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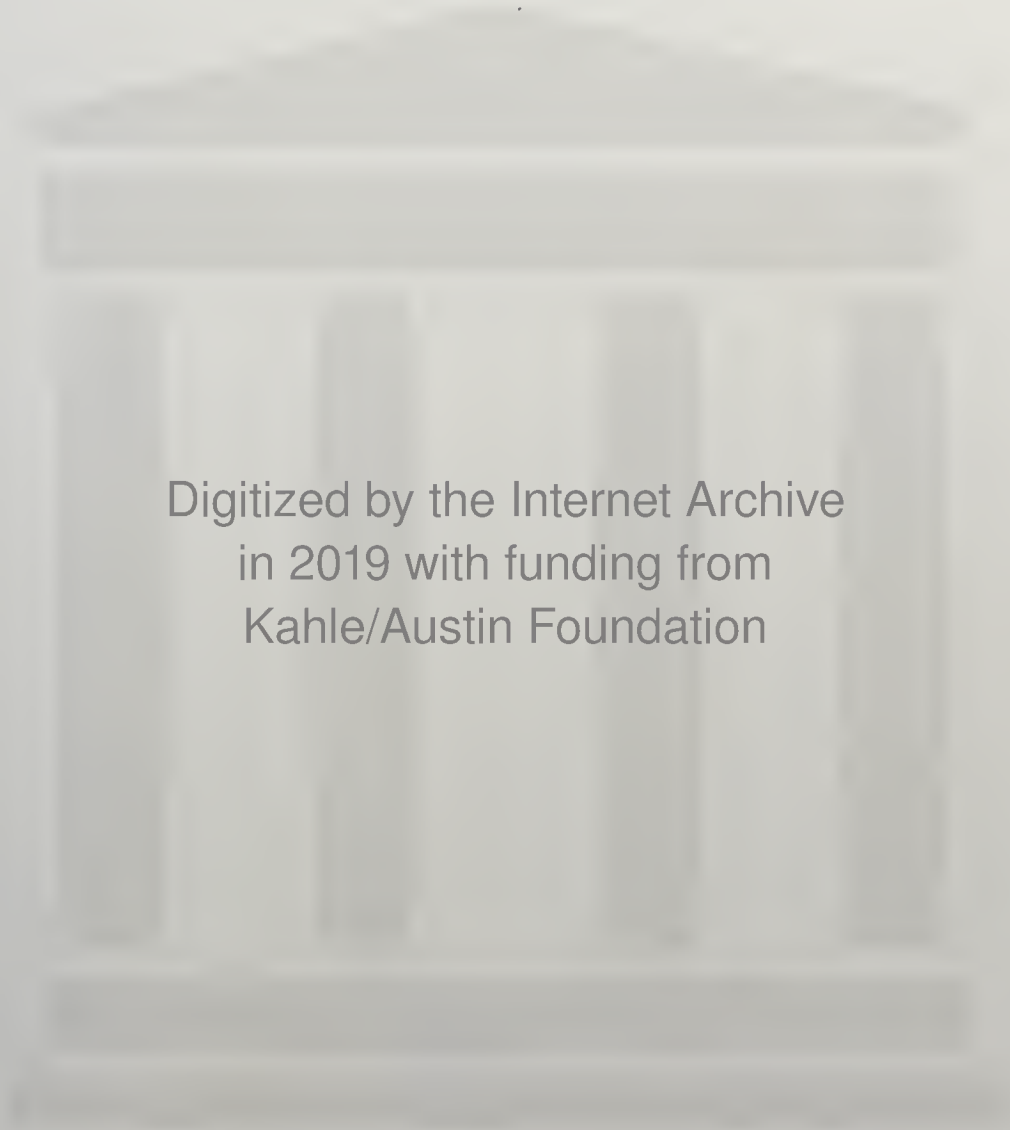
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Behaviour and Ecology of Nocturnal Prosimians

Field Studies in Gabon and Madagascar

Comportement et Ecologie de Prosimiens Nocturnes

Etudes de Terrain au Gabon et à Madagascar

By

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Introduction

The prosimians—commonly referred to as "lower Primates"—are of special interest because of their relationship to man. Study of the biology of prosimians can tell us a great deal about the early evolution of the Primates, and thus about the very early stages of human history. It has often been said that the Primates are mainly distinguished from other mammals by their retention of primitive structures, as can be seen from a general examination of skeletal characters. The main specialisations of the Primates are to be found in the development of the brain, the associated elaboration of general behaviour, and in structural, physiological and behavioural characteristics involved in reproduction. Accordingly, field-studies of the natural behaviour and ecology of Primate species are particularly important. In recent years, there have been many excellent studies under natural conditions of the behaviour of monkeys and apes, and much information has been collected on the larger, diurnal (and hence more monkey-like) lemur species. However, the majority of prosimian species are *nocturnal*, and it is vital that the night-active species should be studied with equal intensity, especially since nocturnal prosimians seem to have retained the greatest proportion of primitive Primate characteristics. The two papers in this volume, one referring to Demidoff's Bush-Baby (Gabon) and the other dealing with the Lesser Mouse Lemur (Madagascar), provide detailed information on two nocturnal species which have apparently undergone relatively little evolutionary modification of structure and behaviour since their origin from the ancestral Primate stock. It will be seen that the results from these two independent studies show surprising similarities, and this fact has already provoked the authors to re-examine current concepts of Primate evolution. It is likely that, in the years to come, more detailed information on the behaviour of nocturnal prosimians will provide an entirely new viewpoint on the early radiation of the Primates.

Introduction

Les Prosimiens, communément considérés comme «Primates inférieurs», présentent un intérêt particulier de par leur parenté avec l'homme. L'étude de leur biologie peut nous apprendre beaucoup sur les premiers stades de l'évolution des Primates, donc sur nos origines lointaines. On a souvent dit que les Primates se distinguaient des autres Mammifères par la rétention de structures primitives comme on peut le constater par l'examen général des squelettes. Les principales spécialisations des Primates concernent le développement du cerveau, en relation avec l'élaboration de comportements généraux, et les caractéristiques morphologiques, physiologiques et comporte-

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mentales de la reproduction. Les études de terrain du comportement naturel et de l'écologie des différentes espèces de Primates sont donc de premier intérêt. Au cours des dernières années, de nombreuses et excellentes études ont été faites sur le comportement des Singes, des Anthropoïdes et des grands Lémuriens diurnes (les plus ressemblants aux Singes). Cependant, les 2/3 des espèces de Prosimiens sont nocturnes; il est donc capital de les étudier avec une égale importance, surtout que les Prosimiens nocturnes semblent être ceux qui ont retenu la plus grande proportion des caractéristiques primitives des Primates. Les deux articles de ce volume, l'un concernant le Galago de Démidoff (Gabon) et l'autre le Microcèbe (Madagascar) donnent des informations détaillées sur deux espèces nocturnes qui, apparemment, ont subi peu de modifications morphologiques et éthologiques depuis leur origine à partir du stock ancestral des Primates. Il ressort de ces deux études indépendantes des similarités surprenantes qui, d'emblée, ont poussé les auteurs à réexaminer les conceptions courantes de l'évolution des Primates. Il est vraisemblable que dans les années à venir, un plus grand nombre d'informations apporteront un point de vue totalement nouveau sur les débuts de la radiation des Primates.

P. Charles-Dominique R. D. Martin

Brunoy and London, October 1971

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Ecologie et vie sociale de *Galago demidovii* (Fischer 1808; Prosimii)

Par Dr. Pierre Charles-Dominique

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Avec 24 figures et 6 tableaux

I. INTRODUCTION

La présente étude a été faite au Gabon, à la Mission Biologique de Makokou (Professeur P. P. Grasse). Certains éléments publiés dans cet article seront repris ultérieurement dans une étude comparative des 5 espèces de Prosimiens sympatriques du Gabon *(Perodicticus potto edwardsi, Arctocebus calabarensis aureus, Euoticus elegantulus elegantulus, Galago alleni, Galago demidovii)*. Cette étude a été faite au cours de 4 séjours au Gabon de 7, 8, 14 et 3 mois, d'Octobre 1965 à Décembre 1969; elle est basée principalement sur des observations ou des expériences de terrain. Des études en captivité sont en cours, quelques résultats sont donnés ici afin de faciliter l'interprétation de certaines observations de terrain.

A. Lieu d'étude, méthodes

Makokou se trouve dans le bloc de la forêt hygrophile (Rain-Forest), à 600 km de la côte atlantique, et à 0,4° au Nord de l'équateur.

L'œil des Prosimiens réfléchit la lumière, et avec une lampe frontale assez puissante, on peut repérer un *Galago demidovii* jusqu'à 100 m. En pratique, la végétation arrête le faisceau lumineux, si bien qu'en forêt, on ne peut explorer qu'une zone de 20 à 40 m de largeur (lampe frontale ELAUL, alimentée par deux batteries sèches accrochées à un ceinturon).

Les animaux repérés sont souvent dérangés par la lumière, et il est rare de pouvoir les suivre longtemps. De toutes façons, du fait de leur agilité et de la grande hauteur à laquelle ils évoluent, l'observation de leurs comportements est difficile. En forêt secondaire, où ils évoluent à plus faible hauteur, l'épaisseur de la végétation rend la progression de l'observateur pénible et bruyante.

Plusieurs méthodes ont été utilisées pour améliorer les conditions d'observation:

1. Ecoute des cris

Nous avons enregistré, à l'aide d'écoutes en plusieurs points du terrain (liaison par talkie-walkie) l'heure, la nature et la localisation de tous les cris d'une population. En connaissant la signification de ces émissions sonores, on peut mettre en évidence les différentes phases sociales de la population au cours de la nuit.

2. Observation de nuit à la lampe, chasse

Pour évaluer la dispersion ou les groupements nocturnes, nous avons compté et situé des *Galago demidovii* rencontrés sur des itinéraires mesurés et jalonnés de numéros. En dehors de ces itinéraires, les distances parcourues peuvent être assez bien évaluées par le temps, à l'aide d'une montre, à condition de noter tous les arrêts et leur durée (570 km de parcours à pied en forêt, 2000 heures d'observation en forêt). Sur certaines zones, nous avons tué au fusil (cal. 12 ou 9 mm) des individus pour des études de la reproduction et de l'alimentation (80 *Galago demidovii* au cours des 4 années).

3. Lâcher des animaux semi apprivoisés

Les Prosimiens peuvent facilement être stabilisés dans une zone boisée. Il suffit de les laisser un mois en cage dans la zone que l'on veut leur faire adopter. Après avoir lâché les animaux, nous avons disposé des points de nourriture, à proximité de leur cage, au moins au début. Ces individus que l'on a pu habituer à la présence humaine retrouvent très vite leurs comportements normaux (construction de nids, reproduction etc. ...) et nous avons pu les observer à quelques mètres sans les déranger. Le terrain dans lequel ils sont lâchés est auparavant aménagé pour faciliter les déplacements de l'observateur (layons et numérotage).

4. Enregistrement automatique

Nous avons pu, à l'intérieur d'une population naturelle, en forêt secondaire, comptabiliser les heures de prise de nourriture à l'aide du dispositif suivant: une cage de $40 \times 30 \times 40$ cm, grillagée et ouverte à sa partie supérieure, ne permet que l'entrée des animaux de la taille de *Galago demidorii* (barreaux espacés de 3 cm). Les animaux sautant à l'intérieur établissent un contact électrique en prenant appui sur un perchoir. L'examen des traces de dents sur la peau de banane nous a permis de vérifier qu'il s'agissait bien de *Galago demidovii* (les petits rongeurs ont été précédemment éliminés par piégeage) et un enregistreur graphique est relié au dispositif.

5. Piégeage

Un piège du type trébuchet a été utilisé en appâtant avec de la banane. Les *Galago demidovii*, très méfiants, sont d'abord habitués à manger dans des paniers de liane, puis sur des pièges, et enfin dans les pièges. Cette méthode progressive permet, après marquage de chaque individu, de faire de nombreuses reprises, en des points différents. Des captures simultanées ont permis d'étudier les liens sociaux d'une population. Pour cette étude, une carte détaillée a été relevée à la boussole et au mètreur "fil perdu".

B. Variations morphologiques et biométriques

De nombreuses différences anatomiques ont été constatées dans la population de *Galago demidovii* étudiée dans la région de Makokou (longueur tête + corps, longueur queue, poids, longueur des oreilles, coloration de la fourture, épaisseur de la fourrure, pilosité de la queue, etc. ...). On verra l'importance que peuvent jouer certains de ces caractères dans la vie sociale de cette espèce assez polymorphe (Fig. 1).



Fig. 1: Galago demidovii adulte (Photo A. R. DEVEZ)

1. Couleur

Elle varie du roux clair au gris foncé, en passant par tous les intermédiaires. Les juvéniles ont un pelage cannelle qui peut encore persister sur les joues après la puberté. La couleur de la queue est particulièrement variable, pouvant passer du gris presque noir au roux clair.

2. Epaisseur de la fourrure

Les différences d'épaisseur sont surtout remarquables sur la queue qui peut être très touffue, et parfois presque nue. Certains individus ont de longs poils seulement à l'extrémité de la queue.

3. Poids

Les ♂♂ sont un peu plus lourds que les ♀♀. ♂♂ adultes: moyenne 62,8 g, extrêmes 46 g—88 g ($N = 54$). ♀♀ adultes: (non gestantes) moyenne 59,6 g, extrêmes 52 g—79 g ($N = 19$).

La croissance se stabilise vers 6 mois (Vincent) et des oscillations de poids de 2 ou 3 grammes peuvent être enregistrées à quelques semaines d'intervalle. Après 1 an, les animaux recapturés dans une population naturelle avaient gardé le même poids, à l'exception de 2 ♂♂ et d'une ♀ qui s'étaient alourdis considérablement. Pour les 2 ♂♂, ce changement de poids était en corrélation avec un changement de classe sociale (voir vie sociale). Le facteur poids a une importance énorme chez les ♂♂. En effet, 10% seulement des ♂♂ dépassent 70 g. Ce sont ceux-là qui avaient des rapports avec les ♀♀ dans une population étudiée. Le poids est d'ailleurs proportionnel à la taille chez les ♂♂ (Fig. 2), et ne correspond pas à un engraissement. Chez les ♀♀, le poids et la taille ont des relations moins nettes, du fait de l'engraissement pendant la lactation.

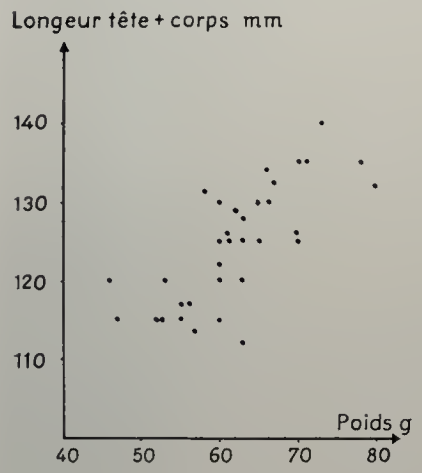


Fig. 2: Relations entre le poids et la taille chez les ♂♂

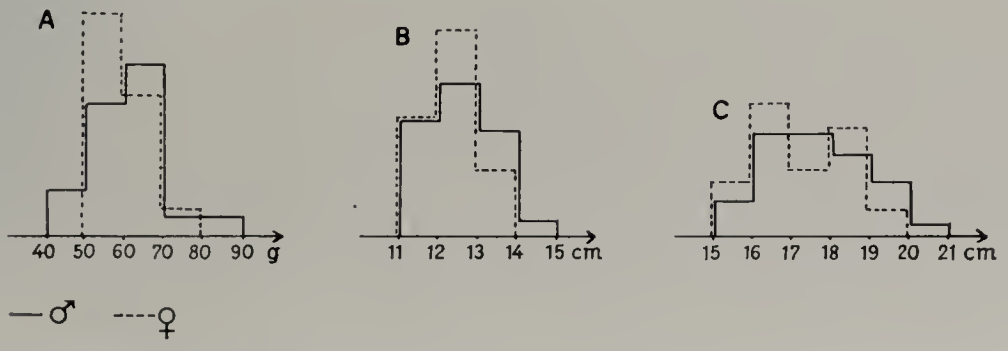


Fig. 3: Biométrie de *Galago demidovii*, comparaison entre ♂♂ adultes (38 mesures), et les ♀♀ adultes (30 mesures). A = Poids, B = Longueur tête + corps, C = Longueur de la queue (sans les poils)

4. Longueur tete + corps

♂♂ adultes: moyenne 124 mm, extrêmes: 110 mm—140 mm ($N = 36$).
♀♀ adultes: moyenne 121 mm, extrêmes: 105 mm—135 mm ($N = 30$).

Les ♂♂ sont un peu plus grands que les ♀♀. La figure 3 indique la répartition de ces dimensions chez les deux sexes.

5. Longueur de la queue (sans les poils)

♂♂ adultes: moyenne 173,6 mm, extrêmes: 152 mm—205 mm ($N = 34$).
♀♀ adultes: moyenne 170,3 mm, extrêmes: 150 mm—192 mm ($N = 29$).

La longueur de la queue n'est pas proportionnelle à celle de la tête + corps au cours de la croissance. Chez l'embryon, le rapport longueur queue: longueur tête + corps est de 0,85 à 0,95 de 3 à 5 g, et de 1,1 à 1,19 de 5 à 6 g. La queue s'accroît rapidement encore après la naissance (moyenne 1,32 de 10 à 20 g) puis se stabilise aux alentours de $1,5 \pm 0,3$. La moyenne de ce rapport tend toutefois à baisser avec le poids des animaux. 1,53 de 30 à 40 g, 1,48 de 40 à 50 g, 1,46 de 50 à 60 g, 1,36 de 60 à 70 g, 1,41 de 70 à 80 g.

6. Longueur des membres

Membre antérieur (longueur totale) ♂♂ = 81 mm, ♀♀ = 77 mm.
Membre postérieur (longueur totale) ♂♂ = 121 mm, ♀♀ = 114 mm
(♂♂, $N = 4$; ♀♀, $N = 3$).

7. Longueur des oreilles

La moyenne est de 23 mm pour les ♂♂ comme pour les ♀♀, mais il existe de grandes variations individuelles (18 à 27 mm dans un lot de 9 galagos mesurés).

C. Sex Ratio

Deux moyennes ont été établies chez l'adulte en considérant deux moyens de capture:

1. *Captures au fusil:* Sur 39 individus adultes tués au fusil pendant les chasses de nuit nous avons obtenu 19 ♂♂ et 20 ♀♀ (49% de ♂♂, 51% de ♀♀).
2. *Captures au piège:* (collets à détente sur les passages). Sur 36 captures d'adultes nous avons obtenu 23 ♂♂ et 13 ♀♀ (62% de ♂♂ et 38% de ♀♀).

Les ♂♂ se déplaçant plus que les ♀♀ il est normal qu'il y en ait d' avantage de pris dans les pièges. Seules les valeurs de 49% et 51% peuvent être retenues; elles correspondent à peu près au *sex ratio* des jeunes (46% de ♂♂ et 54% de ♀♀, $N = 37$).

II. ECOLOGIE

A. Niche écologique

Pour définir la niche écologique du *Galago demidovii*, tous les éléments mesurables ou quantifiables permettant de définir les caractéristiques de ses supports ont été analysés (Fig. 4). Pour cela, nous n'avons considéré que l'endroit où l'animal est surpris par le faisceau lumineux, pour ne pas fausser les résultats. En effet, l'influence de l'observateur est trop importante; un animal observé peut s'en approcher par curiosité ou bien se cacher s'il a peur. Dans ces conditions, les supports qu'il emprunte ne sont pas forcément ceux qu'il utiliserait en temps normal.

La hauteur, le diamètre, l'orientation et la nature du support sont analysés. La hauteur par rapport au sol est évaluée de 5 m en 5 m, et le diamètre de 0 à 1 cm, puis 1 à 5, 5 à 10, 10 à 15 cm etc. ... L'orientation du support est considérée comme horizontale de 0° à 15°, oblique de 15° à 75°, et verticale de 75° à 90°, par rapport au plan horizontal.

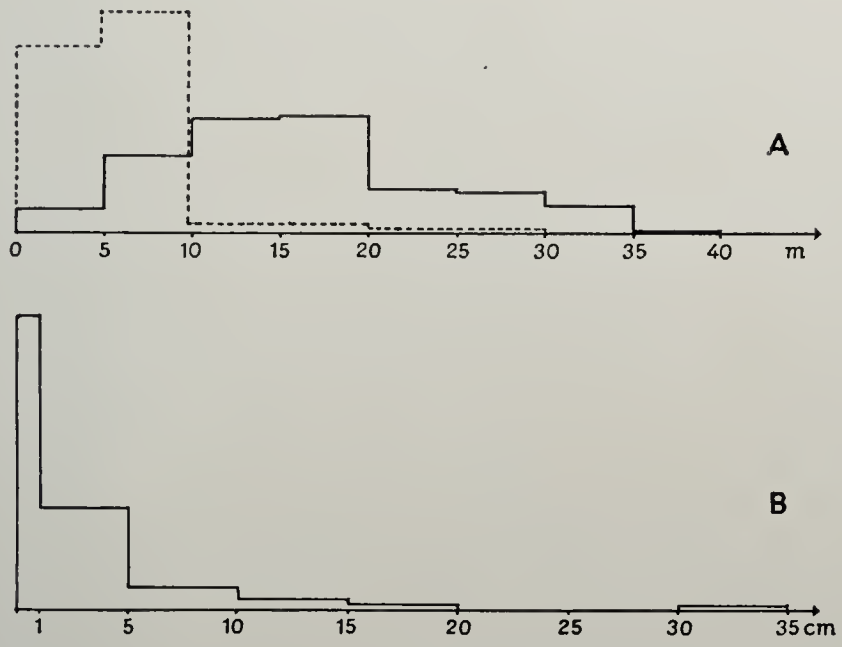


Fig. 4: Analyse statistique des supports utilisés par *Galago demidovii* en forêt. A: Hauteur par rapport au sol (trait plein = forêt primaire, trait pointillé = forêt secondaire). B: Diamètre du support

En forêt primaire, le *Galago demidovii* se trouve surtout entre 10 m et 20 m de haut, parfois jusqu'à 40 m. En forêt secondaire ou en forêt inondée, il évolue à une hauteur plus faible. En réalité, il suit la canopée et les feuillages denses qui se trouvent surtout à grande hauteur en forêt primaire, et près du sol en forêt secondaire (la forêt inondée a une situation intermédiaire). Quand il est observé à faible altitude en forêt primaire, c'est presque toujours dans les feuillages épais de lianes entraînées au sol par la chute d'un gros arbre.

Nous avons analysé statistiquement la hauteur, le diamètre, l'orientation et la nature des supports utilisés par *Galago demidovii*. Sur 154 observations en forêt nous avons rencontré cette espèce au sol (1,3%), sur des départs de lianes (1,3%), sur des lianes (22%), sur des grosses branches (8,4%), sur des petites branches (33%) et dans les enchevêtrements de lianes qui envahissent les feuillages (34%) (Fig. 5). Cette espèce utilise des supports horizontaux (24%), obliques (35%), ou verticaux (41%).

Le diamètre des supports utilisés est généralement inférieur à 1 cm (66%), mais *Galago demidovii* peut grimper sur des grosses branches et des grosses lianes surtout quand leur écorce est rugueuse.

Le déplacement de *Galago demidovii* est constitué en parties égales de course et de sauts. La course est assez rapide, et les sauts (1,50 m à 2 m) lui permettent de prendre des raccourcis au cours de ses déplacements. Avec un peu d'habitude, il est très facile de reconnaître *Galago demidovii*, même à grande hauteur quand on ne voit que ses yeux, à sa course et à ses sauts.



Fig. 5: Enchevêtrement de lianes dans la canopée: Biotope favori de *Galago demidovii* (Photo A. R. Devez)

B. Alimentation

Le *Galago demidovii* est surtout insectivore. Sur 52 contenus stomacaux analysés, 26 ne contenaient que des insectes, 1 seul n'en contenait pas. Quantitativement, les insectes représentent 70% de son alimentation. On trouve souvent des fruits dans les estomacs (52% de cas), mais ils ne représentent quantitativement que 19% de son alimentation. Les gommes (10%), les feuilles et les bourgeons entrent en faible quantité dans son régime alimentaire (Tab. 1).

Tab. 1: Régime alimentaire de *Galago demidovii* d'après l'analyse de 52 contenus stomacaux. F = fréquence qualitative (%) des aliments trouvés dans les estomacs. On peut trouver plusieurs catégories d'aliments mélangés dans le même estomac; par exemple, 98% des contenus analysés présentaient des insectes, mélangés à des fruits, présents seulement en plus ou moins grande quantité 52% des cas. Q = pourcentage quantitatif des aliments trouvés dans les estomacs. Les contenus stomacaux sont triés dans la mesure du possible, et les proportions sont calculées par pesée (paids frais)

	partie animale	fruits	gommes	feuilles	bourgeons
F	98 %	52 %	32 %	5 %	5 %
Q	70 %	19 %	10 %		

Tab. 2: Fréquence et quantité des différents groupes d'arthropodes entrant dans le régime alimentaire de *Galago demidovii* ($N = 52$) F et Q comme pour le tableau 1. Les pourcentages sont ramenés à la quantité totale d'arthropodes ingérés: par exemple, les Coléoptères représentent 46,2% des arthropodes consommés et non pas de l'alimentation totale

	coléoptères	lépidoptères	chenilles	hémiptères	orthoptères	pupes	scolopendres
F	83 %	67 %	42 %	17 %	17 %	17 %	17 %
Q	46,2 %	32,6 %	11,2 %	10 %			

Les insectes qu'il capture sont toujours de petite taille. Coléoptères (46%)s Lépidoptères (33%), chenilles (11%) constituent la majeure partie des insecte, qu'il mange (Tab. 2). Les chenilles trouvées dans les estomacs étaient toujours petites, sans poils urticants.

Dans certains cas, l'ouïe peut le guider dans la recherche de ses proies; quand il s'apprête à capturer un insecte, il oriente les oreilles dans sa direction. Une main ou les deux mains interviennent pour la capture selon la taille de l'insecte. Ce dernier est rapidement porté à la bouche, et tué de quelques coups de dents sur la tête et le thorax. Pendant qu'il le tue et le mange, le *Galago demidovii* plisse les oreilles et ferme en partie les yeux, surtout quand il s'agit d'un gros insecte (Fig. 6). Une proie qui se débat pourrait facilement lui blesser les yeux ou les oreilles (*Protective responses*). Quand un *Galago demidovii* fait fuir un insecte sur son chemin, il peut l'attraper au vol en sautant, ses pattes postérieures restant accrochées à la branche, puis, comme un ressort, revient à sa position initiale. Généralement, il utilise ce système de capture quand l'insecte est sur une petite branche voisine, à 10—20 cm de lui. Quand un *Galago demidovii* rencontre une proie sur la branche qui le supporte, il s'en approche doucement, lève lentement les pattes avant, puis les abat rapidement dessus, en s'allongeant de tout son corps, maintenu à la branche par les pattes postérieures.

Galago demidovii ne mange que des fruits mous et sucrés, ses petites dents pointues ne lui permettant pas d'entamer les fruits trop durs. Cependant, si un gros fruit est entamé par un autre animal (Potto), il profite de l'ouverture pour manger la pulpe.



Fig. 6: Galago demidovii mangeant un papillon. On peut remarquer les yeux mi-clos et les oreilles légèrement plissées (Photo A. R. Devez)

C. Rythmes d'activité

Galago demidovii est strictement nocturne, cependant, il sort de son nid avant le crépuscule, quand la luminosité est d'environ 100 Lux. Le crépuscule est très court sous l'équateur, si bien que 20 à 25 minutes après, la nuit est presque complète. Le matin, le regroupement se fait dès l'apparition du jour, mais quelquefois, des animaux attardés à la construction d'un nid peuvent être encore actifs alors qu'il fait jour depuis 10 à 15 minutes (Fig. 12 voir p. 20).

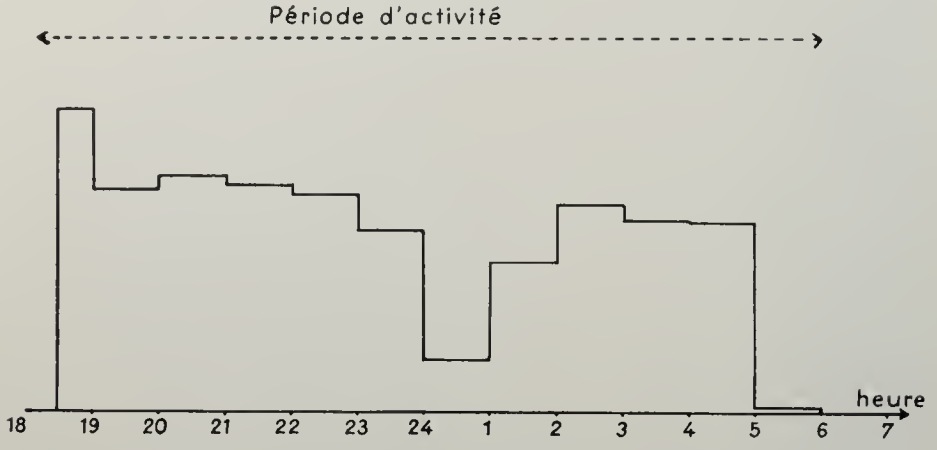


Fig. 7: Rythme d'alimentation en fruits de *Galago demidovii*: les heures de 500 entrées dans un nourrisseur, placé en forêt secondaire, ont été comptabilisées à l'aide d'un enregistreur graphique

Les heures de prise de nourriture et d'émissions des cris enregistrées dans des populations sauvages permettent de mettre en évidence l'activité moyenne de l'espèce aux différentes heures de la nuit.

L'alimentation en fruits a pu être analysée d'une façon précise (voir Méthodes). Le diagramme obtenu sur 500 passages dans le nourrisseur représente l'activité moyenne de 2 galagos pendant plus d'un mois en forêt secondaire (Fig. 7). C'est pendant la première heure de la nuit que l'activité est la plus grande. Entre 23 heures et 2 heures, l'activité baisse considérablement pour ne reprendre que quelques heures avant le matin. Entre 5 et 6 heures, les animaux ne mangent presque pas de fruits, et restent peu actifs dans le feuillage, attendant la venue du jour. La diminution du nombre de repas au milieu de la nuit correspond à une baisse générale de l'activité qui se retrouve dans la courbe de fréquence des émissions vocales (Fig. 10 voir p. 17).

Les périodes de repos, la nuit, ne se passent jamais dans les nids, mais dans le feuillage, à un endroit assez touffu où l'animal se sent en sécurité. Si en captivité les animaux se réfugient dans leur nid pendant la nuit, c'est qu'ils n'ont aucun autre endroit pour se réfugier. Quand il pleut, les animaux se réfugient de la même façon dans le feuillage épais, mais seulement quand la pluie est très forte.

D. Densités de population

Deux méthodes, qui seront détaillées dans une autre publication, ont permis d'estimer les densités de population dans différents milieux. La première est basée sur l'observation directe sur des parcours mesurés, en évaluant la surface explorée par la lampe frontale. La deuxième est basée sur l'écoute des cris sur les même itinéraires. Les nombres donnés correspondent à des

moyennes faites sur 148 km de parcours à pied, mesurés soit au mètreur "fil perdu", soit d'après l'estimation de la moyenne horaire de marche. On a constaté les densités suivantes par km²:

Forêt primaire:	32 *G. demidovii*/km² (1ere méthode),
	46 *G. demidovii*/km² (2eme méthode).
Forêt primaire inondée:	34 *G. demidovii*/km² (1ere méthode),
	103 *G. demidovii*/km² (2eme méthode).
Bords de Fleuve:	60 *G. demidovii*/km² (1ere méthode),
	120 *G. demidovii*/km² (2eme méthode).
Forêt secondaire:	42 *G. demidovii*/km² (1ere méthode),
	63 *G. demidovii*/km² (2eme méthode).
Bordure de route en forêt primaire:	117 *G. demidovii*/km² (1ere méthode),
	113 *G. demidovii*/km² (2eme méthode).

Nous verrons dans le chapitre "Vie sociale" que la répartition est très hétérogène, correspondant à des groupements séparés par des zones peu habitées.

Une population de *Galago demidovii* (environ 30 individus), étudiée par piégeage en forêt secondaire, occupait une surface de 100 000 m², ce qui faisait une densité de 300/km², alors qu'un peu plus loin, le même type de forêt était pratiquement inhabitée (Fig. 8).



