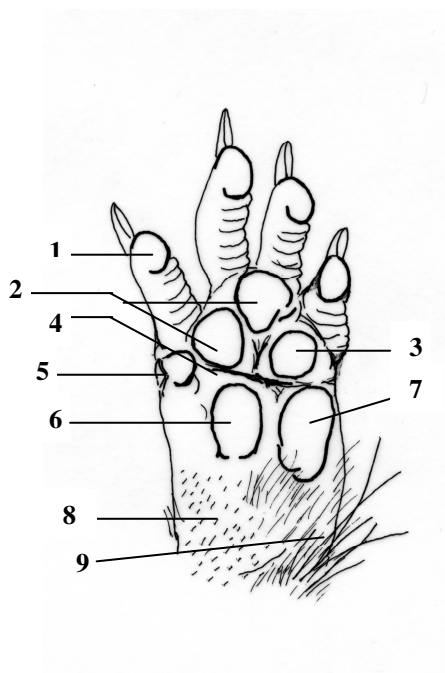


Palma: The palms of *Eliurus tanala* show five distinct pads. Proximal and distal halves of the hand are separated by a marked transverse furrow extending across the entire width of the palm. There is no longitudinal furrow in evidence. The three distal pads (interdigital pads II-IV) only differ slightly in size; the two proximal pads (carpal pads) are clearly larger than the distal pads. The proximal hypothenar pad is markedly larger and more raised than the other pads. As in all examined species, in *E. tanala* the proximal interdigital pad I is merged with the thenar pad to form one large "pollical-thenar pad". Although the carpal pads are considerably more prominent than the distal pads they only stand out slightly towards the transverse furrow. On all pads there are slight punctual indentations; it can be assumed that these are clusters of glands which occur at a higher density at the pad centres. There are no glands visible between the pads. Compared to the other *Eliurus* species listed above, the claws of the fingers are much longer, pointed and yet fine. The flat and broad thumbnail ends with the tip of the thumb. On average, there are six long ulnocarpal vibrissae growing from the carpal hillock. These vibrissae stand further apart than in the other species and do not form a bunch (see Fig. 17, palma of *E. tanala*).

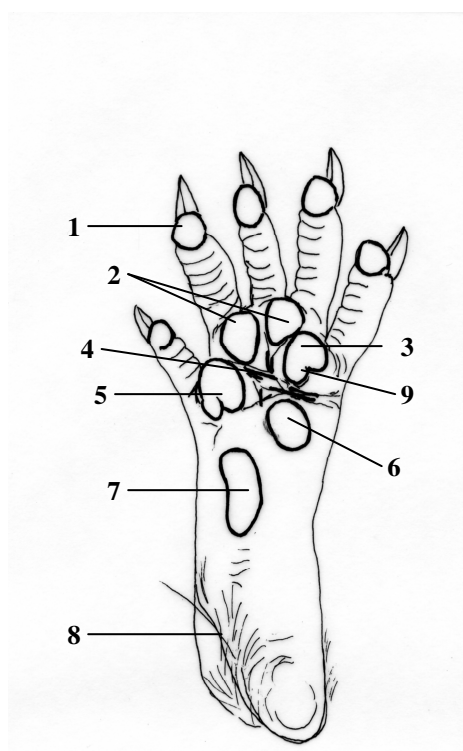
Planta: The feet of *E. tanala* are characterised by six large prominent pads. A transverse furrow divides distal and proximal halves of the sole. The proximal hypothenar pad is notably raised and of similar size as the distal interdigital pads II-IV. The proximal thenar pad is large and of conspicuous, elongated "bean-shape". Smaller subunits such as distal thenar pad and distal hypothenar pad are hardly visible but still present. These two "secondary pads" are merged with the large proximal interdigital pad I and the interdigital pad IV, respectively, to form adhesive cup-shaped pads. In contrast to the palmar pads there are no glands visible on the plantar pads. The claws of the toes are comparatively long, thin and pointed. In relation to the head-body-length the feet are broader than, for instance, in *E. minor*, but can nevertheless be classified as long. Compared to the volar area of the sole, the five toes are also very long. The fourth toe is the longest. The fifth toe is opposable against the hallux for gripping and can be spread wide apart. On the inner side of the foot, near the heel, there is a single stiff posterior vibrissa (see Fig. 18, planta of *E. tanala*).

Fig. 17: Palma of *Eliurus tanala*

1. Apical pad
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Thumbnail
6. Interdigital pad I + thenar pad
7. Hypothenar pad
8. Carpal hillock
9. Ulnocarpal vibrissae

**Fig. 18: Planta of *Eliurus tanala***

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Interdigital pad I + distal thenar pad
6. Proximal hypothenar pad
7. Proximal thenar pad
8. Posterior vibrissa
9. Distal hypothenar pad

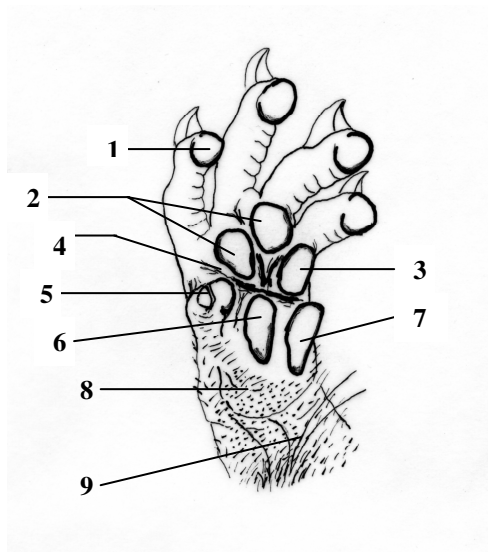


Palma: The palms of *Eliurus webbi* possess five pads. Proximal and distal halves of the hand are separated by a clear transverse furrow extending across the entire width of the palm. A longitudinal furrow is hardly discernible or not present at all. The three distal pads (interdigital pads II-IV) differ only slightly in size; the two proximal carpal pads are somewhat larger and distinctly longer than the distal pads. The proximal hypothenar pad in particular is markedly larger in comparison with the interdigital pads II-IV. The proximal interdigital pad I and the thenar pad are merged to a "pollical-thenar pad". All palmar pads are comparatively strongly raised and the carpal pads stand out noticeably towards the transverse furrow. There are no glands visible either on the entire palm or on or between the pads. The claws of the fingers are short, pointed and, compared to the other *Eliurus* species, particularly strong. As in all species studied the thumbnail does not cover the tip of the thumb but is, in fact, much shorter. A carpal hillock is clearly visible and a bunch of on average four long ulnocarpal vibrissae points distalwards (see Fig. 19, palma of *E. webbi*).

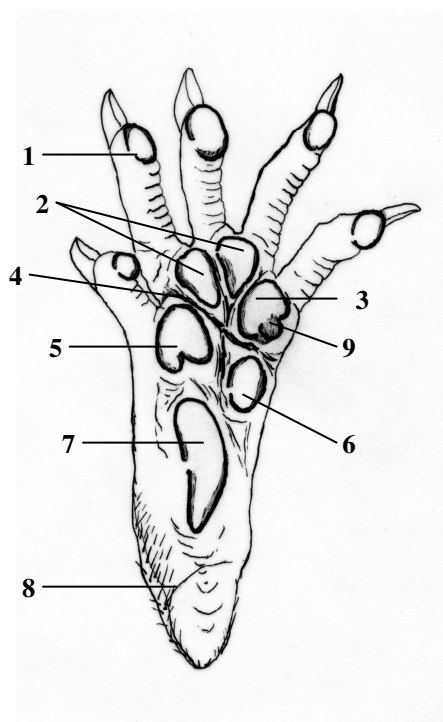
Planta: The feet of *E. webbi* show six large prominent pads. Distal and proximal halves of the foot are divided by a distinct transverse furrow, and a longitudinal furrow divides the right from the left half of the foot. Both furrows clearly intersect at the centre of the foot, which is unique for an *Eliurus* species. The proximal hypothenar pad is a little more raised and slightly smaller than the distal interdigital pads II-IV. The proximal thenar pad is conspicuously large, markedly elongated and lies farther tibiawards than in any of the other examined species. Another peculiarity of *E. webbi* is the presence of smaller pads such as distal thenar pad and distal hypothenar pad. These two "secondary pads" are clearly distinguishable but lie very tightly against the neighbouring pads and are thus merged with the large proximal interdigital pad I and the interdigital pad IV. Both of these "fused" pads have a very conspicuous cup-shape depression at the centre. There are no glands visible on or between the pads. The claws of the toes are short, pointed and markedly strong in comparison with the other species. The feet are noticeably stocky, short and compact in relation to the head-body-length. Hence, the five toes are very long compared to the short volar area of the sole. The fourth toe is the longest. The fifth toe is opposable against the hallux for gripping. On the inner side of the foot, near the heel, inserts a remarkably long posterior vibrissa which points inwards between the feet (see Fig. 20, planta of *E. webbi*).

Fig. 19: Palma of *Eliurus webbi*

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Thumbnail
6. Interdigital pad I +
thenar pad
7. Hypothenar pad
8. Carpal hillock
9. Ulnocarpal vibrissae

**Fig. 20: Planta of *Eliurus webbi***

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Interdigital pad I +
distal thenar pad
6. Proximal hypothenar
pad
7. Proximal thenar pad
8. Posterior vibrissa
9. Distal hypothenar pad

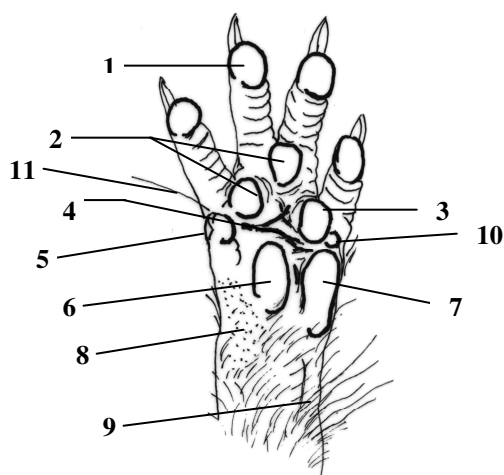


Palma: Among all examined species, *Nesomys rufus* alone possesses six palmar pads. The sixth pad is the distal hypothenar pad which is small but easily distinguishable. Proximal and distal halves of the hand are separated by a distinct transverse furrow extending across the entire width of the palm. There is no dominant longitudinal furrow. The three distal pads (interdigital pads II-IV) are of equal size, the two proximal carpal pads are noticeably larger and more elongated. The proximal hypothenar pad in particular is markedly larger. The proximal interdigital pad I and the thenar pad of *N. rufus* are merged into a rather flat and elongated "pollical-thenar pad". All palmar pads are comparatively little raised. The carpal pads, however, stand out clearly towards the transverse furrow. No glands are visible on the entire palm or on and between the pads. The claws of the fingers are notably long and strong. The thumbnail ends with the tip of the thumb or even projects beyond it in many cases. A long vibrissa grows out of the flexion crease of the thumb. The carpal hillock is clearly visible and supports a bunch of on average six long ulnocarpal vibrissae pointing distalwards (see Fig. 21, palma of *N. rufus*).

