

Journal of Tropical Ecology (1993) 9:101–107. With 2 figures

SHORT COMMUNICATION

Activity patterns of two species of *Nesomys* (Muridae: Nesomyinae) in a Madagascar rain forest

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KEY WORDS: *Nesomys*, rodents, Madagascar, ecology, activity.

The Nesomyinae is a subfamily of muroid rodents endemic to Madagascar (Carleton & Musser 1984). Ten species in seven genera are now recognized (Corbet & Hill 1986, Petter 1972, 1975), but it is likely that the Nesomyinae contains more species than previously recognized (Carleton & Schmidt 1990). The genus *Nesomys* contains a single species, *N. rufus*, with three recognized subspecies: *N. r. rufus*, *N. r. audeberti*, and *N. r. lambertoni* (Petter 1975). Specimens of *N. r. lambertoni* are known only from the type locality in western Madagascar near Maintirano. The other two subspecies inhabit eastern and northern rain forests, with *N. r. audeberti* found in lowland rain forest (from sea level to 1000 m) and *N. r. rufus* restricted to montane rain forests (900–2300 m; Carleton & Schmidt 1990).

During July 1987 we found that both *N. r. rufus* and *N. r. audeberti* co-occurred at 900–1000 m elevation at Parc Nationale de Ranomafana. The syntopic distributions and discrete characters observed near Ranomafana for the two forms suggest their genetic isolation. Taxonomic studies are underway to clarify the status of the two forms. We consider that these two currently recognized subspecies are species, and hereafter we refer to the two forms as *N. rufus* and *N. audeberti*. We undertook a preliminary study of the ecology of *Nesomys* in an area of overlap between lowland and upland forms, with the aim of describing their activity patterns.

The study site is located on a ridge top at 900–1000 m elevation in Parc Nationale de Ranomafana (21° 15' S; 47° 26' E), near the village of Ranomafana, Province de Fianarantsoa. This area is classified as eastern montane rain

forest (Jenkins 1987) and receives an average annual rainfall of between 2000 and 3000 mm. The site is on steep mountain slopes. The vegetation is characterized by a 20–25 m canopy forest and is transitional between lowland rain forest and high elevation sclerophyllous forests (1300–2300 m). Epiphytes, lianas, mosses, orchids, and lichens are very abundant, the herb layer is well developed, and ground litter is extensive with a dense root mat.

When captured in the field, the two forms of *Nesomys* are easily separable by differences in colour of the venter, body weight and hindfoot length. *Nesomys rufus* is the smaller form. The mean body weight of 19 *N. rufus* males was 176.6 gm (SE = 3.44), which is significantly different from that of eight *N. audeberti* males (224.3 gm; SE = 6.86; Mann-Whitney U test, $P < 0.001$). Eleven female *N. rufus* averaged 146.2 gm (SE = 3.7) in body weight compared with 205.7 gm (SE = 13.5) for seven female *N. audeberti* (Mann-Whitney U test, $P < 0.05$). Hindfoot lengths average 49 mm for *N. rufus* (both sexes) and are significantly smaller than those of *N. audeberti* (54.6 mm; Mann-Whitney U test, $P < 0.001$). *Nesomys audeberti* has a white belly, while *N. rufus* has a rufous venter with white hairs confined to the chin and throat region and bright reddish hairs on the cheeks and flanks.

Radiotracking studies were conducted from June to August in 1987–1989, and spool and line tracking was done in 1989. *Nesomys* were captured with live-traps (National live traps) and were sexed, measured, weighed and ear-tagged with numbered fingerling tags. All animals were released at the capture site after handling. Four *N. audeberti* and four *N. rufus* (2 scrotal males and 2 adult females each) were selected for radiotelemetry, anaesthetized with an intramuscular injection of ketamine hydrochloride and fitted with 10 gm motion-sensitive radio transmitters. Transmitters broadcast at two pulse rates depending on the activity of the animal. Animals were located by use of a hand-held three-element-Yagi antenna.