Fig. 8: Jeune *Galago demidovii* âgé d'environ 1 mois $^1/_2$, élevé au biberon (Photo A. R. Devez)

III. VIE SOCIALE

A. Populations

En forêt, le parcours régulier des mêmes itinéraires montre vite l'hétérogénéité des peuplements de galagos. Des zones peuplées sont séparées par des espaces plus ou moins grands (Fig. 9, A, B) où l'on n'en rencontre pratiquement pas. En grande forêt, il est impossible de savoir si ces différences de

concentrations sont dûes à des facteurs sociaux ou écologiques (hétérogénéité de la canopée). Les routes percées en forêt offrent un biotope particulièrement homogène constitué par la végétation secondaire des bas-côtés formant un étroit couloir. Les *Galago demidovii* sont très attirés par ces bordures de route, et il est facile de mettre en évidence l'existence de groupements distincts (Fig. 9, C). Lors de l'étude des groupes sociaux, nous avons piégé sur une surface de 350 000 m² (2 km de long). Toutes les ♀♀ furent capturées sur une zone de 80 000 m² (550 m × 150 m). Les ♂♂ étaient situés sur cette zone ou aux alentours immédiats. Un seul individu (♂ adulte) sur 31 animaux contrôlés fut capturé loin du groupe.

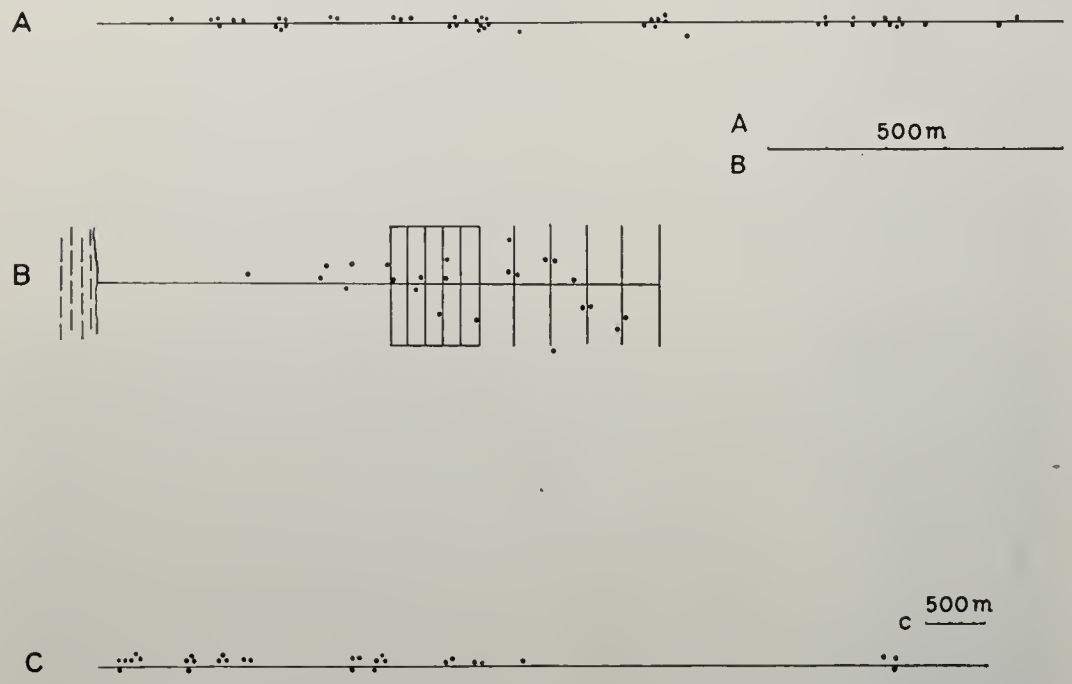


Fig. 9: Répartition de *Galago demidovii* sur 3 itinéraires. A = Forêt primaire d'Ipassa (9 parcours en 1 an), B = Forêt primaire de Mekob (7 parcours en 2 mois), C = Piste de Bengoué (2 parcours en 1 nuit). A et B sont rectilignes, C comporte quelques courbes légères. On peut remarquer la concentration des animaux dans certaines zones

B. La dispersion nocturne

Si le phénomène social est évident le matin, au coucher des animaux et pendant leur sommeil, il ne touche qu'une partie de la vie active du *Galago demidovii*, les groupes se dispersant dès leur réveil, au crépuscule. Au cours de mes sorties nocturnes, 78,5% des animaux rencontrés étaient seuls, 17,6% groupés par deux, 1,7% groupés par trois, 1,1% groupés par quatre, 1,1% groupés par cinq (moyenne établie sur 220 contrôles). Les groupes de deux sont constitués la plupart du temps par une ♀ et un juvénile, ou une ♀ et un ♂.

Tab. 3: Pourcentage de *Galago demidovii* observés seuls ou groupés par deux au cours des 6 premières heures de la nuit ($N = 220$)

Heure	18	19	20	21	22	23	24
Seuls	68 %	85 %	86 %	82 %	80 %	86 %	
A deux	32 %	15 %	14 %	18 %	20 %	14 %	

Ces groupes de deux sont d'ailleurs plus fréquents de 18 à 19 heures (Tab. 3). En effet, les ♂♂ qui ont dormi isolément rendent visite aux ♀♀ en début de nuit; ces visites sont accompagnées d'un petit gémissement émis par les deux partenaires. Des groupements plus importants (3, 4 et même 5) ont été observés, mais très rarement (1,7%, 1,1%, 1,1%). Une fois, j'eus l'occasion de rencontrer, à 22 heures 45, un groupe de cinq individus adultes ou juvéniles très excités, émettant le cri n° III avec des phonoréponses (l'un d'eux émit le cri n° II à notre arrivée). Si les animaux sont dispersés pendant la nuit, cela n'empêche pas qu'ils restent en communication sonore par leurs cris. En début et en fin de nuit, on assiste à une liaison sonore assez particulière donnant lieu à des phonoréponses.

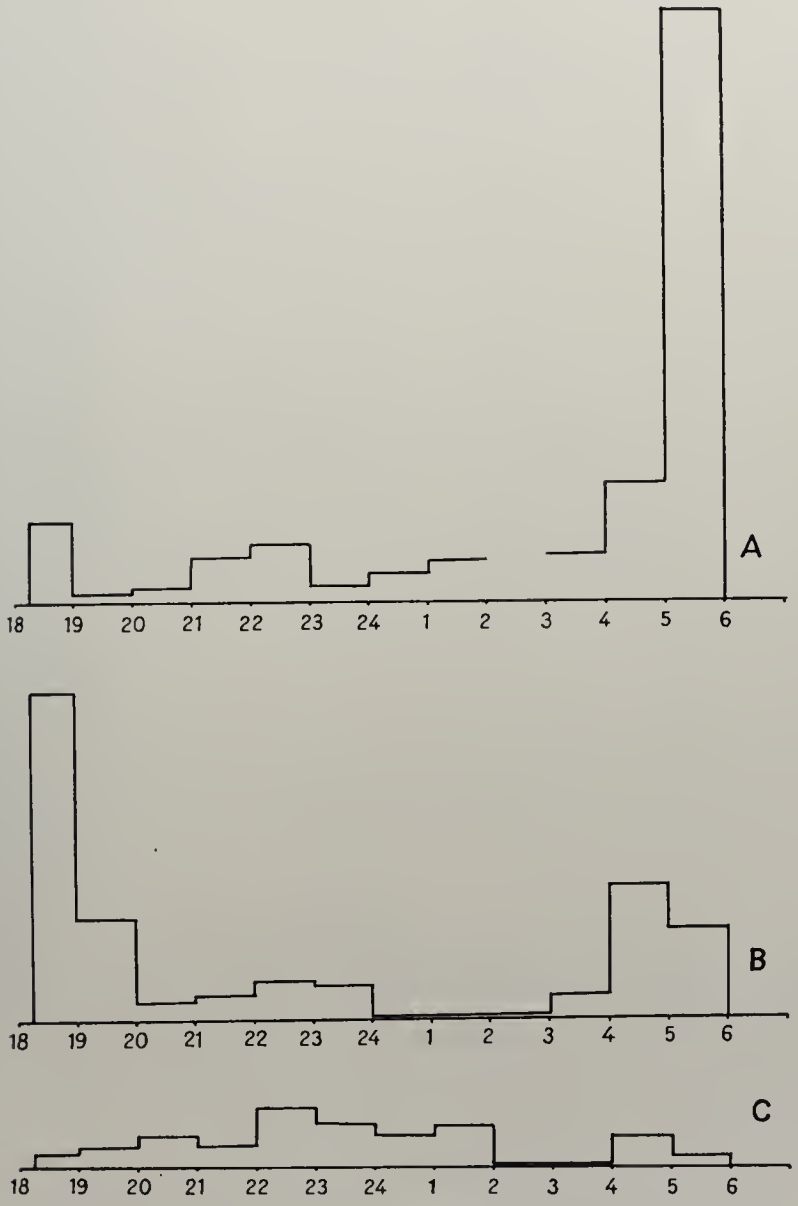


Fig. 10: Répartition moyenne des 3 principaux cris de *Galago demidovii* au cours de la nuit. A = Cri n° III correspondant au regroupement du matin avec phonoréponses, B = Cri n° I correspondant surtout à la dispersion du soir avec phonoréponses, C = Cri n° II correspondant à l'agressivité et au territorialisme, pas de phonoréponses (moyennes établies sur 263 heures d'écoute). On peut établir un parallélisme entre les phases sociales et solitaires de *Galago demidovii* et la fréquence d'émission de ses cris au cours de la nuit

Communications sonores pendant la nuit

1. Cri nº I

On peut entendre ce cri toute la nuit avec un pic très net à 19 heures, au moment de la dispersion des animaux, et un autre plus réduit de 4 à 6 heures, avant le rassemblement du matin (Fig. 10, B). le cri nº I, très aigü et difficilement perceptible pour une personne non avertie, est audible de 25 à 30 mètres pour l'oreille humaine. Il est constitué par un élément bref très aigü, comparable à une stridulation d'orthoptère, pouvant se répéter très rapidement de 1 à 10 fois (parfois plus quand il dérive vers le cri nº II). Il nous est vite apparu qu'il pouvait exister des phonoréponses, mais du fait de la dispersion des animaux et de la faible portée du cri pour l'oreille humaine, ce phénomène n'est pas très évident.

J'ai placé à 200 mètres de moi un aide qui me prévenait immédiatement par radio (talkie-walkie) quand il entendait un cri. A l'aide du chronomètre, je notais l'heure de tous les cris avec une précision de 2 à 3 secondes. En un seul point, 6% des cris émis par des individus différents sont séparés de 0 s. à 5 s., 20% de 0 s. à 30 s., 30% de 0 s. à 60 s., 56% de 0 s. à 120 s. Entre les deux points distants de 200 mètres, 12% des cris sont séparés de 0 s. à 5 s., 28% de 0 s. à 30 s., 47% de 0 s. à 60 s., et 75% de 0 s. à 120 s. Le nombre de cris entendus par station est très faible (10/heure) dans ces conditions, on peut considérer que ces cris correspondent à des liaisons sonores.

Nous avons eu l'occasion d'observer des *Galago demidovii* au moment où un autre émettait le cri nº I. Souvent, il s'ensuit une grande excitation des animaux observés qui courent dans tous les sens et peuvent répondre par un cri identique. La réponse n'est pas toujours immédiate, si bien que pendant une minute ou deux, on entend des cris un peu partout, puis le calme revient. Ces séries de cris, correspondant à une grande excitation des animaux au réveil, peuvent se reproduire toutes les 5 à 20 minutes. La figure 11 représente la fréquence du cri nº I en fonction de la chute de la lumière. La lumière est mesurée à l'aide d'un Luxmètre enregistreur dont les cellules sont dirigées vers le ciel en terrain découvert. En forêt, c'est lorsque la luminosité tombe

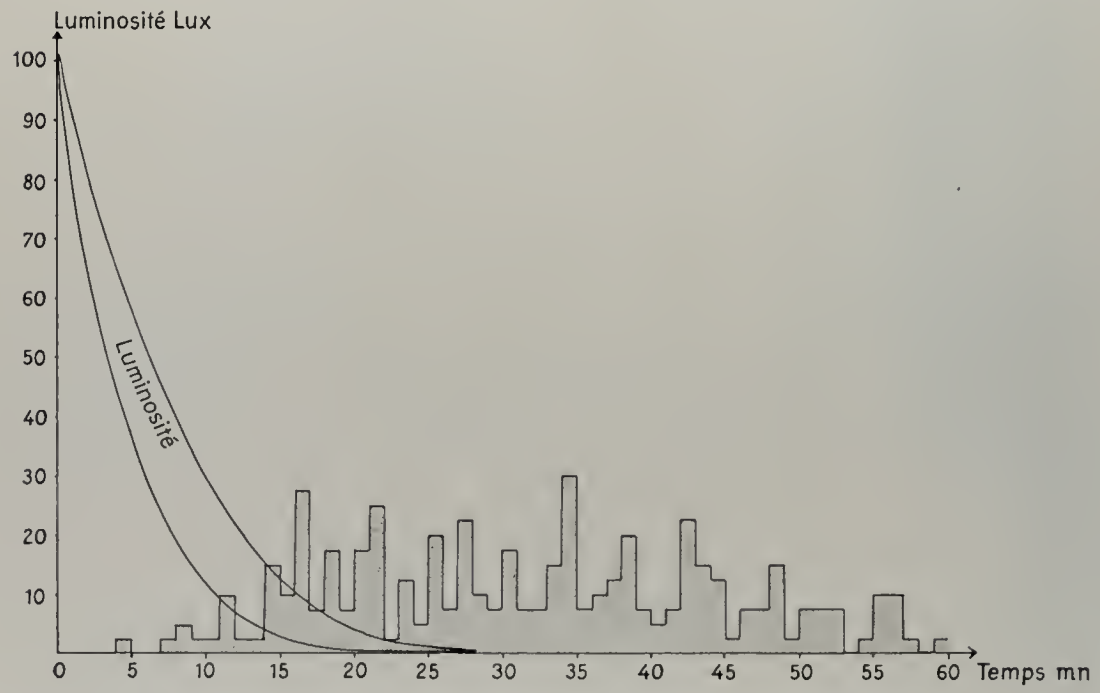


Fig. 11: Répartition moyenne du cri nº I, le soir, en fonction de la chute de la luminosité. Cette chute de la lumière varie selon la nébulosité, les extrêmes sont figurés sur la courbe

vers 100 Lux au ciel que les *Galago demidovii* se déplacent. Ce n'est que 15 minutes après leur réveil et leur dispersion que la fréquence d'émission du cri nº I atteint son maximum. Pendant une demi-heure, il y a un plateau, puis la fréquence baisse rapidement pour être stationnaire le reste de la nuit (Fig. 10, B). La signification de ce cri est difficile à interpréter. Il témoigne d'une grande excitation des animaux au moment de leur dispersion au réveil. Dans certains cas, il peut dériver progressivement vers le cri nº II.

2. Cri nº II

Ce cri est constitué par les éléments du cri nº I, espacés d'environ $^1/_2$ seconde, bien plus puissants. Il s'agit là sûrement du cri décrit par VINCENT comme "3ème type déclenché sous l'effet d'un stimulus à hightcontact". Tous les intermédiaires existent, un animal pouvant passer facilement du cri I au cri II, mais jamais en sens inverse. C'est surtout entre 20 heures et 4 heures que l'on entend le plus fréquemment ce cri (Fig. 10, C). En présence d'un intrus (homme, carnivore, rapace etc. ...), le *Galago demidovii* l'émet souvent: l'animal devient assez agressif, pouvant faire du "mobbing". Ce sont essentiellement les ♂♂ et les ♀♀ allaitantes qui réagissent ainsi. Très souvent, les galagos émettent spontanément ce cri dans certains arbres où ils ont l'habitude de venir crier. Une ♀ venait ainsi crier régulièrement dans un arbre près du bâtiment d'habitation, généralement entre 22 heures et 1 heure du matin. Immobile dans le feuillage, elle criait pendant 1 à 10 minutes, puis repartait.

Ce cri nº II est émis fréquemment lors des manifestations territoriales observées en captivité. Deux individus habitant des compartiments différents sont mis en contact par une trappe. Quand ils ne font pas partie du même groupe social, ils peuvent se battre et et émettent assez souvent ce cri nº II pendant le moment de grande excitation qui suit l'expérience. Chez *Euoticus elegantulus* et *Galago alleni*, des cris homologues au cri nº II de *Galago demidovii* existent et sont également liés à une forte excitation déclenchée par un danger ou un comportement territorial.

Il existe d'autres cris émis par *Galago demidovii*: cri nº III (voir regroupement des animaux). Un gémissement émis par les ♂♂ et les ♀♀, lié au comportement sexuel et aux visites du ♂ en début de nuit. Un roulement très doux émis par la mère répondant à son jeune. Un petit cri très aigü émis par le jeune qui appelle sa mère. Un cri de détresse émis par tous les individus en grand danger (capture, blessure, combat); c'est ce cri qu'imitent les enfants gabonais pour attirer les adultes qu'ils chassent parfois à l'arbalète (normalement, les cris de détresse d'un animal blessé attirent les galagos les plus proches, parfois à moins d'un mètre de l'homme). Un cri de dispute (Kèc Kèc Kèc ...).

C. Regroupement des animaux

Les *Galago demidovii*, dispersés pendant la nuit, émettent à l'aube un cri extrêmement puissant, constitué par un crescendo d'éléments de plus en plus aigüs et rapprochés (cri nº III). Ce cri nº III est émis par tous les individus: ♂♂, ♀♀ et juvéniles. Cependant, chez ces derniers, l'émission est moins longue et moins puissante. Chez le nouveau-né, il consiste en un seul élément très faible, qui de jour en jour devient plus puissant, puis se répète de plus en plus souvent. Plus tard, les éléments sont graves en début, et aigüs en fin d'émission, comme dans une gamme que l'on monte, et les temps de séparation deviennent de plus en plus brefs de façon à former un crescendo très caractéristique d'une durée de 2 à 3 secondes (étude de l'ontogénèse en cours). Il existe des différences individuelles assez importantes dans ce cri nº III, si bien qu'il est très souvent possible, en captivité, de reconnaitre les animaux à leur cri nº III. Il est bien possible que les animaux puissent se reconnaitre indivi-

duellement à leurs vocalisations lors des regroupements. Chez le jeune, ce cri correspond à un appel ou un état d'insécurité: un nouveau-né que l'on sépare de sa mère ou que l'on manipule avec violence l'émet. Le matin, les jeunes l'émettent spontanément quand ils sont isolés. C'est à ce moment que dans la nature la mère récupère alors son jeune qu'elle a laissé toute la nuit dans la végétation. Généralement, elle émet le cri nº III ou un petit roulement sourd en réponse à l'appel du jeune, et peut ainsi le localiser facilement grâce à son cri. Plus tard, le cri nº III est émis surtout le matin, comme le montre la figure 10, et correspond à un regroupement social. A l'aube, en forêt, ce cri provoque des phonoréponses, et les galagos entrent dans une vive excitation. Ils se dirigent très rapidement les uns vers les autres, s'arrêtant de temps en temps pour crier, déclenchant de nouvelles phonoréponses. Il est assez courant d'assister à ce spectacle en forêt vers 5 h. 45. Alors qu'en fin de nuit les *Galago demidovii* sont peu actifs, dès l'apparition du jour, un véritable concert de cri nº III, durant de 1 à 10 minutes, se déclenche brusquement. Me trouvant une fois au point de rassemblement d'un groupe de 5 ou 6 galagos, j'ai pu enregistrer 70 émissions vocales en 9 minutes. Les animaux se dirigent les uns vers les autres à une telle rapidité qu'il est impossible de les suivre, surtout en forêt dense. Une fois rassemblés, ils se taisent et partent vers le lieu de dortoir en file indienne, entre 10 et 50 cm les uns des autres. La cohésion est très forte, et si l'un d'eux se sépare du groupe, il revient vite se replacer dans la file.

Le soir, il arrive de voir, au réveil, certains individus se suivant en file indienne avant leur dispersion. Dans la journée, des animaux dérangés dans leur sommeil adoptent très souvent cette position en file indienne après leur fuite du nid.

Quand un retardataire arrive en criant, les *Galago demidovii* ne répondent que rarement à ses cris. En captivité, il est très rare d'entendre le cri nº III quand plusieurs individus vivent ensemble, alors qu'un animal nouvellement isolé émet ce cri spontanément le matin, et parfois le soir. Un groupe de trois *Galago demidovii* (1 ♂ adulte, 1 ♀ adulte, et 1 ♀ juvénile) ont été lâchés et étudiés dans un bouquet d'arbres isolés de la forêt. Tous les matins, ils se regoupaient en émettant le cri nº III pour aller dormir ensemble dans le même arbre. Il leur arrivait quelquefois de se regrouper sans un cri, mais la surface boisée mise à leur disposition ne couvrait que 1500 m².

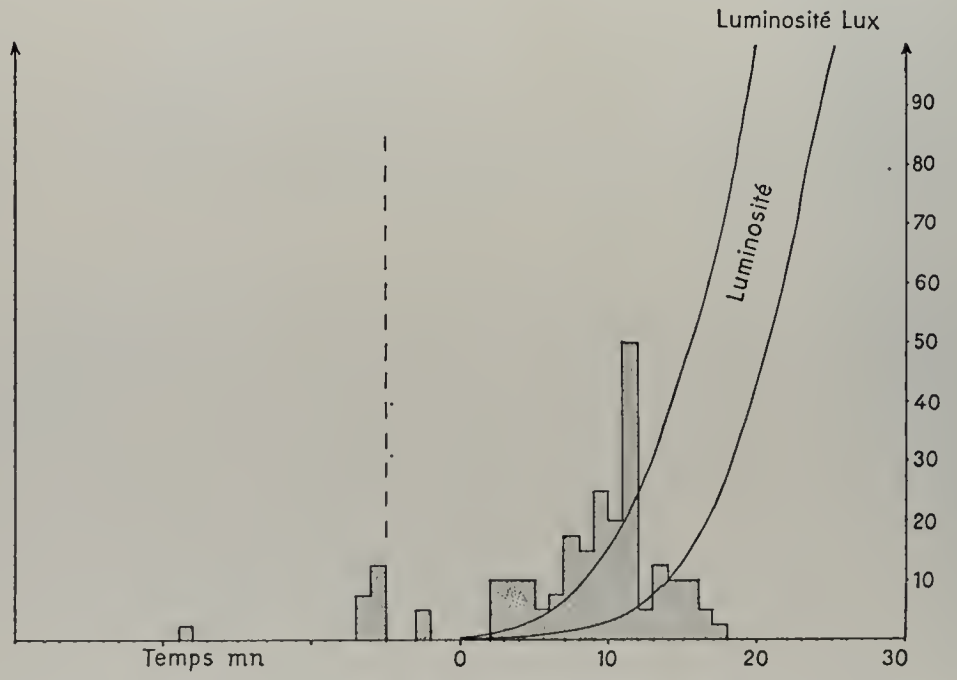


Fig. 12: Répartition moyenne du cri nº III en fonction de l'apparition du jour. L'augmentation de la luminosité varie selon la nébulosité, les extrêmes sont figurés sur la courbe

Le rassemblement n'est pas obligatoire, et concerne les ♀♀ et les juvéniles. Le cri nº III, dérivé du cri d'appel du jeune, a pris une signification sociale chez l'adulte. Il correspond à un besoin de regroupement, et les *Galago demidovii* ne l'émettent plus quand ils sont réunis. Les comptages de cris faits en forêt au cours de toutes les heures de la nuit (Fig. 10, A), indiquent une très grande fréquence du cri nº III pendant la dernière heure d'activité des animaux au moment de leur coucher. On peut noter sur la courbe un léger pic au moment du réveil. La figure 12 représente la fréquence du cri nº III, non pas en fonction de l'heure, mais en fonction de l'apparition du jour. Ce moment correspond à une valeur de $^1/_4$—$^1/_3$ de Lux au Luxmètre enregistreur (cellule dirigée vers le ciel en terrain découvert). En réalité, l'œil humain discerne l'apparition du jour 5 minutes avant que le luxmètre ne réagisse. Ce moment est figuré par la ligne pointillée. La courbe de fréquence du cri est établie sur 8 enregistrements de coucher d'animaux en forêt. Selon la nébulosité, la luminosité n'augmente pas à la même vitesse pendant les 10 ou 15 premières minutes. Ces différences ne peuvent en aucun cas agir sur l'heure du regroupement. C'est l'apparition du jour qui déclenche l'émission du cri nº III, donc le regroupement des animaux. En fin de nuit, une stimulation quelconque (faisceau lumineux, détonation, présence d'un observateur etc. ...) peut déclencher le cri nº III. La pulsion sociale existe donc bien avant le jour (augmentation de la fréquence 2 heures avant le jour, Fig. 10, A), mais les animaux attendent presque toujours la venue de l'aube. Ce n'est qu'à ce moment là que les *Galago demidovii* émettent le cri nº III et se dirigent les uns vers les autres.

La figure 10 indique la fréquence des trois principaux cris du *Galago demidovii* au cours de la nuit. Il est intéressant de signaler que parmi ces cris, I et III donnent lieu à des phonoréponses indiquant un lien social et se situent en début et en fin de nuit. Le cri nº II, témoin d'un état de grande excitation, lié à la territorialité, est le plus fréquemment entendu entre 20 heures et 4 heures. Il existe un parallélisme étroit entre le comportement social de cette espèce et la fréquence d'émission de ses différents cris. *Matin:* abondance des cris nº III avec phonoréponses immédiates et rassemblements de petits groupes de galagos dormant ensemble. *Soir:* dispersion des groupes, liaison sonore pendant la première heure de la nuit, avec excitation des animaux qui se répondent par des cris nº I. *Nuit:* les animaux, après leur réveil, se dispersent et émettent le cri nº II sans qu'il y ait de phonoréponses (grande excitation, territorialité).

Dortoir

Jamais, en quatre ans de séjours au Gabon, nous n'avons observé de *Galago demidovii* dormant dans des trous d'arbres[1]). A ce sujet, les observations en captivité peuvent prêter à confusion. En effet, en enclos, les *Galago demidovii* ne construisent jamais de nids et se réfugient dans des bûches-nichoirs mises à leur disposition (ils y mettent quelquefois des feuilles vertes qu'ils cueillent). Si l'enclos est suffisamment riche en végétation, ils délaissent la bûche-nichoir pour dormir en "groupe de contact", accrochés les uns aux autres dans une partie dense du feuillage.

Ces groupes de contact sont formés par plusieurs individus qui dorment sur un support naturel dans le feuillage (petite fourche, ou entrecroisement de petites lianes), recherchant le maximum de contact entre eux.

Dans un enclos de 3 m × 3,50 m × 2,50 m, contenant un cacaoïer vivant, je n'ai jamais pu observer de construction de nid. Les trois *Galago demidovii* lâchés et étudiés dans un bouquet d'arbres

[1]) Par contre, *Galago alleni* utilise les trous d'arbres pour dormir.

isolé de la forêt, construisirent un nid de feuilles, alors que des bûches-nichoirs étaient mises à leur disposition.

Dans la nature, 20 informations indiquent des rassemblements de sommeil soit dans des nids de feuilles ($N = 15$), soit en "groupe de contact" dans le feuillage ($N = 5$) — (Tab. 3). Nous avons observé trois animaux (2 ♂♂ et 1 indéterminé) qui dormaient isolément dans le feuillage, et un ♂ qui dormait seul dans un nid de feuilles. Sur une trentaine de bûches-nichoirs placées en forêt, aucune ne fut utilisée par *Galago demidovii*.

Même pendant leur sommeil, les *Galago demidovii* sont très craintifs, et le moindre ébranlement de la végétation les fait fuir. D'après les renseignements fragmentaires indiqués (Tab. 4), on peut conclure que les ♀♀ et leurs jeunes se groupent dans des nids de feuilles pour dormir. Les ♂♂ peuvent dormir seuls, mais il n'est pas exclu que certains dorment avec des ♀♀. Cependant, sur huit captures d'adultes rassemblés dans des nids, il n'y avait que des ♀♀. Très souvent, des jeunes animaux sont capturés avec leur mère dans des nids de feuillage.

Tab. 4: Composition des groupements de sommeil de *Galago demidovii*

		Nombre d'individus	Fréquence	Composition (souvent partielle)
Nids	Isolés	1	1	♂ adulte
	En nombre	2	4	(♀ ad. + juv. 19 g) (♀ ad. + juv. 19 g) (♀ ad. + juv. 26 g) (? + ?)
		3	1	(♀ ad. + juv. 15 g + juv. 13,5 g)
		4	4	(? + ? + ? + juv. 18 g) (? + ? + ? + ?) (? + ? + ? + ?) (? + ? + ? + ?)
		6	3	(? + ? + ? + ? + ? + juv. 34 g) (♀ ad. + ♀ ad. + ? + ? + ? + ?) (♀ ad. + ♀ ad. + juv. 43 g + juv. 35 g + juv. 28,5 g + ?)
		10	1	(juv. 30 g + ???....)
		?	1	(♀ ad. + ???....)
Support naturel (Sans nid)	Isolés	1	3	(♂ ad.) (♂ ad.) (?)
	Groupes de contact	4	3	(? + ? + ? + ?) (? + ? + ? + ?) (? + ? + ? + ?)
		10 ?	1	(? + ? + ?.....)

BATES signale des groupements dans des nids d'écureuils. Une fois, un indigène me conduisit à un nid de *Funisciurus* d'où il avait vu sortir 4 *Galago demidovii* la veille. Les animaux ayant abandonné le nid, je n'ai pu confirmer cette observation.

Adultes et juvéniles participent à la construction du nid, qui consiste en un amoncellement de feuilles vertes cueillies généralement dans le même arbre, et disposées dans un entrecroisement de branches ou de petites lianes (Fig. 13). Un nid construit dans un caféïer par une ♀ et son jeune, pesait 110 g (poids frais), et était composé de 104 feuilles, correspondant à 75 voyages: 38 feuilles vertes, 40 feuilles vertes réunies 2 par 2, 9 feuilles vertes réunies 3 par 3, 4 feuilles vertes réunies 4 par 4, et 13 feuilles sèches. Les feuilles reliées les unes aux autres par leur pétiole contribuent à la solidité du nid. Les *Galago demidovii* arrachent les feuilles en les tirant par le pétiole qu'il tiennent dans la gueule. Les feuilles sont ensuite disposées dans le nid à l'aide des mains. Le même nid peut servir plusieurs jours, mais il est abandonné dès que ses occupants ont été dérangés. Je n'ai jamais pu assister à la construction



Fig. 13: Nid de *Galago demidovii.* Ce nid, dont les occupants venaient de fuir, est âgé de plusieurs ours, coïmme en témoigne l'état de dessiccation des feuilles (Photo A. R. Devez)

ɔomplète d'un nid, la présence d'un observateur arrêtant ce comportement. J'ai pu cependant voir l'un des animaux lâchés dans le bouquet d'arbre (♀ juvénile) arracher des feuilles de cacaoïer le matin. Vincent indique qu'au Congo, les nids sont constitués par les feuilles d'arbres voisins; ce n'est pas toujours le cas au Gabon où les feuilles sont souvent cueillies dans l'arbre où est construit le nid, à quelques mètres de celui-ci. Il semble que les ♀♀ ayant un nouveau-né s'isolent: Poids des jeunes capturés dans des nids avec une ♀ isolée: 19 g, 19 g, 26 g, 15 g, 13 g. Poids des jeunes capturés dans des nids avec plusieurs adultes: 18 g, 34 g, 43 g, 35 g, 28,5 g, 30 g.

D. Toilettage social (Social Grooming)

Le toilettage, assez facile à voir en captivité, du fait de la concentration des animaux, existe sûrement d'une façon moins fréquente dans la nature. En captivité, il a lieu surtout au réveil et au coucher des animaux. C'est ce qui doit se passer dans la nature du fait de la dispersion nocturne. Ce toilettage est différent de celui des singes car les mains n'interviennent que pour agripper le partenaire (caractère de Prosimiens). Généralement, l'animal actif tient l'autre par la tête ou les épaules, et lui lèche la face. Ce dernier tend souvent le cou et le bras pour se faire lécher dessous. Les *Galago demidovii* se lèchent à tour de rôle, et il arrive fréquemment que l'un d'eux lâche son partenaire pour se lécher, le toilettage mutuel reprenant après. Quand certains poils sont collés ou que la langue rencontre une aspérité, le peigne, formé par les incisives et "canines" inférieures, intervient pour déméler la fourrure. La sublingua nettoie ensuite le peigne, et les poils tombés sont avalés: on en rencontre fréquemment dans l'estomac.

Les individus captifs, faisant partie du même groupe social, après une séparation de 5 à 15 jours, se lèchent mutuellement pendant plusieurs heures quand on les remet en contact. Au cours de ce toilettage, le dominant se tient un peu plus haut que son partenaire, et lui lèche le haut de la tête. Le dominé lèche au contraire le cou et le museau de son partenaire, rarement le haut de la tête.

Ce toilettage social existe entre les ♀♀ et leurs jeunes, entre les ♀♀, entre les ♀♀ et les ♂♂. Dans ce dernier cas, c'est la ♀ qui prend souvent l'attitude du dominant et quelquefois repousse le ♂ et émet des cris de dispute quand celui-ci étend son léchage un peu trop loin sur son corps. Le toilettage entre ♂♂ est beaucoup plus rare.

