Diet, activity patterns, foraging movement and responses to deforestation of the aquatic tenrec *Limnogale mergulus* (Lipotyphla: Tenrecidae) in eastern Madagascar

Jonathan P. Benstead*, Kevin H. Barnes and Catherine M. Pringle

Institute of Ecology, University of Georgia, Athens, GA 30602, U.S.A.

Abstract

The aquatic or web-footed tenrec *Limnogale mergulus* is a semi-aquatic lipotyphlan insectivore known only from stream habitats of eastern Madagascar. *Limnogale* is considered a high conservation priority because of its rarity, suspected vulnerability to habitat degradation, and unique ecological niche on the island. However, its ecology and behaviour remain poorly understood. Quantitative faecal analysis and radio-tracking were used to study the diet and foraging activity of *Limnogale* in eastern Madagascar. Faecal pellet counts along forest and zero-canopy streams were also conducted to examine the response of aquatic tenrec populations to catchment deforestation. Faecal analysis indicated that the diet of *Limnogale* consists mainly of larval and adult aquatic insects, larval anurans and crayfishes. The most important prey were Ephemeroptera, Odonata and Trichoptera larvae. Diets did not differ substantially between forest and zero-canopy streams. Radio-tracking of two individuals indicated that *Limnogale* is strictly nocturnal and remains in streamside burrows during daylight. Nocturnal movement was restricted solely to stream channels and consisted of active foraging by swimming and diving. Distance travelled per night ranged from 200 to 1550 m along the stream channel (means 1067 and 860 m, respectively). The total lengths of stream channel used by the two aquatic tenrecs during each radio-tracking study were 1160 and 505 m, respectively. Faecal pellet counts along forest and zero-canopy streams suggested that *Limnogale* was at least as abundant in zero-canopy streams. This finding suggests that *Limnogale* is not an obligate forest species; however, it preys on benthic communities that are extremely vulnerable to sedimentation. Control of excessive sedimentation and maintenance of healthy benthic communities are essential to *Limnogale* conservation. We include an updated list of known sites for *Limnogale* and recommend the use of faecal pellet surveys to assess the current distribution of the species.

Key words: activity patterns, diet, *Limnogale mergulus*, Madagascar, Tenrecidae

INTRODUCTION

The aquatic or web-footed tenrec *Limnogale mergulus* is a large (80–100 g) semi-aquatic lipotyphlan endemic to Madagascar (Fig. 1). This monotypic genus is the only semi-aquatic representative of the Malagasy mammal fauna. In its ecology and behaviour, *Limnogale* seems to be most similar to the smaller African otter shrews *Micropotamogale ruwenzorii* and *M. lamottei*, neotropical ichthyomyine rodents *Chibchanomys, Ichthyomys, Neusticomys* and *Rheomys* spp., New Guinean hydromyine rodents *Crossomys* and *Hydromys* spp., Holarctic water shrews *Sorex, Neomys, Chimarrogale* and *Nectogale* spp., Pyrenean desman *Galemys pyrenaicus*, and Ethiopian water mouse *Nilopegamys plumbeus*. This taxonomically diverse group of small mammals represents a remarkable example of convergent evolution for semi-aquatic carnivory (Malzy, 1965; Vogel, 1983; Stone, 1987*a,b*; Voss, 1988; Hutterer, 1992; Flannery, 1995; Peterhans & Patterson, 1995; Barnett, 1997; Churchfield, 1998).

Populations of *Limnogale* seem to be restricted to fast-flowing streams of the eastern highlands and escarpment (450–2000 m) of Madagascar (Fig. 2, Table 1). Only 10 sites are known for the species, and at least two of these may no longer support populations because of habitat degradation (Nicoll & Langrand, 1989). Degradation of stream habitats in the region is caused by extensive clearance of the original eastern rainforest for traditional slash-and-burn (*tavy*) agriculture (Green & Sussman, 1990; Benstead *et al.*, 2000). Deforestation eventually causes accelerated erosion and subsequent sedimentation within stream channels

*All correspondence to: J. P. Benstead.
E-mail: benstead@sparc.ecology.uga.edu

Fig. 1. Aquatic tenrec *Limnogale mergulus* trapped from the Tomaro stream in the peripheral zone of Ranomafana National Park, eastern Madagascar, May 1998. Photograph by Kevin H. Barnes.
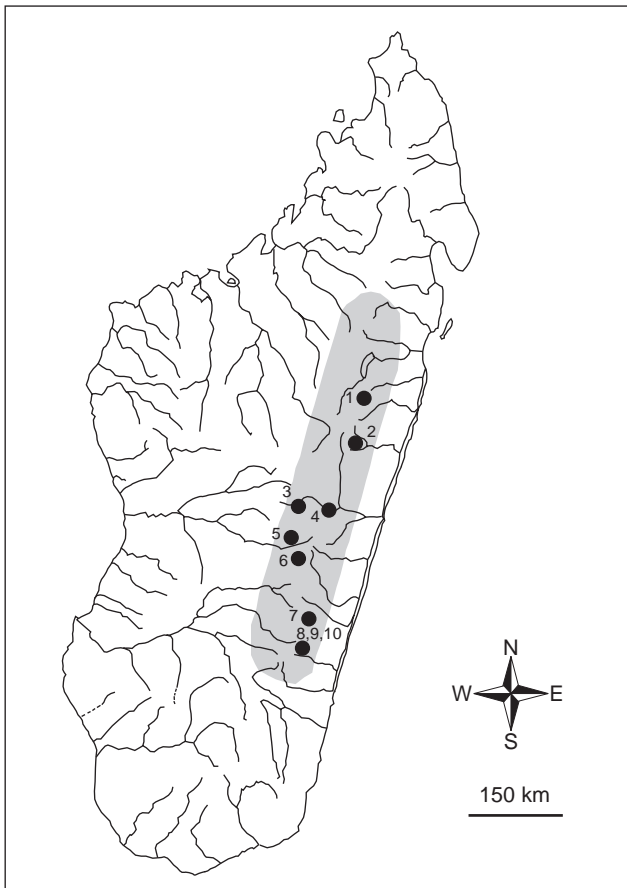
(Le Bourdiec, 1972; Helfert & Wood, 1986). Such sedimentation is expected to cause considerable changes in the benthic invertebrate communities on which *Limnogale* preys. *Limnogale* may also be threatened by accidental drowning in traditional eel and crayfish traps (Nicoll & Langrand, 1989; Nicoll & Rathbun, 1990). Currently, only five sites are known to support populations. Because of its restricted distribution and threatened habitat, and because it occupies a unique ecological niche in the Malagasy fauna, *Limnogale* is considered one of the highest lipotyphlan conservation priorities globally (Nicoll & Rathbun, 1990).