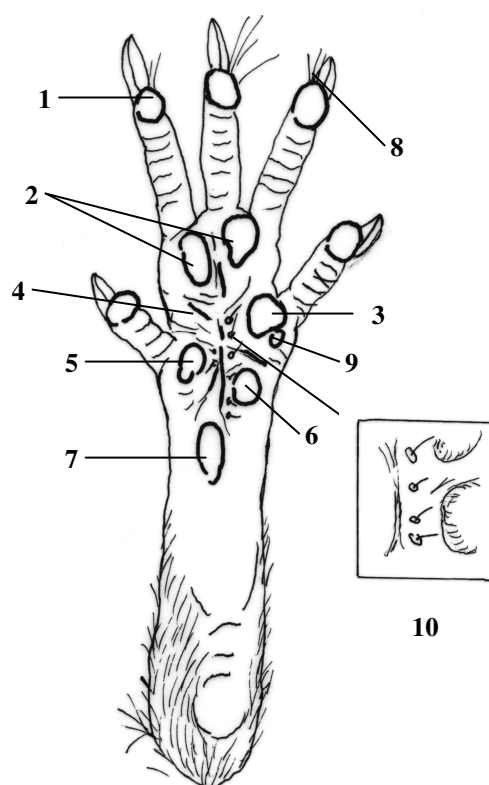
Planta: *N. rufus* has six large prominent foot pads. There is only the hint of a division of the soles into distal and proximal halves by a slight transverse furrow. A distinct longitudinal furrow divides the right from the left half of the foot and two additional furrows between interdigital pad I and II or III and IV divide the foot in diagonal directions. In contrast to the other nesomyines examined, nearly all the proximal pads are smaller than the distal pads. The proximal hypothenar pad is minute; the proximal thenar pad is also small and situated well apart from the heel. The smaller pads such as distal thenar pad and distal hypothenar pad are clearly distinguishable in *N. rufus*. These two "secondary" pads almost stand alone and are clearly distinct from the other pads, thus not forming an adhesive pad but showing a clear separation from interdigital pad IV. Numerous glands are discernible all over the markedly flat pads and particularly between these. Short, bristle-like hairs sprout from circular depressions between the pads (see below for details). The claws are very long and strong and edged by thick long hairs. The feet are especially long in relation to the head-body-length, the five toes therefore have to be classified as being of medium length. The fourth toe is the longest. The fifth toe is opposable against the hallux for gripping and can widely be spread apart. In contrast to the other species *N. rufus* does not possess long posterior vibrissae (see Fig. 22, planta of *N. rufus*).

Fig. 21: Palma of *Nesomys rufus*

1. Apical pad
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Thumbnail
6. Interdigital pad I + thenar pad
7. Hypothenar pad
8. Carpal hillock
9. Ulnocarpal vibrissae
10. Distal hypothenar pad
11. Pollical vibrissa

**Fig. 22: Planta of *Nesomys rufus***

1. Apical pad
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Interdigital pad I + distal thenar pad
6. Proximal hypothenar pad
7. Proximal thenar pad
8. Claw hairs
9. Distal hypothenar pad
10. Plantar hairs (magnified)

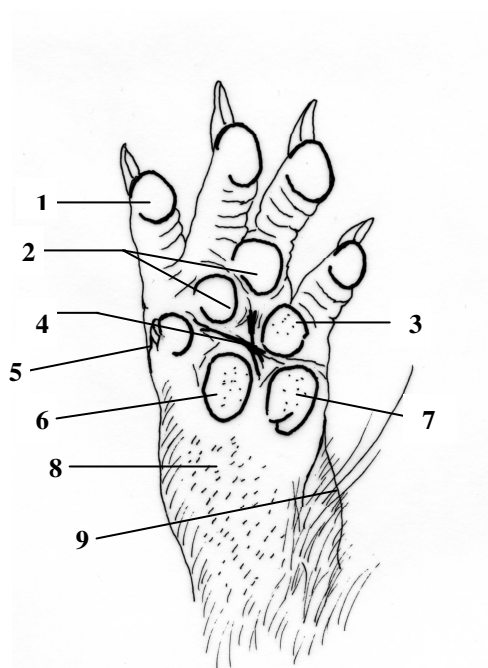


Palma: On the palms of *Gymnuromys roberti* five pads are clearly visible. Proximal and distal halves of the hand are divided by a transverse furrow extending across the entire width of the palm. A longitudinal furrow separates the right half of the hand from the left. There is a distinct intersection of both furrows at the centre of the hand. The three distal pads (interdigital pads II-IV) vary only slightly in size; the two proximal pads (carpal pads), i.e. thenar pad and hypothenar pad are a little larger than the distal pads. The proximal interdigital pad I and the thenar pad are merged into a "pollical-thenar pad" in *G. roberti*. The carpal pads are distinctly raised and stand out towards the transverse furrow. All other palmar pads are moderately raised. There are glands on the pads (interdigital pad IV, proximal hypothenar pad and pollical-thenar pad) but not between them. The claws of the fingers are long and strong. The thumbnail is markedly shorter than the tip of the thumb. The carpal hillock is clearly visible and supports a bunch of on average six long Ulnocarpal vibrissae (see Fig. 23, palma of *G. roberti*).

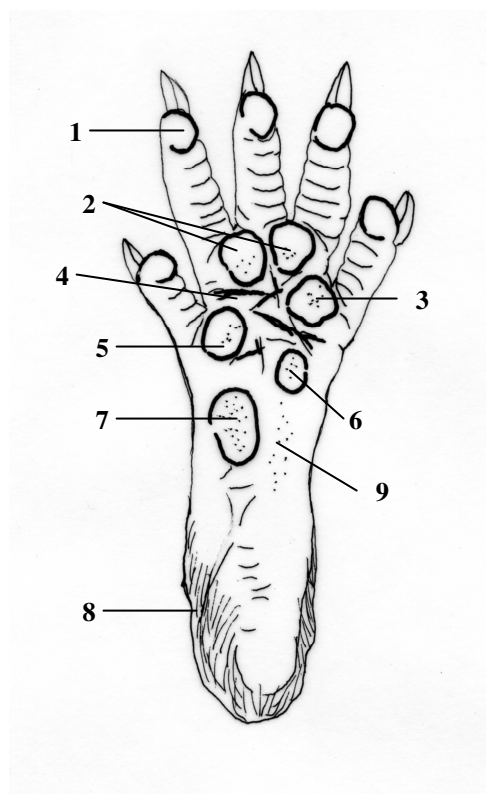
Planta: The soles of *G. roberti* possess six large prominent pads. There is only the hint of a separation into a distal and a proximal half of the foot by a transverse furrow. The proximal hypothenar pad is conspicuously small. The proximal thenar pad is oval or round and not of elongated bean-shape as in most of the other *Eliurus* species. The smaller pads such as distal thenar pad and distal hypothenar pad are not apparent, nor are cup-shaped adhesive pads. All plantar pads are moderately raised. There are numerous glands on but not between the pads. Further glands are found on the sole in parallel with the proximal thenar pad and running in the direction of the tibia towards the heel. The claws are extremely long and strong. The foot is long compared to the head-body-length; the five toes therefore have to be classified as being of medium length in relation to the long volar area of the sole. It is of note that all pads are separated by large gaps and are thus distributed over a large part of the sole. The fourth toe is the longest. The fifth toe is opposable against the hallux for gripping and can be spread apart. On the inner side of the foot, near the heel, inserts a particularly long posterior vibrissa which points inwards between the feet (see Fig. 24, planta of *G. roberti*).

Fig. 23: Palma of *Gymnuromys roberti*

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Thumbnail
6. Interdigital pad I + thenar pad
7. Hypothenar pad
8. Carpal hillock
9. Ulnocarpal vibrissae

**Fig. 24: Planta of *Gymnuromys roberti***

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Transverse furrow
5. Interdigital pad I + distal thenar pad
6. Proximal hypothenar pad
7. Proximal thenar pad
8. Posterior vibrissa
9. Glands



Palma: The palms of *Brachytarsomys albicauda* possess five pads which are noticeably prominent, raised and massive. There are no transverse or longitudinal furrows. The three distal pads (interdigital pads II-IV) are only slightly different in size; the two proximal carpal pads are markedly larger than the distal pads. The proximal hypothenar pad is of similar size as interdigital pads II-IV. A particularly prominent feature of *B. albicauda* is the "pollical-thenar pad" resulting from the fusion of the proximal interdigital pad I with the thenar pad which looks massive and is markedly raised. Compared with all other examined nesomyine species, all palmar pads of *B. albicauda* are distinctly raised and have an almost "inflated" appearance. There are no glands visible on the entire palm nor on or between the pads. All pads, however, show conspicuous epidermal ridges running around and away from them. The claws are short and strong. The thumbnail is much shorter than the tip of the thumb. A carpal hillock is apparent; on this inserts a loose bunch of 9-10 long ulnocarpal vibrissae which point distalwards (see Fig. 25, palma of *B. albicauda*).

Planta: The feet of *B. albicauda* exhibit six large conspicuously prominent pads. There is no transverse furrow dividing distal and proximal pads. The proximal hypothenar pad is markedly raised, even laterally projecting from the foot. The distal interdigital pads II-IV are very similar in size. The proximal thenar pad is the largest of all pads and particularly conspicuous. As in none of the other taxa examined, all pads extend very far towards the tibia. Another characteristic is that one of the smaller pads, the distal thenar pad, is still clearly distinguishable although it is merged on one side with the large proximal interdigital pad. This "fused" pad has a very conspicuous cup-shaped depression at its centre. There are no glands on or between the pads. As with the palmar pads, the plantar pads also show distinct epidermal ridges running around and away from them. The claws of the toes are short and very strong. In relation to the head-body-length the foot is notably stocky and very short, giving rise to the name "*Brachytarsomys*" (= "short-footed rat"). Compared to the short volar area of the sole the five toes can be considered as long. *B. albicauda* is an exception among all taxa examined because the fifth toe is the longest and opposable against the hallux, making it very suitable for gripping, but can also be spread wide apart. On the inner side of the foot, near the heel, inserts a particularly long posterior vibrissa which points inwards between the feet (see Fig. 26, planta of *B. albicauda*).

Fig. 25: Palma of *Brachytarsomys albicauda*

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Thumbnail
5. Interdigital pad I +
thenar pad
6. Hypothenar pad
7. Carpal hillock
8. Ulnocarpal vibrissae

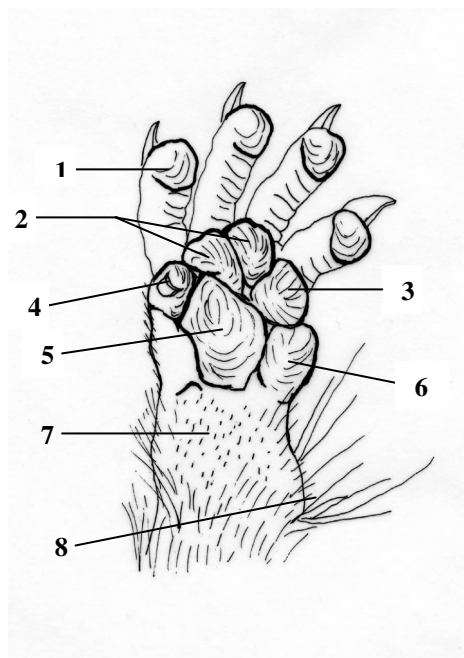
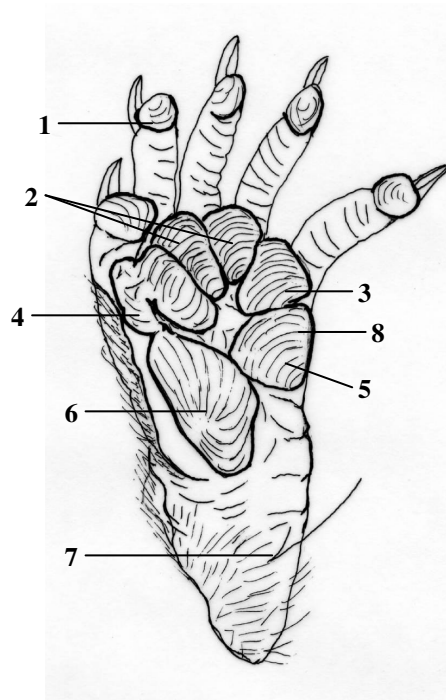


Fig. 26: Planta of *Brachytarsomys albicauda*

1. Apical pads
2. Interdigital pads II+ III
3. Interdigital pad IV
4. Interdigital pad I + distal
thenar pad
5. Proximal hypothenar pad
6. Proximal thenar pad
7. Posterior vibrissa
8. Epidermal ridges



3.3.4 Area ratios

My study shows that the seven species differ most strongly in the morphology of their hind feet. There is considerably less modification in the morphology of the hands, as is commonly the case for all rodents (Mohr 1959). For this reason, only the percentage area ratios of the hind feet (in particular the pad/sole area ratio) are presented and compared for the different species.