We tracked two animals simultaneously on foot. Locations were triangulated from three compass bearings taken at three mapped trail marker numbers. Appropriate trails were selected to ensure the intersection of the three bearings. Bearings were taken nearly continuously (every 5–10 minutes) from pre-dawn until after dark. Animals were also tracked at various intervals during the night to verify that they remained in their dens until just after dawn. We located dens of radio-tagged animals by plotting the bearings on a trail map of the site. Minimum-convex-polygons were calculated for each animal following procedures outlined by Stickel (1954) and Mohr & Strumpf (1966).

We used a spool-and-line tracking method modified from Anderson *et al.*, (1988), Berry *et al.*, (1987) and Miles *et al.*, (1981) to locate den sites and to get a preliminary view of movement patterns and microhabitat use. We attached a spindle of no. 5 nylon reverse-wound thread (Culver Textiles Corp.) between the shoulder blades of the animal and followed the trail of thread that unwound as the animal moved through the forest. Spools contained approximately 175 m of thread that played out from the inside of the spindle so that there was no spool

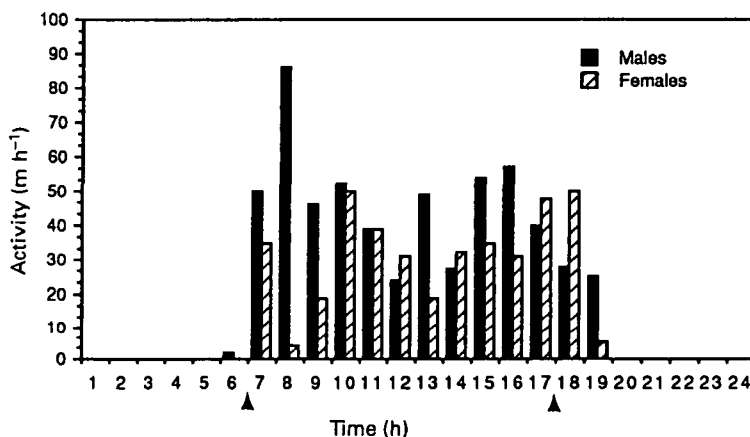


Figure 1. Daily activity patterns of two male and two female *Nesomys rufus* radiotracked in this study. Activity is expressed as the mean distance moved (m h^{-1}) for each sex over the study period. Arrows indicate sunrise and sunset on a 24-hour time scale.

or housing. Spindles ($3 \text{ cm} \times 1 \text{ cm}$) were encased in 0.5 inch heat-shrink electrical tubing, which prevented the outer layers of thread from catching on vegetation and allowed the completed package to be glued directly to the animal's fur using Gel Super Glue. Completed spools weighed 1.96 g (SD = 0.04 g; $N = 10$). On days spools were attached, we set traps at 1500 h and checked them at 1600 h. Ten traps usually captured five *Nesomys* in one or two hours. Spools were quickly glued to unanaesthetized rats without inhibiting their respiration or locomotion. Spools generally remained attached to the animals for several days, even in heavy rains.

We followed thread trails the day after attachment. A trail ended either when the thread was broken and no trail could be found several metres away, when the spool was found, or when the thread ran out. Courses were plotted by taking compass bearings and estimating the length of thread (m) between each direction change. Thread was removed from the forest floor during tracking to avoid confusion with trails of other animals. Plots of thread trails gave a precise topological map of each rat's activity. Thread trails often led to den sites because animals began heading to dens between 1730 and 1900 hours each night. Trails also showed details of habitat use and evidence of foraging (e.g. discarded or partially eaten fruits and seeds).