E. Marquages

Les marquages par urine sont extrêmement fréquents chez les *Galago demidovii* qui utilisent la technique du "lavage des paumes" (EIBL-EIBESFELDT). Ce marquage consiste à déposer de l'urine sur la plante d'une patte arrière et de mouiller les doigts de la patte avant correspondante en les frottant dessus. Les pattes du deuxième côté sont ensuite humectées de la même façon. Quelquefois, l'animal essuie les mains sur la branche après le lavage des paumes.

A leur sortie d'un nid de feuilles dans les arbres, trois *Galago demidovii* avaient l'habitude de marquer abondamment à quelques mètres du nid. En captivité, les botes servant de dortoirs sont également marquées par les urines.

Plusieurs auteurs (SEITZ, EIBL-EIBESFELDT, SAUER) ont émis l'hypothèse que chez les Lorisiformes, le dépos d'urine correspondait à un repérage de l'animal au sein de son territoire, lui permettant de revenir sur ses traces. Après de nombreuses observations des cinq espèces de Prosimiens gabonais dans leurs biotopes, et en expérimentant sur le terrain, cette hypothèse ne semble pas vérifiée. Tout d'abord, il est bien rare qu'un galago (ou un Potto) repasse par le même chemin, à moins qu'une seule voie de passage existe pour aller d'un point à un autre. Quand une forêt a été dégradée par de nombreux abattages, les animaux sont obligés de faire des détours et de connaître certains passages privilégiés. Lorsqu'un nouvel individu y est introduit, il met un certain temps à repérer les passages que ses congénères utilisent régulièrement. Il n'aurait aucune hésitation si ces voies de passage particulières étaient marquées par les urines des autres animaux. Expérimentalement, nous avons détruit de tels passages pour les remplacer par d'autres, éloignés de 10 ou 20 m (liane attachée d'un arbre à un autre). Les animaux voulant passer par leur ancien chemin hésitent un moment, et repèrent immédiatement le nouvel itinéraire qu'ils adoptent très vite. La vision doit intervenir d'une façon importante dans le repérage, car en période de nuit très noire, ils ne se déplacent presque pas. Sur certains parcours très fréquentés, les itinéraires peuvent être les mêmes, et des variations individuelles peuvent intervenir. Dans ce cas, il doit s'agir davantage d'habitudes individuelles basées sur la mémoire visuelle, tactile et olfactive. Ces itinéraires régulièrement fréquentés sont aussi les plus directs, et il serait étonnant que les animaux les aient empruntés à leur premier passage. En dehors de ces voies uniques imposées par la nature de la végétation, les animaux peuvent passer par n'importe quelle zone de leur domaine qu'ils semblent connaître parfaitement. En fait, tous les intermédiaires existent entre les chemins très bien connus et les zones moins explorées où les animaux s'aventurent sans se perdre, sans pour autant revenir par le même itinéraire (les bananes, disposées au hasard dans le domaine vital d'un galago sont mangées dans les 1 à 3 jours qui suivent). Le psychisme et les organes des sens des Prosimiens sont suffisamment développés pour qu'ils puissent facilement se repérer dans leur milieu grâce à leur mémoire visuelle, tactile, olfactive

et peut-être auditive. S'ils ne disposaient que des traces d'urine pour retrouver leur chemin, ils seraient vite perdus après les pluies torrentielles qui tombent dans ces régions.

Le dépos d'urine sur les branches semble d'avantage être en relation avec le marquage territorial, phénomène très généralisé chez les Mammifères. Dans une étude en cours sur *Galago demidovii* en captivité, nous avons observé qu'un individu marque toute nouvelle branche introduite dans sa cage, alors qu'il évite, les premiers temps, les branches marquées par d'autres galagos inconnus. Les dépos d'urine se font presque toujours dans les mêmes points de la cage, ou à proximité des objets introduits, marqués par un individu étranger. Le "lavage des paumes" nous semble être une adaptation à la vie arboricole permettant de disperser le marquage. En effet, un marquage déposé en un point de la végétation pourrait passer inaperçu aux autres congénères. En humectant ses pattes, un galago laisse sur son chemin une partie des urines pendant quelques temps, marquant ainsi selon une "ligne" plus facilement repérable dans les arbres qu'un "point". En captivité, les galagos marquent à l'aide des urines 4 à 8 fois par heure.

Un autre marquage existe, consistant à frotter les parties génitales sur le support. Cette forme de marquage est plus fréquente au moment de l'excitation sexuelle. (Vincent indique également un marquage par étalement des excréments, et un autre par frottement des avant-bras sur les branches).

F. Organisation sociale et domaines vitaux

1. Techniques

Ce travail a été effectué à Makokou, de juillet 1968 à décembre 1968, puis d'Octobre 1969 à Décembre 1969. La Mission Biologique est située en bordure d'un vallon couvert de forêt secondaire où prend source un petit cours d'eau de 400 m de long, se jetant dans le fleuve Ivindo.

Cette zone boisée d'une vingtaine d'hectares, à cinq ou dix minutes de marche du laboratoire, est limitée à l'Ouest et au Sud par des défrichements (route et villages), et à l'Est par le fleuve. Elle est cependant largement en contact avec la grande forêt par un couloir de végétation de 200 m de large longeant le fleuve. La carte (Fig. 14) a été dressée au mètreur "fil perdu" et à la boussole. Des sentiers taillés à la machette, parallèles et distants de 50 m, permettent de circuler (Fig. 15). Des numéros sont disposés tous les 5 m facilitant le repérage. Les animaux capturés ont été marqués et relâchés pour contrôler leurs déplacements et la nature de leurs groupes. Nous avons d'abord habitué les *Galago demidovii* à manger de la banane dans des paniers de liane, disposés en plusieurs points du terrain. Un piège, accroché à quelques mètres du panier, et camouèflé par du feuillage, est appâté par des bananes posées successivement dessus puis à l'intérieur, le piège n'étant pas armé. Ce n'est qu'au bout d'une dizaine de jours que nous les armons, lorsque les animaux y entrent régulièrement et sans crainte pour manger la banane. Les pièges ne sont armés qu'en début de nuit pour éviter que les animaux soient enfermés trop longtemps, s'affolent ou soient victimes des petits carnassiers. Durant six moix, en 1968, nous avons pu opérer en 75 points, avec un jeu de vingt pièges. Pendant le séjour au Gabon, d'Octobre à Décembre 1969, nous avons placé les pièges aux mêmes endroits que l'année précédente, afin de contrôler la population déjà étudiée. Les pièges sont du type trébuchet (33 cm × 55 cm × 55 cm), en bois et grillage. Le poids de l'animal sur le perchoir déclenche la fermeture de la trappe. Une branche flexible attachée à une ficelle tient lieu de ressort, et une petite porte latérale permet d'attraper les animaux (Fig. 16). Pour chaque capture, les animaux sont pesés. L'état sexuel est noté (développement des organes génitaux, ouverture du vagin, lactation etc. ...), et à la première capture, les oreilles sont marquées par des petites encoches faites aux ciseaux.

En 1968, 133 captures furent faites sur 32 animaux (dont 8 vagabonds) constituant la population. Durant Octobre, Novembre et Décembre 1969, nous avons fait 35 captures dans cette même population, et contrôlé 13 individus nouveaux et 9 anciens. Cette saison, riche en fruits, était peu propice au piégeage, et malheureusement, il fut impossible de capturer certains individus.

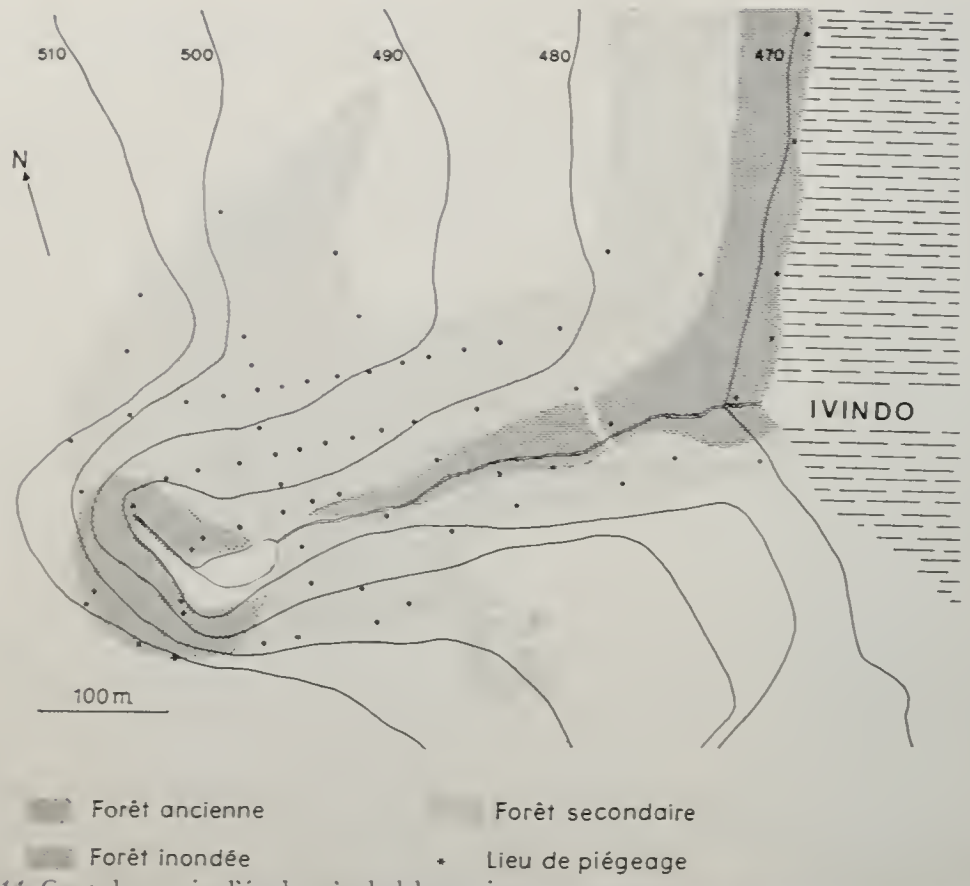


Fig. 14: Carte du terrain d'étude près du laboratoire



Fig. 15: Préparation d'un chemin pour circuler en forêt secondaire sur le terrain d'étude
Fig. 16: Piège installé en forêt secondaire. Le feuillage devant camoufler le grillage n'a pas encore été accroché

Le domaine de capture des galagos est délimité sur la carte par une ligne passant à égale distance des points où ils ont été capturés, et des points où ils ne le furent pas. Ce système ne donne qu'une approximation surtout pour les animaux repris peu souvent, mais il permet une figuration pratique. Les *Galago demidovii* (ainsi que les autres Prosimiens du Gabon) ont une grande mémoire des lieux de fructification ou des nourrisseurs. Un panier de fruits accroché dans la végétation, à un point quelconque de la forêt est généralement découvert dans les 1 à 3 jours qui suivent son installation (les marques caractéristiques des dents sur la peau permettent d'identifier l'animal qui a mangé: Rongeurs, Potto, Nandinie, *Galago demidovii*, *Galago alleni* etc. ...).

Si le hasard permet la découverte d'un panier de fruits, les jours suivants les animaux y arrivent directement. Il en est de même quand un piège amorcé a été bloqué une dizaine de jours auparavant. Les *Galago démidovii* y arrivent très vite dès le début de la nuit, hésitent quelques instants, puis descendent très prudemment le long du grillage. Ils n'y restent que peu de temps (30 à 45 secondes), et en sortent très rapidement en sautant généralement sur l'une des branches déclenchant la fermeture. C'est donc en sortant du piège qu'ils se prennent. Quand plusieurs animaux arrivent ensemble, c'est le premier à sortir et non le premier à entrer qui déclenche la fermeture du piège. Compte tenu de la faible durée des repas (30 à 45 s), il y a de très grandes chances pour que plusieurs animaux capturés ensemble soient venus ensemble au piège. En captivité, nous avons constaté que des individus appartenant à des groupes différents se fuyaient ou se battaient lorsqu'ils étaient mis en contact. On est en droit de penser que deux galagos hostiles l'un vis à vis de l'autre n'entreraient pas ensemble dans un piège même s'ils arrivaient au même instant.

Grâce à 37 captures communes de galagos, entrés ensemble dans les pièges, on peut se faire une idée des liens sociaux existant entre les différents individus de la population. Pendant la nuit, les liens sociaux sont relâchés par rapport à la phase des groupements de sommeil. Ils existent cependant, surtout en début de nuit (Tab. 3). Les captures communes donnent donc des indications importantes sur les liens sociaux.

Une autre technique consiste à lâcher des animaux étrangers aux abords de la population et à les suivre. Trois individus ont été ainsi lâchés: 1 ♀ adulte (N° 76), 1 ♀ juvénile (N° 88), et 1 ♂ adulte (N° 105). Après quelques temps, ils furent inclus dans la population naturelle étudiée, mais en marge de celle-ci.

Chaque soir, muni d'une lampe frontale, nous avons sillonné ce terrain d'étude afin de compléter les observations en localisant les animaux dans les arbres.

2. Répartition des domaines

Le piégeage a été étendu jusqu'à 2 km au Nord de la zone indiquée sur la carte. A l'exception d'un ♂ adulte (vagabond?), tous les *Galago demidovii* furent capturés dans la zone de 20 hectares représentée sur la carte. Aucune raison écologique ne semble expliquer une telle concentration. Plusieurs types de végétation habités par le *Galago demidovii* se retrouvent en marge et en dehors de cette zone.

3. Domaines vitaux des femelles

Le tableau (Tab. 5) indique le temps écoulé entre la première et la dernière capture des ♀♀ durant les six mois d'étude en 1968. Les dernières ♀♀ ont été contrôlées moins longtemps car le piégeage a débuté plus tard dans cette zone. L'astérisque indique une capture un an plus tard en 1969.

Tab. 5: Caractéristiques des ♀♀ capturées sur le terrain d'étude en 1968. * = Individus contrôlés 1 an plus tard en 1969

♀♀ (adultes)	nombre de contrôles en 1968	poids moyens	surface des domaines (en m^2)
G. d No. 28	6	55 g	9 000
G. d No. 6	10	75 g	14 000
G. d No. 36	3	55 g	9 000
G. d No. 5	5	54 g	8 000
G. d No. 1 *	3	54 g	6 000
G. d No. 3	5	68 g	8 000
G. d No. 32 *	2	50 g	?
G. d No. 30 *	1	67 g	?
G. d No. 39	2	55 g	?

Toutes les ♀♀ sont sédentaires et sont groupées sur un espace de 80 000 m², tous les degrés de superposition existent: depuis la superposition totale (1 cas) jusqu'à l'isolement complet (Fig. 17). Le plus grand des domaines couvre 14 000 m², la moyenne se situe aux alentours de 8000 m². Les contours de ces domaines sont sujets à de petites variations. Entre juillet et décembre 1968 ♀ 28 étendit son domaine de 60 m vers le Sud, et ♀ 5 abandonna une cinquantaine de mètres à l'Ouest. L'année suivante, l'une des ♀♀ avait complètemen

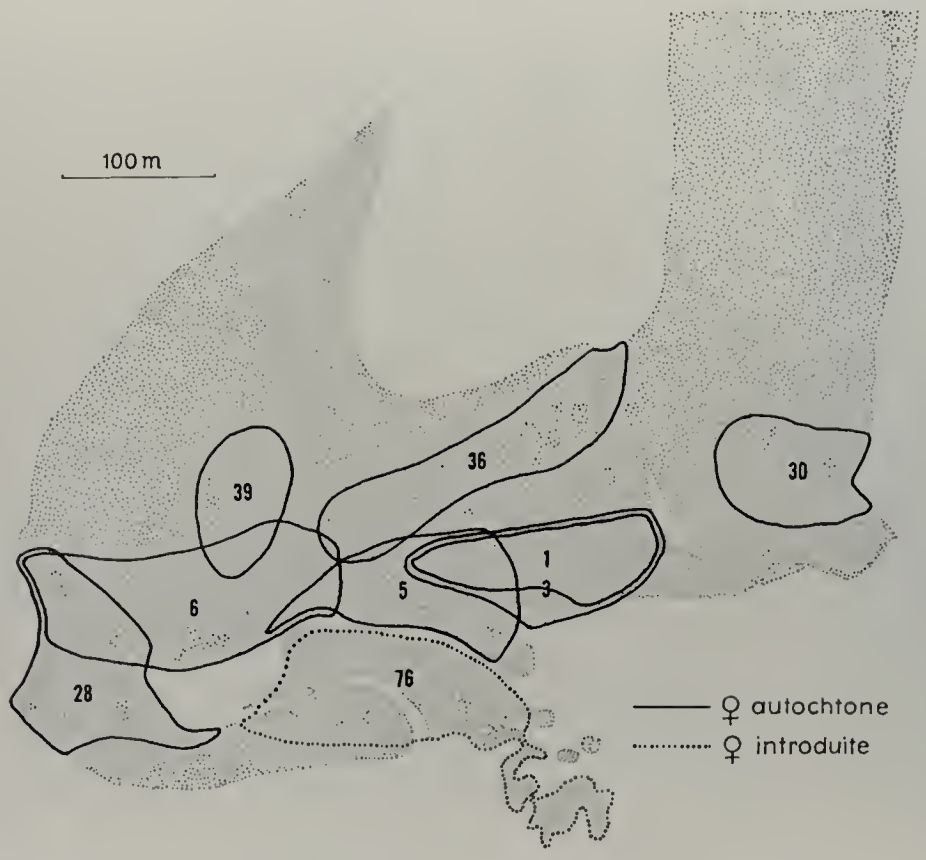


Fig. 17: Répartition des ♀♀ d'après le piégeage et les différents contrôles

abandonné son domaine pour s'installer 200 m plus loin, et deux ♀♀ adultes non contrôlées en 1968 furent capturées en 1969. Les autres ♀♀ contrôlées en 1968, puis en 1969, n'avaient pas changé de place.

4. Domaines des mâles

Le problème est assez complexe: certains ♂♂ sont errants (jeunes ♂♂ pubères), et d'autres sédentaires. Parmi les sédentaires, certains, les plus gros, ont de nombreux rapports avec les ♀♀ (♂♂ centraux A), d'autres, les plus petits, très peu ou pas du tout (♂♂ centraux B et périphériques). Le tableau (Tab. 6) indique les différents caractères permettant de telles distinctions.

Tab. 6: Caractéristiques des ♂♂ capturés sur le terrain d'étude en 1968. * = Individus contrôlés 1 an plus tard en 1969

No.	durée de contrôle (en jours)	poids (g)	nombre de captures avec ♀♀	nombre de contrôles		
♂ 8	177	85	4	9	Centraux A	SEDENTAIRES
♂ 4	179	83	5	17		
♂ 9	66	77	2	6		
♂ 34*	70	70	1	7		
♂ 15	43	61	1	2	Centraux B	
♂ 31	62	57	0	2		
♂ 33*	84	53	0	2		
♂ 11	132	57	0	5	Périphériques	
♂ 13*	90	60	0	6		
♂ 14	69	67	0	5		
♂ 21	3	75	0	2		VAGABONDS
♂ 27	1	47	0	1		
♂ 29	1	61	0	1		
♂ 35	1	69	0	1		
♂ 37*	3	55	0	2		
♂ 41	1	66	0	1		
♂ 42	1	47	0	1		
♂ 43	1	49	0	1		
♂ 105	41	60	1	9	Animal introduit	

Mâles vagabonds

Les ♂♂ vagabonds sont faciles à distinguer, leur temps de contrôle étant très faible. Ces nombres n'indiquent qu'un minimum, et il est probable qu'ils restent plus longtemps aux alentours de la population. Il s'agit toujours de ♂♂ adultes dont beaucoup, à peine pubères, ont encore quelques poils juvéniles à teinte jaunâtre. Il en arrive régulièrement qui gravitent autour de la population. La fréquence des captures au cours de ce travail est la suivante: Juillet: 2, Aout: 1, Septembre: 0, Octobre: 2, Novembre: 2, Décembre: 2. Ces animaux sont sûrement originaires d'autres populations, n'ayant été capturés qu'au stade pubère dans la population étudiée. L'un de ces ♂♂, ♂ 37, portait des marques d'un combat récent très sérieux: oreilles déchirées, œil gauche crevé, queue fracturée. Ce fut le seul vagabond à se fixer dans la population; il fut repris en 1969. Sept nouveaux ♂♂ furent capturés en 1969.

La distribution de poids de ces ♂♂ est très variable.

Mâles sédentaires

Trois catégories ont été distinguées: ♂♂ centraux A, ♂♂ centraux B, ♂♂ périphériques.

Mâles centraux A

Ce sont les plus lourds, et tous ont des rapports avec les ♀♀ (Tab. 9, Fig. 20). Leurs domaines vitaux couvrent ou traversent un ou plusieurs domaines des ♀♀.

♂ 4: 4 ♀♀ (♀ 1, ♀ 3, ♀ 30, ♀ 5),
♂ 8: 3 ♀♀ (♀ 28, ♀ 6, ♀ 36),
♂ 9: 1 ♀ (♀ 76),
♂ 34: 1 ♀ (♀ 39).

Il est intéressant de noter que ♂ 4 et ♂ 8, dont les domaines couvrent plusieurs domaines de ♀♀, sont les plus lourds. La surface des domaines est assez grande: moyenne 18 000 m² contre 8000 m² pour les ♀♀. Maximum: 27 000 m². Les domaines couvrant celui d'une seule ♀ (♂ 9, ♂ 34) sont assez réguliers, et le débordent largement. Ceux couvrant plusieurs domaines femelles, sont au contraire allongés en couloir passant souvent au milieu ou en bordure des domaines femelles (♂ 4, ♂ 8). Ces deux domaines font 500 m de long. Les ♂♂ centraux A sont très peu farouches: 39 captures pour les quatre animaux contre 81 pour les 20 autres *Galago demidovii* sédentaires de la population.

Un an plus tard, les deux ♂♂ les plus gros (♂ 4 et ♂ 8) avaient disparu; ils étaient remplacés par ♂ 9 et ♂ 34 dont les domaines couvraient alors plusieurs domaines femelles. Alors que ♂ 9 était resté au même poids (77 g), ♂ 34 était passé de 70 g à 82 g.

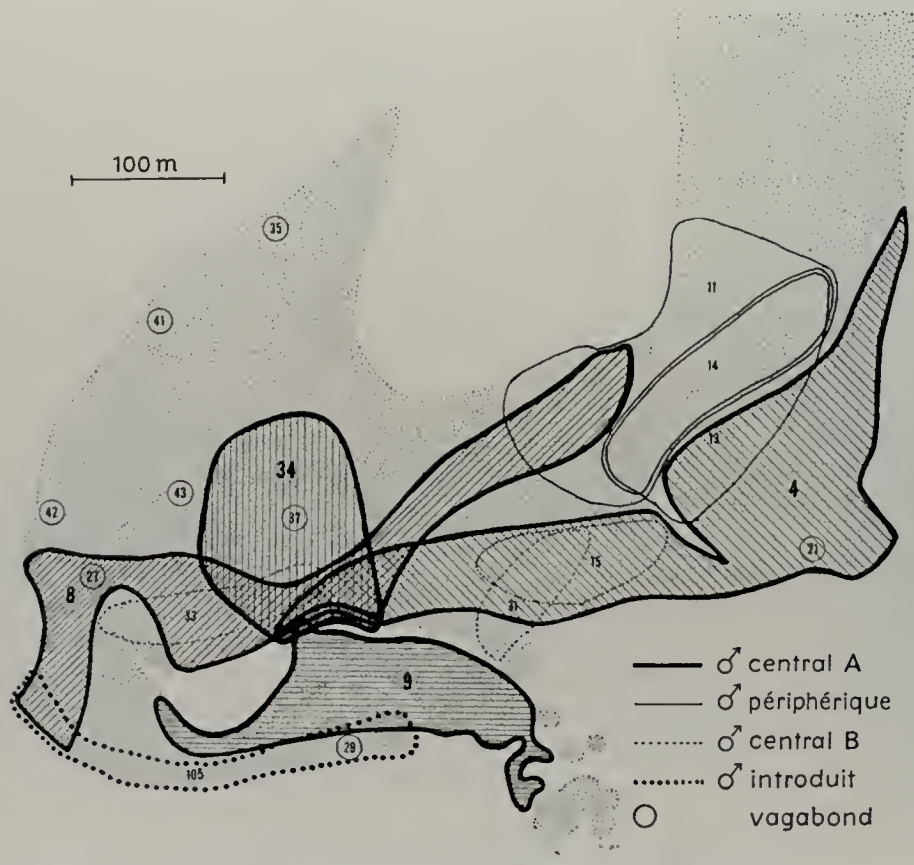


Fig. 18: Répartition des ♂♂ d'après le piégeage et les différents contrôles

Sur la carte (Fig. 18), on voit nettement l'existence d'une zone commune à tous les ♂♂ centraux A. En trois points différents de cette zone, les ♂♂ centraux A furent capturés 8 fois: ♂ 4, une fois, ♂ 8, trois fois, ♂ 34, trois fois, ♂ 9, une fois. Ils ne furent jamais capturés ensemble et jamais le même jour (1 jour d'intervalle entre ♂ 4 et ♂ 8, 1 jour d'intervalle entre ♂ 8 et ♂ 34, 2 jours d'intervalle entre ♂ 4 et ♂ 9, 1 jour d'intervalle entre ♂ 9 et ♂ 8). Cette zone commune ne présente aucune particularité écologique (forêt secondaire sur terrain en pente), le même type de végétation se prolonge bien au-delà. En étudiant la vie sociale du Potto par des techniques voisines (résultats non publiés), nous avons remarqué également que les ♂♂ possédaient une zone commune à la limite de leurs territoires où ils venaient presque tous les soirs, tout en s'évitant. Il est très possible que chez *Galago demidovii*, la zone commune des ♂♂ centraux A ait une signification semblable. Ce comportement pourrait permettre à la fois de connaître les voisins immédiats tout en signalant sa présence grâce aux marquages par urine qui sont si fréquents chez cette espèce (4 à 8 fois par heure en captivité).

Mâles centraux B

Ce sont des animaux bien plus légers que les centraux A: moyenne 56 g contre 75 g. Ils ne semblent pas avoir beaucoup de rapports avec les ♀♀, cependant, ♂ 15 fut capturé une fois avec une ♀. Ces animaux sont assez craintifs, contrairement aux centraux A, et n'ont été capturés que deux fois chacun en des points distants de 40 m, 75 m, 120 m, ce qui indique des domaines assez réduits.

Mâles périphériques

Un groupe de trois ♂♂ adultes (♂ 11, ♂ 13, ♂ 14) capturés plusieurs fois ensemble, vivait en bordure de la population sur une zone presque commune. Ce "Club des célibataires" ne semblait pas avoir de rapports avec les ♀♀; mais seulement entre eux; pourtant, deux d'entre eux débordaient sur les domaines des ♀♀. Les surfaces respectives de leurs domaines sont les suivantes: ♂ 11, 20 000 m², ♂ 13, 13 000 m², ♂ 14, 9000 m². Leur superposition est très importante, et, comme les centraux B, il s'agit d'animaux de petite taille (moyenne 61 g), cependant un peu plus lourds que les centraux B, et leurs domaines sont considérablement plus étendus.

L'un de ces trois individus (♂ 13) fut contrôlé l'année suivante, 300 m plus loin, en compagnie de 2 ♀♀; son poids était passé de 60 g à 66 g. Les deux autres ♂♂ avaient disparu.

Un ♂ adulte et étranger (♂ 105) fut lâché en bordure de la population. Il adopta un domaine comparable à celui des ♂♂ périphériques, en marge de la population, se superposant en partie avec celui de ♂ 8 (central A). Cependant, une capture commune avec une ♀ et le ♂ central A correspondant témoigne de rapports sociaux avec ceux-ci.

5. Domaines des juvéniles

Dans la population étudiée, trois jeunes animaux furent contrôlés: 1 jeune ♀ (♀ 38) de 41 g, âgée de 2 à 4 mois, et très farouche. Elle ne se prit qu'une fois au piège. 2 jeunes ♂♂ (♂ 12 et ♂ 26) âgés de 4 à 6 mois en juillet 1968, qui, eux, furent très souvent contrôlés. La carte (Fig. 19) indique les domaines de ces deux animaux: ♂ 12, le plus âgé, possède un très vaste domaine vital couvrant les $^3/_4$ de celui du ♂ central A de son groupe. ♂ 26, du 29 juillet au 30 août, possède un domaine à cheval sur ceux des ♀♀ (♀ 28 et ♀ 6). Petit à petit, son domaine s'agrandit, débordant même en dehors des domaines du ♂ central A et des ♀♀, passant de 11 000 m² à 24 000 m²: Il est probable qu'à

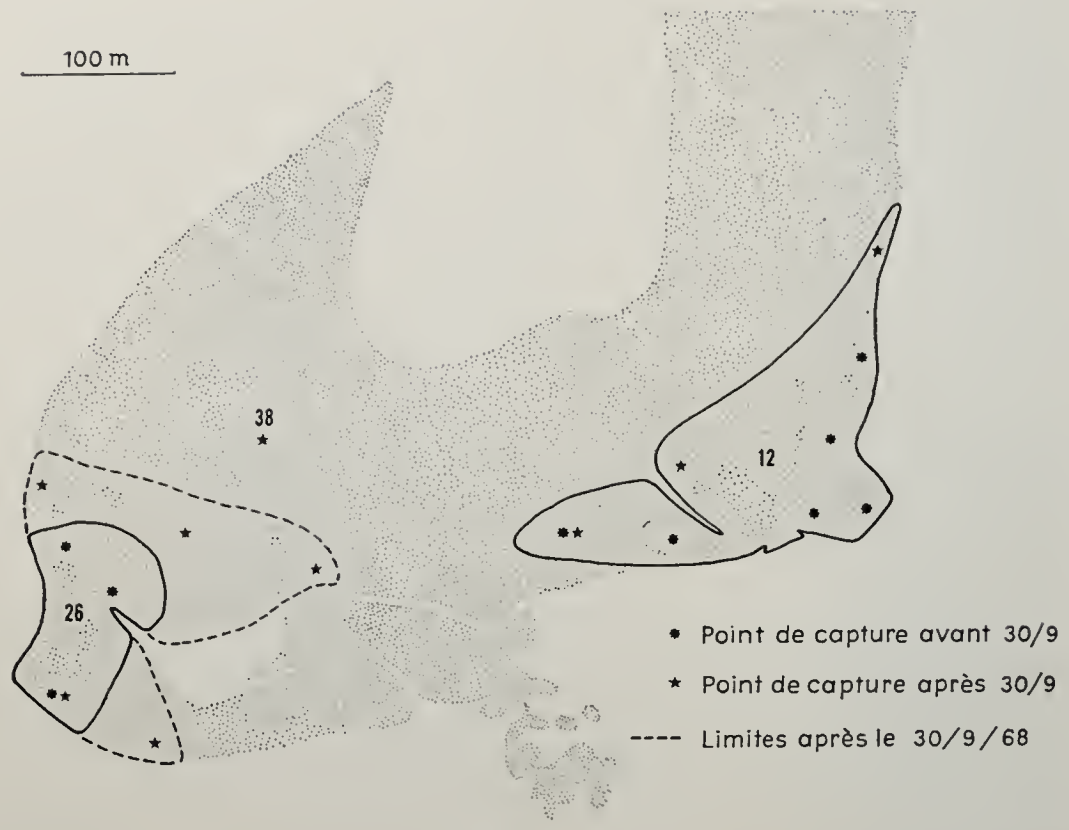


Fig. 19: Répartition des juvéniles d'après le piégeage, évolution des domaines vitaux dans le temps: le jeune ♂ 26 étend progressivement son domaine. Au stade pubère, les ♂♂ auront disparu

la puberté, les jeunes ♂♂ passent par le stade vagabond. En effet, ils ne furent pas retrouvés l'année suivante. Par contre, une ♀ impubère, marquée, fut contrôlée un an plus tard, adulte, au même endroit.