B. albicauda has the highest pad/sole area ratio: 90 % of the plantar surface is covered by massive and strongly raised pads. *E. webbi* has the second highest pad/sole area ratio (73 %). *E. minor* and *E. grandidieri* have a similarly large pad area in relation to their plantar surface: 45-46 % of their sole is covered by pads. In *E. tanala*, though, only 43 % of the plantar area is covered by the pads. *G. roberti* has a still lower pad/sole area ratio: only 41 % of the plantar surface is covered by flat pads. Finally, *N. rufus* clearly has the smallest pad surface compared to its very large plantar area: only 37 % of the sole is covered by small, flat pads (see Fig. 27 and 28).

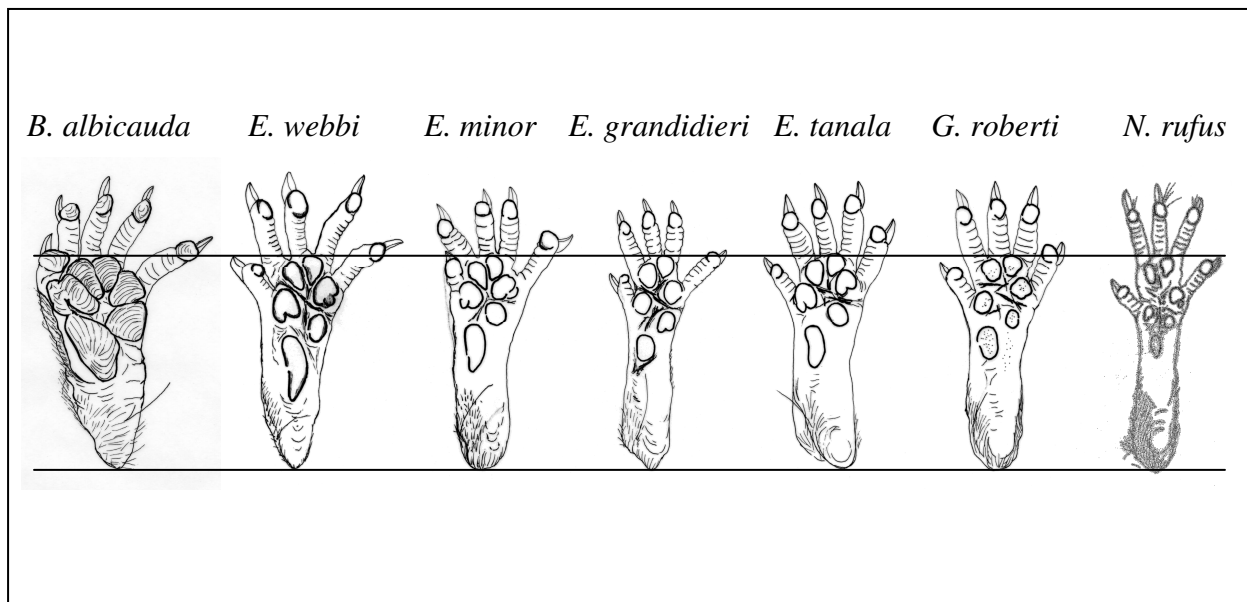


Fig. 27: Comparison of pads in relation to the sole area of left rodent planta (left hind foot of *Brachytarsomys albicauda*, *Eliurus webbi*, *E. minor*, *E. grandidieri*, *E. tanala*, *Gymnuromys roberti*, *Nesomys rufus*). For easier comparison foot prints are presented in the same size, by setting the drawings between two reference lines.

3.3.5 Locomotion behaviour on different vegetation structures

B. albicauda can be considered a downright "large-tree-climber". In my study this species could only be once observed climbing on tall, massive trees. There are no data about digging or swimming/wading behaviour.

E. webbi was also classified as a "large-tree-climber" (65-90 % of all released animals from the trap have shown climbing locomotion behaviour). I could not observe this species on the ground running or digging, but this behaviour is frequently known from literature. There is no information about possible swimming behaviour.

E. minor and *E. grandidieri* both are outstandingly good climbers (65-90 % of all released animals from the trap have shown climbing locomotion behaviour) - on massive tall trees as well as on slender twigs and even on filigree bamboo grass which could not be shown for any of the other five taxa. So I considered these species as good "large-tree-climbers" as well as good "small-branch and bamboo-grass-climbers". Both species could also be observed running on the ground (5-20 %); digging behaviour could, however, only be documented for *E. grandidieri* (5-20 %). No swimming or wading behaviour was observed for either species. Only when collecting food and nesting material on the ground, *E. grandidieri* could be seen using a puddle for immersing nesting materials, however, without entering the water itself.

E. tanala is a very good climber as well (25-60 % of all released animals from the trap have shown climbing locomotion behaviour) and can mainly be classified as a "large-tree-climber", occasionally also using slender twigs so also be classified as a "small-branch-climber". Additionally, *E. tanala* was more frequently recorded on the ground: it could be observed running (5-20 %) as well as digging and was the only rodent species that could be seen swimming and wading in water (up to 5-20 %).

G. roberti can be considered an essentially ground-dwelling species that was observed on the ground after release in 25-60 % of all captures. Contrary to expectations, however, this species could be recorded climbing with equal frequency (25-60 %). Thus, *G. roberti* appears to be a very good climber which could, however, only be observed on broad structures. In 5-20 % of all observations this species could also be recorded digging a burrow or a hole for food storage and clogging the hole later with soil and leaves. There are no data about swimming or wading behaviour.

N. rufus was most frequently seen on the ground (65-90 % of all released animals) and only occasionally used broad vegetation or a fallen tree for climbing (5-20 %). This species was the most infrequent climber of all observed rodents, most of the time running on the ground foraging. *N. rufus* was also recorded digging (5-20 %) but there are no data about swimming or wading behaviour (see Fig. 28).

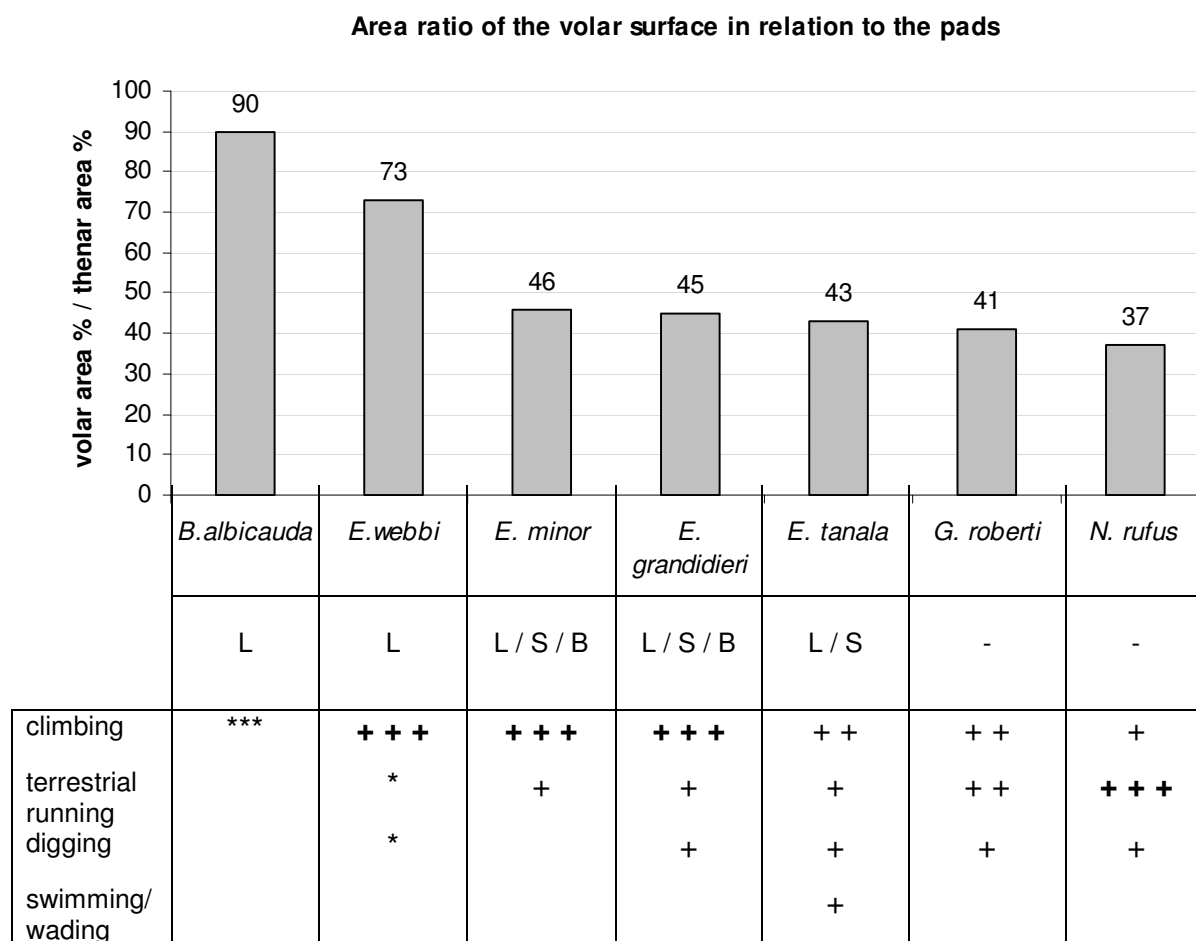


Fig. 28: Area ratio of sole in relation to pads and the observed locomotion mode for nesomyine species investigated, L = large-tree-climber; S = small-branch-climber; B = bamboo-grass-climber; + = 5-20 %; ++ = 25-60 %; +++ = 65-90 %; */*** = data from literature.