Like that of many small semi-aquatic mammals, the ecology of *Limnogale* is poorly understood. Since the species was described in 1896, fewer than 40 individuals have been captured by scientists (Malzy, 1965; Nicoll & Rathbun, 1990; M. Nicoll & L. Olson, pers. comm.). Malzy (1965) trapped 14 individuals from the north and central areas of the species' range and reported physical measurements and qualitative data on diet, as well as observations on feeding in captivity and excavation of a

Fig. 2. Map of Madagascar showing major river systems, presumed range of *Limnogale mergulus* (shaded area; M. Nicoll, pers. comm.) and confirmed sites for the species, including Ranomafana National Park (Site 7). Shading does not imply a continuous distribution. Site numbers refer to Table 1.

Table 1. Locations of all known sites for *Limnogale mergulus* with notes and sources of information. Site number refers to Fig. 1

Site	Site number	Latitude/ Longitude	Notes	Sources
Sihanaka Forest	1	18°05′S, 48°30′E	British Museum specimen	L. Olson, pers. comm.
Andekaleka (Rogez)	2	18°46′S, 48°45′E	Population may be at low density or extirpated due to habitat degradation	Malzy, 1965; Gould & Eisenberg, 1966; Eisenberg & Gould, 1970, 1984; Nicoll & Langrand, 1989; Nicoll & Rathbun, 1990
Antsampandrano	3	19°37′S, 47°04′E	Population may be at low density or extirpated due to habitat degradation	Malzy, 1965; Gould & Eisenberg, 1966; Eisenberg & Gould, 1970, 1984; Nicoll & langrand, 1989; Nicoll & Rathbun, 1990
Tsinjoarivo	4	19°38′S, 47°43′E	Faeces found in 1998	S. M. Goodman, pers. comm.
Antalava (35 km south of Antsirabe)	5	20°11′S, 47°06′E	Faeces found and one individual seen in 1987	Nicoll & Rathbun, 1990
Imasindrary	6	20°17′S, 47°31′E	Type locality	Major, 1896
Ranomafana National Park	7	21°15′S, 47°27′E	Appears to support a large population	Nicoll & Langrand, 1989; Nicoll & Rathbun, 1990; this study
15 km north of Antanifotsy	8	22°02′S, 46°55′E	Presence reported by local villagers	Nicoll & Langrand, 1989; Nicoll & Rathbun, 1990
Maitso Forest	9	22°09′S, 46°57′E	Presence reported by local villagers	S. M. Goodman, pers. comm.
Upper Iantara River and tributaries, east of Andringitra	10	22°13′S, 47°00′E	Presence reported by local villagers	S. M. Goodman, pers. comm.

single maternal burrow. Subsequent literature pertaining to *Limnogale* has been based largely on Malzy's observations (e.g. Eisenberg & Gould, 1970, 1984), with the exception of metabolism data reported by Stephenson (1994; also see Racey & Stephenson, 1996) and new sites reported by Nicoll & Langrand (1989) and Nicoll & Rathbun (1990).

In this paper, we present the first quantitative data on the diet of *Limnogale*, based on faecal analysis. We also report the first data on activity patterns, foraging, and range size of the species, based on the radio-tracking of two individuals. Finally, the results of faecal pellet counts in six streams in Ranomafana National Park and its deforested peripheral zone are presented. Our results are discussed with respect to the responses of *Limnogale* to deforestation and the long-term conservation of the species.

MATERIALS AND METHODS

Study site

This study was conducted within Ranomafana National Park (RNP; 21°15′S, 47°27′E) and in the vicinity of its peripheral zone (Fig. 3). RNP is a 41 300 ha reserve located in south-eastern Madagascar. The park spans elevations of 400–1500 m and its vegetation consists primarily of premontane tropical rainforest. The peripheral zone is a buffer area, extending 3 km from the park boundary, in which land use consists of slash-and-burn agriculture, secondary (fallow) vegetation, riparian rice paddies, and remnant forest patches. RNP is one of the historical sites for *Limnogale*, and the only site for post-1980 captures of the species by scientists (Nicoll &

Rathbun, 1990; Stephenson, 1994; M. Nicoll & L. Olson, pers. comm.).

Seven streams were used in this study (Fig. 3, Table 2); 4 were within the forest protected by RNP while 3 were located in deforested areas within or near the peripheral zone. All were small (5.3–13.7 m mean width), located at 700–1100 m a.s.l., and fast flowing with gravel, cobble and boulder substrata. Canopy cover ranged from 70 to 83% in the 4 forest streams, and was 0% in the peripheral zone streams (hereafter referred to as zero-canopy streams). Benthic invertebrate communities of forest and zero-canopy streams were dominated by aquatic insect larvae (e.g. Ephemeroptera, Trichoptera and Odonata), but differed in the relative dominance of taxa (J. P. Benstead, pers. obs.). Larval anurans were abundant in all streams. Freshwater crabs (Potamonautidae) and crayfishes *Astacoides granulimanus* were present in most streams but were less abundant in zero-canopy reaches, possibly because of collection for food by local villagers. Atyid shrimps *Caridina* spp. were present in at least 2 streams. No fishes were observed in forest streams, although the eel *Anguilla mossambica* may have been present. Introduced tilapia *Tilapia zillii* and green swordtail *Xiphophorus helleri* were present in all 3 zero-canopy streams. A native, undescribed Madagascar rainbowfish *Bedotia* sp. (M. L. J. Stiassny, pers. comm.) was also present at 1 of the zero-canopy streams (Menarano).