* * *

Sur la figure 20, chaque individu est représenté au centre de son domaine par un numéro et un symbole indiquant sa classe. Chaque trait indique une capture commune donc un lien social entre deux individus. On peut distinguer cinq groupes: quatre groupes centrés chacun autour d'un ♂ central A et un cinquième composé de trois ♂♂ périphériques formant une sorte de "Club des célibataires". (Cependant, ♂ 15, ne pesant que 61 g, fut capturé une fois en compagnie de ♀ 32 dans le domaine de ♂ 4, central A, et ♂ 105, introduit expérimentalement, fut capturé en même temps que ♂ 8, central A et ♀ 28). Aucune capture commune d'individus appartenant à des groupes différents n'a été enregistrée. Il existe pourtant une zone commune où les quatre ♂♂ centraux A ont leurs domaines superposés. De la même façon, plusieurs ♀♀ de groupes différents (♀ 39, ♀ 6, ♀ 5, ♀ 76) ont des domaines se chevauchant ou se cotoyant. Cependant, le nombre de captures communes de ♀♀ est très faible. La répartition des captures communes se fait de la façon suivante:

13 captures communes entre ♀♀ et juvéniles,
12 captures communes entre ♂♂ centraux A et ♀♀,
6 captures communes entre ♂♂ centraux A et juv.,
2 captures communes entre ♀♀,
3 captures communes entre ♂♂ périphériques,

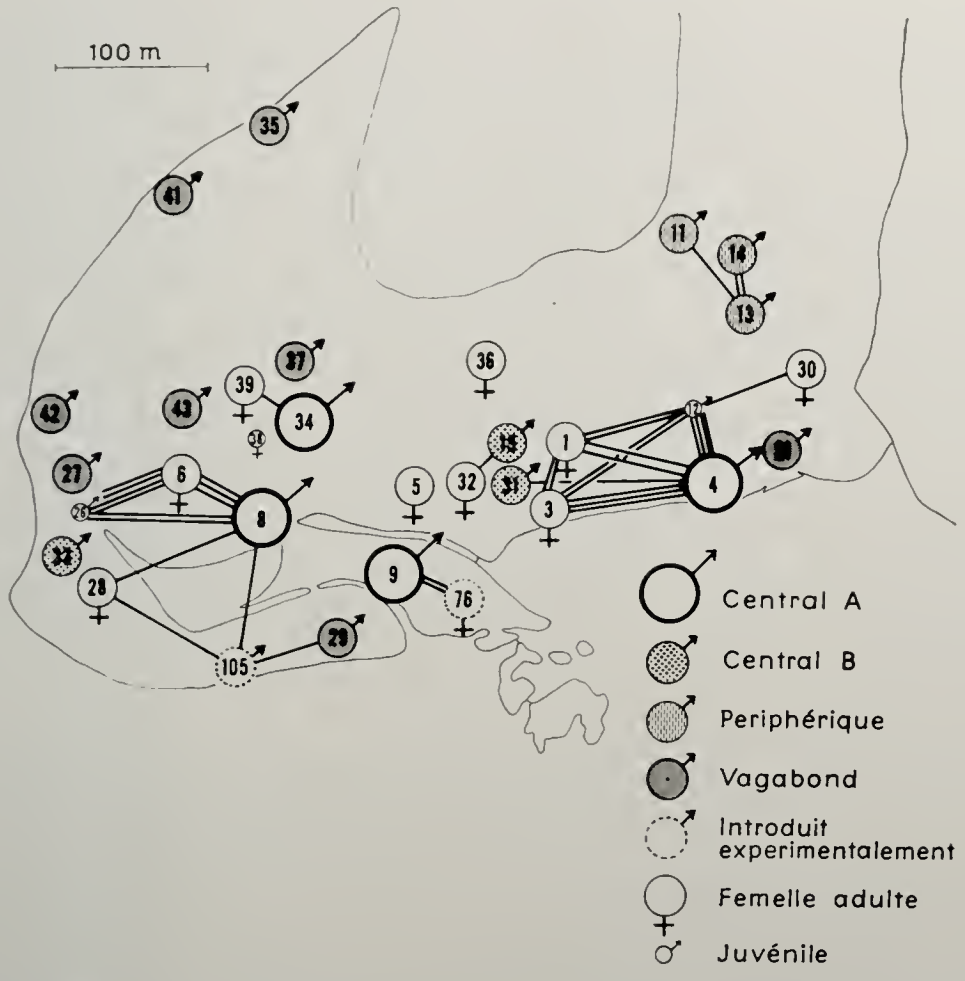


Fig. 20: Schéma des rapports sociaux entre les individus de différentes classes (chaque trait symbolise une capture commune). On remarque les rapports établis autour de chaque ♂ central A et ceux établis entre les ♂♂ périphériques

1 capture commune entre ♂ central A et ♂ central B,
1 capture commune entre ♂ central A et ♂ introduit expérimentalement,
1 capture commune entre ♂ périphérique et ♂ vagabond,
1 capture commune entre ♂ introduit expérimentalement et ♀,
1 capture commune entre ♂ central B et ♀.

Les ♂♂ centraux A jouent donc un rôle prépondérant dans la formation de ces groupes sociaux. Ces individus, très grands (pouvant peser presque le double des ♂♂ les plus petits), ont des rapports avec les ♀♀ et les jeunes, parfois avec certains ♂♂ "tolérés" dans leur voisinage. Leurs domaines couvrent ceux des ♀♀, soit en totalité, quand ils se superposent à un seul, soit en partie, quand ils se superposent à plusieurs. Très actifs, ils circulent énormément et sont toujours les premiers capturés quand un piège est armé en un point quelconque de leur domaine (♂ 4 capturé aux abords du domaine de ♀ 30 fut repris 3 heures plus tard à 100 m de là, dans les domaines de ♀ 1 et ♀ 3).

Pendant 6 mois d'étude en 1968, les ♂♂ centraux A n'ont cessé d'avoir une grande activité, ce qui laisse à penser que la structure est permanente pendant l'année (le début de l'étude coïncidait avec le minimum d'activité sexuelle, et à la fin de l'étude, on était proche du maximum des naissances).

6. Animaux introduits

Les trois individus introduits furent d'abord placés dans un ilôt de végétation relié par des lianes à la forêt, au Sud de la population. Les deux ♀♀ furent lâchées les premières. Elles restèrent un mois sans sortir des bouquets d'arbres. Au moment de l'œstrus, ♀ 76 émit un cri spécial qui attira un ♂ voisin (♂ 9). Ce ♂, pas encore fixé sur le domaine d'une ♀ (vagabond à ce moment), arriva très vite et entraîna la ♀ dans la forêt. Il n'y eut pas de fécondation, mais les deux animaux s'installèrent à l'endroit indiqué sur la carte, en marge de la population. Au début, ♂ 9 venait souvent rendre visite à ♀ 76, mais trop farouche, il se sauvait dès qu'on l'observait. Quelques jours plus tard, la ♀ s'en allait la nuit dans la forêt voisine, mais revenait dormir avec ♀ 88 et ♂ 105 dans le bouquet d'arbres. Un peu plus tard, elle se fixa définitivement dans le domaine marqué en pointillé (Fig. 17), ne venant dans l'ilôt que de temps en temps pour manger dans le nourrisseur. Le ♂ 9 est figuré sur la carte comme central A, car il adopta cette position dès le début de l'étude. L'année suivante, son domaine s'était étendu, couvrant plusieurs domaines femelles. La jeune ♀ 88 suivit ♀ 76, et le ♂ 105 alla se fixer en marge de la population un peu plus à l'Ouest (pointillé, Fig. 18). Sa position sociale est comparable à celle des ♂♂ périphériques, mais il entra en contact avec le groupe de ♂ 8.

7. Interprétation des résultats

Les jeunes ♀♀, après la puberté, restent sédentaires et permettent ainsi la constitution de petits matriarcats. Nous n'avons pu en avoir la preuve absolue par marquage sur le terrain qu'une seule fois, mais il arrive souvent de capturer ensemble une vieille ♀ (longues tétines), et une jeune ♀ adulte (petites tétines). Dans un travail en cours sur la vie sociale de *Galago demidovii*, nous avons reconstitué en captivité de tels matriarcats et les territoires, par des compartiments séparés, communiquant par des portes à glissières. Les contacts sociaux sont très développés au sein de tels matriarcats (toilettage social, jeu, dortoir), et le territoire commun, est défendu par chacune des ♀♀ contre les autres ♀♀. Les ♂♂ étrangers sont très souvent ignorés et repoussés quand ils s'en approchent trop près. Si les ♀♀ d'un matriarcat défendent le même territoire, chacune d'elle possède cependant une zone privilégiée.

Après un séjour d'un mois dans la même cage, d'une ♀ adulte (♀ 76) et d'une jeune ♀ presque pubère (♀ 88), nous avons pu facilement établir un lien social entre ces deux animaux. Lâchées dans un ilôt de végétation à proximité du terrain d'étude, ces ♀♀ occupèrent toutes deux la même zone et construisirent un nid de feuilles qu'elles occupaient pendant la journée. Cependant, les mêmes arbustes n'étaient pas utilisés selon la même fréquence par ces deux animaux. Certains étaient utilisés autant par une ♀ que par l'autre, alors que d'autres arbustes étaient inégalement utilisés. Certaines branches ne servaient qu'à l'une ou l'autre des ♀♀. Un peu plus tard, ces deux ♀♀ allèrent s'établir plus loin dans la forêt, mais revenaient assez souvent chasser des insectes dans les enclos des singes (pendant la nuit, de nombreux papillons sont attirés par les restes de fruits, les galagos venaient les capturer en passant à travers le grillage). Les deux ♀♀ arrivaient souvent ensemble, à 10 ou 20 m de distance, et chacune d'elles pénétrait toujours dans le même enclos pour y capturer les papillons.

En captivité, nous avons remarqué que les ♀♀ d'un matriarcat, vivant dans une même cage, ne déposaient leurs marquages d'urine qu'en certains points, avec des zones préférentielles pour chacune d'elle.

La stabilité des jeunes ♀♀ permet de comprendre facilement la constitution des matriarcats et des agrégations de ♀♀. Le mécanisme n'est cependant pas aussi rigide, et nous avons pu constater plusieurs fois des déplacements plus ou moins importants de ♀♀ adultes. L'évolution d'un matriarcat dépend de la mortalité et de la descendance mâle et femelle. Une hiérarchie existe entre les différentes ♀♀, et il est très possible que, pour des raisons de dominance, ou

d'autres raisons (écologiques?), certaines ♀♀ se séparent de leur groupe pour s'établir un peu plus loin. L'attraction sociale reste cependant assez forte puisque dans tous les cas, les nouvelles ♀♀ s'étaient établies en bordure de l'agrégation des autres ♀♀. Les limites des territoires sont aussi sujettes à de petites variations de plusieurs dizaines de mètres.

Les jeunes ♂♂, après la puberté, passent par un stade vagabond, gravitant autour de populations étrangères. Les jeunes ♂♂ impubères, contrôlés de nombreuses fois sur le terrain d'étude, avaient tous disparu l'année suivante, et les ♂♂ vagabonds, régulièrement capturés à proximité de l'agrégation femelle, provenaient de populations étrangères, n'ayant jamais été capturés sur place avant leur puberté. Ces ♂♂ vagabonds sont jeunes et beaucoup conservent encore des traces de leur pelage juvénile. Ce vagabondage des jeunes ♂♂ est d'ailleurs un phénomène très répandu chez les Mammifères, et doit contribuer à l'homogénéité génétique des populations.

Le poids et la taille de *Galago demidovii* sont très variables, et possèdent une très grande importance sur la future position sociale des ♂♂. Les individus les plus forts établissent des domaines très étendus (jusqu'à 500 m de long), se superposant aux domaines de une ou plusieurs ♀♀, avec lesquelles ils entretiennent des rapports sociaux très nombreux. Les individus les plus petits s'établissent soit au centre de l'agrégation où ils semblent être tolérés par les plus gros ♂♂ (2 captures communes) — sans toutefois avoir beaucoup de relations avec les ♀♀ — soit en bordure de l'agrégation. De nombreux individus montrent des traces de combat, ce qui permet de comprendre l'étroite relation existant entre la taille et la position sociale des ♂♂.

La croissance pondérale se poursuit jusque vers 5 ou 6 mois, et la puberté a lieu entre 7 et 9 mois (Vincent). Dans plusieurs cas nous avons constaté un alourdissement appréciable d'individus déjà pleinement adultes. Dans deux cas, il s'agissait de ♂♂ adultes dont la position sociale s'était élevée (il s'agit vraisemblablement d'un alourdissement et non d'une croissance, mais nous n'avons pu le vérifier, les animaux étant vivants). Les autres ♂♂ que nous avons contrôlés après un an, et dont le poids était resté stationnaire, n'avaient pas changé de classe sociale. Alors que toutes les ♀♀ adultes étaient restées à un poids stationnaire après un an, l'une d'elles était passé de 54 g à 74 g. Ce phénomène peut être en partie masqué par la gestation, mais il semble que chez les ♀♀, il existe une relation entre le poids des individus et l'étendue du domaine (Tab. 5).

Sur la figure 21, nous avons schématisé le mécanisme de la structure sociale de *Galago demidovii* et de sa dynamique.

Chez *Galago demidovii*, on assiste à un stade intermédiaire entre le territorialisme de mammifère solitaire, et la vie sociale de type primate.

Chaque individu possède un territoire défendu, signalé par des cris, et marqué par les urines. La nuit, pendant la phase active, les petits groupes se dispersent, chaque individu allant dans une zone préférentielle quand le territoire est commun (78% d'observations d'individus isolés pendant la nuit).

La vie sociale est caractérisée par plusieurs points:
— Constitution de petits matriarcats au sein desquels les rapports sont nombreux (nids communs à plusieurs ♀♀ adultes, toilettage social très fréquent).
— Rapports sociaux entre ♂♂ et ♀♀ en dehors des périodes d'activité sexuelle (visite du ♂ en début de nuit, avec émission d'un cri particulier des deux partenaires et toilettage mutuel très actif).

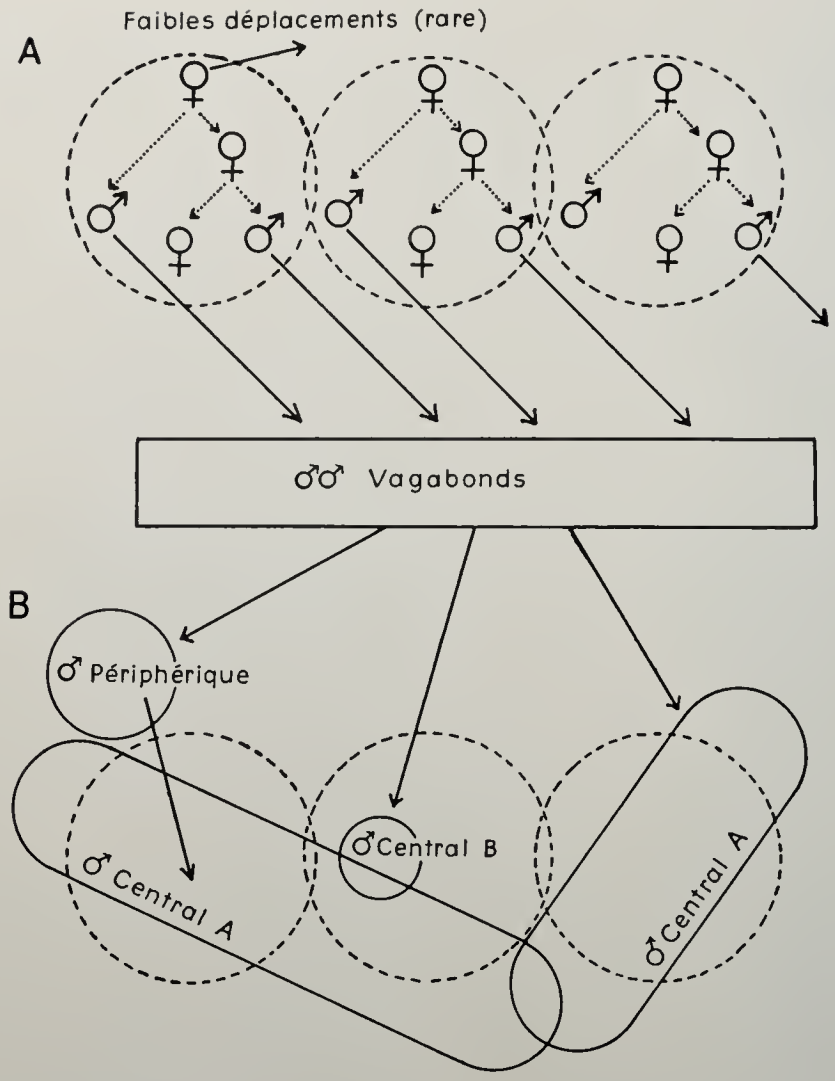


Fig. 21: Reconstitution schématique de la structure d'une population de *Galago demidovii* et de sa dynamique. A = Evolution des ♀♀ et de leur jeunes (formation de matriarcat), B = Situation sociale des ♂♂ d'après leur taille par rapport aux populations de ♀♀ (·····→ = descendance, → = déplacements)

— Rapports sociaux entre juvéniles et adultes après le sevrage, jusqu'à la puberté pour les ♂♂, et au stade adulte pour les ♀♀ (les ♂♂ juvéniles ont été capturés en compagnie du ♂ central A et de plusieurs ♀♀ du groupe, jamais avec des individus étrangers au groupe).

IV. REPRODUCTION

La période de naissance est étalée sur toute l'année, avec un pic en Décembre—Janvier. A la naissance, le jeune est peu développé: le poil est clairsemé, les yeux entr'ouverts, et il ne peut s'agripper à sa mère comme le font d'autres Prosimiens. Posé sur une surface plane, il ne peut se déplacer (Fig. 22, 23). Poids à la naissance: 7 g, 9 g, 10 g.

La mère fabrique un nid de feuilles et s'y isole les premiers temps avec son jeune. Ce nid sert surtout au repos de la journée, car la nuit, elle emmène

son petit dans la gueule, en le tenant par le flanc (Fig. 24), le dépose dans la végétation et chasse aux alentours. Si on capture le jeune, il émet des cris de détresse qui la font accourir dans les 15 à 30 secondes qui suivent (premier cri entendu à l'âge de trois semaines). Les premiers temps, le jeune est laissé dans le nid pendant le nuit. Chez *Galago alleni*, où le jeune nait au même stade de développement, la mère ne l'emmène avec elle qu'au bout d'une semaine Une ♀ *Galago demidovii*, tuée la nuit dans un piège à collet, avait avec elle un jeune de 14 g, âgé de 5 à 7 jours. En captivité, nous avons observé le premier transport d'un jeune hors du nid, à 3 jours, et ce même jeune était capable de se déplacer aisément hors du nid à 17 jours.

Le matin, le jeune émet un "clic" très aigü, semblable à celui émis par tous les jeunes Lorisiformes. La mère répond par un petit roulement sourd et le cri III et peut le localiser dans le feuillage. Les premiers temps, elle le



Fig. 22: Galago demidovii nouveau-né. A la naissance, le jeune est incapable de se déplacer (Photo A. R. Devez)



Fig. 23: Galago demidovii nouveau-né. On peut remarquer les yeux mi-clos (Photo A. R. Devez)



Fig. 24: Galago demidoviiç ♀ emportant son jeune dans la gueule. La mère prend toujours son jeune par le flanc, la queue de ce dernier passant autour de son cou (Photo A. R. Devez)

prend dans la gueule, par le flanc, et l'emmène jusqu'au nid. Un peu plus tard, les "clic" du jeune ont évolué vers le cri social des adultes, la mère ne transporte plus son jeune, mais vient le chercher, puis se fait suivre jusqu'au nid. Ce n'est qu'au stade adulte que le cri du jeune finit d'évoluer (cri N° III permettant le rassemblement des petits groupes du matin).

Summary

Ecology and social behaviour of *Galago demidovii* (Fischer 1808; Prosimii)

1. The field-study of *Galago demidovii* discussed in this paper was part of a wider study of prosimian ecology at the Mission Biologique, Makokou, Gaboon, and was conducted over 4 periods of 7, 8, 14 and 3 months, between October 1965 and December 1969.

The methods of observation and study are outlined, especially with respect to release of semi-tame animals and live-capture techniques.

2. Biometric variation is illustrated, and the sex ratio determined (150 individuals). The ecological niche and diet were established statistically (200 observations; 50 stomach-content analyses). *Galago demidovii* is a species specialised for living in dense foliage in the canopy zone, which is frequently invaded by creepers. The diet is predominantly insectivorous, based particularly on capture of small lepidopterans and beetles.

3. The second section deals with social organisation. The first step is the demonstration of the existence of individualised populations. Notes of vocalisation (260 hours of audition) show that the species passes successively through a social phase and a solitary phase during each 24-hour cycle: morning — reassembly of small groups by means of vocalisations eliciting numerous phonoresponses; daytime — sleeping phase in leaf-nests (Groups of ♀♀ and young) or simply attached to one another in vegetation; evening — dispersal

of individuals accompanied by emission of a vocalisation evoking phonoresponses during the first hour of darkness; night-time — dispersal accompanied by emission of a vocalisation with an aggressive (territorial) character and lacking evocation of phonoresponses.

4. Social organisation and range are described on the basis of systematic live-trapping conducted with a selected population (134 captures for 24 animals; 8 controls of vagabond ♂♂). In addition, 34 simultaneous captures indicated social bonds between different individuals.

The ♀♀ occupy ranges of about 8000 m² (approx. 200 m long), with varying degrees of overlap occurring between the ranges in each localised group. A number of ♂♂ *(A-centrals)* circulate over the ranges of one or more ♀♀ and exhibit a liason with the residents (simultaneous captures). These ♂♂ are the heaviest (approx. 80 g), and their ranges may be up to 500 m long. Certain smaller ♂♂ (*B-centrals*; approx. 60 g) live in contact with former, but have little or no contact with ♀♀. Their ranges are smaller in size. Other ♂♂ of similar small body-size live on the perimeters of the group and exhibit contact only with one another *(peripheral ♂♂)*. Finally, there are regular arrivals of strange ♂♂ *(vagabond ♂♂)* — frequently on the fringe of puberty — which gravitate around the population and may become involved in fights.

5. Genuine social contact only exists between an A-central ♂, one or more ♀♀ and their offspring. There was no case of capture of an individual belonging to the group of a particular A-central ♂ at the same time and place as an individual belonging to a different A-central ♂ group.

The 4 A-central ♂♂ exhibited a common overlap zone, but they were never captured together there during the course of one night.

6. The third section briefly deals with reproduction. The young *Galago*, unable to move around at birth, is very soon carried out of the nest by the mother, to be left in the vegetation during the night activity period. The mother relocates her offspring relatively easily thanks to a highpitched vocalisation uttered by the latter. This vocalisation undergoes a rapid development, and in the adult the resulting vocalisation has acquired a social significance, aiding in regrouping of the *Galagos* in the morning.

Zusammenfassung

1. Im Rahmen von Untersuchungen über Halbaffen in Gabun wurden Gruppen von *Galago demidovii* im Freiland während vier Besuchen der Biologischen Station von Makokou jeweils 7, 8, 14 und 3 Monate lang von Oktober 1965 bis Januar 1970 beobachtet.

2. Fangtechnik, Freilassung halbzahmer Tiere und allgemeine Methodik werden dargestellt und an Hand von 150 Tieren die biometrische Variabilität und das Geschlechtsverhältnis besprochen, ökologische Nischen und Ernährung erläutert. *Galago demidovii* lebt in dichtem Blattwerk und wuchernden Lianen vorwiegend von Insekten, besonders von kleinen Schmetterlingen und Käfern.

3. Der zweite Teil der Arbeit beschreibt das soziale Verhalten. Die Gruppenmitglieder kennen einander persönlich. Wie die Lautäußerungen in 260 Abhörstunden lehrten, zerfällt der Tag in eine soziale und eine solitäre Phase: Morgens finden sich kleine Gruppen zusammen. Tagüber schlafen ♀♀ und Jungtiergruppen in gemeinsamen Nestern oder nebeneinander im Bewuchs hängend. Abends zerstreuen sie sich, rufen bisweilen und antworten

einander in der ersten Nachtstunde. Nachts sind sie einzeln unterwegs. Man hört aggressive, aber keine Antwortlaute.

4. Die soziale Organisation: Die Lebensräume werden auf Grund von 134 Fängen von 28 Gruppenangehörigen und 8 umherschweifenden ♂♂ beschrieben. 34 Gruppen-Fänge trugen dazu bei, die sozialen Bindungen der verschiedenen Tiere besser kennenzulernen.

Die ♀♀ leben in Gebieten von etwa 8000 m² (etwa 200 m lang), welche sich mehr oder weniger überschneiden und einen Kern bilden. Einige *zentrale* ♂♂ *A* bewegen sich in den Gebieten eines oder mehrerer ♀♀ und unterhalten Beziehungen mit ihnen (gemeinsame Fänge). Diese ♂♂ sind am schwersten (80 g), und ihre Wohngebiete können 500 m Länge erreichen. Einige kleinere *zentrale* ♂♂ *B* (60 g) leben mit ihnen in Kontakt, haben aber keine oder fast keine Beziehungen zu den ♀♀; ihre Wohngebiete sind kleiner.

Weitere, ebenfalls kleine ♂♂ leben in der Randzone der Gruppe und haben nur untereinander Beziehungen *(periphere ♂♂)*. Schließlich gibt es fremde ♂♂ *(Vagabunden)*, die meist kaum geschlechtsreif sind, um die Population herumstreichen und sich auf Kämpfe einlassen.

5. Soziale Beziehungen bestehen ausschließlich zwischen einem zentralen ♂ A, einem oder mehreren ♀♀ und ihren Jungen. Niemals wurde ein Tier aus der Gruppe eines zentralen ♂ A zusammen mit einem aus der Gruppe eines anderen ♂ A gefangen. Die 4 zentralen ♂♂ A hatten eine gemeinsame Zone, wurden aber niemals in der gleichen Nacht gefangen.

6. Der dritte Teil der Arbeit behandelt kurz die Fortpflanzung. Die Mutter trägt das Neugeborene, das sich noch nicht selbständig fortbewegen kann, abseits und legt es für die Nacht im Gebüsch ab. Der hohe Schrei des Jungen, der ihr den Abliegeplatz wiederfinden hilft, dient beim erwachsenen Tier der Gruppierung der *Galogos* am Morgen.

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A Preliminary Field-Study of the Lesser Mouse Lemur (*Microcebus murinus* J. F. Miller 1777)

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With 23 figures and 2 tables

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INTRODUCTION

Any overall consideration of evolution within the Order Primates (lemurs, lorises, tarsiers, monkeys, apes and man) must include a treatment of the "*prosimian*" forms (lemurs, lorises, tarsiers) as well as the simians. Such treatment should, ideally, include reference to the behaviour of prosimians under natural conditions, since the functional significance of morphology can only be appreciated in this light. Within the framework of Primate evolution as a whole, the prosimians are important for two reasons: Firstly, they widen the scope of information about descendants from the ancestral Primate stock (Fig. 1); and secondly, they have generally retained a greater proportion of ancestral characters, or characters which are only slightly modified from the ancestral form. Therefore, an understanding of the functional morphology of living prosimians is particularly valuable for inferring probable functional mechanisms in the ancestral stock of all living Primates.

The prosimians are often referred to as "lower Primates" (as their scientific name implies); but this crude, short-hand term tends to imply that the animals concerned abruptly stopped evolving at a certain stage, and that — perhaps given the right environmental conditions and pressures — they would have continued evolving into "higher Primates". This implication is definitely spurious, since the fact that the *majority* of characters of a living lemur species (for example) may be relatively primitive does not prevent that species from possessing a number of extremely specialised adaptations to its particular way of life. It is much more rewarding to refer to *ancestral characters* and to look for the retention of such characters in species derived from the ancestral Primate stock. In this restricted sense, the prosimians are closer to the ancestral Primate condition than are the living monkeys, apes and man. For various ecological reasons, they appear to have evolved at a generally slower pace, with marked specialisations occurring only in a minority of their characters. The main aim of any essentially evolutionary study is to distinguish such specialisations from ancestral retentions and to attempt to trace the evolution of the various living Primates from the ancestral pattern which emerges (Martin 1968).

In recent years, studies based mainly or exclusively on morphological characters of Primates have been greatly enriched by studies of behaviour. Consequently, through considerations of functional morphology, we are gradually coming closer to an integrated understanding of the possible forms

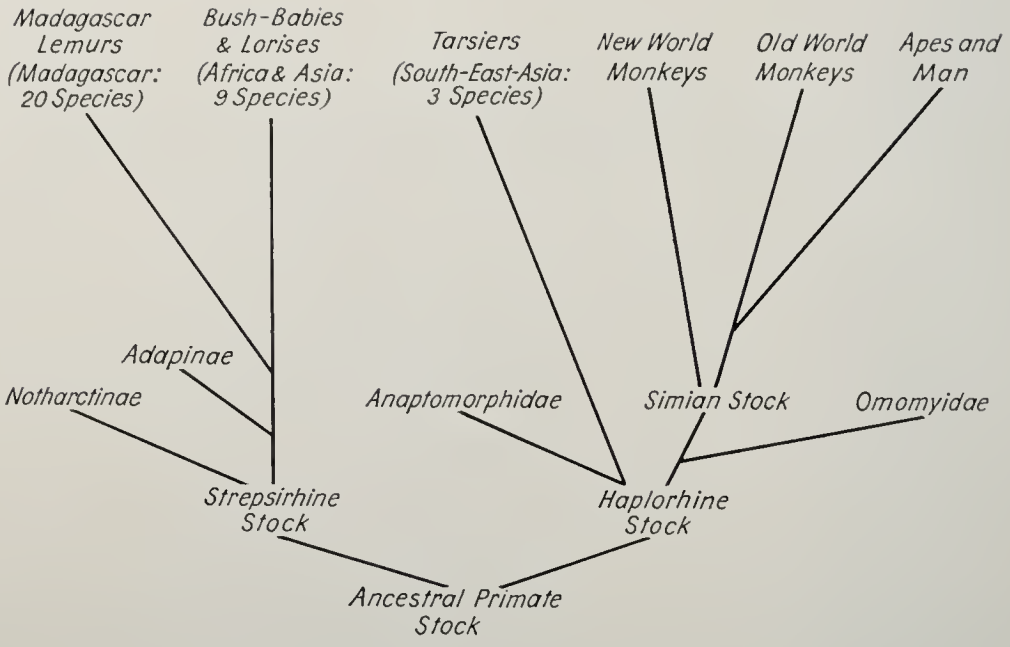


Fig. 1: A generalised, hypothetical diagram of evolution within the Order Primates. The "Strepsirhini" have, on average, departed less from the ancestral condition than the "Haplorhini"

and habits of early Primates and of the conditions under which these radiated to produce the range of living forms. However, relatively little work has been carried out on the *prosimians* — particularly in the realm of behaviour under natural conditions — and there is therefore a conspicuous gap in our knowledge of the Primates. There are approximately 32 species still to be found (lemurs — 20; loris and bush-baby group — 9; tarsiers — 3), and of these almost two thirds are restricted to the island of Madagascar. The classical explanation for this bizarre distribution is that Madagascar became separated from Africa at a time when various prosimian stocks were prevalent in the Old and New Worlds (i. e. at some time before or during the Eocene period), and that the prosimians outside Madagascar were gradually replaced to a large extent by new simian forms. Accordingly, it is only on Madagascar that one can see a full prosimian radiation, free from interaction with simian competitors and relatively free from predation pressure. By studying the lemurs of Madagascar, one can see the end-products of an exclusive prosimian radiation, and by studying the prosimians still surviving in the Old World one can identify the special characteristics necessary for survival in a habitat also occupied by simians. In view of this, it is likely that any similarities shared by the least specialised of the Madagascar lemurs and by the survivors in other parts of the Old World will reflect the ancestral prosimian condition (and thus the ancestral Primate condition).

As far as the Madagascar lemurs are concerned, an excellent series of publications by Petter (1959, 1962a, 1962b, 1962c, 1965) has laid the basis for a general consideration of lemur behaviour. However, until recently, our knowledge of the lemurs was limited by a lack of long-term field studies of individual species, and Jolly's (1966) intensive investigation of the Ringtail *(Lemur catta)* and the Sifaka *(Propithecus verreauxi verreauxi)* represented a major advance. Jolly's study showed that, particularly in terms of social behaviour, some prosimians have developed characteristics almost as complex as those found in some monkey species. However, the two species chosen are

rather exceptional in that they are *diurnal*, whereas the majority of lemurs are *nocturnal*, in common with all prosimian species which occur outside Madagascar. Thus, it is extremely important to study species such as the Ringtail and the Sifaka in order to determine the extent to which parallel evolution may produce forms resembling simians; but such studies tell us very little about the early ancestry of the prosimians. It seems extremely likely that the common ancestor of the Madagascar lemurs was *nocturnal*, since even forms which now seem to be exclusively diurnal in habits (e. g. Sifaka, Indri) possess a reflecting membrane in the eye *(tapetum)*, which may well represent an adaptation to vision under poor light conditions. There is, then, a pressing need for extended field studies of nocturnal lemur species in order to obtain information about the overall radiation of lemurs and of Primates in general.