3.4. Discussion

3.4.1 *Ecological adaptations among the species at the study site*

Using three different capture levels and observational data on release of the animals after capture, it was possible to determine habitat preferences and to draw first conclusions about life history and ways of locomotion. Thus, the seven rodent species included in this study can be assigned to different categories. For animals that were frequently trapped at a particular forest layer it can safely be assumed that they also preferably live at this vegetation level and use it for foraging or to build nests for roosting. The high number of captures revealed clear preferences for the species:

E. minor, ***E. tanala*** and ***E. grandidieri*** were most frequently caught at medium height (level II: 1.30 m up to 1.70 m). This forest layer is characterised by a large variety of structural elements suitable for climbing, as shown by the results of the vegetation analyses presented in the previous chapter: fine twigs, dense undergrowth, many bushes and lianas but also larger tree trunks. It is interesting to note, however, that *E. minor* and *E. tanala* were caught at top layer (level III: 2.60 m up to 3.00 m) with the second highest frequency whereas in *E. grandidieri* this was the case at ground level up to a height of 40 cm. These results can be explained by the ecological niches the respective species occupy: *E. minor* is characterised by a low body mass and is thus able to climb along very thin vegetation structures, even culms of bamboo grass, and to leap up into the very highest tree tops. *E. tanala*, on the other hand, is of much heavier build and therefore prefers larger tree trunks and very tall dragon trees at the same level. By contrast, *E. grandidieri* with its medium body mass can utilise the fine vegetation structures at medium height but was also observed digging and foraging on the ground; such was not the case for *E. minor*, e. g., for which no digging behaviour could be recorded. Singularly among all species studied, *E. tanala* shows another interesting aspect: this species was frequently caught in the vicinity of running water and could be recorded swimming or wading. Trapping events on both banks document active crossing of water bodies for this species.

N. rufus and ***G. roberti*** were most often trapped at level I on the ground; additionally, their mode of locomotion could also be described as mainly terrestrial.

Only occasionally, *N. rufus* was caught on taller vegetation (level II: 1.30 m up to 1.70 m) or was observed climbing. In comparison of both species, *E. rufus* can be classified as a sustained runner with a wider "home range radius" than *G. roberti* (Garbutt 1999). Surprisingly though, *G. roberti* occasionally proved to be a more adept climber (only documented by observations, not by trappings) and less of a "long-distance-runner" than *N. rufus*. Both species could be observed digging in the soft ground and were also caught inside ground excavations they used as roosting sites and as food caches. Possibly, these two ground-dwelling species avoid competition for food, e.g., by *N. rufus* as a partly diurnal species covering larger distances during daylight whereas *G. roberti*, a nocturnal species, shows high site fidelity and occasionally also climbs on taller vegetation for foraging. Roosting sites of both species were found on the ground and for *G. roberti* once in a dead wood hole, it was a fallen hollow tree trunk with a nesting hole at approximately 1.50 m height lined with dry bamboo leaves and containing fresh fleshy and hard shelled fruits.

E. webbi and *B. albicauda* were exclusively trapped at the topmost forest layer (level III: 2.60 m up to 3.00 m) in the highest tree tops. These last two species are marked climbers and use broad and massive vegetation elements. *B. albicauda* in particular is a species of very large and heavy build that lives in tree cavities and can be attested high site fidelity. *B. albicauda* is described in literature as well, as almost exclusively arboreal (Goodman & Benstead 2003). *E. webbi* however, could be observed by several authors foraging, digging and nesting on the ground (Garbutt 1999, Goodman & Benstead 2003), but this was not the case in my study. It is possible that this species also digs burrows for use as roosting sites or to cache food, for instance, when there are no suitable natural cavities in massive trees. At periods of high precipitation during the rainy season, *E. webbi* mainly appeared to be a climbing species, being caught near tree cavities but not in traps on the ground, as for instance *G. roberti*. It is still unclear, in how far *E. webbi* might adapt digging behaviour and roosting site choice to weather conditions and in consequence to the availability of food in the rain forest outside the rainy season.

3.4.2 Morphological differentiations of the chiridia for different locomotion

The dermal structures of the chiridia (hands and feet) allow inferences about a species' ecological niche (Niemitz 1990). Their differentiation and special characteristics such as, for instance, number and shape of the foot pads reflect an

organism's adaptations to certain constraints (Dukelski 1927, Niemitz 1990, Ade & Ziebur 1999). The findings for **habitat use** and **locomotion** are discussed in relation to the **morphological** results in the following paragraphs.

E. grandidieri can be characterised as a typical **tree-dwelling, arboreal species** that could mostly be recorded on slender twigs, stems, lianas and bamboo grass at medium height ("small-branch-climber" and "bamboo-grass-climber"). The observations on locomotion are corroborated by the results of the trappings: *E. grandidieri* mostly used vegetation for getting about. It is a very nimble and swift climber. Its small body mass is advantageous for climbing on stems and grasses, as are the strongly raised foot pads which increase the surface area of the soles when pressed against the substrate, thus improving grip. This species could also be observed on the ground, running and digging as well as foraging and collecting material. **Its hands** are visibly subdivided by transverse and longitudinal palmar furrows, suggesting a very flexible and mobile hand that is used for digging or grabbing food. The latter is first picked up by mouth, then transferred to the hand and eaten. *E. grandidieri* was caught with the second highest frequency at the lowest level and on the ground and was also observed digging. The marked transverse furrow between interdigital and hypothenar pads hints at a high flexibility of the hand - such a flexion might, for instance, occur when *E. grandidieri* scratches at the earth surface for worms and insects, or else during active digging for food. *E. grandidieri* could also be observed dexterously opening seeds etc. with its hands, although the food item always was picked up by mouth first. The enlarged proximal pads of the hand also suggest excellent gripping abilities. As these pads are larger than the distal pads and also stand out against the transverse furrow they can be pressed against the distal pads very efficiently to secure grasped items in the furrow. The shortened thumb with its interdigital pad and the thenar forms a thumb-thenar-pad. This entire complex also fulfils a special adhesive function: when climbing, the whole surface gets into contact with the substrate and the grip on thin twigs and stems is improved by adhesive forces. The short, pointed and comparatively fine claws can also serve as anchors on the climbing surface. The thumb nail is of equal length with the tip of the thumb or shorter, thus increasing tactile sensitivity of the thumb's periphery; this characteristic appears to be important for climbing species. All seven species in this study possess a carpal elevation (Caruncula carpalis) on the medial side of the wrist. There were, however, species-specific differences in the size of this area as well as

in the number of ulnocarpal vibrissae. For all *Eliurus* species it can be assumed that this particular region with its short bristles serves as a brush. It could be shown without doubt that the whole genus including *E. grandidieri* is also carnivorous or omnivorous, respectively, and preferably uses insects and invertebrates as a protein-rich food source, in addition to sweet fruit and nectar. These food types which soil the coat more strongly than, for instance, plant material or seeds and therefore call for a particularly effective preening tool. Vigorous brushing of head and belly with the insides of the arms could often be recorded for *E. grandidieri* in particular. In contrast with the preening function of the short hairs, the longer ulnocarpal vibrissae of the hand probably perform tactile tasks. The presence of these vibrissae is generally regarded as ancestral for mammals (HersHKovitz 1977, Ade & ZieKur 1999) and could also be confirmed for all study species. It could not be resolved, however, in how far the number of vibrissae might be important for tactile perception. **The foot of *E. grandidieri*** with its six large and prominent adhesive pads also appears to be adapted to climbing. The presence of a transverse furrow allows a higher flexibility and pliability of the foot when running along fine structures. The fifth toe serves *E. grandidieri* to clasp small twigs and to hold on to them, even when climbing down vegetation head-first. Here, the opposable gripping toe is used just like pliers or a locking anchor. During sitting position the fifth toe can be also spread wide apart, maybe for a better balance, especially when the whole bodyweight is on the hind leg, e. g. during preening, feeding or observing. The foot is long and slender, which in turn is advantageous on stems and grass blades. The strongly convex and notched proximal hypothenar as well as the proximal interdigital pad I (in conjunction with the small distal thenar pad) act like a suction cup: the slight central depression creates negative pressure when the raised periphery of the pad is pushed against the ground, thus providing secure grip on, for instance, wet surfaces, which is of great advantage in a rainforest with high precipitation levels. The vibrissae present on the heels of *E. grandidieri* presumably facilitate the coordination of the hind limbs, being pointed inwards between the feet, and also serve tactile perception in locomotion. It is possible that the shorter hairs of the inner sides of the feet are also employed for preening: the animals could be observed brushing their back, belly and flanks vigorously with their hind feet, whereas the hands were mostly used when preening the facial area.

Like *E. grandidieri*, *E. minor* can be characterised as a **very good climber** and a **tree-dwelling, arboreal species**. Across all study years, this smallest of all *Eliurus* species was also mainly trapped at medium vegetation heights. Observations of locomotion correlated with the trapping results showed that the species preferably uses slender twigs in dense filigree vegetation and, like *E. grandidieri*, can skilfully move along bamboo grass ("small-branch-climber" and "bamboo-grass-climber"). Its low body mass and the markedly raised foot pads as well as the flexible hands and feet are optimally suited for climbing on fine structures. *E. minor*, however, also used high vegetation (with the second highest frequency) which can be explained by the fact that this species is a very good jumper: when leaping, the animals could be observed raising their long, markedly bushier tail high for balance, unlike the other species. The ability to jump must be essential for small animals as *E. minor*, for a fast locomotion among the tree-tops. **The hands of *E. minor*** are subdivided by a clear lateral and a rather indistinct longitudinal furrow, pointing at a very flexible hand. The disparity of the furrows might be evidence for the hand mainly being used for grasping, e.g. food items (leading to lateral flexing) rather than for holding on to fine vegetation structures for locomotion (leading to longitudinal flexing of the palms for folding around twigs). This corresponds with observations on locomotion: *E. minor* more frequently leaps from branch to branch and thus is less dependent on good "lateral adhesion" than, e. g., *E. grandidieri* (for instance, when climbing down head-first). The slightly enlarged proximal pads stand out from the transverse furrow also indicating a strong but not quite as specialised grasping function as described for *E. grandidieri*. In comparison of the two species, the hypothenar pad is less pronounced in *E. minor* and thus presumably serves a holding rather than a gripping function. Furthermore, the shortened thumb (forming a thumb-thenar-pad in conjunction with its interdigital pad and the thenar) has special adhesive functions, as is also the case in *E. grandidieri* (see there). These two species have a lot more in common: the short pointed fine claws providing better grip when climbing; the thumbnail abutting with the tip of the finger to increase tactile sensitivity; the carpal elevation which possibly serves as a preening brush; and the ulnocarpal vibrissae of the hand which support tactile perception. **The foot of *E. minor*** with its six large, prominent and adhesive pads also appears to be adapted to climbing. There is only a slight indication of a lateral furrow characterising a foot that is less flexible than that of *E. grandidieri* and thus is not adapted to grasping fine structures but instead, due to a more rigid sole,

allows better adhesion, for instance, when leaping. Also, the proximal hypothenar is particularly raised in *E. minor* and of similar size as the distal interdigital pads; the proximal thenar is noticeably bean-shaped, larger and more elongated, thereby facilitating a still better grip on broad structures. In contrast to the more slender and mobile foot of the similar-sized *E. grandidieri* the foot of *E. minor* appears stockier and wider. Noticeable is the presence of the smaller pad units, the so-called lesser pads (distal thenar and distal hypothenar) which are fused with the proximal interdigital pads to form suction-cup-shaped structures. This is another morphological adaptation to climbing and leaping: the "suction cups" provide greatly improved grip - slight pressure along the periphery of the pad structure causes negative pressure as already mentioned for *E. grandidieri*. If, as in *E. minor*, two such "suction cups" face each other, even stronger adhesive forces can be assumed. As in all nesomyines, the fifth toe is opposable for grasping and serves *E. minor* as a gripping tool when running or leaping. During sitting position the fifth toe can be also spread wide apart. As in *E. grandidieri*, the vibrissae at the heels presumably also improve coordination of the hind limbs as they project inwards between the feet and also serve tactile perception during locomotion.