Diet analysis

During 1996–8, faecal pellets were collected from 6 streams within RNP and its peripheral zone (Fig. 3, Table 2). Faecal pellets were collected from *Limnogale*

Table 2. Physical descriptions of stream reaches sampled in Ranomafana National Park and peripheral zone, south-eastern Madagascar, 1996–98. FA, faecal analysis; FC, faecal counts; RT, radio-tracking; n.d., no data

Stream	Fieldwork conducted	Mean width (m)	Mean maximum depth (m)	Mean temperature (° C)	Substratum	Mean canopy cover (%)	Land use
Forest streams							
Mariavaratra	FA, FC, RT	6.0	0.31	17.0	Cobble, with boulders	71	Primary forest; some logging in early 1980s
Fompohonona	FA, FC	5.3	0.38	17.0	Cobble, with sand and boulders	74	Primary forest; some human disturbance
Vatoharanana	FA, FC	9.6	0.51	17.0	Boulders, cobble and gravel/sand	83	Primary forest; some human disturbance
Sakaroa	FA	6.0	0.5	n.d.	Cobble, with boulders	c. 75	Primary forest; some logging in early 1980s
Zero-canopy streams							
Tomaro	FA, FC, RT	13.7	0.72	18.5	Cobble, with boulders	0	Rice agriculture
Tolongoina	FA, FC	7.2	0.56	17.3	Cobble, with boulders	0	Rice and sugar cane agriculture
Menarano	FC	9.7	0.48	17.5	Cobble, gravel and sand	0	Rice and cassava agriculture
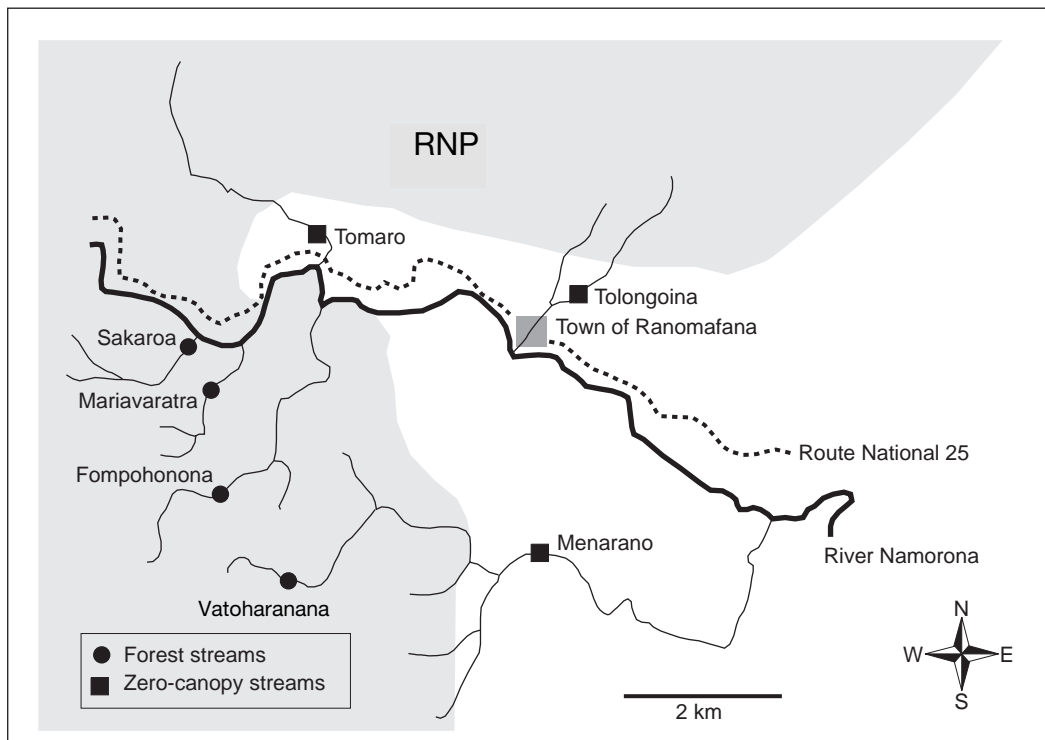
Fig. 3. Locations of the seven study streams in relation to the boundary of Ranomafana National Park (RNP; shaded region). Only part of the Park is shown; the peripheral zone extends 3 km from the park boundary.

latrine sites in each stream and preserved immediately in 70% ethyl alcohol. Latrine sites are usually emergent, mid-stream rocks with little or no growth of bryophytes or other plants, although woody debris is also sometimes used. Crevices and rocks with overhanging cover are particularly favoured. Latrine sites are rarely on the bank (unless on that of a mid-channel island) or > 20 cm above the water surface (J. P. Benstead, pers. obs.). It is not known if latrine sites are communal or whether they serve a territorial purpose. The latter seems probable,

based on the ecology of other semi-aquatic mammals (e.g. Kruuk, 1992).

Faecal pellets of *Limnogale* are 5–25 mm long, 3–7 mm wide, and generally black. When fresh, they are soft, moist and glossy, with a faint odour. Their colour becomes duller and paler upon drying. Recognizable arthropod remains are often visible on the exterior. Faecal pellets containing crustacean remains may be off-white and composed almost entirely of carapace fragments.