Of course, the nocturnality of such species presents difficulties for studies of behaviour, and this adaptation to night activity has been one of the major barriers to investigation of most prosimian species (more than two thirds of the species being nocturnal). However, this barrier is not insurmountable, and a number of recent studies have demonstrated special techniques for analysing gross behavioural characteristics of nocturnal prosimians. Indeed, there are some aspects of nocturnal prosimians which make them easier to study than diurnal forms. Most workers who have worked on nocturnal lemurs (Bluntschli 1933; Petter & Petter-Rousseaux 1964) and members of the loris/bush-baby group (Jewell & Oates 1969; Charles-Dominique 1971; Vincent 1969) have found it relatively easy to locate individuals of the various species at night because the tapetum at the back of the eye will reflect light from a headlamp. As a result, it is actually easier to spot a nocturnal prosimian when active at night than to spot many diurnal prosimians and simians when they are simply resting quietly in the forest canopy. (One can even locate sleeping groups of diurnal lemurs if they open their eyes and permit the light from the headlamp to strike the tapetum.) Using this technique as a basis, it is easier than might be expected to establish some idea of the overall patterns of nocturnal activity. Petter (1962c) has given a good general description of the nocturnal Madagascar lemurs, while Charles-Dominique (in prep.) is at present writing a detailed account[1]) of a long-term field study of 5 sympatric prosimian species of the lemur-loris group in Gabon *(Galago demidovii, Galago alleni, Euoticus elegantulus, Perodicticus potto, Arctocebus calabarensis)*, greatly expanding upon the information provided about the same species by Jewell & Oates 1969. Charles-Dominique's report on the behaviour of *Galago demidovii* under natural conditions (1971) undoubtedly represents the most complete study of any nocturnal prosimian species. Thus, the major gaps left to fill are the following:

1. Intensive study of the behaviour of individual nocturnal lemur species in Madagascar.[2])
2. Study of the behaviour of Asiatic lorises *(Loris tardigradus; Nycticebus cougang)*.[3])
3. Investigation of the behaviour of the tarsiers in South-East Asia.

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[1]) Charles-Dominique, P. (1971): Eco-éthologie et vie sociale des prosimiens du Gabon. Thèse de Doctorat d'État (Faculté des Sciences; Paris).

[2]) This gap has new been partly filled by: Charles-Dominique, P. and C. M. Hladik (1971): Le *Lepilemur* du Sud de Madagascar — Ecologie, alimentation et vie sociale. Terre et Vie (in press).

[3]) See: Petter, J.-J. and C. M. Hladik (1970): Observations sur le domaine vital et la densité de population de *Loris tardigradus* dans les forêts de Ceylan. Mammalia **34**, 394—409.

This paper is presented as a modest contribution towards filling the first gap. The Lesser Mouse Lemur *(Microcebus murinus)* was selected because it seems, in many features, to be the least specialised of the living Madagascar lemurs, and because its small body size permits coverage of a meaningful area with the techniques at present available. The results reported here are extremely fragmentary; but it is felt that publication at this point is justified because the tentative conclusions which can be drawn throw doubt on the common tendency to describe nocturnal lemurs as "solitary" and because they provide a preliminary basis for more intensive studies. In particular, the general behavioural resemblances between *Microcebus murinus* and *Galago demidovii* are so striking that some interesting conclusions may be drawn about the early evolution of the Primates (Charles-Dominique & Martin 1970).

The Species Studied

The exact taxonomic status of the various forms of the Lesser Mouse Lemur has yet to be established. Petter (1962c: p. 15) reports 3 forms:

1. A rufous form with small ears inhabiting the rain-forest areas of the East Coast of Madagascar.
2. A basically grey form with large ears inhabiting the remaining forest areas (North-West, West and South), which range from deciduous forest with a marked annual variation in rainfall to the extremely dry forest of the South.
3. A rufous form co-existing with type 2 in some areas and distinguished from type 1 (apart from its geographical separation) by its larger ears.

The third form is so rare that its status remains completely obscure; the other 2 forms are generally regarded as subspecies of *Microcebus murinus* — *M. m. murinus* being the grey form and *M. m. rufus* being the rufous form. There is also some confusion over the nomenclature of the latter subspecies, since it is sometimes referred to as *M. m. smithii* (the name used by Petter in 1962c), but has recently been referred to by Petter-Rousseaux as *M. m. rufus*, following Schwarz 1931.

This present field-study involved observations on both the grey and the rufous forms, and new information on their geographical distribution and morphology indicates that they may well be separate species. A survey of the literature shows that *rufus* is probably the valid name for the rufous form. Accordingly, these 2 forms are probably best designated as *Microcebus murinus* and *Microcebus rufus*. However, in order to avoid this taxonomic question, reference will be made to the "Grey Mouse Lemur" and the "Brown Mouse Lemur". The bulk of the observations relate to the grey form, which can in either case be correctly referred to as *Microcebus murinus*, and the small number of relevant observations on the rufous form will be added parenthetically. Thus, it can be correctly stated that this account concerns the behaviour of *Microcebus murinus*, whatever the outcome of the taxonomic issue.

Aims, Methods and Study Areas

Aims

The field-study was conducted as a general survey of the lemurs in 5 different areas of Madagascar, incorporating a concentrated field-study on the behaviour and geographical distribution of the Lesser Mouse Lemur. In the 6-month period July—December 1968, 13 of the 19 extant lemur species were located and observed to various extents. Observations on species other than the Mouse Lemur will be outlined in a subsequent publication. Several of these species were filmed for inclusion in a 16 mm colour-film ("Ghosts at the End of the Earth") by Mr. G. Blanchard on behalf of the B. B. C. (Natural History Unit, Bristol).

The large, and extremely rare, Coquerel's Mouse Lemur *(Microcebus coquereli)* was not observed in the field, so the observations in this paper relate exclusively to the Lesser Mouse Lemur.

The general aims of the study were to obtain a wide range of information on all species sighted, in order to supplement the data provided by Petter, and to obtain specific information about the Lesser Mouse Lemur.

Study Areas

In order to fulfill these aims, 5 main areas were visited during the 6-month field trip. The selection of these areas was planned to cover representative sections of the range of different forest

types. The coastal forest can be roughly divided into 3 basic sectors (Fig. 2) on the basis of annual rainfall, seasonality of rainfall, soil types and vegetation types (HUMBERT 1927, 1955; JOLLY 1966):

1. Eastern Domain (East Coast rain-forest with high rainfall and little seasonality).
2. Western Domain (deciduous forest with relatively high rainfall and marked seasonality, forming a gradient from the North-West to the South-West).
3. Southern Domain (semi-arid forest with low annual rainfall and marked seasonality, covering the extreme South-West and the South).

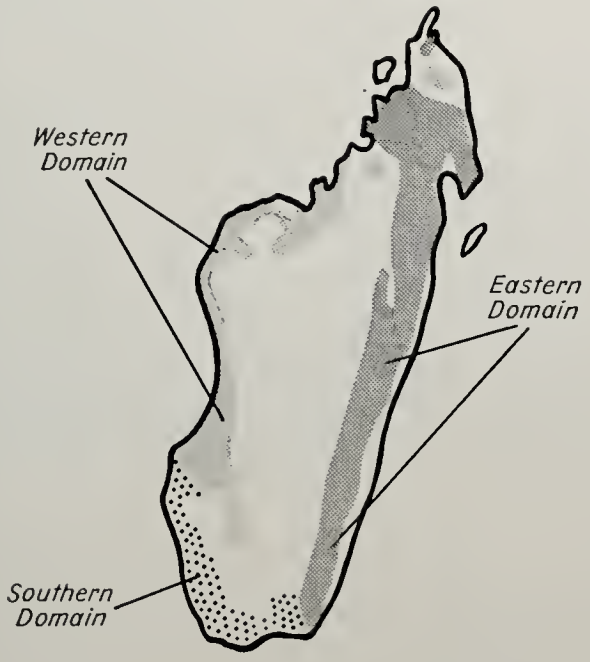


Fig. 2: Map showing the 3 main coastal forest domains of Madagascar. Note the overlap zone in the North. Eastern Domain: habitat of Brown Mouse Lemur. Western Domain + Southern Domain: habitat of the Grey Mouse Lemur

The distribution of these areas is such that a peculiar climatic boundary is present in the South-East. In the North of the island, there is a relatively smooth transition from rain-forest to a deciduous forest with relatively high rainfall; but in the South-East the Anosy Chain of hills divides typical East Coast rain-forest from the dry forest typical of the Southern Domain. One therefore finds 2 distinctive vegetational zones, with their associated faunas, which are separated by a transitional zone only a few miles wide.

In most areas of Madagascar, there is a distinct rainy season (approx. November—April) and a distinct dry season (approx. May—October), though in the Eastern Domain this amounts to little more than a cyclical variation in comparatively heavy rainfall. At the other extreme, in the Southern Domain rainfall is almost entirely confined to the "rainy season", and even during this season may be extremely limited.

Accordingly, the 6-month study covered the latter half of the dry season (July—October) and the first half of the rainy season (November—December) in 1968. The 5 study areas (Fig. 3) were visited in the following sequence:

1. North-West deciduous forest — Forestry Station of Ampijoroa (between the forestry reserve of Ankarafantsika and the River Betsiboka); July 1968.
2. East Coast rain-forest — Forestry Reserve of Perinet; August 1968 (briefly revisited in early October 1968).
3. Southern arid forest — Private Nature Reserves at Berenty (estate of the de Heaulme family); September 1968. (N. B. These reserves include both representative sections of the dry forest and sectors of the lush, green gallery forest lining the River Mandrare).
4. South-East boundary between the East Coast rain-forest and the Southern arid forest, close to the Anosy Chain — Forestry Reserve of Mandena (near Fort Dauphin); October—December 1968 (briefly visited in September 1968).
5. West Coast deciduous forest near Morondava — Private estate of the de Heaulme family (Analabe); briefly visited in December 1968.

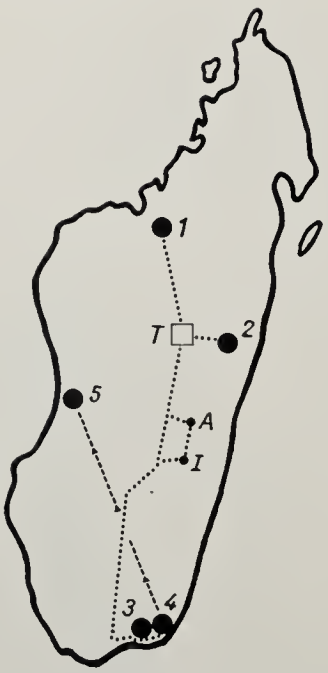


Fig. 3: Map showing the 5 main study areas, with routes taken (see text).

Main study areas:
1 = Ampijoroa
2 = Perinet
3 = Berenty (close to Amboasary)
4 = Mandena
5 = Analabe

T = Tananarive
A = Ambohimanga-du-Sud
I = Ifanadiana

Lesser Mouse Lemurs were observed in all of these areas; but the most intensive study was carried out at Mandena (area 4), covering a period of 3 months at the changeover from the dry to the wet seasons. At Ampijoroa, Berenty and Analabe (areas 1, 3 and 5), only the Grey Mouse Lemur was observed, whilst at area 2 only the Brown form was seen. At Mandena, because of the juxtaposition of the Eastern and Southern Domains, both kinds of Mouse Lemur were found in different forest types. The Grey form was found in the littoral rain-forest, whilst the Brown form was found in the much more humid rain-forest on the flanks of the Anosy Chain.

Some information was also collected whilst travelling from one area to another. In particular, a few Mouse Lemurs were seen in the residual forest patches on the Central Plateau (generally poor in animal life), and quite detailed information was collected at Ifanadiana (I) and Ambohimanga-du-Sud (A) in the East Coast rain-forest between Perinet (area 2) and Mandena (area 4). As a general rule, Lesser Mouse Lemurs were relatively common, though they were more-or-less confined to the vicinity of regions where considerable areas of endemic forest are still preserved. Since they tend to live on the fringes of the forest, rather than in the interior, they were relatively easy to discover by surveys along existing pathways.

Data Collection

Apart from simple observations on the occurrence of Lesser Mouse Lemurs (and other lemurs) in the areas visited, the following data were collected for the Grey and Brown forms:

1. General behavioural observations: activity, interactions and locomotion.
2. Investigation of diet under natural conditions, supplemented by feeding tests on captured Mouse Lemurs.
3. Study of the occurrence, localisation, nesting and social tendencies of recognisable individuals.
4. Investigation of reproduction, including a study of occurrence of oestrus, pregnancy and birth and rearing of offspring with and without their mothers in captivity. Collection of gravid uteri.
5. Collection of representative skins and skulls for later identification.

Methods

In any proposed study area, a suitable population of Mouse Lemurs was first located by a series of exploratory tours using dry battery headlamps powered by 3 U2 batteries (supplied by courtesy of the EVER-READY Co. Ltd.). In the case of the Mouse Lemur, individuals can be



Fig. 4: Flash-assisted night photographs of a tail-marked ♀ Grey Mouse Lemur (natural habitat: Mandena). Arrow indicates tail-mark

a: Note removal of hairs at tip of tail for easy identification. Pupil size is small with direct light from nearby

b: Pupil size has increased with the head turned away from the light-source. Note reflection from *tapetum* at the back of the eye

readily spotted over a range of up to 30 m, and can sometimes be sighted at even greater distances, with the weak light source utilised. In using this technique, it was found that the Mouse Lemurs are most likely to be first spotted at the fringe of the light-beam (or towards the centre when the batteries are beginning to lose power), at the range generally involved (5—20 m). Probably, the Mouse Lemurs turn their heads away from a *strong* light beam (thus becoming unnoticeable), whilst they will tend to look towards a weak source of light (see Fig. 4).

Once spotted, a Mouse Lemur could usually be followed on foot (provided that the vegetation was not too dense), and it was often possible to approach to within 5 metres. Surprisingly, the animals were in many cases only mildly disturbed by such close observation, and would often complete ongoing activities (feeding, grooming, etc.) unless induced to flee by loud noise, abrupt movement or displacement of foliage.

Attempts were made to conduct observations using an infra-red telescope (weapon sight) hired from the Ministry of Defence (London); but this instrument proved to be of little value for observing Mouse Lemurs owing to difficulties in relocating moving animals and in adjusting the focus. Tests indicated that infra-red telescopes would probably be more effective for observing the larger, more sedentary lemurs such as the Avahi *(Avahi laniger)* and the Sportive Lemur *(Lepilemur mustelinus)*, which are both active at night.

Once Mouse Lemurs had been located in a given area, it was possible to obtain data about their habits and ecological relationships:

1. Mapping of small study areas of approximately 4,000 sq. metres.
2. Performance of nightly surveys in order to record localised sightings of Mouse Lemurs, their movements, and any general behavioural activities. (In many cases, it was possible to identify the *sex* of unknown individuals by examination with 10×40 binoculars used in alignment with the headlamp.)
3. Trapping, marking and release of Mouse Lemurs within the study areas. With a team of 4 people, it is often possible to isolate Mouse Lemurs on low bushes or trees at night and to trap them by hand. Marking was carried out by clipping the hairs on the tail with scissors. ♀♀ were marked by clipping the tip to varying extents (Fig. 4a/b), and ♂♂ by clipping out a segment of variable length from the centre of the tail.

Clipping of the tail is sufficient for short periods of a few months, and the bare area is identifiable with binoculars from a distance of up to 10 m. Marking of the ears with small triangular incisions — already used successfully in the laboratory by PETTER and PETTER-ROUSSEAUX (pers. comm.) — would be necessary for longer periods. Experience from the laboratory shows that such ear incisions will remain identifiable for two years or more.

Some individuals which were not trapped were recognisable through distinctive physical features (e. g. one female in Mandena showed no reflection from the tapetum of one eye).

4. By day, the study areas were examined for identification of food-plants, measurements of precise locations and distances, and for location of nests. If nests were found, the occupants were trapped, examined, marked and released.

This procedure permitted gradual construction of a simple plan of the occurrence of Mouse Lemurs within each study area and of possible relationships between them. Unidentified sightings permitted identification of "areas of activity" on a scatter principle, whilst identified sightings gave some indication of actual home ranges. (See section on "Distribution Patterns" — p. 61 etc..)

Data were also collected from nests containing Mouse Lemurs brought in by various helpers (usually local villagers) or discovered outside the study areas. General observations in all areas were supplemented by nocturnal photography using a CANON FX SLR camera with a 135 mm lens and a small flash using AG 1B and AG 3B bulbs.

Trapping of Mouse Lemurs also permitted collection of the following data:

i. Simple measurements of weight, etc.,
ii. Stomach contents,
iii. Blood samples,
iv. ♂ and ♀ reproductive characteristics.

(N. B. Small canvas bags fitted with 2 tapes for tying off proved to be invaluable for holding, transporting and weighing captive Mouse Lemurs and other specimens.)

Biometric Data

All animals trapped were weighed and examined prior to release. (Weighings were conducted to an accuracy of ± 1 gm with a "PESOLA" spring balance of 300 gm capacity.) With some individuals, measurements were taken of the lengths of the head, body, tail and limbs, using a flexible tape-measure. Because of the difference between the two types of Mouse Lemur, special attention was given to the height of the ears.

Table 1: Weights of Brown Mouse Lemurs from various areas

Sex	Origin	Date	Weight (gm)
♂	PERINET	7. 8. 1968	36
♂	"	10. 8. 1968	40
♂	"	11. 8. 1968	41
♂	"	15. 8. 1968	53
♂	"	15. 8. 1968	40
♂	"	24. 8. 1968	43
♀	"	28. 9. 1968	48
♂	"	29. 9. 1968	48
♂	AMBOHIMANGA-DU-SUD	12. 10. 1968	44
♂	"	12. 10. 1968	51
♂	IFANADIANA	13. 10. 1968	46
♀	"	13. 10. 1968	47
♀	FORT DAUPHIN (Besavona)	6. 12. 1968	76 *
♂	FORT DAUPHIN (Col de Manangotry)	7. 12. 1968	55

* probably pregnant

Most data came from Grey Mouse Lemurs trapped in Mandena (area 4; Fig. 3). For reasons to be discussed later (section on "Distribution Patterns"), these were predominantly ♀♀. Data for Brown Mouse Lemurs are given in Table 1, and weights of ♂ and ♀ Grey Mouse Lemurs are given in Figs. 5 and 6, respectively.

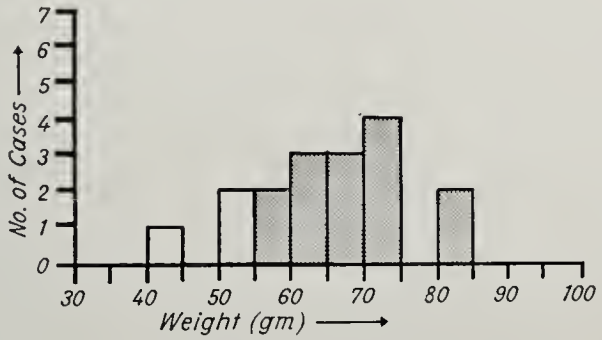


Fig. 5: Histogram of weights of ♂ Grey Mouse Lemurs trapped in various areas (N = 17), Jul. to Dec. 1968. Blank areas = "peripheral ♂♂". Stippled areas = ♂♂ associated with aggregations of ♀♀

The overall range of weights of captured Mouse Lemurs was 40—100 gm, with the average at about 70 gm. Since many weights were taken from pregnant or lactating females (68 out of 163 readings), the average weight prior to breeding is probably nearer 60 gm (cf. Fig. 6). It is also likely that average body weights are even lower at the peak of the dry season (June/July), and higher at the peak of the rainy season (January/February), since weights were only recorded for the period September—December in the main study area

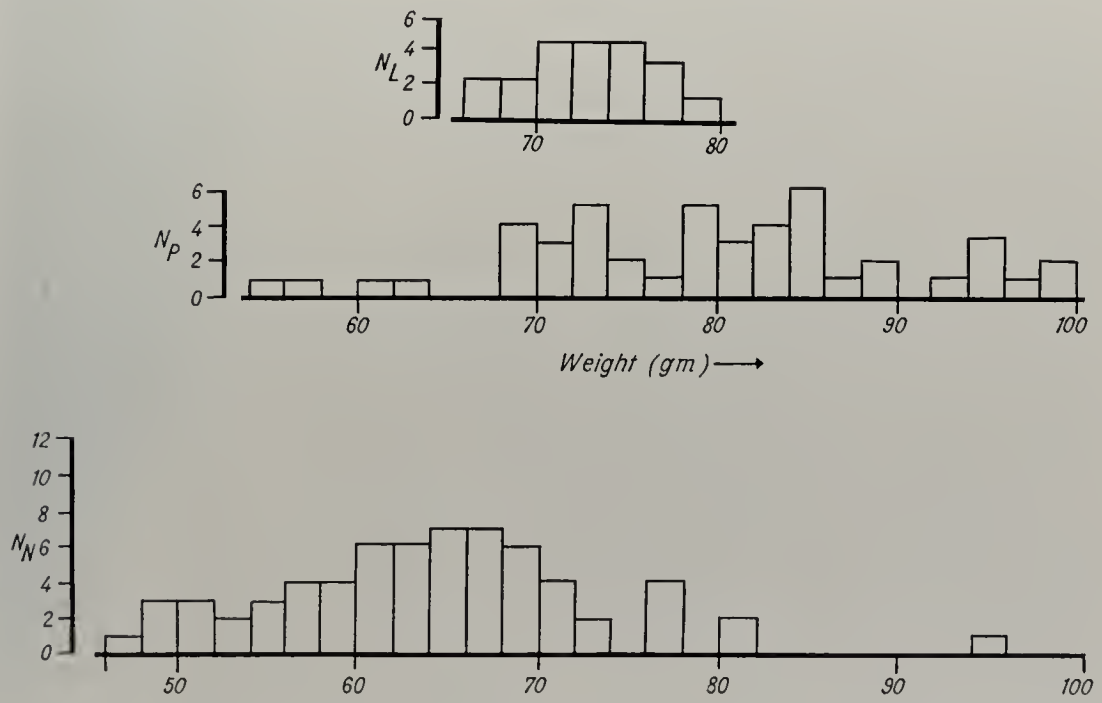


Fig. 6: Histogram of weights of ♀ Grey Mouse Lemurs trapped in various areas (N = 132)
N_N = non-pregnant, non-lactating ♀♀ captured Sept.—Dec. 1968
N_P = pregnant ♀♀ (mid- to late-) captured Oct.—Dec. 1968
N_L = lactating ♀♀ with offspring captured Nov.—Dec. 1968

(Mandena). On the whole, it is probably correct to take a figure of 60 gm for the average annual body weight of adult Lesser Mouse Lemurs.

Since body measurements on live individuals are not very accurate, they were only taken from a few individuals ($N = 12$). The averages were as follows:

Head Length (tip of snout to occiput):	42	(38— 45) mm
Body Length (occiput to root of tail):	91	(82—101) mm
Tail Length (root to tip):	138	(123—149) mm

Thus, on average the tail was just slightly longer than the head + body (138 vs. 133 mm). It has been stated that the Grey Mouse Lemur differs from the Brown form in having a relatively longer tail (Hill 1953, p. 332); but the small number of measurements taken here (6 Grey; 6 Brown) adequately demonstrated that there is no clear-cut distinction of this kind.

On the other hand, there was a clear difference between the 2 types of Mouse Lemur in the maximum height of the ears (measured from the lower margin of the external auditory meatus to the tip of the pinna):

Grey Mouse Lemurs	Brown Mouse Lemurs
22 (21—23) mm	18 (17—19) mm

This distinction in ear-size is matched by differences in pelage colouration in all cases, and no intermediates were found in either respect, though there is a small range of variation for each type of Mouse Lemur.

Ecological Characteristics

1. General Habits

Despite vast differences in annual rainfall and vegetation types in the different study areas, Mouse Lemurs were generally found to occupy the same kind of ecological niche: They were always found in relatively dense foliage zones containing large numbers of fine branches, narrow lianes, etc. (Fig. 7). This may be referred to as the *fine branch niche*. Even in dry forest areas (e. g. Berenty area), dense leafy zones are found to afford cover for mouse lemurs.

Petter (1962c) gave the following description of locomotion in *Microcebus* (my translation):

"When moving along branches, *Microcebus murinus* generally progresses in a jerky fashion. Rapid bouts of running covering one metre or more alternate with pauses of varying duration. The animal can also progress by means of small thrusts with the hind-legs, with the body maintained in a horizontal position, which gives it a hopping gait entirely comparable to that of a mouse.

Thanks to its small body weight and size, it can move around upon the finest branches and weave in and out of matted vegetation. The animal leaps with ease from one branch to another and uses its tail as a balancing device."

Walker 1967 is essentially in accord with this description, noting that small gaps between branches may be crossed by the animal "reaching for the next branch and holding it with the hands before swinging the hind limbs across". Walker classifies *Microcebus* as essentially quadrupedal, lacking the marked adaptations for vertical clinging and leaping or for slow climbing found in other prosimians. However, the Mouse Lemur does show some elongation of the tarsus, involving the navicular and calcaneus (Weber 1928,



Fig. 7: Flash-assisted night photograph of ♂ Grey Mouse Lemur (Mandena), showing typical *fine branch habitat*. Note lateral application of hands and feet on the broad support

p. 736) and possibly the cuboid (Hill 1953); though this is by no means as marked as in the bush-babies (Galaginae) and the tarsiers (Tarsiidae). In fact, the pes of *Microcebus murinus* is extremely similar to that of *Galago demidovii*, except that the pes of the latter is more elongated and has a number of more specialised features (e. g. in the arrangement of the digital pads). On the basis of its *intermembral index* (ratio of fore-limb length to hind-limb length), Walker (1967) classifies *M. murinus* as an arboreal quadruped, but the indices of this species and *G. demidovii* are not greatly different (72.6 vs 65.1), and since the index is somewhat variable within each species, this difference is not very pronounced. It is true that adaptations for vertical clinging and leaping have proceeded farther in *Galago demidovii* (in morphological terms); but the differences from *Microcebus murinus* are more likely to indicate distinction in *degree of development* of particular locomotor types, rather than clear-cut differences in locomotion. Primate species with a greatly elongated tarsus and a low intermembral index (e. g. *Galago species*, *Tarsius species*) are quite obvious vertical clingers and leapers, whilst various prosimians with only moderate development of these features can be either typically quadrupedal (e. g. *Cheirogaleus*) or typical vertical clingers and leapers (e. g. *Hapalemur griseus*). This suggests that behavioural adaptation of locomotion is probably achieved some time before appropriate morphological adaptations emerge. It is therefore extremely important to establish typical modes of locomotion in the field before giving a detailed explanation of morphology.

In actual fact, the Mouse Lemur is extremely versatile in its locomotion under natural conditions, and the descriptions given by Petter and Walker can be expanded to give the following list of locomotor patterns:

1. Slow to fast quadrupedal movement along horizontal, inclined or vertical supports (including the pattern of slow passage from one branch to another described by Walker).
2. Rapid, skipping locomotion along essentially horizontal supports.
3. Leaps over distances up to 3 metres, landing on all fours (i. e. with the hind-limbs swinging round prior to impact when landing on vertical surfaces).
4. Hopping over the ground, in frog-like fashion (i. e. largely based on thrusts with the hind-limbs, but not fully bipedal).

In effecting these different patterns, the Mouse Lemur can exhibit all kinds of body-posture, and its grasping hands and feet can be utilised and oriented in a number of different ways. On large surfaces, the hands and feet are generally held laterally (Fig. 7), and close examination shows that the fingers are usually flexed with the digital pads appressed to the substrate (e. g. see figures provided by Starmühlner 1960). On fine branches, the mobile digits of the hand and the opposable hallux on the foot are used to grasp the support directly (Figs. 4 & 8).

This versatility in locomotor pattern and use of the extremities seems to be unique among prosimians. The Mouse Lemur combines possibilities of slow and rapid arboreal quadrupedalism with a tendency to hind-limb dominated locomotion, whilst most other living prosimians have become restricted to vertical-clinging-and-leaping, arboreal quadrupedalism or slow climbing as their major form of locomotion in the trees. This generalised repertoire of motor possibilities may well represent a retention of the ancestral Primate condition, and its tendency towards hind-limb domination would accord with the widespread appearance of morphological adaptations for vertical-clinging-and-leaping during and since the Eocene period, described by Napier & Walker (1967).

Apart from general locomotion, Mouse Lemurs also have 2 (partially overlapping) patterns associated with feeding. One was described by Shaw (1879): "I have often seen them swing themselves down from their perch holding by the hind limbs, grasp their food in the two forehands, and then gradually draw themselves back again into their former position on the perch". This observation was based on captive specimens; but in the course of the present field-study, it was frequently observed when Mouse Lemurs were feeding on plant food (e. g. berries of *Vaccinium emirnense;* Mandena). The second pattern, which has apparently not been described previously, is a rapid movement used for trapping live *insects:* The Mouse Lemur squats in a retracted position on a branch, launches itself rapidly outward with the grasp on the branch firmly maintained by the hind feet, grabs at the prey with the hands, and then rapidly retracts to its former position. The rapid retraction phase is just as characteristic of the movement as the rapid extension phase, and it may well provide a safety mechanism in case the prey is able to defend itself in some way. This pattern was only rarely seen under natural conditions, since trapping of insects in the trees was not a frequent event under the conditions of observation (with a headlamp). However, it has been extensively studied under laboratory conditions[4]), and it is a characteristic pattern. Various observations indicate that where an insect (e. g. a mealworm) is tethered within reach of the hands, the Mouse Lemur will move around on available branches until the appropriate distance for the predatory pattern is achieved.

[4]) Experiments conducted at the Muséum National D'Histoire Naturelle (Ecology Section), Brunoy, France.

On a number of occasions, Mouse Lemurs were also seen to hold their bodies horizontal with only the hind-feet maintaining a grasp on a branch ("flag-posture"). This was only observed when the feet were grasping a *vertical* branch (i. e. with one foot above the other); but it seems likely that the Mouse Lemur could also hold itself in a horizontal position with the feet attached to a horizontal branch.

Opinions vary about the *height* at which Mouse Lemurs typically occur in the trees. SHAW (1879) maintained that they typically move around "on the tops of the highest trees", whilst PETTER (1962b) stated that he had observed no spatial restriction of this kind for any lemur species. The present field-study confirmed PETTER's statement, as far as the Grey Mouse Lemur is concerned, since the animals were observed at all levels in the forest, provided that dense foliage and fine supports were available. In marginal, bushy vegetation, Mouse Lemurs can be found from ground level to the tops of the available bushes; whilst in dense primary forest they can be observed moving around in the leafy crowns of trees 30 m and more in height. In secondary forest, where there are many relatively thin, vertical trunks and relatively little ground-level vegetation, Mouse Lemurs typically occur at intermediate heights among the leafy branches and lianes of the young trees (i. e. at 2—10 m height). In all kinds of habitat, provided that there is sufficient foliage cover and fine branch support, Mouse Lemurs can be seen moving up and down, even descending to the ground on occasions. Thus, vertical distribution appears to be a function of vegetational substrate rather than of specific altitude preference.



Fig. 8: a. Night photograph of a ♀ Grey Mouse Lemur (Mandena) feeding upon the small, green berries of *Vaccinium emirnense*. Note the density of the fruit
b. Drawing based on the photograph, clarifying the positions of the hands and feet. Note that the berry is held exclusively in the right hand, with the thumb probably opposed

In both locomotion and altitude of activity, the Mouse Lemur contrasts sharply with its close relative the Dwarf Lemur *(Cheirogaleus sp.)*, which is usually sympatric except in low-grade forest areas. *Cheirogaleus* is a slow-moving, essentially quadrupedal form which rarely descends below 3 m altitude, even when dense cover is available. Both factors probably relate to the fact that *Cheirogaleus* moves primarily on the large branches, rather than in the fine branch zone, in association with its larger body size (250 gm vs. 60 gm).

2. Diet

Mouse Lemurs (both Grey and Brown types) were frequently observed whilst feeding at night. If they were seen frequently on a particular type of tree or plant in successive nights of observation, samples were taken in a plant press for later identification. In addition, captive animals were given samples of leaves, buds, flowers and or fruit from any such plant in order to see whether they would readily take these as food. In some cases, Mouse Lemurs were actually seen feeding on particular food-plants (Fig. 8), providing a certain identification of natural food-sources. As a rule, food debris was found under any frequent food-source, and this provided further information. On this basis, a list of common food-plants was established for the various study areas (Table 2).