E. tanala could be observed and caught far more often in traps at ground level than, for instance, *E. minor* but is also considered **arboreal** and a **good climber**. *E. tanala* also preferred traps at medium vegetation height across the years of this study but unlike the smaller *Eliurus* species not on fine structures but instead always favoured traps on broad structures, large trunk diameters and massive branches. Observations of locomotive behaviour showed *E. tanala*, the largest *Eliurus* species, to be less nimble when moving along slender branches and on grass stems but instead to be sure-footed on broad structures and even in water. This species can thus be classified as a "large-tree-climber" and a "small-branch-climber" and was the only species that could be recorded swimming or wading in water. Its heavy body as well as the comparatively broad and less flexible hands and feet are well adapted to climbing on broad structures or slippery surfaces. **The hands of *E. tanala*** are subdivided by only a clear transverse furrow, pointing at a hand with good grasping and digging abilities allowing, for instance, picking up food items by hand, pushing away earth, or catching prey in water. There is no longitudinal furrow, suggesting that a hand which could be flexed in two dimensions (e.g. for grasping slender twigs) is of less importance for moving along broad and slippery structures such as stones in

watercourses and massive tree trunks or when catching prey. The two proximal pads are markedly larger than the distal pads; the proximal hypothenar in particular is visibly bulkier and more conspicuous than the other pads, but stands out less towards the transverse furrow which might be connected to *E. tanala*'s habits: proximal pads that stand out less impede the grasping of vegetation but improve grip on smooth surfaces due to an increased contact area. The punctual glands on all the larger pads of the hand might further improve adhesion. The long but comparatively fine claws are useful for digging and can be anchored in the surface when climbing. In contrast to the smaller species, the thumbnail is flatter and wider and always abuts with the tip of the thumb; possibly to enhance tactile sensitivity in water or when digging. A carpal elevation with a preening brush is also always clearly visible in *E. tanala* - observations on food intake have shown that *E. tanala* preferably consumes insects such as beetles, larvae and moths as well as minute aquatic animals. It is conspicuous that the ulnocarpal vibrissae stood in bunches in all arboreal and terrestrial *Eliurus* species, with the single exception being *E. tanala* with its aquatic habits: its vibrissae were not bundled but stood well apart, possibly to improve tactile perception in water at night, for instance when catching prey. **The foot of *E. tanala*** with its six large and prominent well-adhesive pads also appears to be adapted to climbing along broad and slippery structures. A marked transverse furrow is a sign of an articulated and flexible foot; presumably facilitating moving the distal and proximal parts of the foot against each other, thereby in turn improving adhesion on, for instance, slippery surfaces. As in *E. minor*, the proximal hypothenar pad is visibly raised - this appears to be of advantage for a safer grip. The proximal thenar is large and elongated to bean-shape, again improving grip on broad structures. The foot of *E. tanala* in general appears markedly wider, e.g. in comparison with *E. minor*. Compared to *E. grandidieri* the foot width of *E. tanala* is even greater. The smaller pads are not easily identifiable because they are merged with the other pads to form "suction cups". This is particularly obvious for the suction cup formed by the proximal interdigital pad I and the distal thenar - as described for the previous species, slight force on the periphery of the pad structure causes negative pressure. In *E. tanala*, two of these "suction cups" are facing each other, thus optimising adhesion. All toes are very long in relation to the volar surface of the foot sole - a clear advantage in water: when spread, the toes can thus provide better grip on uneven ground. As in all nesomyines, the fifth toe is opposable and can be used for grasping; it serves *E.*

tanala as "locking pliers" to keep hold when climbing, or can be spread wide apart, for a better balance, especially on slippery surfaces. In contrast to the other species described above, a single vibrissa at the heel seems to be sufficient for *E. tanala*, possibly to facilitate directed coordination of the hind limbs and a more sensitive perception even when in water.

E. webbi - like *E. tanala* - can be described as an **excellent climber** and an **arboreal** species. *E. webbi*, however, only used the highest tree-tops and was exclusively caught on the tallest trees. During the entire study period, this species was never observed or trapped on the ground or on low bushes and lianas. On the other hand, this species is described as tree- as well as ground-dwelling in literature (Garbutt 1999), which hides in ground burrows up to one meter in depth (Carleton 2003). Goodman (1994) describes the behaviour of *E. webbi* as "probably nests and forages at different levels in the forest", and recorded the species sharing the same burrow system with a nesting bird (Groundroller). It is possible that this behaviour depends on the time of year - during the more humid rainy season it might well be of advantage to retire to dry tree cavities. Like *E. tanala*, this species always favoured traps on broad structures. Observations of *E. webbi*'s locomotion also showed this species to be more of a "large-tree-climber". The species' relatively heavy body mass and its comparatively wider and less flexible hands and feet represent optimal adaptations to climbing on broad structures. **The hands of *E. webbi*** are marked by a clear transversal furrow; a longitudinal furrow is hardly noticeable or lacking entirely, pointing at good grasping and digging abilities, thus corroborating descriptions in literature of *E. webbi* as possessing good digging skills. Thus, lateral bending of the hand for digging appears to be of greater importance for *E. webbi* than a longitudinally flexible hand for grasping thin twigs. Like *E. tanala*, this species therefore appears to be adapted to climbing on broad structures such as massive tree limbs. The distal pads differ only slightly in size; the hypothenar pad is markedly larger and more elevated, however, and leans towards the lateral furrow, thereby allowing a better grasping function than, for instance, in *E. tanala*. It is interesting to note that the hypothenar pad and the interdigital pad I (forming a thumb-thenar-pad in combination with the thenar) are a lot more elongated than in the other *Eliurus* species. It almost appears as if *E. webbi*'s hand is adapted to grasping and digging at ground level, whereas the foot with its marked surface adhesion proves to be particularly adapted to "climbing on broad surfaces". The strong and short claws -

compared to all other *Eliurus* species - are probably especially useful for digging but are less suitable to be used as anchors to the substrate when climbing, as is the case, for example, in *E. grandidieri*. The shape of the thumbnail also differs from the other species: it is particularly short, not reaching the tip of the thumb but markedly shorter, thereby possibly increasing tactile sensitivity when digging in earth and leaf litter. A carpal elevation with a preening brush could also be documented; ulnocarpal vibrissae supporting tactile perception are also present. **The foot of *E. webbi*** is of noticeably wide but stocky shape. The six large, prominent and strongly adhesive pads appear to be particularly adapted to climbing on broad structures - similar as in *E. tanala* - the foot, however, looks even more compact and stockier in shape, the pads covering visibly more of the surface. The proximal and distal foot halves are separated by a clear transverse furrow; a longitudinal furrow separates the left from the right half of the foot. Both furrows cross at the centre of the foot - as was the case in none of the other *Eliurus* species - but rather characterises the flexible "grasping hands" of, for instance, *E. grandidieri* and *E. minor*. The transverse furrow present in *E. webbi* points at an articulate and flexible foot that is pliable and thus can be "rolled" on massive structures. Additionally, both halves of the foot can be moved against each other, signalling an improved "adhesion" and an enhanced function of the suction-cup-like pads. As in *E. minor*, the proximal hypothenar pad is markedly raised - this also appears to be advantageous for a better grip. The proximal thenar is large and particularly elongated to bean-shape and is situated further tibiawards than in all other species studied. In this manner, the pad area on the foot is strongly enlarged and grip on broader structures is improved still further. Noticeable in *E. webbi* is the presence of the smaller pad components such as distal thenar and distal hypothenar. These two minor pads are clearly visible but are closely adjacent to the other pads, merging with the large proximal interdigital pad I and interdigital pad IV. Both merged pads have a very conspicuous suction-cup-like depression at their centre. As described for the previous species above, slight force on the periphery of the pad structure creates negative pressure, thus increasing adhesion - lengthwise flexion of the foot might further enhance this effect for optimal alignment of opposite suction cups. The claws are short, pointed and very strong, compared to the other species - this might be of advantage when climbing along broad, hard structures: sturdy claws provide grip, but are not used as "anchors" in the substrate. All five toes are very long in relation to the very short volar surface of the foot sole - this might be

of great advantage when climbing on broad structures: the toes can be spread for better grip. As in all nesomyines, the fifth toe can be opposed for grasping and serves *E. webbi* as "gripping pliers" when climbing. Like *E. tanala*, *E. webbi* appears to need only one single, particularly long vibrissa at the heel - possibly to aid precise coordination of the hind limbs.

N. rufus was never caught on high vegetation and could only occasionally be trapped on vegetation of medium height. Instead, *N. rufus* most frequently occupied traps at ground level and can therefore be described as a **purely ground-dwelling species** and can be considered a **good "long distance runner"**. If this species was seen climbing, it was exclusively on broad vegetation of medium height, such as fallen trees or stumps. When climbing, the animals moved swiftly along broad, preferably horizontal structures; they were never observed climbing down head-first or even hanging, as was the case for the small arboreal *Eliurus* species, for instance, *E. grandidieri* or *E. minor*. *N. rufus* could frequently be observed digging in loose litter. Here, the tuftless tail with its short inconspicuous hairs serves *N. rufus* as a prop when digging and sitting up. Uniquely among all species studied, **the hands of *N. rufus*** exhibit six pads. The sixth pad is the distal hypothenar which is small but clearly visible. A possible reason why this pad is not merged with the adjacent one might be the fact that *N. rufus* is not adapted to climbing and therefore does not need to increase adhesion by merging pads to form a suction cup. The morphology of the hand appears to be an adaptation to digging. This becomes apparent in the distal pads which are smaller and less bulging. The spaces between the pads are wider, resulting in easier flexion of the hand across the lateral furrow, thus allowing it to be used as a digging tool. The carpal pads are markedly larger, more elongated and form - together with the apical thumb pad - a stable support against which the long fingers (2-5) can be flexed. This also improves the digging abilities of the hand. The fingers are - in comparison to the other nesomyines studied - relatively long and bear strong claws that are useful for digging, e.g. when building burrows in the ground. The glands on and between the pads presumably have a shared function: by pressing together both sides of the hand, a secretion might be applied to the substrate, either as olfactory marker or to enhance adhesion when climbing on smooth broad structures that cannot be grasped around by hands or feet and on which therefore adhesion of the entire pad surface is necessary. The nail of the thumb is as long as the tip of the thumb or even longer, as tends to be characteristic