Faecal pellets were subsequently broken apart, washed on a 363-μm mesh sieve to remove very fine particles, and examined under a stereomicroscope (12.5–53 × magnification). Undigested prey remains (e.g. keratinized jaw sheaths, centra and hyoid bones of larval anurans, crustacean carapace fragments, and insect head capsules, mandibles and legs) were identified using a reference collection of potential prey items collected concurrently from the streams of RNP. We examined 108 faecal pellets from 6 streams (12–20 from each of 4 forest streams and 20 from each of 2 zero-canopy streams; see Table 2). Diet analysis data are reported as percentage occurrence (number of faecal pellets n in which a prey category c occurred, n_c, divided by the total number of faecal pellets examined at each site × 100) and as percentage frequency (n_c divided by Σn_c for all prey categories × 100) (Shiel *et al.*, 1998).

Faecal pellet counts

Initial observations indicated that *Limnogale* faeces seemed to be at least as abundant, if not more abundant, in zero-canopy reaches of streams draining partially deforested catchments in RNP's peripheral zone. In order to investigate the relative abundance of faecal pellets in forest and zero-canopy streams, during July–September 1998 we selected 3 streams of each type and conducted faecal pellet counts along 250-m reaches in each. In each reach, we measured off successive 10-m segments of known width. All potential latrine sites (i.e. emergent rocks) in each segment were exhaustively searched for faecal pellets. Data are expressed as mean (± 1 SE) number of faecal pellets/100 m^2 stream channel along 10-m segments in each stream. Because the presence of faecal pellets is governed partly by the availability of potential latrine sites, we also visually estimated the percentage area of stream channel occupied by emergent rocks in each 10-m segment. The number of faecal pellets in each segment was divided by this index (m^2 emergent rocks) to standardize data with regard to latrine site availability. These data are expressed as mean (± 1 SE) number of faecal pellets per m^2 emergent rocks along 10-m segments in each stream.

Radio-tracking

Limnogale were trapped using unbaited Tomahawk live-traps (Model 102; 40 × 13 × 13 cm) and self-assembled, spring-loaded box traps (30 × 10 × 10 cm). Trapping began on 21 October 1997 in the Mariavaratra forest stream within RNP (Fig. 3) using 35–50 traps along a 50 m reach. Most traps were partially submerged and placed facing upstream between rocks that formed a constriction in stream flow. Some traps were placed on mid-stream emergent boulders, under overhanging rocks (i.e. actual or potential latrine sites) and faced downstream. When possible, traps were soiled with faeces collected from another stream. Traps were

Table 3. Capture information and physical data for two *Limnogale mergulus* individuals, Ranomafana National Park, south-eastern Madagascar

	LIMNOGALE I	LIMNOGALE II
Site of capture	Mariavaratra	Tomaro
Stream type	Forest	Zero-canopy
Date of capture	30 Oct 1997	15 May 1998
Sex	Male	Male
Weight (g)	80	105[a]
Length (mm)[b]		
Total	283	293
Head and body	145	138
Tail	138	155
Hindfoot	34	35
Ear	7	9

[a] After feeding.
[b] Measurements were taken while animals were anaesthetized.

checked every 4 h throughout the day and night. On 30 October 1997, after 165 trap-nights (nights of trapping × number of traps used), a male *Limnogale* (LIMNOGALE I) was captured in a soiled trap placed facing downstream under a mid-stream overhanging rock. The animal was anaesthetized using Metofane® (methoxyflurane; Mallinckrodt Veterinary, Inc., Mundelein, IL, U.S.A.), weighed with a Pesola balance, measured (see Table 3) and fitted with a sealed Advanced Telemetry Systems (ATS) radio-transmitter (Model 384; weight 1.6 g; frequency 150 MHz) attached between the shoulder blades using Araldite Rapid epoxy adhesive. The animal was released at the capture site 2 h after it was found.

Radio-tracking began on 2 November 1997, using an ATS Fieldmaster receiver and 3-element Yagi antenna. The location of the tenrec was noted using a compass bearing taken from marked way points along a stream-side trail (<20 m from the stream). Location was recorded every 10–15 min during 12-h tracking sessions that started or ended at approximately 05:30. We also noted whether the tenrec seemed to be actively foraging (immersion of the transmitter during dives resulted in an abrupt weakening of the transmitter's signal). To minimize disturbance to the tenrec, no attempt was made to observe its behaviour during tracking. The tenrec was tracked for 16 nights and 8 days before the transmitter detached on 13 December 1997. The stream and trail were then mapped using a compass and field tape. The stream reach and way points were subsequently plotted to scale, and the locations of the tenrec were determined with respect to distance (in m along the stream channel) from the burrow site.

Our second period of trapping began on 25 November 1997 in the Tomaro zero-canopy stream within RNP's peripheral zone (Fig. 3). Trapping was suspended on 8 December 1997, after 468 trap-nights, when storms repeatedly washed traps from their locations. Trapping was resumed in the Tomaro on 11 May 1998. Traps were placed in locations similar to those in the Mariavaratra and checked daily at dawn. On 15 May 1998,

Table 4. Percentage occurrence and percentage frequency (in parentheses) of prey categories in *Limnogale mergulus* faeces collected from six streams within Ranomafana National Park and its peripheral zone, 1996–98

Prey category	Forest streams				Zero-canopy streams	
	Mariavaratra	Fompohonona	Vatoharanana	Sakaroa	Tomaro	Tolongoina
Insecta						
Ephemeroptera	72.0 (27.8)	70.0 (26.4)	66.7 (22.9)	87.5 (30.4)	100.00 (31.7)	95.0 (31.7)
Odonata	55.0 (20.4)	35.0 (13.2)	25.0 (8.6)	81.3 (28.3)	55.0 (17.5)	65.0 (21.7)
Hemiptera	5.0 (1.9)	0	16.7 (5.7)	6.3 (2.2)	0	5.0 (1.7)
Trichoptera	55.0 (20.4)	65.0 (24.5)	33.3 (11.4)	43.8 (15.2)	65.0 (20.6)	60.0 (20.0)
Lepidoptera	20.0 (7.4)	5.0 (1.9)	16.7 (5.7)	62.5 (21.7)	30.0 (9.5)	35.0 (11.7)
Coleoptera	25.0 (9.3)	45.0 (17.0)	33.3 (11.4)	6.3 (2.2)	30.0 (9.5)	15.0 (5.0)
Diptera	5.0 (1.9)	15.0 (5.7)	16.7 (5.7)	0	0	5.0 (1.7)
Crustacea						
Crabs (Potamonautidae)	0	0	16.7 (5.7)	0	0	0
Crayfish (*Astacoides* spp.)	15.0 (5.6)	15.0 (5.7)	8.3 (2.9)	0	0	15.0 (5.0)
Anuran larvae	15.0 (5.6)	15.0 (5.7)	58.3 (20.0)	0	35.0 (11.1)	5.0 (1.7)