Table 2: Plant food of Mouse Lemurs

Study area	Date (1968)	Plant species	Parts eaten	
			Leaves	Buds
AMPIJOROA (Fig. 3 : 1)	July	unidentified plant bearing small fruits	–	–
		"Jujube" shrub (buckthorn group) ; *Zizyphus mauritianus*	–	–
PERINET (Fig. 3 : 2)	August & October	Short pathside plant bearing mauve berries; *Clidemia hirta*	–	–
		Rambling thorny climber with fleshy flowers ; *Rubus roridus*	–	–
AMBOHIMANGA-DU-SUD (Fig. 3 : A)	October	Shrubby tree bearing small fruits ; *Eugenia jambosa*	–	–
		Pathside plant with mauve berries ; *Clidemia hirta*	–	–
MANDENA (Fig. 3 : 4)	September & October - December	Shrubby tree with white flowers and green pods ; *Brexia madagascariensis*	–	–
		Shrubby tree with white flowers and green berries ; *Vaccinium emirnense*	–	–
		Large tree with buttress roots and fairly large green to yellow fruits *Uapaca sp.*	+	–
ANALABE (Fig. 3 : 5)	end of November & beginning of December	Small , shrubby tree with small , squarish green pods (Malgache name: FANTSIKAKOHOLAHY)	–	–
		Small , shrubby bush with small , white to pink berries (Malgache name: ARONGAFANIHY)	–	–

It is important to note that such observations indicated that the plant diet of the Lesser Mouse Lemur is not confined to *fruit*, as has commonly been supposed. In several areas, it was found that the Grey Mouse Lemur was feeding upon *flowers*, usually concentrating on the base of the flower and allowing the petals to fall to the ground (e. g. on *Vaccinium emirnense* in Mandena). In Mandena, where the most intensive observations were conducted, it was also found that *leaves* were occasionally eaten; on 3 separate occasions, Grey Mouse Lemurs were definitely observed eating the leaves of *Uapaca* trees, and many of the leaves of these trees were found to be chewed in the same fashion as those actually observed being eaten by Mouse Lemurs. This supported previous observations of chewed liane leaves in Ampijoroa, and it seems likely that the Mouse Lemur — at least occasionally — includes some leaf material in its diet. This means that the range of plant food taken by Mouse Lemurs is quite wide (leaves, flowers, fruits) and that these animals are even less specialised in their diet than has been supposed.

Apart from feeding upon plant products, Mouse Lemurs also eat a certain amount of animal food, as reported by Webb (1953), Hill (1953), Starmühlner (1960), Petter (1962c) and Walker (1967), who all state that insects are the primary source. Despite the difficulties of observation by night with a headlamp, direct confirmation of this was obtained in various areas

in various study areas *Table 2*

Parts eaten		Source of data *	General comments
Flowers	Fruits		
–	+	S	Most of the small fruits seen were on lianes and small shrubs
–	+	O ; F ; R	Species introduced relatively recently ; small yellow to brown fruits with a sweet , insipid taste
–	+	S ; O ; F ; R ; C	Introduced via Tamatave in 1918 ; now a common roadside species in East Coast rain-forest
+	+	O ; F ; R ; C	Apparently introduced quite recently ; forms a thick tangle of fine , spiny branches
–	+	F ; R ; C	Pathside species belonging to the "clove" family
–	+	O ; F ; R ; C	(see above)
+	?	O ; F ; R	Found alongside paths in secondary forest ; pods may be chewed by Mouse Lemurs
+	+	O ; F ; R ; C	Found alongside paths in secondary forest ; relatively common in Mandena
?	+	O ; F ; R ; C	Occurs in relatively dense forest and yields large quantities of fruit ; almost certainly endemic to Madagascar
–	+	O ; F ; R	Probably a pathside shrub ; extremely thorny , as with most trees and shrubs in this forest
–	+	O ; F ; R	Pathside shrub ; bears large quantities of fruit. Name in colloquial tongue indicates that fruit is also eaten by fruit-bats (FANIHY)

of Madagascar. Mouse Lemurs were seen eating the following animal food; beetles, moths, praying mantids, Fulgorid bugs and spiders; and in captivity small tree-frogs and chamaeleons were completely devoured, along with various grasshopper species which formed the bulk of insect food for captive animals.

Stomach contents were collected from 2 Mouse Lemurs from each of 4 Study areas (Fig. 3: Ampijoroa, Perinet, Ambohimanga-du-Sud, Mandena), and analysis confirmed that the major part of the diet consisted of plant material and insects. The main constituent of the insect remains in the stomach contents were fragments of beetles, and this correlated both with the fact that most cases of predation at night involved beetles, and also with the common occurrence of beetle elytra in nest debris. However, the quantitative relationship between plant remains and insect remains in the stomach contents indicated that animal food provides less than half of the food intake. It is extremely difficult to draw reliable conclusions from partly digested material; but in two animals which had been feeding on fruit with hard kernels (Ampijoroa specimens), the large number of kernels indicated a fruit intake far in excess of the volume of insect food witnessed by the chitin fragments in the stomach contents. It was also noticeable that the chitin fragments were extremely small, indicating extensive mastication prior to swallowing. In *Galago demidovii*, which *is* predominantly insectivorous (Charles-Dominique 1966), the chitin is fragmented to a much lesser extent (Charles-Dominique, pers. comm.). This, in correlation with the lower crowns of Mouse Lemur molar teeth, indicates that *Microcebus* is adapted for a greater percentage intake of plant food (requiring more intensive mastication) than is the Dwarf Bush-Baby. This impression is confirmed by observations in captivity, which indicate that the Mouse Lemur will take a relatively large proportion of plant food (bananas, apple, orange, grapes, etc.), whilst *Galago demidovii* feeds almost exclusively on insects (mealworms, crickets, locusts, etc.). It is therefore unlikely that the Mouse Lemur is "highly insectivorous", as stated by Hill 1953 (following Webb); it is best regarded as an omnivore. In this context, it is interesting to note that damaged mollusc shells and fragments of such shells were frequently found in the nest debris of Mouse Lemurs under natural conditions. It is possible that these molluscs, which often frequent crevices in trees, are also included in the diet.

Surprisingly, most observed cases of predation upon insects occurred on the ground, although there were cases of predation upon Fulgorid bugs and large spiders in the trees. On several occasions, a Mouse Lemur was seen exhibiting the following behaviour: The animal would descend to a height of about 1 m on a tree-trunk or bush and remain motionless for a while, exhibiting alternating movements of the ear pinnae. It would then make a rapid dash across the leaf-litter on the forest floor, seize an insect with its hands, bite the prey and then dash back to its former vantage point to eat its prey. On one occasion, in Mandena, a Grey Mouse Lemur was seen to dart to the ground and trap a green praying mantis almost as long as its own body. (Predation on large insects is not uncommon; Petter [1962c] reports a Mouse Lemur sitting on a branch and eating an enormous migratory locust.) Predation on the ground was only observed 8 times in all; but the behaviour involved is strikingly reminiscent of the behaviour of Mouse Lemurs and bush-babies in captivity, seen when they locate and trap insects (e. g. mealworms and crickets) in wood-shavings on the cage-floor. It may well be that the large ear pinnae in these prosimians, along with the alternating movement of the pinnae prior to predation, represent an adaptation for precise location of insects moving in leaf-litter and other matter.

3. Dietary Specialisation

One important observation was the fact that Mouse Lemurs seem to specialise upon different plant food-sources according to locality. For example, in the rainforest at Perinet, the Brown Mouse Lemurs were primarily feeding upon a small hedgerow plant bearing mauve berries about the size of a black-currant *(Clidemia hirta)*, and a suitable study-area for Mouse Lemurs was later found at Ambohimanga-du-Sud and Ifanadiana in rain-forest 140 miles to the South (Fig. 3) by first locating an area in which this plant was common. In the drier, littoral rain-forest of Mandena, on the other hand, Grey Mouse Lemurs were seen predominantly eating the flowers and fruits of a forest-fringe shrub (*Vaccinium emirnense;* Fig. 8). In the North-West deciduous forest at Ampijoroa, analysis of stomach contents showed a predominant intake of a small fruit containing a hard kernel (unidentified), and Grey Mouse Lemurs in the West, at Analabe were mainly observed feeding on a small shrub with tiny white/pink berries (Malgache name: Arongafanihy). In all of these cases, the main item of food seemed to be the fruit ("berries"), which were usually less than 1 cm in diameter. In 2 cases, observation showed that fruit were available over at least 3 months (*Clidemia hirta:* August—October; *Vaccinium emirnense:* October—December). However, the brief duration of this field study ruled out any conclusions about continuous food-sources. All that can be said for the present is that there seems to be some local specialisation, which may persist for a number of months.

Feeding upon *animal food* seems to be much more opportunistic. The diet seems to include a wide range of arthropods and other small animals, though there is some specialisation on essentially terrestrial beetles. Particularly in areas with a marked annual variation in rainfall (e. g. Mandena, Berenty, Analabe, Ampijoroa), various arthropods are taken as and when they appear, with a probable peak of availability during the wet season. In one



Fig. 9: Drawing of a Grey Mouse Lemur close to the larvae of the Fulgorid bug *Phromnia.* (Taken from a poorly exposed photograph from the Analabe study area.)

case (at Analabe), rapid concentration upon a newly emergent food-source was seen, as a particular insect species appeared in large numbers at the end of November. The insect — a member of the Homopteran Family Fulgoridae (genus: *Phromnia*) — has already attracted attention as possessing an apparently protective adaptation known as "flower mimicry". (See Wickler 1968 for an account of an African representative of this Family.) The adult insects assemble in groups on fine branches, and their laterally flattened form and colour give each group a striking similarity to a group of flowers or a single inflorescence. Such mimicry has only been widely reported for the adults, and Wickler states that the African form *Ityraea nigrocincta* has 2 morphs — a green one and a yellow one — which arrange themselves such that the green morph occurs at the top of a branch, giving the impression of "unopened buds". In the Madagascar form, *Phromnia*, there is no dimorphism in the adults — all of which are pink/red. However, the genus is noteworthy in that the *larvae*, which are completely white, aggregate in the same way as the adults and also have a flower-like appearance. These larvae lack the flattened wings of the adults; but the posterior end of the abdomen bears waxy, white appendages which have a sugary taste. The larvae, like the adults, group themselves on fine branches or lianes, and they resemble bundles of white flowers. It is not known whether this resemblance to flowers (to the human eye) really does limit predation by birds and other predatory animals; but it certainly does *not* safeguard *Phromnia* against predation by Lesser Mouse Lemurs. As soon as the first larvae appeared in the Analabe study area, the local Grey Mouse Lemurs were seen feeding upon them or adjacent to them on several different occasions, and one ♂ was seen with them in a particular clump of bushes every single night over a whole week[5]). Thus, Mouse Lemurs seem able to profit rapidly from newly expanding animal food sources (Fig. 9).

4. Activity Patterns

Lesser Mouse Lemurs sleep in some kind of nest during the daylight hours (p. 61 et seq.). Most individuals emerge soon after sunset, and all have returned to the cover of a nest by sunrise; at least some individuals can be seen active every hour of the night, but the periods of greatest activity seem to be the first and last thirds of the night, with a general reduction in sightings around midnight. During this phase of relative inactivity, Lesser Mouse Lemurs (both Grey and Brown) were occasionally seen in rough "resting nests". However, there is no clear-cut bimodal pattern of activity applicable to all individuals.

As far as *annual* patterns of activity are concerned, it has often been said (usually following Grandidier) that Lesser Mouse Lemurs exhibit a fixed seasonal activity rhythm, in that there is a period of dormancy (sometimes misleadingly called "aestivation") comparable to the hibernation of certain mammals of Northern temperate areas (e. g. see Kaudern 1914, Vallois 1955 & Walker 1968). According to Starmühlner 1960 (citing Grandidier), both *Microcebus* and *Cheirogaleus* are dormant from July to September. However, there are no detailed accounts of such "dormancy" of *Microcebus*, and certainly no evidence for it was found in the course of this field-study. Mouse Lemurs were observed in fairly large numbers in all areas visited between July and September 1968 (i. e. both Grey and Brown forms), and there was no obvious

[5]) The Mouse Lemurs were actually observed eating these larvae on 3 occasions, whilst the majority of observations simply showed them near to the larvae. It has been pointed out by Dr. J.-J. Petter (pers. comm.) that the main source of attraction may be *sap* liberated whilst the larvae are feeding on lianes.

increase in frequency of sightings in the period October—December, as would have been expected if there were some period of *relative* inactivity from July to September. Probably, such accounts of a "dormancy" period are based on finds of groups of Lesser Mouse Lemurs in hollow trees; these nesting groups in fact have a quite different significance (p. 68 etc). The best evidence *against* "dormancy" in *Microcebus* is provided by data from *Cheirogaleus*, which really does seem to have a natural period of dormancy in the field. In the period 14th July to 14th September 1968, *Cheirogaleus* was not seen out in any of the study areas, whilst *Cheirogaleus major* was sighted on 12th October in Ambohimanga-du-Sud (Fig. 3: A) and *Cheirogaleus medius* was seen on 22nd October in Mandena (Fig. 3: 4). Thereafter, sightings of *Cheirogaleus* were frequent. *Cheirogaleus medius* were found in tree nests in mid-September in Mandena, so it can be safely assumed — for that area, at least — that *Cheirogaleus* remain inactive in their nests for part of the year[6]). The date of emergence of *Cheirogaleus* must have been somewhere between 14th September and 12th October for the year 1968.

Another characteristic of *Microcebus* which led to the assumption of "dormancy" is the animal's ability to store fat in its tail — an ability which it shares with *Cheirogaleus*. In the latter case, the stored fat probably acts as a reserve over a period of several weeks of dormancy. In the case of the Lesser Mouse Lemur, however, the fat is probably laid down during periods of food abundance in order to *supplement* food gathered during periods of scarcity. It seems likely that such fat stores are laid down during the rainy season (December—April) and used up during the dry season (May—November), and this supposition is supported by the fact that the Brown Mouse Lemur (both in the field and in the laboratory) is far less prone to store fat in its tail. In the East Coast rain-forest, seasonal availability of food is likely to be less marked than in the areas inhabited by the Grey Mouse Lemur. It seems quite probable that such seasonal storage of "emergency reserves" in the tail was an evolutionary precursor to the full dormancy adaptation of *Cheirogaleus*. PETTER (1962c) has already noted that *Cheirogaleus* exhibits periods of marked inactivity in captivity, whilst *Microcebus* only does so if the external temperature is lowered from the normal laboratory temperature of 25 °C to one of 18 °C. (See also: BOURLIERE & PETTER-ROUSSEAUX 1953; BOURLIERE, PETTER & PETTER-ROUSSEAUX 1956.) Since daily air-temperatures in the dryer forests inhabited by the Grey Mouse Lemur are usually far in excess of 18 °C, only falling below that figure for part of the night, it is unlikely that these animals would exhibit a period of torpor because of low external temperatures, particularly since the period July—September is usually quite hot in Madagascar.

Distribution Patterns

1. Nesting Patterns

During the daytime, Mouse Lemurs (both Grey and Brown forms) can be found in nests of 2 basic types:

(i) *tree-hollows* — often containing a basal platform of leaves and debris (Fig. 10).

(ii) *leaf-nests* — spherical leaf-aggregations with a central chamber and (usually) one lateral entrance. The entire nest is usually wedged between the fine branches of a tree (see Fig. 21).

[6]) It is important to note, however, that the *Cheirogaleus medius* were not in an obvious state of torpor when found in nests in September. Thus ,there is probably a restriction of activity during the dry season, but not necessarily a special physiological withdrawal state.



Fig. 10: Grey Mouse Lemur at entrance to tree-hollow (Analabe study area)
Photo taken at night

In a few cases, Mouse Lemurs were found simply curled up (singly or in groups) in natural foliage cover; but as a rule, a more elaborate retreat (type (i) or (ii)) was used. When Mouse Lemurs were resting in foliage cover or leaf-nests, shaking of the supporting branches invariably elicited an escape response; the occupant(s) would always dash away and 'freeze' several metres from the original retreat. With tree-hollows, on the other hand, striking the trunk or probing with a fine branch in the hollow always induced the occupant(s) to cower at the farthest corner of the nest, though the initial disturbance usually evoked an explosive vocalisation (see p. 74).

As a general rule, most nests were found in *tree-hollows*, and it seemed that leaf-nests or simple foliage cover were mainly used where no suitable hollows were available (e. g. in roadside vegetation and in areas where hollow trees had been opened by local villagers in search of food items). Of 32 nests discovered in this field-study, 22 were in hollow trees, 7 were spherical leaf-nests, and 3 were simple retreats in dense foliage.

This provides an interesting contrast to *Galago demidovii*, which will build leaf-nests quite similar to those of the Mouse Lemur or rest in natural foliage cover, but apparently does not occupy tree-hollows (Charles-Dominique 1971; Vincent 1968). This may be explained by the relative absence of competition in the Mouse Lemur's habitat; the only potential competitors seem to be a few, rare endemic rodent species, some of the small nocturnal prosimians (particularly *Cheirogaleus spp.*), and some arboreal lizards. In fact, because of various ecological distinctions between these potential competitors, it seems

likely that the Mouse Lemur encounters little serious competition for the use of tree-hollows within its own ecological niche.

By searching systematically through forest areas known to contain Mouse Lemurs, it is possible to locate many hollow trees, and the latter can then be probed with a fine branch to determine whether they are occupied. Local villagers were enlisted as guides and helpers, and a team of 4 people was usually sufficient to find about 6 nests per day. In every case, all of the Mouse Lemurs in a nest were carefully examined, except where escapes occurred, and the nest was measured in order to identify any consistent character (dimensions of entrance(s) to nest; internal diameters of trunk; height of entrance above ground; length of cavity within tree). In a number of cases, tree-hollow nests containing Mouse Lemurs were brought in by villagers, and these nests were also measured, provided that each nest could be reliably assumed to be genuine.

Essential information is provided by the measurements of internal diameter of the nest cavity (Fig. 11: I) and the external diameter of the trunk (Fig. 11: E). The histogram in Fig. 11 shows that the cavity and the trunk tend to be of standard size, though the trunk itselfmay in some cases be extrem-

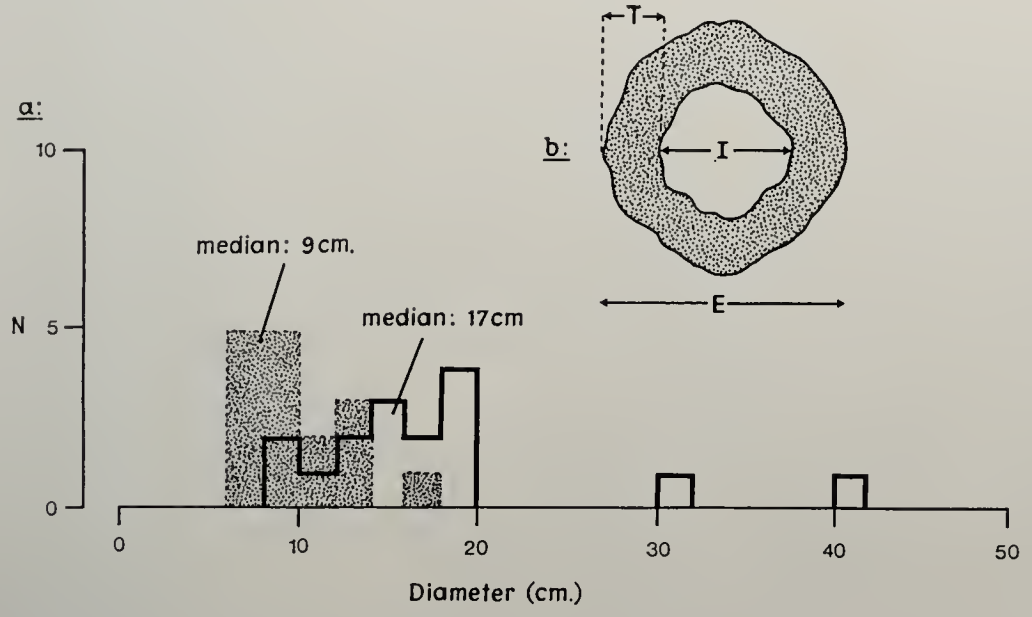


Fig. 11: Histogram of the internal and external diameters of hollow trees used as nests by Mouse Lemurs (N = 16; a), with a diagram of the dimensions taken of the nest cross-section (b):
I = internal diameter
E = external diameter
T = thickness of wood

ely massive (cavity diameter: 6—14 cm, median 9 cm; trunk diameter: 9—42 cm, median 17 cm). Taking individual values for I and E, the median thickness of the wood surrounding the hollow can be calculated ($T = 3.5$ cm). These values are important for 2 reasons: Firstly, they indicate that a forest must be of considerable age to support a population of Mouse Lemurs using tree-hollow nests. Secondly, it is likely that the average thickness of the wood is important with respect to thermal insulation of the adults and/or young when they are in the nest.

Another key parameter of the tree-hollow nest is the size of the entrance/exit hole(s), which is presumably related to predation. (Most nest-hollows had only one entrance; but some had 2 or pehaps more.) Fig. 12 shows that most nest openings are relatively small, vertical slits on the side of the trunk (group 1: average 7 cm × 3 cm), while some are fairly large horizontal or sub-

vertical main trunk orifices continuous with the nest hollow (group 2: average 15 cm × 11 cm). Many of the latter are actually man-made holes, and in many cases where there are 2 orifices, one is a small lateral hole, while the other is a horizontal main trunk opening caused by breakage of the trunk.

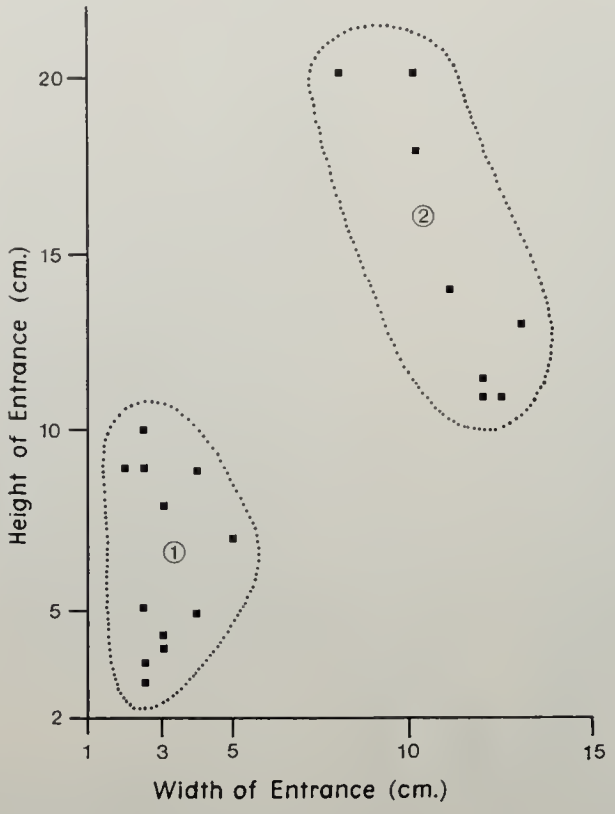


Fig. 12: Plot of entrance/exit size for tree-hollow nests (N = 16; 4 nests had 2 orifices).
1 = small, lateral orifices
2 = main trunk orifices

Predation is probably limited by the *depth* of the nest-hollow as well. This parameter proved to be very variable in the 16 nests examined (range: 11—450 cm), and there was no firm correlation between depth of the hollow and entrance-size. However, 75% of the hollows were more than 40 cm in depth (median depth: 75 cm), and the 3 deepest hollows (150 cm, 280 cm, 450 cm) were all associated with large openings. It is thus obvious that Mouse Lemurs, despite their small size, tend to use fairly large tree-hollows as nests, and this throws some doubt on Petter's statement (1962c: p. 16): 'Un trou d'arbre peu important suffit à sa petite taille et il lui et aisé d'en trouver'. Most of the small tree-hollows found proved to be empty, although they could have contained one or more Mouse Lemurs. This is an important point for any lemur conservation programme.

The depth of the tree-hollows used by Mouse Lemurs also reduces the possibility of competition with other vertebrates, since there is room for other occupants. In the Analabe study area (Fig. 3: 5), several of the Mouse Lemur tree-hollow nests were also occupied by a large arboreal lizard (body-length ca. 25 cm).

Tree-hollow nests are sometimes lined with leaves of various kinds, usually collected close by. (Up to 12 different leaf species may be used in a single nest.) Such linings can be extensive, as was the case with one tree-hollow nest found by PETTER (1962c) in the Ankarafantsika area (N. W. Madagascar). Since this nest was in a rotting trunk with a 10 cm opening, it is likely that the large nest (a loose ball of approx. 30 cm cross-section) compensated for the relatively poor cover. PETTER described the lining material as 'brins d'herbe'; but in all other recorded cases leaves from trees have been used as nest-material. One nest found in a bamboo hollow at Perinet (Fig. 3: 2) during this field-study contained 130 leaves stripped from the bamboo stand itself. In other cases ($N = 4$), an average of 120 leaves had been collected from neighbouring trees. Most tree-hollow nests were scarcely lined at all, however ($N = 11$). At the most, there was a small platform of leaves and debris in the hollow, with a few fresh leaves on top. This applied to *all* tree-hollow nests found in the Analabe study-area, where the available leaves were all extremely small.

One special kind of 'tree-hollow nest' is provided by the 'traveller's-tree' *(Ravenala madagascariensis)* in the East Coast rain-forest habitat of the Brown Mouse Lemur. In this relative of the banana tree, the leaves are arranged in a fan-like manner in a single plane; the bases of the leaves are semi-circular in cross-section, thus forming a linear series of inclined cavities up to 100 cm in length. These cavities can collect water in some cases, and they then contain what is essentially a micro-biotope of small forest organisms. Indeed, this capacity to contain water gave the tree its name, since early visitors to Madagascar were told that the cavities could be opened with a spear in order to obtain drinking-water. When the cavities are somewhat drier, they are frequently occupied by Brown Mouse Lemurs. This was reported by BLUNTSCHLI 1933 (p. 892 & Fig. 19), who found many such "nests" near Maroantsetra (extreme North East coast); and during the present study Brown Mouse Lemurs were found in traveller's-trees in the rain-forest near Fort Dauphin (see Fig. 14). Use of this special nesting facility may thus be typical over the whole range of the Brown Mouse Lemur, since this coincides with the distribution of the traveller's-tree. In fact, availability of such palms may be a factor influencing the distribution of the Brown form.

When nests are found *outside* a natural cavity, they are usually extremely well constructed ('spherical leaf-nests'). SHAW (1879) was one of the first to describe such structures, stating that they looked like birds' nests when viewed from below, and PETTER (1962c) reported that his guides often pointed out nests roughly 20 cm in diameter made of interwoven leaves, stating that they had been constructed by Mouse Lemurs.

Recently, STARMÜHLNER (1960) has questioned these observations, on the grounds that a few specimens never constructed such a nest in captivity, stating that HOFER assumes the Mouse Lemur to occupy empty bird's nests in the wild. STARMÜHLNER and HOFER seem to have misinterpreted SHAW's remarks, since the latter only wrote that the nests resembled those of birds *when viewed from below*. When viewed from the *side*, a Mouse Lemur nest is not easily confused with any known birds' nests. Apart from this, it is simple inadmissible to base assumptions on *negative* observations in captivity, as was pointed out some time ago by LORENZ (1970, p. 98—99). In fact, a female Grey Mouse Lemur kept in captivity in Mandena in 1968 *did* build the foundation of a leaf-nest when kept in a large cage with several small trees and plenty of leaf cover. Unfortunately, it has not yet been possible to observe

Mouse Lemurs building leaf-nests under natural conditions; but it can at least be assumed that they *do* collect nest-material, since Mouse Lemurs in captivity will collect leaves and other debris in nest-boxes, and since all of the Mouse Lemur nests found in the wild contained at least a few fresh, green leaves. It is difficult to understand why Starmühlner's captive Mouse Lemurs failed to line their nest-boxes, or to make use of such nest-boxes when already lined with material. Perhaps the ambient temperature was abnormally high (the cage was heated with an electric radiator).

All 7 leaf-nests discovered in this field-study were of the same general size (20—25 cm diam.); they were all wedged between branches and hidden from view by fairly dense foliage. An important structural detail is the fact that many of the leaves (approx. 30%) involved are gathered in groups of 2—6 attached to one stem. This stabilises the nest framework. Presumably, a nest-building Mouse Lemur bites through the leaf petioles, carries the leaves (singly or in attached groups) to the nest-site and then interlaces them with the natural, fine branch foundation. (Mouse Lemurs were on 3 occasions seen biting off leaves and carrying them away in this fashion; but no actual nest-building was seen.) The average size of the leaves used probably plays an important part as well. The largest leaves had an area of 100 cm^2, the smallest an area of 8 cm^2, while most leaves had an area of approximately 40 cm^2.

The spherical balls constructed with such leaves contained a central hollow of 8—10 cm diameter, approached by a lateral entrance 3—5 cm in diameter, and the average thickness of the leaf wall of the nest was thus 6 cm — larger than the median thickness of wood surrounding tree-hollows (3.5 cm).

In some cases, the natural vegetation is so dense in places that it is not really necessary for the Mouse Lemur to construct a special shelter. When discussing the dry, spiny forest zone of S. and S.-W. Madagascar (typified by the bizarre Didiereaceae and Euphorbiaceae), Jolly (1967, p. 12) wrote: 'The plants grow close together, their long spines and fleshy fingers interlaced. Each plant, however, has reduced its leaf area to a minimum, so there is no shade in the tangle of branches'. The latter is doubtless true for human observers and the larger lemurs (e. g. *Propithecus verreauxi; Lemur catta*), but it certainly does not apply to the Mouse Lemur. In a small, isolated patch of dry forest near Amboasary (close to 3, Fig. 3), a thriving population of Mouse Lemurs was found at night, and 3 nests were located during the daytime. One nest was a fully-fledged spherical leaf-nest wedged between the finger-like twigs of *Euphorbia leucadendron*, made with small leaves taken from *Rhus perrieri*. The two others were made by the naturally intertwining, fleshy leaves of *Euphorbia plagianthra*. In fact, this state of affairs was reported by Bluntschli 1933, who worked in the dry forest to the South of Amboasary, at a time when it was more extensive. At heights of 2—4 m, he found large, greyish-green tangles of vegetation formed by the leaf-less "twigs" of certain *Euphorbia* species and by lianes of various kinds. In a proportion of these bundles of vegetation, Mouse Lemurs were found by probing with sticks. Petter (1962c) also reports a "nest" of the Brown Mouse Lemur made of intertwined leaves and lianes, 4 m up in a bush near Maroantsetra; so it would seem that Lesser Mouse Lemurs in general make extensive use of natural vegetation cover for their nests.

A striking feature of Mouse Lemur nests of all kinds is their low position: most nests are found at heights between 2 and 4 m (Bluntschli 1933; Petter 1962c; this study). Shaw's statement that Mouse Lemurs live and nest "on the tops of the highest trees" is thus not generally accurate, though it is

possible that there *are* nests at such heights which are difficult to locate. The low siting of the nests found in this study means that there is at least partial exclusion of competition with *Cheirogaleus*, which tends to live and nest above the 4 m level.

Sporadic searches for Mouse Lemur nests do not permit reliable conclusions about long-term nest use. Some (but not all) of the leaf-nests were composed of old, dried leaves (SHAW 1879; personal observations), and in some of the tree-hollow nests there was a large accumulation of old, decaying leaves and other debris. Both facts indicate that some nests, at least, are occupied regularly over a considerable length of time; though this does not mean that the *same* individuals occupy the *same* nest night after night. In various study areas (Perinet, Mandena, Analabe: Fig. 3), unoccupied nests of both kinds were found, and it is possible that a given Mouse Lemur can occupy several nests within a particular area, especially if several available tree-hollows are present in the animal's area of activity. It is important to recognise that "abandoned nests" in such an area may well be alternative resting sites not actually in use at the time of finding.

In Analabe, Mouse Lemurs were seen on 2 separate occasions entering (and "investigating"?) tree-hollows which they did not use as retreats during the subsequent daytime rest period. However, the need to be acquainted with available vacant tree-hollows (etc.) in a given area of activity, and the expenditure of energy involved in constructing an adequate leaf-nest, probably requires that each Mouse Lemur should remain in a restricted, familiar "home-range", where several retreats are available as required. This is particularly the case with nursing females, which will apparently abandon a nest if it is disturbed, and transfer their offspring to a separate (predetermined?) nest.

Rudimentary "resting nests" (possibly representing decayed leaf-nests) were found on 2 occasions (Perinet; Mandena), when the "owners" (in each case a ♂) occupied them at about midnight. On another occasion (Analabe), a ♀ Grey Mouse Lemur retreated temporarily into a hollow tree during the night, but did not use that hollow as a nest the following day. Some Mouse Lemurs in captivity will often use a distinct nest-box for resting during the nocturnal activity phase, and this further indicates use of a range of available retreats in the wild.