We defined activity as movement determined by changes into radio-transmitter pulse-rate and/or sequential radio-locations (Emmons 1988). An animal that was feeding or grooming (behaviourally active) would be determined to be inactive. Although sample sizes are small, the daily activity patterns of individuals of both species in this preliminary study were entirely diurnal and crepuscular. Male *N. rufus* tended to leave their dens earlier than females, usually at or just before sunrise (0630 hours; Figure 1). Males had three periods of increased activity (early morning, mid-day, and early afternoon). Females

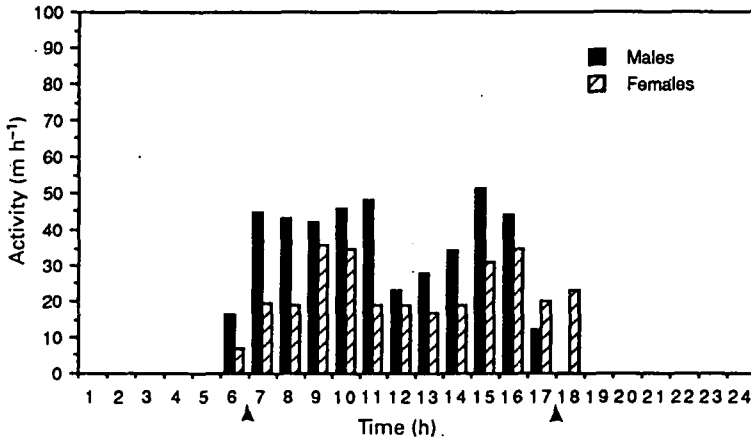


Figure 2. Daily activity patterns of two male and two female *Nesomys audeberti* radiotracked in this study. Activity is expressed as in Figure 1.

showed a trough in activity at mid-day and remained active until just before dusk (Figure 1). Male activity declined steadily from 1600 h to dusk. Activity of male and female *N. audeberti* was bimodal during our study period (Figure 2). Male and female *N. audeberti* left their dens just before sunrise. Both sexes were active in the morning and afternoon with a decline in activity at mid-day. All rats returned to their dens by 1900 h and remained there until the following morning. Male *N. audeberti* were more active than females for all but the last few hours of the day. Females tended to enter their dens later in the evening than males.

Male *N. audeberti* had home ranges of approximately 1.4 ha compared with only 0.5 ha for females. Male and female *N. rufus* had home range areas between 0.4 and 0.6 ha. Home-range area was not correlated with the number of radiolocations (Spearman's rank correlation, $r = -0.166$, $P > 0.5$), indicating that variation in home range area was not caused by variation in the number of radiolocations.

Nesomys species did not use exclusive home ranges either intra- or intersexually. For example, male *N. audeberti* home ranges overlapped with both conspecific males and females. Live-trapping in the study area showed that each individual (of each species) shared its home-range with between two and eight other animals. For example, *N. rufus* female no. 325 shared a portion of its area with at least three other *N. rufus* (two males and one female). *N. rufus* male 318 overlapped with two male *N. audeberti* (308 and 311) and two female *N. audeberti* (376 and 326), as well as a conspecific male and female. There was similar intra- and interspecific overlap in the home-ranges of male and female *N. audeberti*. Aggressive chases were rarely observed even though animals were occasionally observed within several metres of one another.

Average daily movements of individuals were fairly uniform. Distances represent underestimates because certain days were incompletely sampled (lost

transmitter signals over various time spans). On average *N. rufus* travelled 400 m (SD = 39 m) day⁻¹. Females seemed to travel shorter distances per day and per hour than males. *Nesomys audeberti* of both sexes travelled 441 ± 56 m day⁻¹ on average. We regularly observed solitary *Nesomys* travelling through vegetation on the forest floor. Typical undisturbed movement patterns were erratic and consisted of short bursts of running interspersed with slow walking or stationary periods. The movement rate was between 34 and 84 m h⁻¹. These observations were consistent with data from thread tracking.

We tracked *N. audeberti* and two *N. rufus* with spool-and-line. These records gave precise movement patterns for an undetermined portion of the day. Thread trails showed that both species stayed close to downed logs, brush piles, and dense tangles of herbaceous vegetation when travelling. Movement was characterized by short (<3 m) zig-zags, with occasional straight runs of up to 10 m and numerous instances of doubling back on existing trails. Long straight runs tended to be across more open ground or when the animals crossed trails. All movements were terrestrial and only rarely did animals move along the top of fallen logs.