after 136 trap-nights, a male *Limnogale* (LIMNOGALE II) was captured in an unsoiled, partially submerged trap facing upstream between two emergent rocks. The animal was kept in an aquarium ($80 \times 40 \times 60$ cm; filled to a depth of 20 cm and provided with an emergent rock for resting) during the day. It was fed, photographed and observed for several hours before being measured and weighed (see Table 3), and fitted with a transmitter as above. The tenrec was released at the capture site at dusk. Radio-tracking and mapping were carried out as above, except that the location of the animal was noted approximately every 30–60 min. The animal was tracked for 12 nights and 6 days before it was found dead on 9 June 1998. The tenrec had drowned after the transmitter became entangled on discarded fabric lodged between submerged rocks. It was preserved in formalin and deposited at the University of Antananarivo Département de Biologie Animale (UADBA), Madagascar (UADBA 11606).

Radio-tracking data were used to calculate the mean distance travelled per night, the range in distances travelled per night, and the total length of stream channel used by each tenrec during radio-tracking studies. The total length of stream channel travelled was used as an approximation of the range size of each animal. We emphasize that our reported distances are minimum estimates of distances travelled – animals were assumed to move directly between successive positions and assumed not to have moved during periods between identical successive positions.

RESULTS

Faecal analysis of diet

Larval and adult aquatic insects were the dominant prey items recorded from faecal analysis (Table 4). Ephemeroptera nymphs were the single most important prey category, followed by Odonata nymphs, Trichoptera and Lepidoptera larvae, and Coleoptera larvae and adults. Diptera larvae and Hemiptera were of minor importance. Decapod crustaceans and larval anurans formed the only other major prey categories and were of approximately equal importance in most streams. Larval anurans were of major importance (58.3% occurrence) in the Vatoharanana forest stream but were not recorded from faeces in the Sakaroa forest stream. We found no evidence of predation on fish or adult amphibians.

Limnogale diets varied between the six streams but we found no evidence for distinct differences between diets in zero-canopy and forest streams. However, there was a slightly higher reliance on Ephemeroptera larvae in the two zero-canopy streams (Table 4). Percentage occurrences of all other prey categories in zero-canopy streams were within the ranges recorded in forest streams.

Faecal pellet counts

No faeces were found in one of the zero-canopy stream reaches (Menarano), which contained no suitable latrine sites such as emergent boulders. However, faeces have subsequently been found upstream of the original survey site in this stream in an area with abundant potential latrine sites. In each of the three forest streams, 10–30 faecal pellets were found in the 250-m survey reaches (Table 5). Higher numbers (32 and 68 pellets) were found in the remaining two zero-canopy stream reaches. This pattern of more faecal pellets in zero-canopy streams was also reflected in the density of faecal pellets, expressed both as number per unit area stream channel and number per unit area emergent boulders. These standardized densities indicated that the higher number of faecal pellets in zero-canopy streams was not a function of stream size or latrine site availability (Table 5).

Observations in captivity

On 15 May 1998, a male *Limnogale* (LIMNOGALE II) was kept in an aquarium for *c*. 10 h. During the first

Table 5. Results of *Limnogale mergulus* faecal pellet counts in three forest streams within Ranomafana National Park, and two zero-canopy streams within its peripheral zone, July–September 1998

Stream	No. of faecal pellets in 250 m stream reach	Density of faecal pellets (mean ± 1 SE)	
		No./100 m^{-2} stream channel	No./m^{-2} emergent boulders
Forest			
Mariavaratra	30	2.00 ± 1.26	0.10 ± 0.07
Fompohonona	10	0.75 ± 0.68	0.16 ± 0.14
Vatoharanana	13	0.54 ± 0.50	0.02 ± 0.02
Zero-canopy[a]			
Tomaro	68	1.99 ± 0.70	0.26 ± 0.11
Tolongoina	32	1.78 ± 1.09	0.16 ± 0.11

[a] No faeces were found in the third zero-canopy stream reach (Menarano), possibly because of a lack of potential latrine sites (see text).

2–3 h, the tenrec was fed three parastacid crayfish *Astacoides granulimanus* from which the chelae were first removed. While swimming, LIMNOGALE II moved using primarily the hind feet, and using the tail as a rudder. Foraging behaviour consisted of short (10–15 s) dives to the bottom of the aquarium, accompanied by sweeping movements of the head. Prey encountered by contact with the vibrissae was seized in the mouth and brought to the surface. At the surface, the animal rolled onto its back and vigorously kicked the prey with its hind legs to subdue it. Moribund prey were subsequently brought up onto the rock, held with the fore feet, and eaten. Crayfish were consumed entirely in small successive bites. Between diving bouts, the *Limnogale* engaged in licking and grooming behaviour. After *c*. 3 h of observation, the tenrec was provided with an artificial sleeping chamber (a 1.5 l plastic bottle, with the base removed, lined with dry bamboo leaves) which it immediately entered to sleep.

Activity patterns

After being released, both *Limnogale* seemed to experience 3–5 days of disorientation, during which they slept at a different streamside location each day. Subsequently, they seemed to re-locate to what was assumed to be their permanent burrow (i.e. it was used for sleeping every day thereafter). Data recorded during the initial release period were excluded from our analyses of foraging movement.