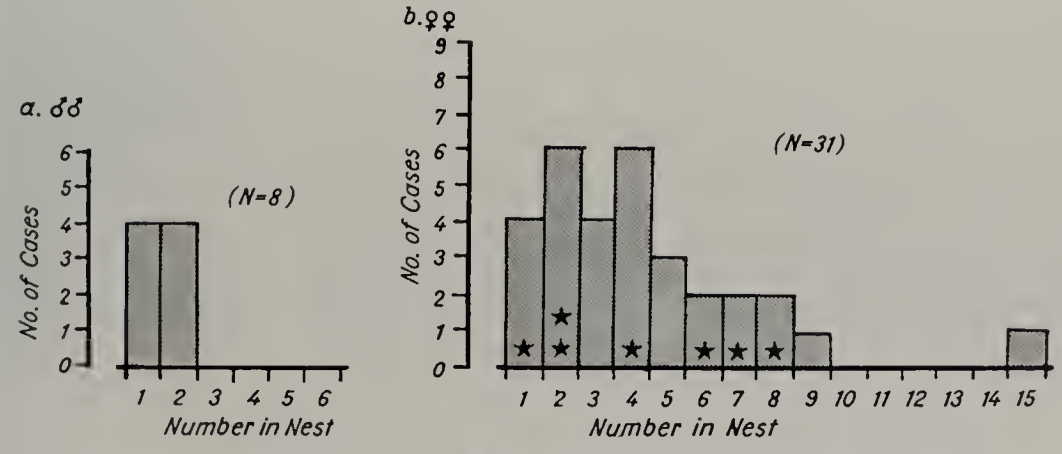


Fig. 13: Histograms showing number of Mouse Lemurs (mainly Grey type from Mandena and Analabe) found in 39 separate nests where the sexes were segregated
a = nests containing ♂♂ only; *b* = nests containing ♀♀ only (stars indicate single cases where babies were found with mothers, showing that the groups probably do not break up for birth)

2. Nesting Groups

There are 2 striking features about the occupancy of Mouse Lemur nests found during this field-study:

1. The sexes are generally segregated; it was very rare to find a ♂ together with ♀♀.
2. The ♀♀ tend to nest in large groups, particularly in tree-hollows. On occasion, 15 ♀♀ were found together in one tree-nest, while the average and median numbers of ♀♀ per nest were 4 · 3 and 4 (Fig. 13b; $N = 31$). This grouping in nests was also found, on a lesser scale, in leaf-nests and simple foliage cover.

♂♂, on the other hand, generally nest singly or in pairs (Fig. 13a; $N = 8$); no larger aggregations were found. Only on 3 occasions was a ♂ found with a group of ♀♀ (1+5; 1+7; 1+3).

Large aggregations of Mouse Lemurs in tree-hollow nests have been reported by other authors, notably by PETTER (1962c), who cited 2 cases:

(i) $N = 8$: 4 dependent young, 1 lactating ♀, 1 non-lactating adult ♀, 1 ♂, 1 unidentified (escaped).

(ii) $N = 7$: 3 almost independent young, 2 adult ♀♀, 1 ♂ and 1 unidentified (escaped).

PETTER suggested that these groups represented "families", where the young had not yet left the parents. However, he later stated (1965): "... in *Microcebus murinus* we have observed sleeping groups that we are still unable to interpret, and it is possible that a slight amount of gregariousness is present in this animal at least under certain circumstances." In both cases quoted by PETTER, a single ♂ was present; but it is notable that there were more ♀♀ than ♂♂ in each nest. Further, PETTER's observations were conducted in March (Banian; Mangoky River), and at that time the ♂♂ found in the two nests could have been fully-grown adolescents from the first litter in December (see p. 78 etc.).

Obviously, this pattern of nest-occupancy must be related to the system of social interactions; though, as PETTER has pointed out, such sleeping groups tend to disperse for feeding during the night. The fairly large ♀ groups probably represent loose social groupings, and there is some evidence that the ♂♂ found together in nests are also linked together in some way. On 2 separate occasions, social grooming was seen between two ♀♀, in each case close to a communal nest which was found and examined the next day. Social grooming was also seen between 2 ♂♂ which habitually moved around together in the Mandena study area (Fig. 16a; top right-hand corner). In all of these cases, 'social grooming' consisted of one participant grooming the head and neck area of the other, using the tooth-scraper with rapid, jerky movements. During such grooming bouts, the head fur (or ears) of the recipient were grasped by the hands of the groomer. It is interesting to note that social grooming of this kind was always observed when the 2 participants were alarmed when approached by the observer (with headlamp), and the immediate effect of the grooming seemed to be one of "reassurance", since both animals at once stopped retreating and temporarily ignored the observer.

Once again, nothing can be said about the *stability* of such nesting groups, since the nests were examined only at one point in time. However, it seems likely that the groups *are* relatively stable, though ♀♀ may possibly combine in varying sub-groups in areas where several suitable nest-sites are available. Evidence for the stability of ♀ groups is provided by the fact that such groups

are still found when young are present (Fig. 13b — stars; see also p. 79). The ♀♀ do not seem to separate prior to birth; mothers and babies are found mingled together in nests examined during the breeding season. This must indicate either that ♀ Mouse Lemurs are remarkably lacking in animosity towards one another (and each other's babies) — a fact which is indirectly refuted on p. 73 — or that members of each nest are personally acquainted with one another on the basis of some stable population distribution pattern.

3. Population Distribution Patterns

The first noticeable feature about the localised *distribution* of Mouse Lemurs is the apparent existence of discrete *population nuclei* of the kind described by PETTER (1962c; p. 80) for *Lepilemur mustelinus* ('noyaux' de peuplement). In an apparently homogeneous belt of forest, one can find localised concentrations of Mouse Lemurs, with sizeable gaps between them. The population nuclei found during the present study were stable throughout the observation periods, and they probably represent genuine established pop-



Fig. 14: Plan of Fort Dauphin area (S.E. Madagascar) adapted from Flle. 62, Service Géographique de Madagascar and aerial photographs provided by the Institut National Géographique de Madagascar (Area shown = 20 km × 20 km)

F.D. = Fort Dauphin
A.M. = Aerodrome de Marrilac
B = Bezavona
A = Ampasy
M = Mandena
P.L. = Pic St. Louis
L.A. = Lac Ambavarano
M.A. = Lac Mananivo
L = Lac Lanirano
P.E. = Pointe Evatra

Dense stippling = littoral forest (habitat of Grey Mouse Lemur); spaced stippling = rain-forest on slopes of Anosy Mountain Chain (habitat of Brown Mouse Lemur)
⩲ = marshy areas; ▲ = hilly areas

ulations. This situation was found in Mandena, Amboasary and Analabe (Fig. 3; 3, 4 and 5), and it is probably typical throughout the range of the Lesser Mouse Lemur, since there was some evidence of the same kind of spatial distribution in Perinet and Ambohimanga-du-Sud (Fig. 3: 2, A). It is possible that such localised nuclei are determined by concentrations of food-availability, nesting sites, etc.; but no such correlation was indicated by a cursory investigation.

Having localised a population nucleus of this type, a study area was marked out in every region visited. In what follows, the study area of Mandena (Fig. 3: 4) will be used as the main example — since this area was most intensively studied — but the same general situation was found in Ampijoroa, Perinet, Amboasary and Analabe.

Fig. 14 provides a general view of the Fort Dauphin area, showing the humid East coast rain-forest zone on the flanks of the Anosy mountain chain, and the dryer, littoral forest zone on the flat coastal area. (The R. N. 7 — the main coastal road passing northwards — provides an easily recognisable dividing line between these 2 forest types.) Surprisingly, although the Brown Mouse Lemur is found in the hilly rain-forest zone (as expected), the *littoral forest* is occupied by the Grey Mouse Lemur. Although rainfall in the 2 zones differs only slightly, the water run-off is probably much more rapid in the littoral forest (sandy soil). This is borne out by the fact that the traveller's-tree *(Ravenala madagascariensis)* — which is typical of the rain-forest — is only found bordering water-courses in the littoral forest. Elsewhere, the humidity usually falls fairly rapidly following each burst of rainfall. This may explain why the Brown Mouse Lemur does not occur there. (N. B. The same distribution is found with *Cheirogaleus; C. major* occupies the rain-forest zone and *C. medius* occupies the littoral forest zone.)

The Mandena study area (Fig. 14: M) was located in the forestry reserve of that name, since the area was protected to some extent against poaching and wood-felling. The actual study area (Fig. 15) lies on the fringe of a block of endemic littoral forest reconstituted over the last 25 years under the direction of the Eaux et Forêts administration. It therefore contained a large number of fairly young trees with thin, almost vertical trunks, and there was dense foliage cover from 1 m up to the canopy (10—20 m up). Grey Mouse Lemurs are common in the endemic forest, particularly in the smaller segments and in vegetation bordering paths and roads. The study area (MS) covered about $1^1/_2$ hectares in a small 12 hectare block of forest isolated to some extent by the Iarindrano River and plantations of introduced trees (*Eucalyptus*; Indo-Chinese pines). Even within this small area, the Mouse Lemur population was concentrated around the study area itself; there seemed to be a definite nucleus (noyau), with few animals occurring to the North.

The outline of the study area was defined by existing paths (2—4 m wide), and a number of narrower, overgrown paths passed through the centre of the area. A brief visit to the area was made in mid-September 1968, followed by intensive study from mid-October to mid-November.

On the basis of repeated nocturnal excursions through the study area, using a headlamp to locate and observe Mouse Lemurs, a "scatter diagram" of sightings throughout the study period was compiled. In many cases (approx. 70%), it was possible to identify the *sex* of the animals, and this was also shown in the scatter diagram (Fig. 16a). On the basis of a preliminary diagram produced half-way through the study, searches were made for nests during the daytime, and a leaf-nest containing 4 adult ♀♀ (2 pregnant; 2 in oestrus) was found in this way. (Fig. 16a: top right-hand corner.) Some of the Mouse Lemurs were marked, and subsequent sightings gave some idea of their ranges of activity (shown by lines linking points in Fig. 16a). In no case was a marked individual seen farther than 50 m away from the original point of sighting. For example, the ♀ shown in the top left-hand corner of Fig. 16a had a defective tapetum in one eye, so that reflection was obtained only from

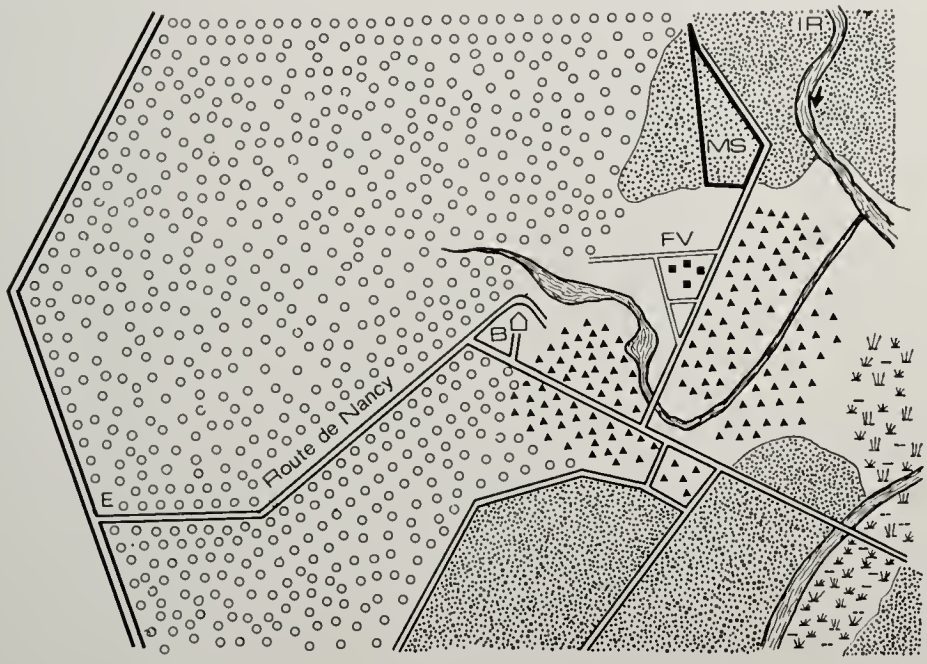


Fig. 15: Detailed map of vegetation around Mandena Study Area (MS). IR = Iarindrano River; FV = Forestry Village; B = house used as base; E = entrance to Mandena Forestry Reserve; open circles = *Eucalyptus* plantation; black triangles = introduced pine plantation; fine stippling = reconstituted endemic forest. Total forest area surrounding study area on left of river = 12 hectares; forest to right of river = part of block of 80 hectares; forest at bottom right = part of block of 250 hectares enclosing the "Jardin Botanique"

the intact eye, thus providing a sure means of identification. Other Mouse Lemurs were trapped and marked by clipping the tail fur (♂♂: middle of tail; ♀♀: tip of tail; see Fig. 4). By the end of the study, 9 animals (3 ♂♂; 6 ♀♀) were marked in some way. Using this figure, a very rough calculation of the likely number of animals in the study area was made during the last 2 weeks of the study: the ratio of unmarked to marked animals sighted was multiplied by 9 — viz. $44/14 \times 9 = 28$. Since this calculation can only be very approximate, all that can be concluded is that the Mouse Lemur population in the study area was probably between 20 and 40. Using this estimate, some idea of the Mouse Lemur's habits can be obtained by taking the following factors into consideration:

1. ♂♂ and ♀♀ tend to nest separately; ♂♂ singly or in pairs, and ♀♀ in groups of average size 4.
2. Within a population nucleus, ♀♀ heavily outweigh ♂♂ in number. (Of 120 Mouse Lemurs found in nests in the Mandena area, only 7 were males!) This fact was also noted by Bluntschli (1933; p. 30) in his study of Mouse Lemurs in the Amboasary area. The actual ratio of observed ♂♂ to observed ♀♀ in Fig. 16a is actually about 1 : 2; but the proportion of ♀♀ is probably higher than this, since many of the animals of unidentified sex were seen close to other ♀♀, and moved off before they could be identified. On the other hand, the proportion of ♀♀ indicated by actual nest discoveries is probably *too high*, since there was some indication that ♂♂ use rather more rudimentary nests which are less likely to be discovered when one is searching for well-defined tree-hollows. In the Analabe study area, where the nest search was more thorough, the ratio of ♂♂ to ♀♀ found was 1 : 4 (viz. 7 : 26),

and this correlated with a ratio of 1 ♂ for every 3 ♀♀ observed at night. Overall, a ratio of 1 ♂ to 4 ♀♀ would seem to be a good average for population nuclei of the Grey Mouse Lemur.

3. Where single, recognisable Mouse Lemurs were found in roadside or low-grade forest vegetation on a number of nights, their areas of activity were

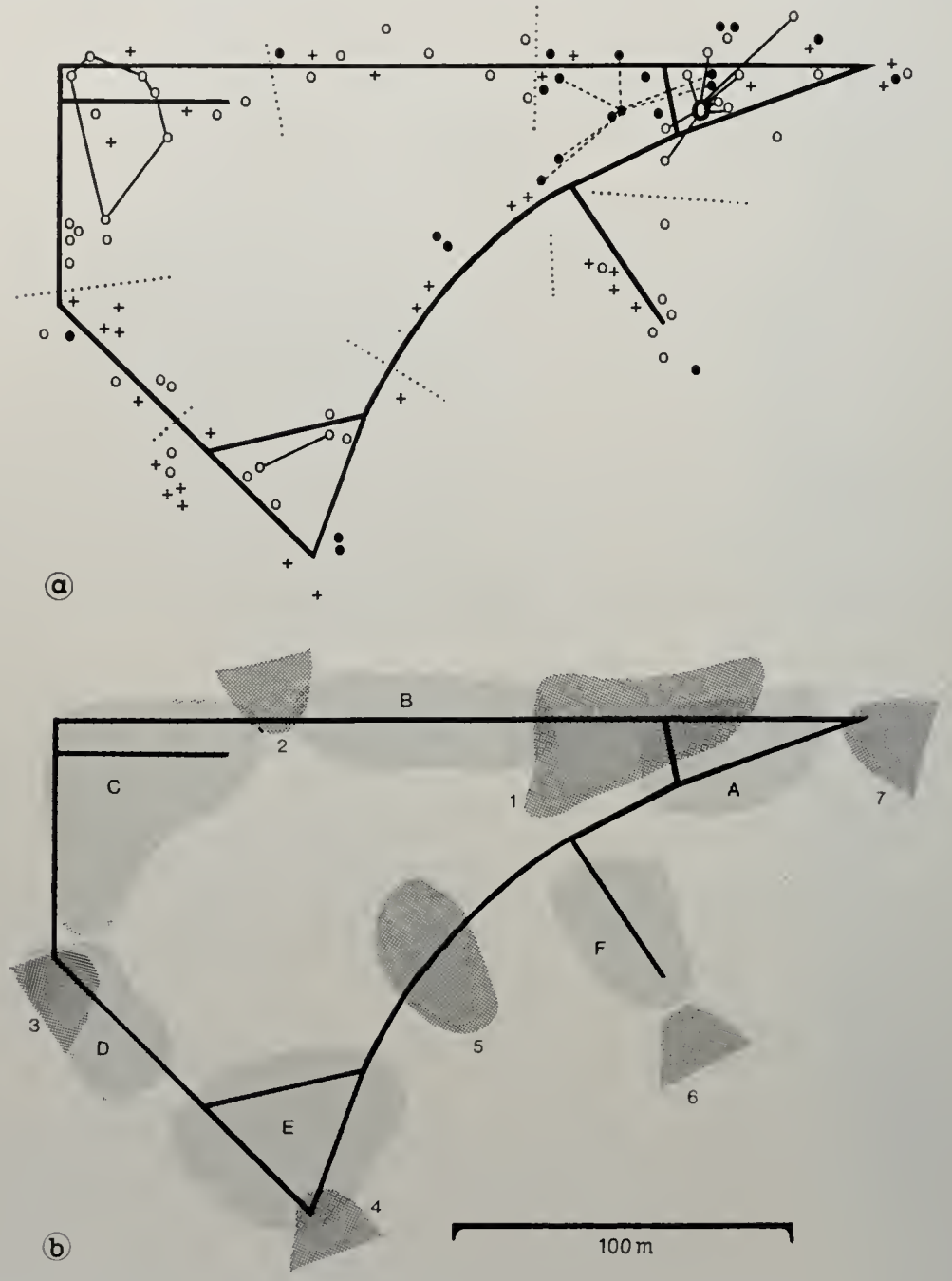


Fig. 16: Detailed maps of Mandena study area (approx. surface area: 1.5 hectares). *a:* "scatter diagram" of points indicating Grey Mouse Lemurs observed at night; open circles = ♀♀; black circles = ♂♂; crosses = sex unidentified; heavy circle = nest. Lines linking observation points show subsequent appearances of marked animals. Weak dotted lines indicate possible borders between neighbouring areas of activity. — *b*: Interpretation of *a* in terms of partial areas of activity of ♀ groups (fine stippling; A—F) of average size 4 and resident ♂♂ (heavy stippling; 1, 2, 3 & 5). Area 1 possible represents the joint range of 2 ♂♂, overlapping with ♀ groups A & B. The ♂♂ represented by areas 4, 6, and 7 were only seen once or twice, and may have been "peripheral"

generally confined within a diameter of 50 m (15 cases). This agrees with the range indicated by marked animals within the Mandena Study area and suggests that "home ranges" are probably small.

4. Within the study area, the fact that about 30% of the population was marked by the end of the study permitted some conclusions about the ranges of *non-marked* animals.

All of these criteria together suggest that the Mandena study area probably supported a population of something like 24 resident ♀♀ and about 6 resident ♂♂. If these animals had fairly restricted, stable home ranges (as the movements of marked animals in Fig. 16a indicate), then the diagram in Fig. 16b may be taken as representing partial *areas of activity* of the resident Mouse Lemurs (6 ♀ groups, A—F; 5—6 resident ♂♂ in areas 1, 2, 3 and 5). These areas do not necessarily represent exclusive home ranges, still less defended territories. However, one piece of circumstantial evidence does indicate that migration into the population nucleus is not usual. 15 ♀ Mouse Lemurs with distinctive tail-marks (double clipping) captured from an area of forest several kilometers away were released near points D and 3 (Fig. 16b) half-way through the study. None of these ♀♀ was re-sighted within the study area. However, 3 were later found in peripheral vegetation lining the plantations (between FV and B, Fig. 15), despite the fact that there was apparently plenty to eat in the study area. (Numerous *Vaccinium emirnense* shrubs were at that time in full fruit.) One such ♀ was captured, and was found to have lost at least 12 gm in weight, at a time when other Mouse Lemurs were increasing in body-weight. The remaining 12 ♀♀ were never sighted again; they had presumably disappeared to the North of the study area.

This picture of a local population aggregation with a low ♂: ♀ ratio fits most of the observed facts, but it does not accord with the 1 : 1 sex ratio found among neonates (p. 80). It is possible that this is to be explained by much higher ♂ mortality; but a more likely explanation is that many ♂♂ are

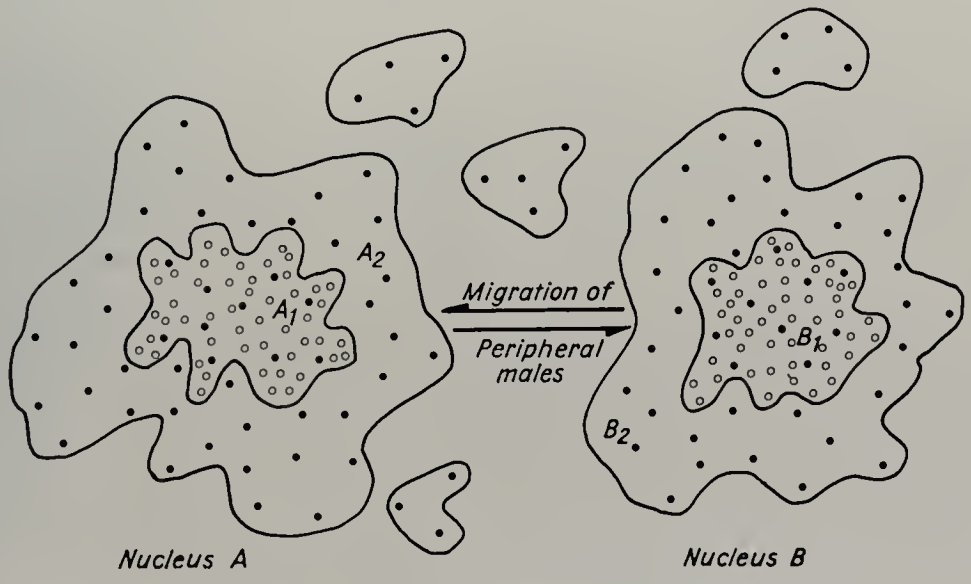


Fig. 17: Hypothetical diagram showing the possible relationship between neighbouring "population nuclei" (A & B). Open circles = ♀♀; black circles = ♂♂. The cores of the 2 nuclei (A_1; B_1) contain ♀ groups, with a ratio of approximately 4 ♀♀ for every "central ♂". The fringes of the nuclei (A_2; B_2) contain "peripheral ♂♂" without breeding access, which can migrate between population nuclei (ensuring exogamy and sexual selection)

peripheral to the main aggregations. Most of the somewhat isolated Mouse Lemurs found at roadsides and on the very fringes of forest areas are *males*, and this indicates that they are in some way excluded from the main population nuclei. (For example, 6 out of 7 Brown Mouse Lemurs trapped at the roadside in Perinet were ♂♂, and 4 separate Grey ♂♂ were found isolated in roadside vegetation near the Mandena study area.)

If this interpretation is correct, one can think in terms of *central males* coexisting with ♀ groups in local population nuclei, with *peripheral males* living on the fringes of, and between, such nuclei. (Fig. 5 provides some evidence that such peripheral ♂♂ are lighter in body-weight than central ♀♀.) Such an arrangement would have a number of advantages, since the peripheral ♂♂ would be able to migrate between localised populations and take up residence elsewhere (exogamy). The exclusive possession of central home ranges, and thus access to ♀♀ in the reproductive season, apparently exhibited by a small proportion of the adult ♂♂ would ensure a certain amount of sexual selection and exclude juveniles and the weaker adults from breeding (see Fig. 17).

Vocalisations

Mouse Lemurs are extremely vocal, but (as Petter 1962c has pointed out) their vocalisations tend to be very high-pitched, probably falling largely in the ultrasonic range. They are therefore difficult to perceive under natural conditions, particularly for people (such as the author) whose hearing is not good in the ultrasonic range. However, since the vocalisations can throw some light on possible interactions between Mouse Lemurs, it is worth providing a provisional list. This list is actually rather striking, in that there are close similarities to the vocalisations of *Galago demidovii;* the basic categories seem to be identical in the 2 prosimians. (See Charles-Dominique and Martin 1970 for a discussion of the importance of this fact.)

The following brief survey of Mouse Lemur vocalisations is essentially based on Petter (1962c), with some additional information gleaned from the present field-study:

1. Explosive snort. This is the most noticeable vocalisation, heard when adult Mouse Lemurs are disturbed in a nest, or when one animal responds aggressively to another (e. g. in disputes over food in captivity). Petter has described this as a "grognement" ("gri gri gri, etc."), while Starmühlner has referred to it as a "ket ket ket" sound. The vocalisation is given with the mouth open and the teeth exposed, and can be generally interpreted as a *threat* call. Many small hole-nesting birds and mammals have a similar call. (Petter: call no. 5.)

2. High-pitched squeals. During fights in captivity, drawn-out squeals can be heard, especially if one animal is chased by another. This call has also been heard from a ♀ which was being chased by a ♂ at the beginning of the mating season (p. 76).

3. Crescendo call. Successive series of 3 or more short, high-pitched notes, each series forming a melodious crescendo. (Petter: call no. 3.) Uttered by a hand-reared ♂ at dusk and dawn. Petter states that this call is uttered at moments of great excitement and when a mother calls to her young. The indications are that this represents some kind of "social contact call".

4. High-pitched squeaks. Series of brief, sharp calls which are clearly audible to people with high-frequency hearing. (Petter: call no. 1.) These calls, which are slightly longer than other single-note vocalisations, are heard principally

in the evening in captivity, with sporadic appearance throughout the night. During nocturnal observation of Mouse Lemurs under natural conditions, this is the call most frequently heard. Its sporadic occurrence throughout the night suggests that this call may have some spacing function, particularly since it is the only call regularly heard when the animals are dispersed for feeding.

5. Rhythmic squeaking. Described by PETTER as a high-pitched "fit-si" sound, this rhythmic vocalisation is only heard when a ♂ is chasing a ♀ in oestrus, and is presumably sexually excited. (PETTER: call no. 4.) The vocalisation seems to be uttered by the ♂, as was stated by PETTER.

6. "Purring". Hand-reared Mouse Lemurs were heard to utter a series of clicks when settled down after feeding. This call was also described by PETTER: "Les petits émettent aussi une sorte de faible ronronnement quand ils sont au chaud avec leur mère ou, pour des petits très aprivoisés, quand ils sont couchés dans le creux de la main". The vocalisation appeared in situations analogous to those which evoke purring in a cat (e. g. when the head is repeatedly stroked), and PETTER's term is entirely appropriate. In fact, this "purring" seems to persist in hand-reared Mouse Lemurs at least to the age of 6 months, and it is quite possible that it represents some kind of social signal in sleeping groups. This, combined with social grooming, would speak for stable bonding within ♀ groups and paired ♂♂.

7. Distress Calls. Nest young of the Mouse Lemur utter two types of distress call, which may represent no more than extremes on a scale. The first is a plaintive, high-pitched squeak, which is uttered in a slow series when the nestling is cold and/or hungry. The second is a piercing, high-pitched vocalisation (PETTER: call no. 6) given when an infant is frantically trying to escape. PETTER represented this call as "criiiiiiii", and it is best described as a *screech.* PETTER-ROUSSEAUX (1964) has pointed out that adult ♀♀ are very responsive to this call, stating that the mother will utter a weak reply call (probably the *crescendo call*, above). In Mandena, all of the captive ♀♀ rushed to the front walls of their cages when a screeching infant was held nearby. Distress-calling of the infant and reply-calling of the mother probably represent an integrated system ensuring that the mother feeds, warms and defends her infant(s) as required.

In sum, a number of these calls indicate some basis for social interaction between Mouse Lemurs (particularly ♀♀), and there is a suggestion that special vocalisations are used for spacing during the nocturnal activity period.

Reproduction

1. General Reproductive Activity

In common with all other Madagascar lemurs, the Lesser Mouse Lemur exhibits a well-defined, exclusive breeding season, as was demonstrated by PETTER-ROUSSEAUX 1962 (p. 51 et seq.). This season roughly coincides with the rainy season, beginning somewhat beforehand and tailing off as the rainy season ends (see chart on p. 72, PETTER-ROUSSEAUX 1962). It was thus possible, at the end of the present field-study, to follow the first half of the reproductive season of the Grey Mouse Lemur in Mandena (September—December), and to collect a few supporting observations from Analabe (beginning of December).

During the main part of the dry season (approx. May—August), the testes of the ♂ are reduced in size and retracted to the orifices of the inguinal canals on each side. (The testes are scrotal throughout life.) Thus, Grey ♂♂

studied in Ampijoroa (July) and Brown ♂♂ examined in Perinet (August) had very small testes. At some time in August, or perhaps earlier, the testes begin to increase in size, so that they are large and functional some time in September. At their peak size, the testes are approximately 8 times larger than during the middle part of the dry season[7]). Accordingly, Grey ♂♂ trapped in the Berenty area and in Mandena (mid-September onwards) and Brown ♂♂ trapped in Ambohimanga-du-Sud, Ifanadiana and the Mandena area (mid-October onwards) all had greatly enlarged testes. The decline in testis-size probably begins some time in April or May (i. e. some time after the end of this field-study).

In the ♀ Mouse Lemur (both Grey and Brown forms), the vulva is sealed off with a membrane, which is only temporarily ruptured at birth and during oestrus. During the dry season, the vulva remains sealed, and this condition was found with all ♀ Mouse Lemurs (both types) examined prior to mid-September. The oestrus condition was only observed from mid-September onwards. When the ♀ comes into oestrus, the skin surrounding the vulva reddens, dilates and eventually ruptures to present an expanded, wrinkled "oestrous swelling" surrounding the opening. At this time the ♀ apparently produces some kind of olfactory signal, which is noticeable to the human observer as a pronounced musky odour. PETTER-ROUSSEAUX (1962) describes ♂♂ in captivity nosing the ano-genital area of ♀♀ in oestrus, prior to copulation. Under natural conditions, a signal of this kind could advertise to a nearby ♂ that a ♀ is in oestrus. The ♂ must mate with the ♀ within a period of about 10 days, since the swelling rapidly collapses, and the vulva is soon re-sealed.

PETTER-ROUSSEAUX has shown with captive specimens that many ♀♀ come into oestrus twice in each season, and that some may exhibit 3 oestrous cycles. The duration of the cycle is generally between 45 and 55 days, though some ♀♀ exhibit intervals larger or smaller than this (range: 36—78 days). This means that ♀♀ in captivity may be receptive 2 or 3 times over a period of 2—6 months, and the same may apply to ♀ Mouse Lemurs under natural conditions.

2. Synchronisation of Breeding

In Mandena, a chance decision to collect Mouse Lemurs in the littoral forest in mid-September provided detailed evidence for the onset of the breeding season in that area. Normally, the appearance of oestrus might have gone unnoticed. Of 31 ♀♀ trapped in the Mandena area on the 11th and 12th of September, 50% (15) had large vulval openings, while a further 20% (3+3) showed either pro-oestrous swellings or signs of post-oestrous collapse in the vulval area. This means that at least 70% of the ♀♀ captured had (or would have) entered oestrus within a 2-week period. At the same time, several kilometres away (9th September), a ♂ Grey Mouse Lemur had been observed chasing a ♀ and uttering the rhythmic "mating call" (p. 75). Although actual mating was not observed, it can be assumed that the ♀ was in (or near) oestrus. It therefore seems that, in 1968, the breeding season in the general Mandena area started at some time in the first half of September, and that there was extensive synchronisation of the first appearances of oestrus in the ♀♀ of that area.

These observations accord well with those made by BLUNTSCHLI in 1931. In the Amboasary area (70 km to the West of Mandena, in the dry forest

[7]) For details see: SPÜHLER, O. (1935): Genitalzyklus und Spermiogenese des Mausmaki, *Microcebus murinus*. Z. Zellforsch. **23**, 442—463.

zone), he discovered that most of the female Grey Mouse Lemurs captured in late November were in early or mid-pregnancy — indicating both genera-synchronisation of pregnancy *and* an onset of breeding activity in about midi October. (See BLUNTSCHLI 1933, and HINTZSCHE 1940 for dates.) BLUNTSCHLI apparently did not find many *early* stages of pregnancy during his stay in Amboasary, and this indicates that mating was rare after the initial spate of breeding activity.

The gestation period of the Mouse Lemur has been demonstrated by PETTER-ROUSSEAUX (1962) to be 59—62 days in captivity. Thus, births should be expected approximately 2 months after matings in the wild. Consequently, a second trapping session was conducted in the Mandena area in mid-October (20. 10. 1968), approximately 1 month after the observed onset of mating, and a search was made for nests with babies as from the beginning of November. All expectations were fulfilled, in that over 75% of the ♀♀ found in mid-October (35 out of 46) were judged to be in mid-pregnancy. (Estimation of pregnancy was based on palpation, and the reliability of diagnosis was confirmed by examination of the uteri of 6 ♀♀ selected at random from those judged to be gestating. In addition, several of the pregnant ♀♀ were kept in captivity, and all subsequently gave birth.) ♀♀ with babies were found regularly in the field from 12th November onwards, and the approximate dates of birth were estimated from the developmental state of the offspring.