for digging species (Ade & Ziekur 1999). Possible reasons why the thumb nail of *N. rufus* is longer than the tip of the thumb might be protection of the delicate thumb tip or a strengthening of the inside of the hand when digging by the creation of a larger area for shovelling when the hand is flexed. There is an additional long vibrissa in the flexion furrow of the thumb, possibly for tactile perception when digging in the ground and for detection of food items. The carpal elevation with short bristle-like hairs as well as several bundles of distalwards ulnocarpal vibrissae appears to play a role for preening and tactile perception in *N. rufus*, too. The variable food items used by *N. rufus* comprise fruits and seeds as well as insects (Manesimana 2007). **The foot of *N. rufus*** is noticeably slender and long. Given the mainly terrestrial locomotive habits of *N. rufus*, the distal foot pads appear to be more important than the proximal pads: in this swift runner, the more prominent pads serve as "shock-absorbent" cushions; the more raised interdigital pads II, III and IV suggest that the distal part of the foot is exposed to particularly high pressure. It is possible that *N. rufus* steps onto the tips of its foot, spreading out toes 1 and 5 as lateral props, thereby distributing most of its weight onto these three distal pads. Distal and proximal halves of the foot are only vaguely separated by a slight transverse furrow which is created by the sequential movement of the pads when walking. The longitudinal furrow is far more obvious, pointing at a mediolateral flexing of the foot-sole. The "lesser pads" are well visible, lie almost singly and are clearly separated from the other pads, thereby not forming a "suction-cup-like" pad structure; instead, the larger spaces between the pads increase flexibility. Possibly, toes 1 and 5 are folded in beneath the sole when the foot is lifted. This makes the foot narrower as it is moved forwards and the speed of running increases due to reduced aerodynamic drag. Additional diagonal furrows between interdigital pads I and II or III and IV, respectively, which could only be documented for *N. rufus*, also support such a movement of the outer toes when walking: spreading of the toes when putting the foot down and contraction when moving forward, respectively. The striking length of the foot is connected with fast running because as a diurnal and crepuscular species not protected by darkness *N. rufus* has to be fast. The longer its chiridia, the longer strides it can take. It can be assumed that *N. rufus* does not put its heel down on the ground when running, as the proximal thenar is comparatively minute, not much raised and particularly far away from the heel, thus not being able to serve as a cushion for the heel in running. If *N. rufus* uses its hands to hold food it sits on the entire hind foot including the heel,

additionally propping itself up by its tail. Here, the toes can be spread wide apart to achieve more stability. As in all nesomyines studied, the fifth toe is opposable and can be used to grasp substrate when sitting on rough ground, thus providing additional stability. The very long feet also help lifting the heavy body when the animal assumes the so-called "watch-and-sniff-posture" (Manesimana 2007). The numerous glands on and between the pads possibly excrete a substance to the ground when both foot sides are pressed together. As discussed above for the hand, possible functions might be the distribution of olfactory markers and an improved adhesion when climbing on smooth broad structures. The bristle-like hairs between the pads on the foot soles might serve a special tactile function. They appear shorter than the raised pads: thus, they presumably only get into contact with the underground when *N. rufus* puts its feet down more forcefully, thereby flattening the pads, or on rough ground. Possibly, these bristles pass on certain information, e.g. about the qualities of the ground or about what moves under the feet when it is too dark to see in the dusk. In this way, the bristles are not permanently stimulated but only under certain conditions. The toes of *N. rufus* bear long, strong claws that can be used to scratch away earth loosened by the front paws to the animal's rear end. Additionally, these claws have a fringe of longer hairs exceeding the tips of the toes, possibly for feeling around in the earth, but a preening function is also conceivable: it could frequently be observed that the hind legs were used for brushing the relatively rough and dense fur up to behind the ears. Here, the long claws and bristles are useful for brushing and to penetrate the thick fur to the skin. Long vibrissae at the heels with a possible function in signal transmission are not present in *N. rufus*. Climbing species are more dependent on good coordination of the feet; "long distance runners" like *N. rufus*, on the other hand, run in a more steady and constant manner and thus do perhaps not need these additional signals.

G. roberti was exclusively caught in traps on the ground or up to 40 cm on vegetation, and could therefore be categorised as a **primarily ground-dwelling species**. Additional observations, however, showed *G. roberti* also to be a nimble climber, mainly on broad structures such as slanted tree trunks and only at medium vegetation height. *G. roberti* used broad structures for climbing even more frequently than, for instance, *N. rufus*. Therefore, *G. roberti* is not only characterised by its marked digging behaviour but also by its tendency to **climb on broad structures**. *G. roberti* was considered to be a pure ground-dweller by many authors (Garbutt 1999,

Goodman & Benstead 2003, Wilson & Reeder 2005) and was supposed not to climb at all but to build its roosts chiefly in the leaf litter and in the ground. It could be shown by this study that according to its hand and foot morphology, *G. roberti* has to be classified as a runner spending a lot of time in ground burrows but also tends to climb.

The hands of *G. roberti* possess five pads which in comparison with the other species are only moderately raised. It is striking that all five pads are very much alike in size and shape, this being the case in none of the other species studied. The hypothenar in particular is rather rounded in shape. All climbing species in this study showed larger and above all more elongated proximal and distal pads on their hands which enhance adhesion when climbing, thus providing a better grip. Possibly, the hand of *G. roberti* is adapted both to climbing and digging: the pads are small compared to the massive hand and of such uniform shape as to make them well suited for moving loose earth. Distal and proximal pads are of similar size, which, however, results in the lack of support for the distal half of the hand when this has to be bent along the transverse furrow when digging in hard earth, as could be recorded for *N. rufus* as a ground-dwelling, digging species. *G. roberti* therefore cannot be said to have a hand specialised for digging, instead, the transverse and longitudinal furrows might serve as so-called "grasping furrows", e.g. for better holding of food items or to improve grip when climbing which, however, is not as strongly pronounced as in the climbing species. Both furrows clearly cross at the centre of the hand, also pointing at a more flexible use in grasping and digging, but not providing the same grip for climbing as larger proximal pads standing out towards the transverse furrow would produce. A "thumb-thenar-pad" is present which is advantageous for climbing on broad structures as it prevents slipping by allowing contact with the substrate across the entire pad area. The long and strong claws of the fingers are useful for digging and moving loose earth. The thumbnail is markedly shorter than the tip of the thumb, thereby increasing tactile sensitivity along the thumbs periphery; this trait appears to be of high importance for climbing species. The glands present on the proximal pads as well as on interdigital pad IV also point at the climbing abilities of this species: it is possible that when both sides of the pads are pressed together a secretion is released to improve adhesion when climbing on smooth broad surfaces. As in all species studied, the carpal elevation with its bundles of ulnocarpal vibrissae appears to have tactile and brushing functions; this region is

noticeably thick and prominent in *G. roberti*; this might also be connected to digging in the earth: loose earth can be moved more effectively with a broader carpal hill region. Moreover, having a larger carpal hill region makes it easier to brush the fur when this has become soiled with earth or food, which might frequently be the case, considering the species' subterranean way of life.

The foot of *G. roberti* also seems to be adapted to running as well as to climbing: firstly, distal and proximal halves of the feet are only slightly separated by a transverse furrow which points at a foot that can be rolled but has no furrow for grasping climbing substrate as is, for instance, the case in the climbing *Eliurus* species. The foot of *G. roberti* is generally broader and more massive; the spaces between the pads are wider. Therefore, unlike in the climbing species, not the adhesive function of the pads seems to be vital; instead, the foot has to be flexible enough to adjust to the ground when running. Possibly, *G. roberti* might be able to tuck the first and fifth toe under the sole of the foot to make it narrower and increase running speed by reducing resistance, as was also the case in the long distance runner *N. rufus*. This theory is supported by the many short furrows between the pads. The conspicuously small hypothenar as well as the oval to rounded proximal thenar also appear not to be adapted to adhesive climbing: they are neither enlarged nor elongated. The smaller pad components are not visible either nor do they form suction-cup-like pad structures as would be the case in exclusively climbing species. The strong and very long claws again are useful for digging and scratching. Thus, *G. roberti* appears to be more adapted to life on the ground. It is interesting to note that there are glands present on all foot pads but not between them. Possibly, the numerous glands help *G. roberti* compensate for the absence of adhesive pads and thus improve adhesion when climbing on broad slippery surfaces by sticky secretions. As there are additional glands on the foot sole in parallel with the proximal thenar towards the heel, these might improve adhesion even further. As in all nesomyines, the fifth toe is opposable for grasping and can be pressed against the hallux to improve stability, especially when climbing. *G. roberti* could not be observed climbing downwards head-first; therefore, the function of this toe does not seem to be that of an anchor as in purely climbing species. Maybe the opposable toe could also improve stability during sitting on the ground, but sometimes the fifth toe is also spread apart, for a better balance during sitting. The bare-looking tail without a tuft is used as an additional prop when sitting on the ground. There is a particularly

long vibrissa near the heel on the inside of the foot which might function as a transmitter of tactile signals.

Like *E. webbi*, ***B. albicauda*** can be characterised as a **purely tree-dwelling, arboreal species** which could exclusively once be recorded on a tall massive tree with a wide trunk diameter. Observations of this species also proved *B. albicauda* to show very high site fidelity. This species only left its tree cavity for shorter excursions in the immediate vicinity and climbed slowly and unhurriedly through the highest tree-tops when foraging, repeatedly returning to its tree-cavity during each observational period. This climbing behaviour is well adapted to the broad structures of massive tree trunks; climbing down head-first also occurred; leaps, as for instance in the small *Eliurus* species, could not be observed. There are five conspicuously bulging and massive pads on **the hand of *B. albicauda***, as was the case for none of the other species studied. The extraordinarily massive pads are a clear sign of the importance of a large pad area for this species which has to climb along smooth, broad structures. The palms of the hands show neither lateral nor longitudinal furrows. Thus, bending of the hand or clinging to twigs is not possible. *B. albicauda* does not seem to depend on a high flexibility of the hand - the large pads would present an impediment - rather, the pads serve as adhesive organs that stick tightly to the ground under pressure. This results in increased friction and prevents slipping. Additionally, suction-cup-like depressions on the pads can create a vacuum for an improved grip on tree-trunks. Fusion of individual pads also occurs in *B. albicauda*, resulting in a particularly conspicuous thumb-thenar-pad which is massive and strongly convex, thus increasing the surface of the hand still further. All pads show conspicuous dermal ridges running around the pads and radiating from them. These dermal ridges are yet another adaptation to climbing on broad, smooth structures, as they as they provide additional grip. All claws are short and strong and can be anchored in the substrate thus increasing grip still further. The thumbnail is visibly shorter than the tip of the thumb which therefore is compressed when getting in contact with the substrate, thereby increasing adhesion and tactile sensitivity of the thumb. The carpal elevation is only moderately pronounced but appears to have a preening function, as in all species studied. The many long and clustered ulnocarpal vibrissae are particularly conspicuous and possibly fulfil a special tactile function. **The foot of *B. albicauda*** shows the same extreme adaptation to climbing on broad structures: six large and conspicuously prominent pads cover more than half the foot

sole and due to their profile prevent slippage. As was the case in none of the other species studied, the foot pads extend very far towards the tibia, thereby maximising the area covered by pads. As in the hand, there are no transverse or longitudinal furrows visible, making it unlikely that the foot is bent or rolled in walking. Instead, *B. albicauda* seems to achieve secure footing by its broad pads which even stick out sideways from the foot, e.g. the proximal hypothenar. It is also noticeable, that the distal thenar - one of the smaller pad components - is clearly discernible despite being merged with the large proximal interdigital pad I. At the centre of this "fused" pad there is a suction-cup-like depression providing adhesion to the substrate when compressed. Moreover, all other pads in conjunction with the large proximal thenar form a circular depression at the centre of the foot which also serves as a suction cup when compressed. Just as those of the hands, the foot pads show conspicuous dermal ridges running around the pads and radiating from them, thus increasing grip still further. The particularly long vibrissa at the heel points inwards between the feet and might transmit tactile information about the movement of the feet, thereby improving coordination in climbing. Literature describes *B. albicauda* as a somewhat ungraceful animal with a small range of movement (Garbutt 1999) which could be corroborated by the morphological results presented here. Only by careful steps and positioning of the chiridia, *B. albicauda* can move safely as an adhesive climber on broad and frequently slippery structures. Here, it is of interest that all five toes are very long in relation to the short volar surface of the soles and that in *B. albicauda*, as the single exception among all species studied, the fifth toe is longest. It can therefore be assumed that the fifth toe does not only serve as an opposable toe for grasping and can be pressed against the hallux when climbing but that this toe with its strong claw also functions as an exceptionally strong locking anchor that is dug into the surface when climbing down head-first. The long fifth toe can also be very helpful as balance on slippery surfaces when spread wide apart.