Diurnal activity was never observed in the two *Limnogale* that remained within their streamside burrows during every diurnal radio-tracking session. Activity typically began at, or just after, sunset and ended 60–90 min before sunrise (Figs 4 & 5). The *Limnogale* often returned to their burrows during the night; LIMNOGALE I never passed its burrow without entering it. These nocturnal resting periods often lasted 3–4 h (Figs 4b & 5a,b). Time outside the burrow was spent mostly in active foraging, as indicated by frequent immersion of the transmitter (Figs 4 & 5). However, short periods of inactivity (*c*. 1 h) outside the burrow were also noted (Fig. 5c, 20:30–21:30 and 23:00–00:00). It is not known if these periods were spent in temporary streamside burrows, but this is possible.
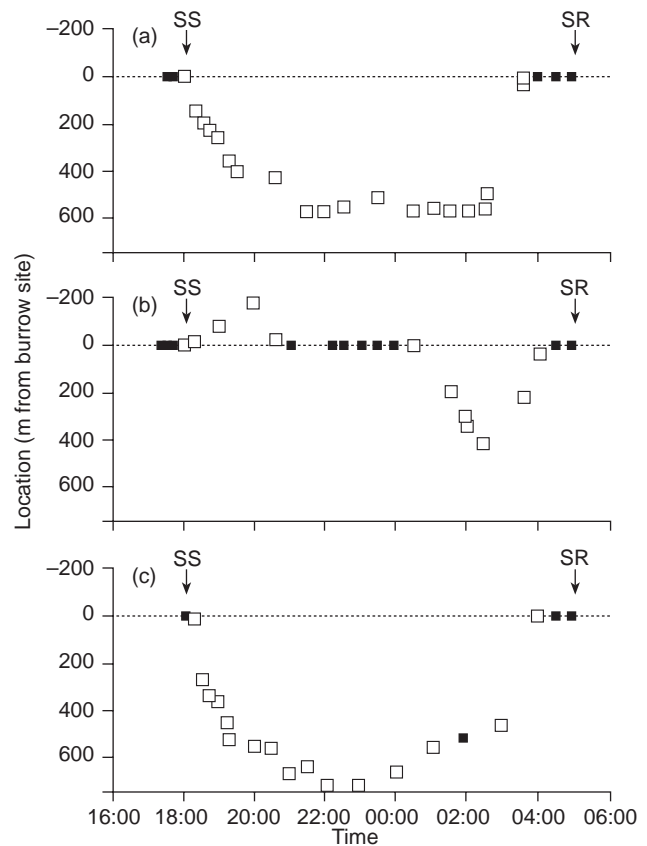

Fig. 4. Location and activity of LIMNOGALE I along the Mariavaratra forest stream (distance in m along the stream channel from the burrow site) during representative nights: (a) 7–8 November 1997; (b) 11–12 November 1997 and (c) 14–15 November 1997. □, tenrec assumed to be actively foraging based on frequent immersion of the transmitter (see text); ■, tenrec assumed to be inactive. Burrow site at 0 m (dashed line); negative distance values indicate upstream movement. The confluence of the Mariavaratra stream with the Namorona River is at 730 m (i.e. at the *x*-axis). SS, sunset; SR, sunrise.

Foraging movement and range size

Movements of both tenrecs were restricted to the stream channel. Total distance travelled per night and maximum distance travelled from the burrow varied
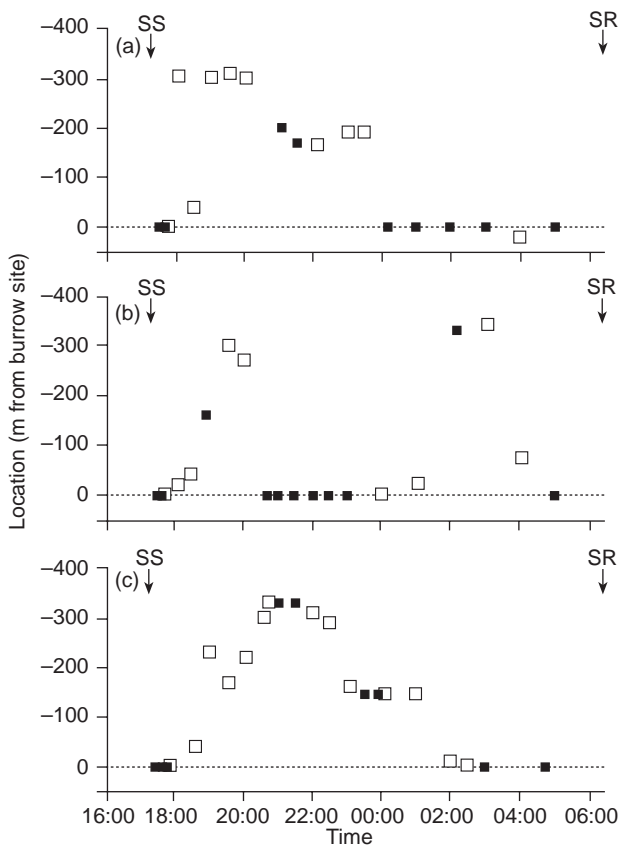
Fig. 5. Location and activity of LIMNOGALE II along the Tomaro zero-canopy stream (distance in m along the stream channel from the burrow site) during representative nights: (a) 2–3 June 1998; (b) 3–4 June 1998; and (c) 4–5 June 1998. □, tenrec assumed to be actively foraging based on frequent immersion of the transmitter (see text); ■, tenrec assumed to be inactive. Burrow site at 0 m (dashed line); negative distance values indicate upstream movement. SS, sunset; SR, sunrise.

between nights and differed between LIMNOGALE I and LIMNOGALE II. LIMNOGALE I travelled further each night and exhibited a broader range in distances travelled per night (Table 6).