Each animal had several widely dispersed dens in its home-range. Five den sites (of three animals) were located with thread trails. Three of these dens were excavated later by hand. Typically, a den was located under brush piles or at the base of large trees with extensive root systems. Each den had several entrances that were approximately 7 cm in diameter and 2–3 m apart. All excavated dens were multichambered, with chambers located on two levels. Burrows leading into these chambers were always lined with freshly clipped grasses. Deeper chambers appeared to be used for sleeping, as they were lined with very finely shredded palm fronds (made by tearing thin strips from the dried petioles of dead fronds found lying on the ground). These palm trees (local name 'lafa'), grow to 8 m and are scattered throughout the study area. The bedding, 2–3 cm thick, was dry, and looked like pine-needles. It covered only the floor of the chamber and was arranged in a circular pattern approximately 20 cm in diameter. There were no food caches or latrines found in the three den systems excavated.

Dens were used primarily during the night. Several times animals went to den sites during mid-day, but this was unusual. Some rats used different dens on different nights, but most repeatedly returned to preferred sites. Although difficult to confirm, we believe that males and females (of a species) occasionally share dens. For example, on 3 August 1989, a *N. rufus* male (318) and female (321) had nearly identical radiolocations at sunset and afterwards.

Of three *N. rufus* marked in 1988, one was recaptured in 1989 only 10 m from its original capture site. Three male and six female *N. audeberti* were marked in 1988. Of those nine animals, only one male and one female were recaptured in 1989. Both animals were recaptured within 100 m of their 1988 capture sites. These data suggest that individuals of both species retain approximately the same home-range for more than one year.

The data presented here demonstrate that both species of *Nesomys* are

exclusively diurnal. Diurnal murid rodents are rare in tropical rain forests (Emmons & Feer 1988). Indeed, rain forests in Borneo lack diurnal murids entirely. In African rain forests, only species in the genera *Hybomys* and *Lemniscomys* are terrestrial and at least partially diurnal (Duplantier 1982, Kingdon 1974). Diurnality may be linked to lower energetic costs associated with high elevations or may be made possible by the deep litter/root layer which allows these rats easy access to escape routes. Alternatively, lack of competitors and/or fewer diurnal predators may have allowed *Nesomys* species to exploit the diurnal niche.

In addition to *Nesomys*, there are four other rodent species at our study site in Madagascar (*Brachytarsomys albicauda* Gunther 1875, *Eliurus minor* Major 1896b, *E. myoxinus tanala* Major 1896a, and *Gymnuromys roberti* Major 1896a, pers. obs., Carleton & Schmidt 1990). At our study site the two species of *Nesomys* occur at high densities and are probably the most abundant rodents in this community. *Brachytarsomys* and both *Eliurus* species are nocturnal and exclusively arboreal. *Gymnuromys roberti* is nocturnal and terrestrial. Thus, the terrestrial niches are occupied by the two diurnal species of *Nesomys* and a single nocturnal species, *G. roberti*.

The eastern rain forests of Madagascar provide a unique opportunity to study a murid rodent community of manageable diversity and accessibility. However, because of the preliminary nature of this study, many questions remain unanswered. Long-term data are needed to document seasonal fluctuations in activity patterns for *Nesomys* species and to determine home-range size and use. Likewise, data are needed on the level of competition between the two species, the role predators play in regulating population density, duration of the pair bond, and the type of reproductive system exhibited by *Nesomys* species.

ACKNOWLEDGEMENTS

This research was supported by grants from the Smithsonian Institution and Hobart and William Smith Colleges. Dr P. Wright provided invaluable logistical support along with the use of her field site near Ranomafana. Thanks also go to A. Wright, P. Daniels, A. Yoder, E. Raholimavo, D. Quammen, and the people of Ambatolahy and Ranomafana. We are grateful to M. Carleton for reading earlier drafts of this manuscript.

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Accepted 2 July 1992