3.4.3 Area ratios of the hind feet as indicators for a first classification of each species regarding habitat use and locomotion

It could be demonstrated by the present study that the morphology of the hind feet allows a tentative classification of a species according to "habitat use and locomotion" using analysis of the area ratios of the hind feet. For this classification,

the percentage of foot pad area relative to the entire sole area was calculated for each species and compared between species.

It could be clearly shown that the one exclusively climbing species hardly ever found on the ground possessed the largest pad area in relation to the entire sole area. The foot surface of this climbing species (*B. albicauda*) is covered by pads to almost 90 %. If, additionally, the pads are also somewhat raised, massive and altogether look thick and swollen the foot cannot be bent and the respective species has to be categorised as an "adhesive climber" on massive broad structures. The presence of pronounced foot pads increases friction when climbing along broad vegetation structures and when the pads are pressed against the surface they acts as "suction cups" and thus prevent slipping on slick and broad substrate. Some species with a large pad area (in relation to the entire sole area) can also be classified as „adhesive climbers“ and “good diggers” in loose substrate due to their broad pads (e.g. *E. webbi* whose sole area is covered with pads to up to 73 %). For this species it can be assumed that its broad massive foot pads are advantageous for climbing as well as for shifting loose earth on the ground. Species that climb along fine thin structures clearly show a smaller pad area ratio in relation to the sole area. The smaller pads on the soles create inter-pad spaces which allow more flexibility of the feet. The feet can be bent and pressed together to hold on to twigs and stems. The pads stand just as far apart that they touch again when bending or grasping and thus help with fixing the substrate between them, in so-called "gripping grooves". In addition, a more flexible foot is also useful for scratching away hardened earth when digging. Species with these characteristics have between 45 and 46 % of their sole area covered by pads (*E. minor* und *E. grandidieri*) and can thus be classified as "grasping climbers" on fine structures. Additionally, one species at the study site could also be identified as an "adhesive climber" on wide structures, but possessed a smaller pad area ratio (*E. tanala* with only 43 % of the sole covered by pads). For this species, in addition to climbing and digging, a unique swimming and wading behaviour could be recorded. It might possibly be an advantage of smaller pads to decrease drag when moving in water, although this species has to be primarily regarded as arboreal and a climber on wide structures and therefore ought to have broad massive pads. Here, it showed that other morphological traits could make up for the lack of broad massive pads in relation to the sole area (e.g. a distinct lateral furrow for flexibility of the foot parts, a bean-shaped elongated thenar, or "suction

cup"-like merged pads). As the pad area decreases in relation to the sole area, a species can be increasingly categorised as a ground dweller and good runner. Here, it is also important to distinguish between species that occasionally "climb" and "dig" (*G. roberti*, with 41 % pad area in relation to the sole surface) but also primarily move on the ground and at the other end of the spectrum a downright "long distance runner" with a pad area ration of only 37 % (*N. rufus*). Here, morphological adaptation to "running" comes in the shape of a smaller pad area and less prominent pads that reduce friction against the ground and larger spaces between the pads allowing better, easier and more flexible bending of the foot.

4. Chapter – Conclusion and outlook

Seven endemic rodent species were recorded at Maromizaha comprising *Eliurus grandidieri*, *E. minor*, *E. tanala*, *E. webbi*, *Nesomys rufus*, *Gymnuromys roberti* and *Brachytarsomys albicauda* as well as the non-endemic *Rattus rattus*. Compared to other rainforest areas nearby (Ampitambe or Ambohimitambo, with 3-5 rodent species per locality (Carleton 1994)), Maromizaha is very rich in rodent species. The highest diversity of indigenous rodents after the richness of Maromizaha was encountered on the slopes of the Réserve Spéciale d'Anjanaharibe-Sud (Goodman and Carleton 1998), with nine endemic nesomyine species in more different habits (like a slightly disturbed lowland moist forest, primary montane and sclerophyllous forests). Species distribution depended on particular vegetation characteristics such as the density of trees and their different size, the degree of vegetation cover, vegetation strata and the rate of light transmission of the canopy. Some sympatric species were unique in their ecological requirements and habitat use; e.g. *E. webbi* and *E. minor* used the same general area but differed in the use of their microhabitats. As a typically arboreal species *E. webbi* was exclusively found on tall, sturdy trees with a large trunk diameter. *E. minor*, by contrast, was mainly caught on bushes, lianas and filigree vegetation in dense undergrowth. In conclusion, the endemic rodents at the study site at Maromizaha can be assigned to four categories, according to their use of vegetation and niche occupation: **1.) Exclusively arboreal** rodents such as *B. albicauda* and *E. webbi* occupy niches on **trees with a large trunk diameter**: these two species were trapped at sites with a high density of very large trees, a low herb cover and a high degree of cover at the upper canopy level. A dense herb layer can only thrive where lacking or sparse tree cover allows enough light to reach the ground (Mühlenberg 1989). The results therefore point at a preference for denser, more closed microhabitats with a continuous canopy which provides better protection from birds of prey and might also be advantageous for locomotion on big trees and to find suitable roosting sites. **2.)** The sometimes **ground-dwelling and arboreal** species *E. tanala* mainly occurs on **massive large trees** in **riverine** habitats. It was often trapped in the vicinity of large dragon trees where it shelters in tree cavities. Additionally, it appears to be closely associated with fresh water because of its feeding habits. **3.)** Sometimes **Ground-dwelling and**

arboreal species that can be considered good **climbers of bushes** such as *E. grandidieri* and *E. minor* were caught significantly more often at sites characterised by a high density of trees with many lianas as well as plenty of bushes and low vegetation. They are not exclusively adapted to dense filigree vegetation by their mode of locomotion but are also able to climb small thin and long branches in the shrub layer. Moreover, these two species became independent of tree holes by their roosting habits in open vegetation structures. **4.)** Primarily **ground-dwelling terrestrial** species such as *G. roberti* and *N. rufus* showed a preference for drier habitats with a particularly high density of bushes, undergrowth and plenty of hiding places at ground level, frequently situated on slopes. They were caught significantly more often at sites with a high percentage of ground, shrub and medium high cover. As predominantly ground-dwelling and partially diurnal species they appear to prefer areas with high ground cover that hides the small mammals from predators.

All of the endemic rodent species are threatened by habitat loss through deforestation for conversion to agricultural land and for charcoal production. Additionally, some of the larger rodent species (like *B. albicauda*) are hunted, as local people do not consider them as rodents but assume that they belong to the lemurs. The endemic rodents are very sensitive to forest change and logging. *E. tanala* was the only endemic rodent species which could be recorded along watercourses in a degraded area. This species appears to have acquired a higher tolerance towards anthropogenic influenced habitats by adapting to riverine ecosystems. It is still unclear, how this species avoids competition with the introduced Black Rat, which was the most common species at the burned agricultural site. There is strong evidence of other authors, that all nesomyine species (especially those found above 800 m) suffer 100 % mortality from plague carried by introduced rodents (Duplantier et al. 2003, Laakkonen et al. 2003).

Combining the results of habitat preferences with the morphology of the hands and feet, referring to the dissertation of Ziekur (2004) which describes morphological differentiations of the chiroidia of 24 African muroid species, and interprets as well functional and ecological adaptations, nearly the same typical characteristics of certain modes of locomotion became apparent for the Malagasy species: **1.) position and relative size** of the individual pads in relation to each other, **2.) pad prominence**, **3.) claw length and width** and **4.) flexion furrows**. In addition, there are two more characteristics of the hand which are of functional relevance: **5.) size**

of the proximal pads in relation to the distal pads of the hand and **6.) length of the thumb nail**. **7.) The ratio of the respective sizes of proximal and distal pads of the feet** provides a characteristic which is useful for the analysis of functional features. **8.) Finally, the ratio of foot sole surface and the combined area of all volar pads of the feet** can be used to characterise a species' habitat use.

Trait 1.) Position and relative size of the individual pads: The so-called "pad configuration" indicates whether a species is a climber or a ground-dweller. Large and wide pads that stand closely together and are partly merged with other pads point at an arboreal, climbing species. Small pads, separated by wide gaps not merged with neighbouring pads, signal a ground-dwelling, running species. In case the distal pads are smaller and more widely spaced than the carpal pads, the species can be attributed digging abilities. A pronounced apical pad of the thumb can serve as support when bending the long fingers of a digging hand. If the proximal pads of the hand are larger and of more elongated shape than the distal pad this indicates a **grasping climber**. If the pads of the hand are extraordinarily massive and wide and form a large pad area this characterises an **adhesive climber**. **Trait 2.) Prominence of the pads:** If the pads are prominent and raised this indicates a climbing, arboreal species. If the pads are visibly flattened, this in turn points to a running and digging species living on the ground. **Trait 3.) Claw length and width:** Climbing species are characterised by short claws. Short and fine claws can be anchored in the climbing substrate. If, by contrast, the claws are short and strong, they are not used as anchors in the climbing substrate but rather point at locomotion on broad hard climbing structures. Ground-dwelling and digging species have long claws. Particularly long, sturdy claws on the toes are useful for scratching. **Trait 4.) Flexion furrows:** Bisection of the hand by a traverse furrow is a sign of its "pliability". A traverse furrow which is strongly pronounced points towards a hand that is used for grasping and holding. Such species usually are climbers that prefer an arboreal life style. If, additionally, there is a marked longitudinal furrow, this indicates an extremely good climber preferring slender filigree vegetation, a so-called "grasping climber". In these species, the two furrows intersect at the centre of the palm. If the furrows are only slight or almost absent this, in conjunction with broad pads, characterises another group of arboreal species: so-called "adhesive climbers". Slight furrows in combination with small pads, on the other hand, indicate mainly ground-dwelling species that are "good runners". A weak traverse furrow points at terrestrial species

with digging habits. This also applies to the foot: If the traverse furrow is visible, this characterises a grasping climber. If the flexion furrows of the foot are only slight or absent this, in combination with broad pads, indicates an adhesive climber. If there is no clear traverse furrow and the pads are small, this points to mainly ground-dwelling species and good runners. Flexion of the foot during running causes the presence of several smaller furrows on the sole. **Trait 5.) Size of the proximal pads of the hand in relation to the distal pads of the hand:** If the proximal pads are large in comparison with the distal pads and stand out towards the traverse furrow, the animal has excellent grasping abilities. The enlarged and projecting proximal pads of the hand can be pressed against the distal pads very efficiently when grasping and the furrow helps to firmly hold items. This trait does not only fulfil a "grasping function when climbing" but also can be useful when "digging and grabbing on the ground". Less projecting proximal pads are less suited to grasping vegetation but provide improved adhesion on slick surfaces, which is of particular advantage when climbing on broad or slippery substrate. **Trait 6.) Length of the thumbnail:** If the thumbnail is shorter than the thumb or of equal length, the thumb has an important tactile function. The periphery of the thumb, uncovered by a nail, has increased tactile sensitivity which is important for climbing and grasping. Furthermore, a nail-free tip can be deformed by pressure, thus improving adhesion to the substrate which is useful for climbing. A thumbnail of equal length with the tip of the thumb or longer serves as protection of the sensitive tip when digging. Additionally, a long nail can create a wider „shovel“, when digging by stabilising the bent hand. **Trait 7.) The ratio of the respective sizes of proximal and distal pads of the feet:** Proximal pads that are smaller or of equal length in relation to the distal pads characterise species that depend on a high flexibility of the foot for running or digging. Larger proximal pads (the proximal thenar frequently being the largest and elongated to bean-shape) in relation to the distal pads are typical of climbing species. If the proximal pads are much larger than the distal pads, the climbing species is not able to gain foothold by grasping but rather relies on the adhesive powers of its pads when moving on broad substrate. **Trait 8.) Area covered by all volar pads of the foot in relation to the area of the sole:** If the volar pads cover almost the entire sole of the foot, this characterises an arboreal species. If, in addition, the pads also form larger units the species can be classified as an adhesive climber on massive, broad structures. Furthermore, a large pad area is also useful for digging in loose ground, but usually

reflects mainly arboreal habits. A markedly smaller pad surface area characterises grasping climbers on fine, thin structures. As the pad area decreases in relation to the entire sole surface, a species can be classified more and more as a ground-dweller and good and fast runner. So-called long-distance runners show the smallest pad area.