Greater movement by LIMNOGALE I was reflected in the total length of stream channel used by the two tenrecs during the respective radio-tracking studies. The total length of channel travelled by LIMNOGALE I was more than twice that of LIMNOGALE II (Table 6). The two *Limnogale* also differed in their pattern of movement relative to stream flow. LIMNO-

GALE I generally moved downstream after emergence from its burrow (Fig. 4a,c), but also moved upstream (Fig. 4b). In contrast, LIMNOGALE II always moved upstream after emergence (Fig. 5), possibly because the stream channel immediately downstream from its burrow had an extremely high gradient.

DISCUSSION

Diet analysis

Previous qualitative reports of the diet of *Limnogale* included small frogs, crayfish, aquatic insects, small fish, and freshwater shrimps as important prey categories (Malzy, 1965; Gould & Eisenberg, 1966; Eisenberg & Gould, 1970, 1984; Nicoll & Rathbun, 1990). Although our data show some correspondence with these qualitative reports, we found that aquatic insects formed the bulk of the diet of *Limnogale* individuals in our study streams, and that larval anurans, a previously unreported prey category, were of relatively high importance. We also found no evidence of predation on fish, adult amphibians or freshwater shrimps, which were present in either all or some of the study streams. It is possible that these groups form an occasional part of the diet of *Limnogale* but were not present in the faecal pellets examined.

Our results can be compared with quantitative diet data and anecdotal reports from available studies of ecologically similar small mammals. In its diet, *Limnogale* is most similar to the Tibetan water shrew *Nectogale elegans* (Voss, 1988; Hutterer, 1992), the Pyrenean desman *Galemys pyrenaicus* (Santamarina & Guitian, 1988), and ichthyomyine and hydromyine rodents (six genera; Hooper, 1968; Voss, 1988; Barnett, 1997), all of which consume mostly aquatic insects. This heavy reliance on aquatic insects differs from the diet of the Eurasian water shrew *Neomys fodiens*, which also consumes terrestrial invertebrates (Churchfield, 1979, 1984, 1985), and the pygmy otter shrew *Micropotamogale lamottei*, which consumes mostly fishes and freshwater crabs (Vogel, 1983).

Our faecal analysis technique did not account for differences in the mean biomass of individuals in prey categories. Remains of larval anurans were from individuals at least 40 mm long (R. Altig, pers. comm.), and the most abundant prey category (Ephemeroptera) was represented by the smallest prey items (< 10 mm). It is

Table 6. Distance travelled per night and total length of stream channel used by *Limnogale mergulus* individuals in the Mariavaratra stream (2 November–13 December 1997) and Tomaro stream (15 May–9 June 1998), Ranomafana National Park, south-eastern Madagascar

Animal	Stream	n^a	Approximate distance travelled per night (m)		Length of stream channel used during study (m)
			Mean ± 1 SE	Range	
LIMNOGALE I	Mariavaratra	16	1067 ± 127	200–1550	1160
LIMNOGALE II	Tomaro	12	860 ± 84	340–1260	505

[a] Nights radio-tracked.

possible that prey categories consisting of large taxa (e.g. larval anurans, Odonata and Lepidoptera) are energetically more important than is indicated by our data.

Apart from a slightly higher reliance on Ephemeroptera larvae in zero-canopy streams, we found few differences in the diets of *Limnogale* in zero-canopy and forest streams. However, the faecal analysis technique used (presence/absence of prey categories) may have been relatively insensitive to differences in diet between stream types. Estimates of prey abundance are extremely difficult to make based on the fragments we found in faeces. Based on our knowledge of prey communities in the study streams (J. P. Benstead, pers. obs.), we would have expected differences in diets between the two stream types. However, all of the important prey categories were abundant in both stream types and differed only in their relative abundance. Our diet data clearly indicate that *Limnogale* can persist in streams draining deforested catchments if prey communities are not depleted by sedimentation.

Responses to deforestation

Faeces of *Limnogale* were at least as abundant, if not more abundant, in reaches of two of the zero-canopy streams. Although we conducted only a single survey in each stream, pers. obs. over 3 years suggest that these results reflect long-term patterns in the forest and zero-canopy streams. Relatively high densities of faeces in zero-canopy streams draining deforested areas suggest that *Limnogale* is not an obligate forest species and that it is able to maintain populations in modified habitats. However, our results should be interpreted with caution. In many of the river systems of Madagascar, particularly those of the central highlands, deforestation has resulted in greatly accelerated erosion of lateritic soils and subsequent massive sedimentation (Benstead *et al.*, 2000). The streams of RNP's peripheral zone sampled in this study seem to be unusual in that excessive sedimentation is not apparent, for which there are several possible explanations. First, the headwaters of all the zero-canopy streams used in this study are still forested and are located within RNP. Second, clearance of forest in the area is patchy and typically small scale (< 1 ha), leading to a mosaic of land use within these catchments. Such land-use patterns may prevent accelerated erosion. Third, the stream slope of the reaches used in the study may be too high for sedimentation to be an important process. Finally, erosion and sedimentation are processes that often act over long time scales (Waters, 1995). Large-scale deforestation in the Ranomafana region dates only from the 1940s (Ferraro, 1994), and so its consequences for stream habitats are yet to be seen.

Consideration of the potential impacts of deforestation on erosion and sedimentation is important because our diet data show that *Limnogale* preys on taxa known to be susceptible to increased sedimentation rates (Waters, 1995; Wood & Armitage, 1997). Fine sediment affects benthic invertebrates in many ways, including clogging of respiratory structures, filling-in of interstitial habitat, and smothering of food resources (Waters, 1995). Changes in benthic communities or reductions in prey density caused by sedimentation would inevitably impact *Limnogale* populations. We believe that sedimentation processes, caused by forest clearance and acting through changes in benthic invertebrate prey communities, pose the greatest threat to remaining *Limnogale* populations in eastern Madagascar. Prevention of sedimentation, either through maintenance of original forest habitat or by other means, is crucial to future efforts to conserve the species.