In conclusion, applying these general morphological characteristics of hands and feet, the endemic rodent species of Madagascar can be newly classified concerning to their ecology. The traits are the result of a functional adaptation to the habitat and thus allow detailed insights into a species' way of life and its behaviour. The morphological traits therefore provide an entirely new method for an ecological classification of nesomyine rodents reflecting their habitat use and mode of locomotion. In the future, the protection of the last remaining rainforests and the reconnection of forest fragments by reforestation are the most important requirements for the survival of the Malagasy Nesomyines. International and local conservationists in Madagascar urgently need ecological data on microhabitat preferences of small mammals for a more improved reforestation planning and further detailed environmental education. The sensitisation of the rural population, the training for reforestation projects and the training of local tourist guides, is one of the major aspects relevant for nature conservation. This study provides a first insight into the ecology and niche separation of many specialised Malagasy rodents. Apart from further research in the primary forests, the effects of reforestation on species diversity have to be examined. The species inventory of the Malagasy primary forests is still incomplete. Further small mammal surveys will most likely discover new species and future research will enable us to better understand the ecological requirements of the diverse taxa. Nevertheless the endemic rodents of Madagascar could provide a model for the protection of microhabitats of small mammals in general.

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Appendix

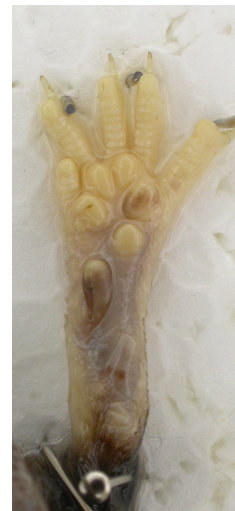
Fig. 29: Pictures of Chiridia and life pictures of all seven rodent species



Eliurus grandidieri



Eliurus minor

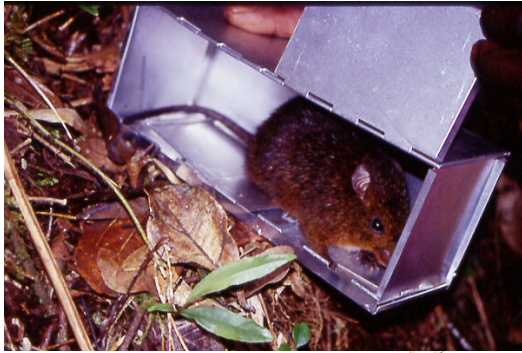


Eliurus tanala



Eliurus webbi





Nesomys rufus



Gymnuromys roberti



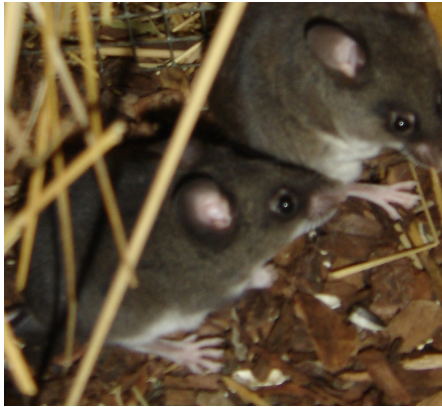
Fig. 30: Picture of the Maromizaha Forest and a posed Sherman life trap



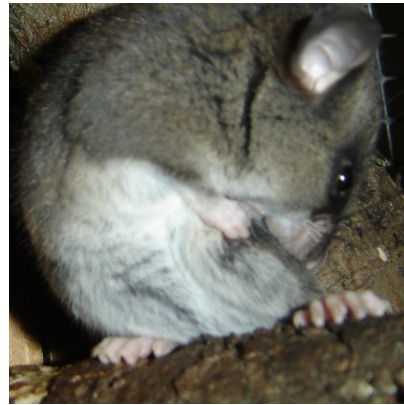
Brachytarsomys albicauda



Fig. 311: Pictures of locomotion and position behaviour of *Eliurus grandidieri*



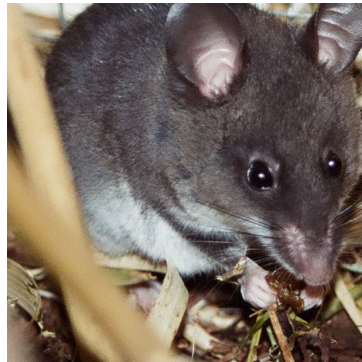
Flexible hands for digging and grasping



Preening with the carpal elevation on the wrist, brushing belly and back



Climbing down vegetation head-first, opposable gripping toe is used like pliers or a locking anchor



For feeding, hands are able to hold food



During sitting position, the fifth toe can be spread wide apart



A nesting-group with several adults and 2-3 juveniles



Swiftly climber on fine structures

Curriculum vitae

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- 04/2010 – 3/2011 Elternzeit
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- 01/03 - 01/05 **Wissenschaftliche Volontärin** am SMNS, in der Abteilung Zoologie /Mammalogie. **Die Arbeitsgebiete** umfassten: Wissenschaftliche Datenerfassung, Taxonomie, Inventarisierung und Leihverkehr. Öffentliche Führungen, wissenschaftliche Mithilfe von Sonderausstellungen, Vorträge, Führungen und Publikationen. In den Jahren 2003/ 04/ 05/ 06 Planung und Vorbereitung der Forschungsreisen nach Madagaskar, zur Erfassung der Kleinsäugerfauna mit jeweils dreimonatigen Forschungsaufenthalten im Regenwaldgebiet von Andasibe, Ost-Madagaskar.
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2004	3. Posterpreis im Rahmen der 7. Jahrestagung der Gesellschaft für Biologische Systematik (GfBS) in Stuttgart: Marquart, Kathrin (2004): Diversität und Ökologie endemischer Nagetiere (Nesomyinae) im „Drachenbaum-Regenwald“ von Ost-Madagaskar.

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05/2006	Austauschstipendium von Synthesys (European-funded Integrated Infrastructure Initiative grant) zur Bearbeitung der Nesomyinen am BMNH (British Museum Natural History) in London.
09/2005	Austauschstipendium von Synthesys zur taxonomischen Überarbeitung der Nesomyinen am MNHN (Muséum National d'Histoire Naturelle) in Paris.

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2005 u. 2006	Betreuung der Diplomarbeit von Michael R. Manesimana an der Universität Antananarivo, Faculté des Sciences, Département de Biologie Animale, mit dem Thema: Contribution a l'étude de la biologie, de l'écologie et de l'éthologie de deux rongeurs: <i>Eliurus tanala</i> et <i>Nesomys rufus</i> , dans la forêt Maromizaha – Andasibe.
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List of publications

- Dieterlen, F., Turni, Marquart, K. (2013): Type specimens of mammals in the collection of the Museum of Natural History Stuttgart. – Stuttgarter Beiträge zur Naturkunde A, Neue Serie 6: 291-303.
- Marquart, K. & Harisoa, V. V. (2006): Biodiversity and Ecology of Endemic Rodents (Rodentia: Nesomyinae) at the "Dragon Tree Rainforest" Maromizaha, Andasibe, Eastern Madagascar. - Proceedings of the German-Malagasy Research Cooperation in Life and Earth Sciences, 16: 191- 202. Berlin Concept Verlag.
- Marquart, K. (2004): Geheimnisvolle Ratten im "Drachenbaum-Regenwald". Die Quastenschwanzratten in Ost-Madagaskar. - Rodentia, 52-55.
- Marquart, K. (2003): A comparative analysis of population densities of mouse lemurs and other lemur species at two dry deciduous forests in the region of Ankarafantsika, north-western Madagascar..- Lemur News, 8: 27-28.
- Marquart, K. (2002): Vorkommen und Populationsdichte von Mausmakis und anderen Lemuren in zwei unterschiedlichen Trockenwald-Gebieten in der Region Ankarafantsika, Nordwest-Madagaskar: Diplomarbeit, Tierärztliche Hochschule Hannover/Universität Hohenheim, Zusammenfassung. - Rundbrief der Gesellschaft für Primatologie, 29: 23-24.

Posters

- Marquart, K. & Dieterlen, F. & Steidle, J. (2009): Ecology and morphological adaptations of the chiroidea in Malagasy rodents (Muroidea: Nesomyinae). Willi Hennig Symposium vom 29.09.-2.10.2009 an der Universität Hohenheim, Stuttgart.
- Marquart, K. & Dieterlen, F. (2009): Morphological adaptations of the chiroidea in Malagasy rodents (Muroidea: Nesomyinae). 6. International Tropical Zoology Symposium zum Thema Tropical Vertebrates in a Changing World, vom 3.-8.05.2009 am Zoologischen Forschungsmuseum Alexander König in Bonn.
- Marquart, K. & Voahangihirinirina, V. H. (2004): Distribution, composition et écologie des rongeurs (Rodentia: Nesomyinae) de la Forêt des arbres Dragons Maromiza á

Andasibe, l'est de Madagascar. Internationale Tagung / Symposium zum Thema:
Madagascar- un jardin d'évolution en danger. German-Malagasy research
cooperation in natural sciences. 5.-6.10.2004 an der Universität Antananarivo,
Madagaskar.

Marquart, K. (2004): Diversität und Ökologie endemischer Nagetiere (Nesomyinae)
im „Drachenbaum-Regenwald“ von Ost-Madagaskar. 7. Jahrestagung der
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Museum für Naturkunde Stuttgart.

Stuttgart, 10. November 2014

Kathrin Marquart

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Kathrin Marquart

Eidesstattliche Versicherung

Anlage 2 zur Promotionsordnung der Universität Hohenheim zum Dr. rer. nat.

Eidesstattliche Versicherung gemäß § 7 Absatz 7 der Promotionsordnung der Universität Hohenheim zum Dr. rer. nat.

1. Bei der eingereichten Dissertation zum Thema

**Habitat use and morphological adaptations of endemic rodents
(Muroidea: Nesomyinae) of East Madagascar**

handelt es sich um meine eigenständig erbrachte Leistung.

2. Ich habe nur die angegebenen Quellen und Hilfsmittel benutzt und mich keiner unzulässigen Hilfe Dritter bedient. Insbesondere habe ich wörtlich oder sinngemäß aus anderen Werken übernommene Inhalte als solche kenntlich gemacht.

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Stuttgart, 10. November 2014



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Kathrin Marquart