Although our faecal pellet counts show that *Limnogale* is at least present in zero-canopy streams, estimations of relative population densities in forest and zero-canopy streams are difficult to make based on faecal pellet density. We found more faecal pellets in zero-canopy streams. However, it is possible that *Limnogale* in these streams consume prey with a higher indigestible content and so produce more faeces per individual, although substantially different diets between the two stream types were not suggested by our diet data. Alternatively, faecal pellets may persist longer in zero-canopy streams (e.g. because of lower numbers of coprophagous insects), giving rise to higher densities of faecal pellets. If higher faecal pellet densities *do* reflect higher densities of *Limnogale* in zero-canopy streams, this could be for at least two reasons. First, higher production of prey (relative to forest streams) in the algal-based food webs of these zero-canopy streams might support higher numbers of *Limnogale*. Second, predation on *Limnogale* may be lower in zero-canopy streams if their main predators are obligate or specialist forest species. Unfortunately, no information exists on the predators of *Limnogale*.

Behavioural observations

Malzy (1965) recorded the only previously published observations of *Limnogale* based on the behaviour of two captive individuals. He noted similar swimming and diving behaviour with extensive grooming after emergence from water. These two *Limnogale* were fed small fish, grasshoppers, small beetles and larval anurans. Prey items were brought out of the water and eaten while held with the forefeet (Malzy, 1965). Our observations support and add to those of Malzy. Apparently, *Limnogale* is a tactile predator, finding its prey by sweeping the stream bed with its vibrissae. It also seems capable of catching and subduing large prey items such as crayfishes. Although anecdotal data report predation on fishes, and Malzy (1965) fed fish to captive individuals, it remains unclear as to whether *Limnogale* is capable of capturing such fast-moving prey under natural conditions.

Activity patterns and foraging movement

Before this study, no information existed on the activity patterns and foraging movements of *Limnogale*. Although a small sample size precludes our drawing firm conclusions about the behaviour of the species, our results suggest that *Limnogale* is strictly nocturnal and that it maintains a permanent streamside burrow to which it returns each morning. We were not able to locate the entrances to either of the burrows used by the two animals radio-tracked in this study. The single burrow excavated by Malzy (1965) was situated in a high-gradient reach on a small (10×3 m) island and dug horizontally into the bank *c*. 0.5 m above water level. The burrow was 10 cm in diameter, 17 cm in depth, and lined with grass and twigs. The two burrows used by *Limnogale* in this study were also located in areas of high-gradient ($> 25°$ slope) channel. Further studies may reveal the relationship between channel characteristics and burrow location.

Our radio-tracking data also show that *Limnogale* is a strongly aquatic species. Movement was restricted solely to the wetted stream channel. In this respect, *Limnogale* seems to be similar to other exclusively aquatic foragers such as *Galemys pyrenaicus* (Stone, 1987*a*), *Nectogale elegans* (Hutterer, 1992) and *Micropotamogale lamottei* (Vogel, 1983). *Galemys pyrenaicus* is the only other small semi-aquatic mammal to have been radio-tracked (Stone, 1985, 1987*a,b*). These studies have shown that *Galemys* displays a predictable pattern of foraging activity and movement. Desmans were active during short afternoon periods and during each night (Stone, 1987*b*). Movement alternated between upstream and downstream travel along the channel to the limit of the individual's range; this pattern of alternation was extremely regular (Stone, 1987*a*). The home ranges of females were smaller than those of resident males and were located within each male's home range. Males and females maintained separate burrows (Stone, 1987*a*).

The two *Limnogale* radio-tracked in this study showed no such regular pattern of foraging movement. Although activity was strictly nocturnal, level and timing of activity and direction and extent of movement of *Limnogale* were very unpredictable. *Galemys* seem to occur at relatively high densities (2.8–7.3 individuals/km stream channel; Nores *et al*., 1998) and it seems possible that their regular pattern of movement is an evolutionary response to the need to defend territories. In contrast, our data show no regular movement pattern. This unpredictable movement may indicate that *Limnogale* occurs at naturally low densities (also see Nicoll & Rathbun, 1990) and, consequently, does not defend its home range strongly. However, direct evidence for low densities is lacking.

Unpredictable movement by the animals in this study, combined with the linear nature of their habitat, makes the estimation of range sizes difficult. For this reason, we report the total length of stream channel used as a proxy for range size, but these values must be treated with caution. Our radio-tracking studies were short and we were unlikely to observe the total range in movement patterns. However, the range sizes of the two radio-tracked *Limnogale* differed considerably; the range size of LIMNOGALE I was more than twice as long as that of LIMNOGALE II (Table 6). This could be explained by higher prey production in the zero-canopy stream inhabited by LIMNOGALE II (see Responses to deforestation). Alternatively, the relative size of the two streams could be an important factor. The stream in which LIMNOGALE II was radio-tracked was more than twice the mean width of the stream inhabited by LIMNOGALE I. This suggests that total stream channel area available for foraging may be an important determinant of range size.

Implications for future research and conservation efforts

The results of this study highlight three main areas for future research and conservation efforts. First, faecal pellet counts offer a rapid means of surveying for *Limnogale*. The use of faecal pellet surveys are recommended to identify additional sites for this poorly recorded and rarely seen species. Combined with faecal DNA techniques (Kohn & Wayne, 1997), collection of faecal pellets also offers a potential method of answering many questions relating to the population genetics and social ecology of remaining *Limnogale* populations.

Second, the vulnerability of benthic prey communities to sedimentation implies that prevention of erosion and sedimentation is of paramount importance for conservation of the aquatic tenrec. New and existing sites for the species must be protected from the effects of sedimentation wherever possible, either by inclusion of forested catchments in the protected areas network or by other means (e.g. effective terracing of agricultural fields and maintenance of vegetated riparian zones).

Finally, movement of the two *Limnogale* radio-tracked in this study was restricted to the channels of their home streams. This may mean that aquatic tenrecs use stream networks as their sole routes for dispersal, and that populations may be subject to fragmentation if isolated by degraded stream habitat. This further highlights the importance of maintaining healthy stream habitats and the benthic communities upon which *Limnogale* depends.

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