Altogether, the following findings provided a large number of estimated and observed dates of birth (Fig. 18):

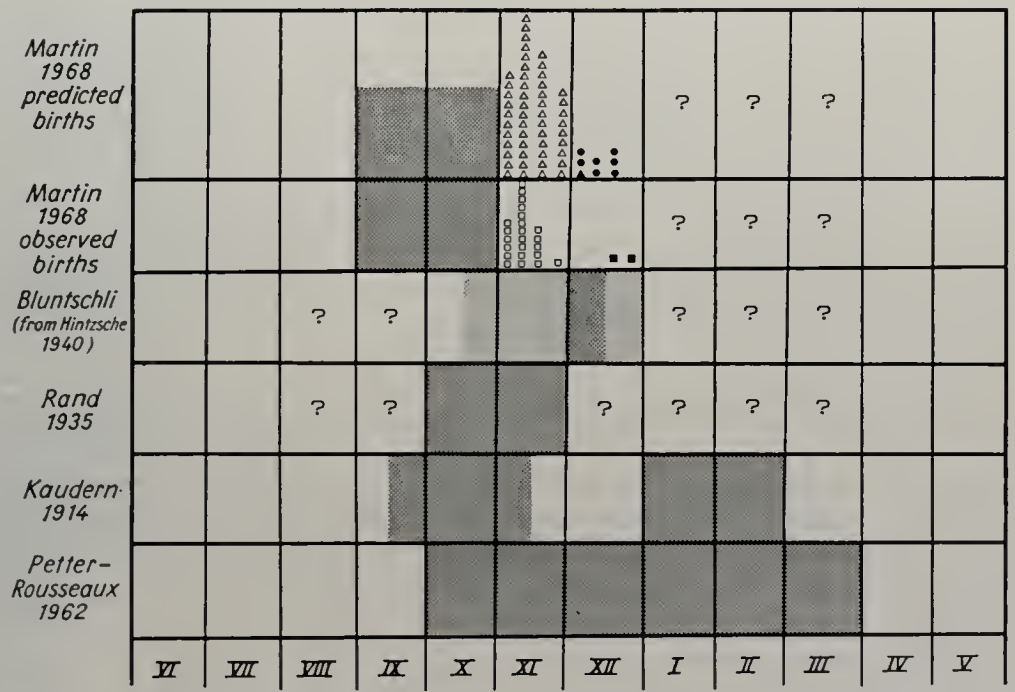


Fig. 18: Diagram showing occurrence of breeding activity in the Lesser Mouse Lemur over the year. Heavy stippling = gestation (observed or suggested); light stippling = theoretical extension of BLUNTSCHLI's brief observations. (N.B.: KAUDERN's schema is also largely theoretical) Open squares = dates of 23 births established from Grey Mouse Lemur offspring born in Mandena; open triangles = dates of 51 births predicted for oestrous and pregnant Grey Mouse Lemurs in Mandena; black triangle = latest possible date of birth for Brown Mouse Lemur offspring found near Besavona; black squares = dates of 2 births observed for Grey Mouse Lemurs taken from Analabe; black circles = dates of 7 births predicted for Grey Mouse Lemurs in Analabe; question-marks = essential periods not covered by observation

(i) projected dates of birth for ♀♀ found at various stages of oestrous activity (estimated date of copulation + 2 months),
(ii) projected dates of birth for ♀♀ palpated during pregnancy,
(iii) actual dates of birth of young born in captivity in Mandena,
(iv) estimated dates of birth for offspring found in nests with their mothers in the wild.

Fig. 18 shows that all of the estimated and observed dates from the Mandena area fall within the month of November, and that the first matings probably occurred in the first week of September, with a peak of matings in the second week of September and a peak of births in the second week of November. Petter-Rousseaux (1962; p. 55) states that the duration of lactation is about 40 days, so all of the offspring represented in Fig. 18 should have been weaned by the first week of January.

It is interesting to note that an early stage of pregnancy found in a ♀ Brown Mouse Lemur on 9th October in Ambohimanga-du-Sud, and a ♀ Brown Mouse Lemur found with young in the rain-forest near Mandena (Besavona: Fig. 14 — B) both fitted the general range of dates determined for the Grey Mouse Lemur from the littoral forest of Mandena. The Grey ♀♀ examined in Analabe (W. Coast, Fig. 3: 5), on the other hand indicated a much *later* onset of breeding activity in that area (Fig. 18). Although the data from Analabe are fragmentary, there is some evidence that the ♀ Grey Mouse Lemurs from that area were synchronised, and that the synchronisation peak was 4—5 weeks later than in the general region around Mandena. In fact, the data from Mandena agree with those indicated by Kaudern 1914 for the East Coast rain-forest area (near Tamatave and Perinet), while the data from Analabe agree with those of Bluntschli 1933 for Amboasary and those of Rand 1935, who reported that *all* of the ♀ Grey Mouse Lemurs caught near Tabiky (N. W. of Ankazoabo on the West Coast) were pregnant in October and November. It is thus possible that the first births in the dryer forest areas of the South, South-West and West are about a month later than in the East-Coast rain-forest and the South-Eastern littoral forest. This difference, if it is a real one, could be explained by the abrupt, and generally later, onset of the rains in the dryer forest areas. It remains to be seen whether this difference will be substantiated by more detailed study.

3. Total Rearing Capacity

Since the field-study was completed towards the end of December, 1968, little can be said about the period from January to April, for which both Petter and Kaudern have provided evidence of breeding under natural conditions. Kaudern in fact suggested for the rain-forest Mouse Lemurs that the ♀♀ may have 2 litters per breeding season, and outlined a hypothetical 2-phase system (Fig. 18) which would account for approximately the following succession:

(i) first pregnancy (60 days),
(ii) rearing of first litter (45 days),
(iii) second pregnancy (60 days),
(iv) rearing of second litter (45 days).

This would give a total reproductive phase of about 7 months, which would fit the overall reproductive activity period suggested by Petter-Rousseaux (Fig. 18). Indeed, all known dates of birth seem to fit a distribution of this kind. However, this does not necessarily mean that some ♀♀ may have 2 litters during the breeding season, if the second batch of pregnancies is

confined to a few ♀♀. If, on the other hand, a considerable number of ♀♀ produce young during the second pregnancy phase, some females *must* have 2 pregnancies, since 75% of the females were found to be pregnant in the first phase in Mandena, and RAND found 100% of pregnant females during the first phase in Tabiky.

In order to obtain some information about the second part of the breeding season, despite the cessation of the present field-study in December 1968, an arrangement was made with Miss P. CORNFORTH (at that time teaching in Fort Dauphin) to employ local villagers to find Mouse Lemur nests at some time during the early part of 1969 (i. e. towards the end of the rainy season). 3 nests were found on 25th March 1969, containing 11, 4 and 15 individuals, respectively (sexes unidentified). The weights of these individuals have been pooled in Fig. 19, which shows wide variation in body-weight among the nest occupants. Taking the system suggested by KAUDERN (Fig. 18), and the dates suggested by the first phase of breeding in the Mandena area, one would have expected at the end of March the following 3 classes in weight:

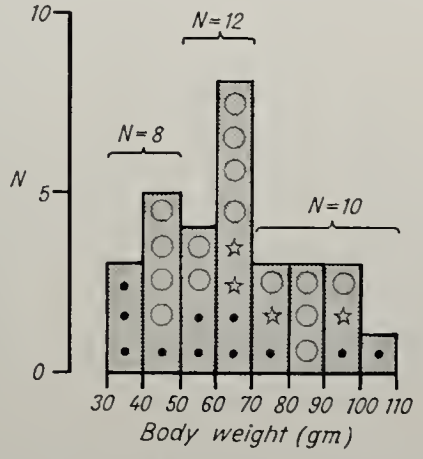


Fig. 19: Histogram of weights of 30 Grey Mouse Lemurs (sexes unidentified) taken from 3 nests in the Mandena area on 25. 3. 69. The 3 brackets indicate possible presence of adults from the previous year, together with offspring from 2 successive litters (see text). Symbols indicate occupancy of the three separate nests

1. Adults from previous years, gaining weight during the last weeks of the rainy season and weighing 70 gm and above.
2. Almost fully-grown offspring from the first batch of litters, aged about 4 months and weighing 50 gm and above.
3. Offspring from the second batch of litters, born towards the end of February, weighing about 30 gm.

It can be seen that the weights represented in Fig. 19 cover all 3 classes, though there were apparently no young below 1 month in age, so the second batch of litters (if it was present) would have appeared in *early* February, and not late February as KAUDERN's diagram indicates.

Laboratory experience shows that Grey Mouse Lemurs from Mandena will increase in weight tremendously (up to 140 gm) when given copious food, particularly towards the end of the equivalent of the Madagascar wet season, and it is therefore reasonable to assume that only the weights between 70 and 110 gm in Fig. 19 represent adults from the previous year. Even if all of these were ♀♀, the ratio of adults to growing young would be 1 : 2 (10 : 20).

Since the average litter size is 2 (see below), this would imply that there is *no* infant mortality if each ♀ gives birth only once during the rainy season. Any appreciable infant mortality would require that at least some ♀♀ can produce 2 litters during the breeding season, and since the first batch of pregnancies is synchronised, there is likely to be some (though perhaps less marked) synchrony of the second batch. Kaudern's diagram may therefore apply approximately to the Mandena situation, with the proviso that the second batch of births occurs in *early* February. This hypothesis is supported by the fact that 75% of the ♀♀ found in October were pregnant. The later births cannot be adequately explained as products of the 25% of ♀♀ which did not mate in the first round.

4. Birth Data

Information on births was obtained from births in captivity ($N = 11$) and from babies discovered with their mothers in tree-nests. In the latter case, the date of birth was estimated from the physical appearance of the offspring, and the litter-sizes were determined by comparison of weights of the infants and observation of the mothers' behaviour. (In 3 cases, single ♀♀ were found with their infants; but in 3 other cases several litters were mingled with a number of adult ♀♀ in the nests.) Of a total of 27 litters, 19 contained two offspring, 3 contained 3 offspring, and 5 were single young. This gives an average litter-size of 2, and there is probably a slight tendency to litters *larger* than this, since ♀♀ may sometimes kill or abandon their young, and would therefore arrive in captivity with reduced litters. This accords well with Rand's (1935) statement that Grey Mouse Lemur females from Tabiky usually had 2 embryos and sometimes 3, and Kaudern actually reported one Brown Mouse Lemur ♀ with 4 embryos. The 6 female Grey Mouse Lemurs dissected in Mandena had 2, 1, 2, 2, 3 1 embryos, respectively. Petter-Rousseaux (1962) reported litter-sizes of 3, 2, 2, 1, 1, 2 and 2, respectively; so it is generally established for the Lesser Mouse Lemur that there are typically 2 young per litter.

As far as the sex-ratio is concerned, there were 24 ♀♀ to 26 ♂♂ among the infants examined, giving an approximately 1 : 1 ratio at birth. This is in agreement with the data in captivity provided by Petter-Rousseaux (1962; p. 52).

5. Infant Survival

5 nests discovered between 12. 11. 1968 and 15. 11. 1968 contained a total of 2 pregnant ♀♀, 13 apparently lactating ♀♀, and 2 non-lactating, non-pregnant ♀♀ along with 23 offspring. This indicates that at least 85% of ♀♀ in those nests had carried pregnancy to term, and when this figure is compared with the overall estimate of 75% ♀♀ pregnant in mid-October, it would seem that intra-uterine mortality is relatively low.

However, in 2 nests found on 19. 11. 1968 — containing only 7 young of a week old or more — there were 13 adult ♀♀ altogether, none of which were still noticeably pregnant. The offspring apparently belonged to only 4 of these ♀♀, indicating that less than 25% of them had successfully reared offspring beyond one week of age. Unless these nests represented "spinster's clubs" of some kind, the implication is that there had been heavy post-natal mortality. One cannot, of course, make generalisations from such scanty data; but this does suggest that — in some cases at least — young Mouse Lemurs may be extremely vulnerable during their first days of life. In one of the nests, there were only 2 infants, apparently belonging to one mother. Since these 2 young were born relatively late, it is possible that the nest had been cleaned

out by a predator while the mothers were away feeding at night, and that only the 2 babies born afterwards had survived.

If infant mortality *is* generally as high as these 2 examples indicate, the data represented in Fig. 19 are more likely to indicate the surviving infants of 2 successive litters, rather than 100% survival of all offspring from one early litter and a few later births. Indeed, it may be necessary for the Grey Mouse Lemur of the Mandena area to have 2 litters per rainy season in order to counteract the effects of predation (e. g. by snakes and small carnivores). An average production of 4 offspring per breeding ♀ per year, with an average survival of 2 out of the 4, would provide the Mouse Lemur with a potential for relatively rapid colonisation of its typical habitat — secondary forest areas. (Lemurs other than the Cheirogaleinae typically produce only 1 offspring per year, and there are indications that even in these there is appreciable infant mortality in the early stages of development.)

6. Infant Development

Following births to ♀♀ kept in captivity, it was possible to establish the state of the young at birth. In 5 cases, the offspring ($N = 12$) were found within 24 hours of birth, and in 3 cases the infants ($N = 6$) were discovered within 72 hours of birth. Petter-Rousseaux (1962; p. 52) has described the state of the neonates as follows (my translation):

"The head and the dorsal areas of the body are covered in grey-brown hairs, with a black dorsal stripe. The head is very large with respect to the rest of the body; the eyes, which are closed at birth, open within 4 days. The incisors and the canines are already through at birth, and the cheek teeth can be seen through the transparent gums." This description is generally applicable to the young born at Mandena, except that the eyes were normally open *within 48 hours*, and that pale hairs were also present on the ventral surface soon after birth. It is also noteworthy that the hallux is widely divergent on the hind-foot; much more so than in the adult Mouse Lemur (Fig. 20a). This is associated with an early ability to cling; soon after birth the neonate can support its entire body-weight in hanging from a twig by one hind foot. At the age of 8—10 days, the infant can cling quite firmly (Fig. 20b), and by the age of 15 days it can move around actively. The first leaps were seen at the age of 3 weeks, and by $1^1/_2$ months of age the young Mouse Lemur can move around and feed fairly independently. Despite this early ability to cling, however, the infant never clings to its mother's fur outside the nest, as noted by Petter-Rousseaux. However, it seems likely that such clinging is important when the infant somehow moves outside the nest. The ability to cling would safeguard it until the mother is able to give assistance. This is likely to be particularly important with leaf-nests, where the response of the adults to shaking of the branches is dispersal in all directions (p. 62). The babies would be able to drop to a branch somewhere below the nest and freeze until the mother returned to retrieve.

When retrieving the baby or transporting it to a different nest-site, the mother carries it in her mouth (demonstrated in a film made by Petter & Petter, 1955). When the nest is disturbed, the mother will pick up one of the babies in her mouth and escape with it (Fig. 21). Having deposited the baby somewhere, she will return for the others(s) — presuming that they are still there. In fact, the clinging ability of the infants may be necessary so that the mother can leave a baby attached to a branch some distance from the nest and return for it later on. Unfortunately, such behaviour was not observed



Fig. 20a: Photo of neonate Grey Mouse Lemur born in captivity in Mandena. Note relatively enormous head, marked presence of fur and wide divergence of hallux in foot. — *b:* Sketch of 10-day-old Grey Mouse Lemur from Mandena. Note ability to grasp twigs

under natural conditions; but in a large cage in captivity, babies were occasionally found clinging to branches when the nests had been disturbed. In fact, oral transport by the mother provided great difficulties when the babies were weighed, since the mother would frequently carry off one of the babies when the nesting-tubes were opened. Indeed, one of the mothers eventually abandoned the nesting-tubes altogether (10 were available), and built a rudimentary leaf-nest (p. 65). Such oral carriage at weighing times was not seen with infants older than 10 days; but various infants in captivity were seen in their

mother's mouths up to the age of about 3 weeks. After that time, oral carriage seems to disappear, probably because the young are by then too large and too heavy.

The only major difference from PETTER-ROUSSEAUX's observations lay in the state of development and weight of the young at birth. PETTER-ROUSSEAUX (1962) recorded only 2 weights on the first day of life: 2.7 and 4.3 gm, respec-



Fig. 21: Sketch of mother Grey Mouse Lemur carrying baby in mouth from leaf-nest

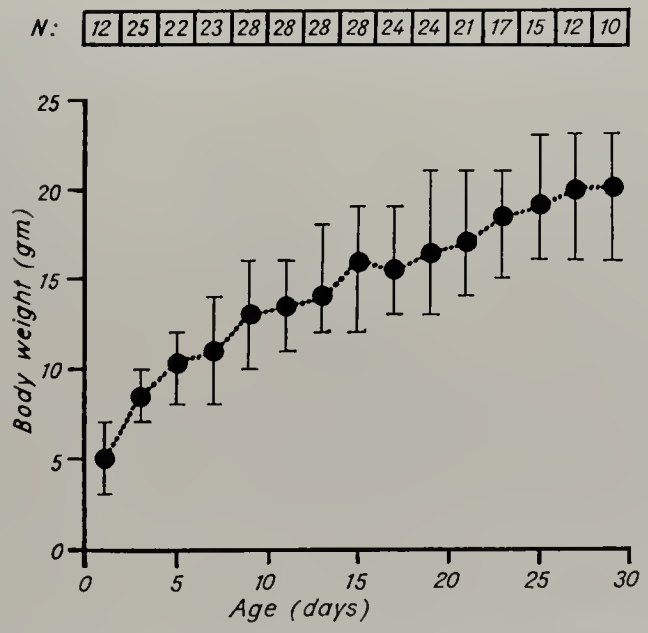


Fig. 22: Growth-curve (means and ranges) for an average of 20 Grey Mouse Lemurs from Mandena, kept with their mothers in captivity. (N.B.: Day. 1 = day of birth) The boxes above the points give the numbers of animals weighed for each point

tively. These weights would seem to be exceptionally *low*, and it is possible that the 2 infants concerned (neither of which survived) were premature, or in some other way abnormal. The 12 offspring weighed within the first 24 hours in Mandena weighed 5 gm on average (range 3—7 gm), and 4 out of the 5 infants weighing less than this average (3, 3, 4 and 4 gm) failed to survive more than a week. The 2 infants weighing 3 gm seemed to be definitely undeveloped, and since these were the first babies recorded in the Mandena area, they may well have been premature.

All offspring born in captivity were weighed at 2-day intervals, and a provisional growth-curve can be constructed from the average values (Fig. 22). Since the ♀♀ were kept with their infants under extremely rudimentary conditions in captivity, this growth-curve probably represents a *minimum* rate of growth for the Mouse Lemur, rather than a typical rate of development. Approximately 33% of the babies kept in captivity died at some stage in development — usually within the first week of captivity.

7. Hand-Rearing

In 2 cases, litters were taken without their mothers; so hand-rearing was attempted. As it happened, 2 of the offspring were Brown Mouse Lemurs, while the other 2 were Grey Mouse Lemurs.

The infants were given milk made up with "Domo" milk-powder provided by UNIGATE Ltd. (as a donation to the field-study). During the first 2 weeks, the milk was made up to half the strength of cow's milk; thereafter, the concentration of normal cow's milk was used. These infants were fed every 2—3 hours daily, then left in a ventilated plastic container with pieces of lint as "nest-material" for 8—10 hours overnight. The milk was given at each feed with an eye-dropper (which was boiled from time to time), and feeding was continued until the infant refused to swallow any more milk. Before and after each feed, the inguinal area was rubbed with a warm, damp

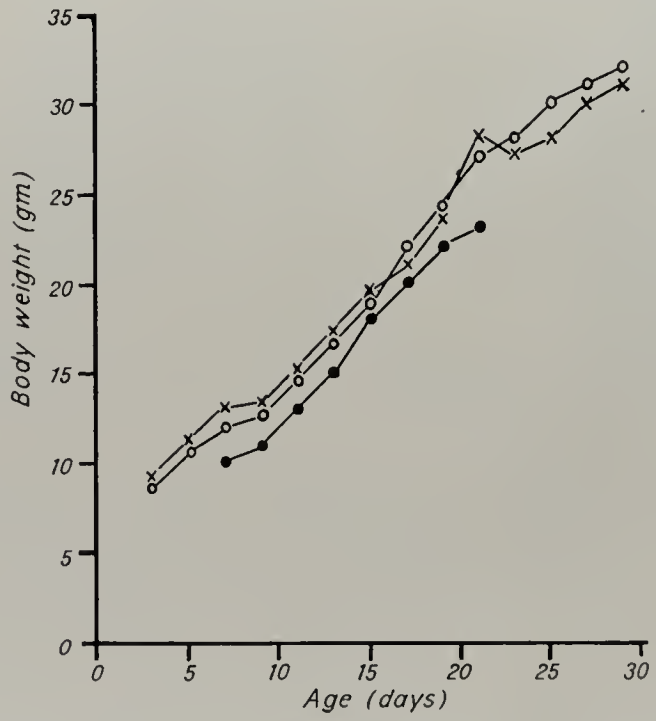


Fig. 23: Individual growth-curves for 3 Mouse Lemurs reared by hand in captivity

cloth. The mother Mouse Lemur usually licks this area during suckling bouts, and her licking actions elicit urination and defaecation. The damp cloth acted as an effective substitute for the mother's licking, and it was noted that the infants uttered a soft, twittering vocalisation at the time when urine or faeces were expelled. Since the mother usually ingests these waste products, this vocalisation may act as a signal marking the moment of elimination.

The hand-reared infants were also weighed every 2 days, giving an average curve (Fig. 23). One of the Grey infants unfortunately wandered off one week after hand-rearing began, and it succumbed before it could be found; so the curve only gives averages for 3 infants. However, it is noticeable that all 3 grew appreciably faster than the infants left with their mothers (Fig. 22). It is possible that the hand-reared infants were "over-fed", and therefore grew much faster than normal; but this is not very likely, since hand-rearing usually represents a trauma which causes artificially-nourished animals to grow *more slowly* than usual — at least for the first few weeks of life. In view of this, Fig. 23 probably represents a more typical growth-curve for young Mouse Lemurs during the first month of life. Certainly, the true growth-curve is likely to lie between the two extremes represented in Figs. 22 and 23.

The hand-reared babies seemed to develop at the same general rate as those left with their mothers. The lower milk teeth were all through by Day 3—4, and by Day 7 the upper milk teeth were also all through. (The incisors and canines were through at birth, as noted by PETTER-ROUSSEAUX.) At 1 week of age, the infants were able to bite quite well as an alarm response. From quite early on, the young were seen to lick one another when kept together, and at about 3 weeks of age this was seen to give way to definite "social grooming", in which the groomer would grasp the head fur and/or ears of the recipient and comb the head and neck fur with the developing tooth-scraper. Early on, reciprocal licking often led to "erroneous" elicitation of urination or defaecation, when applied to the inguinal area, and for this reason the infants were separated at night, so that they were not soaked to the skin when taken out for the first feed in the morning. At about the 7th day of life, the "purring" vocalisation described on p. 75 was heard for the first time. It was subsequently heard whenever the infants were warm and dozing, for example just after feeding. From about 2 weeks of age, this vocalisation was also elicited by stroking of the head after feeding.

Overall, it can be said that Mouse Lemurs are born at a relatively advanced state (considering that this is a *nest-living* mammal), and that they develop fairly rapidly. By $1^1/_2$ months of age, they are virtually self-sufficient, though weaning may occur later than this.

Summary

1. This preliminary account of the behaviour of the Lesser Mouse Lemur *(Microcebus murinus)* is based on observations conducted in several areas of Madagascar (Fig. 3), July—December 1968. There are 2 types of Mouse Lemur, of uncertain taxonomic status: "Brown Mouse Lemur" in East coast rainforest; "Grey Mouse Lemur" in dryer forest areas (Fig. 2). A $2^1/_2$-month detailed study (Oct.—Dec.) of the Grey Mouse Lemur in Mandena (Fig. 3: 4) covered the first half of the breeding season.

2. At night, studies of behaviour were carried out, using a headlamp to reflect light from the tapetum of the animals' eyes. During the daytime, searches were made for nests. Over 200 Mouse Lemurs were trapped by hand

at night or taken from nests during the daytime. All were weighed and examined; some were marked (tail-fur clipping) for later identification (Fig. 4).

3. Average adult body-weight is 60 gm, though some weigh as little as 40 gm (especially in peripheral vegetation). Weights probably increase markedly during the rainy season, when fat may be stored in the tail, and at the beginning of the rainy season pregnant or lactating ♀♀ weighed 70—100 gm. No evidence was found for the oft-repeated statement that Mouse Lemurs are dormant during the dry season.

4. Mouse Lemurs typically occupy the *fine branch niche* at all forest levels where there is dense foliage cover, relying heavily on the grasping ability of their tiny hands and feet. Locomotion is generalised; it is essentially quadrupedal, with some tendency to hind-limb dominated locomotion. One marked feature is the ability to hold the body *horizontal* with the grasp maintained solely by the hind-feet. There is also a special launch-and-recoil pattern for predation on insects, where the grip is maintained on the branch with the hind-feet.

5. The main foods are fruits and arthropods (mainly insects); but Mouse Lemurs were also observed eating leaves and flowers. Small chamaeleons and tree-frogs were eaten in captivity, indicating an essentially omnivorous diet. Individual populations seem to be specialised on a small range of local plant species, usually concentrating on small berries less than 1 cm in diam., whilst animal food seems to be taken more opportunistically.

6. Mouse Lemurs typically rest in some kind of nest during the daytime, though they occasionally rest in dense foliage. The main retreats are: *spherical leaf-nests* and *tree-hollow nests*. Several nests of both types were found in different areas of Madagascar, and their essential dimensions were recorded and analysed. In the East coast rain-forest, the rolled-up leaves of the traveller's-tree *(Ravenala madagascariensis)* provide natural hollows used as nests by Brown Mouse Lemurs. Surprisingly, most nests are relatively close to the ground (2—4 m).

7. Most nests contained ♀ groups of up to 15 members (median: 4), while ♂♂ were usually found separately, nesting singly or in pairs (Fig. 13).

8. Local populations of Mouse Lemurs apparently occur as "nuclei" ("noyaux" of Petter), separated to a greater or lesser extent from one another. The core of each nucleus contains a high proportion of ♀♀ to ♂♂ (at least 4 : 1); there are probably many excess ♂♂ existing as peripheral individuals, since the sex-ration at birth is 1 : 1. There is probably a distinction between *central males*, co-existing with ♀ groups, and *peripheral males* occurring isolated from ♀♀.

9. A population nucleus of Grey Mouse Lemurs was studied in Mandena (Fig. 3: 4), many of the members having been marked at various stages. A "scatter diagram" (Fig. 16a) of observations gave a very approximate idea of the *areas of activity* of the resident Mouse Lemurs (Fig. 16b). Each Mouse Lemur is probably confined to an area of about 50 m diameter, including one or more nests used as retreats during the daytime.

10. A brief survey of the high-pitched vocalisations of this animal is provided.

11. The Mouse Lemur has a clear-cut breeding season, approximately coinciding with the rains (September—March vs. December—April). The first infants become independent just as the rains begin, and the last are probably self-sufficient before the rains end. There is some circumstantial evidence that each ♀ may be able to have 2 litters (generally of 2 infants) during each breeding season.

12. 18 babies were born in captivity, and a further 34 were found in nests with their mothers. The ♀ groups do not apparently split up for birth of the offspring (Fig. 13). Weight curves were obtained for 28 babies reared by their mothers in captivity (Fig. 22) and for 3 infants reared by hand (Fig. 23). Brief details of hand-rearing and early development are given. The infants are extremely advanced at birth, in comparison to typical nest-living mammals, and can cling to branches from Day 1 onwards (Fig. 20b). The mother retrieves the infants in her mouth, and can transport them (one-at-a-time) to a new nest if the original nest is disturbed. At no stage do the infants ride on the mother's fur.

Zusammenfassung

1. Das Verhalten des Mausmaki *(Microcebus murinus)* wurde nach Beobachtungen in verschiedenen Gebieten Madagaskars von Juli bis Dezember 1968 vorläufig beschrieben. Man unterscheidet dort zwei Mausmaki-Typen, den „braunen" vom Regenwald an der Ostküste und den „grauen" in den weniger feuchten Waldgebieten (Abb. 2). In die zweieinhalb Monate Beobachtungszeit für den grauen Mausmaki in Mandena (Abb. 3, 4) fiel auch die erste Hälfte seiner Fortpflanzungszeit.

2. Nachts beobachtete ich mit der Kopflampe, die die Augen der Tiere leuchten machte, bei Tag suchte ich Nester und entnahm ihnen Tiere. Mehr als 200 fing ich nachts mit der Hand. Alle wurden gewogen und untersucht, manche auch durch Kerben im Schwanzhaar markiert.

3. Das Durchschnittsgewicht erwachsener Tiere beträgt 60 g; einige (besonders aus extremen Waldzonen) wogen nur 40 g. Am Anfang der Regenzeit steigt das Körpergewicht wahrscheinlich stark an; vermutlich wird Fett im Schwanz gespeichert. Am Anfang der Fortpflanzungszeit wiegen laktierende ♀♀ 70—100 g. Nichts stützte die weitverbreitete Meinung, daß Mausmakis einen Winterschlaf halten.

4. Der charakteristische Lebensraum der Mausmakis ist im Wald die Zone der dünnen Zweige mit dichter Blätterdeckung. Die Tiere bewegen sich quadruped, springen aber manchmal auch vertikal („vertical clinging and leaping" von Napier u. Walker 1967). Auffallend ist ihre Fähigkeit, den Körper waagerecht zu halten, selbst wenn sie sich nur mit den Hinterfüßen am Zweig festhalten. Für den Insektenfang haben sie eine spezielle Spring- und Landebewegung, wobei wieder die Hinterfüße das Tier halten.

5. Hauptbestandteile der Nahrung sind Früchte und Arthropoden (vorwiegend Insekten), doch wurden Mausmakis auch beim Blätter und Blütenfressen beobachtet. In Gefangenschaft wurden kleine Chamäleons und Baumfrösche erbeutet; Mausmakis sind also Allesfresser. Einzelne Populationen scheinen auf wenige ortsgebundene Pflanzenarten spezialisiert zu sein, wobei sie gewöhnlich kleine Früchte von weniger als 1 cm Durchmesser bevorzugen. Tierische Nahrung wird dagegen je nach Gelegenheit gefressen.

6. Mausmakis ruhen tagsüber normalerweise in irgendeinem Nest, manchmal auch in dichtem Blättergewirr. Die meisten Nester sind entweder runde Blätter-Nester oder Baumhöhlen-Nester. Aus verschiedenen Gebieten Madagaskars wurden mehrere Nester von beiden Typen gemessen und analysiert. Im Regenwald (Ostküste) bilden die gerollten Blätter des „traveller's tree" *(Ravenala madagascariensis)* natürliche Höhlen für das Braune Mausmaki. Erstaunlicherweise sind die meisten Nester ziemlich nah am Boden (2—4 m hoch).

7. Die meisten gefundenen Nester enthielten ♀♀-Gruppen von durchschnittlich 4, maximal 15 Tieren. ♂♂ fanden sich gewöhnlich einzeln oder paarweise (Abb. 13).

8. Örtliche Mausmaki-Populationen kommen anscheinend als „Bevölkerungs-Kerne" („noyaux" von Petter 1962c) vor, die mehr oder weniger streng voneinander getrennt sind. Das Zentrum von jedem Kern enthält verhältnismäßig viele ♀♀ (mindestens 4 ♀♀ für jedes ♂), und es gibt am Rande der Population höchstwahrscheinlich viele überzählige ♂♂, da das Geschlechtsverhältnis bei der Geburt 1 : 1 beträgt. Wahrscheinlich kann man zwischen „Zentral-♂♂" und „Rand-♂♂" unterscheiden, wovon nur die ersteren Kontakt mit den ♀♀ haben.

9. Ein solcher Mausmaki-Bevölkerungskern wurde in Mandena (Abb. 3:4) untersucht; viele Mitglieder davon wurden zu verschiedenen Zeitpunkten markiert. Ein „Punkt-Schema" (Abb. 16a) der Beobachtungen zeigte annähernd die Streifgebiete der ansässigen Mausmakis (Abb. 16b). Jedes Mausmaki beschränkt sich höchstwahrscheinlich auf ein Gebiet von etwa 50 m Durchmesser mit einem oder auch mehreren Nestern als Tages-Schlafstätte.

10. Eine kurze Übersicht der hohen Lautäußerungen wird gegeben.

11. Das Mausmaki zeigt eine klar begrenzte Fortpflanzungszeit, die annähernd mit der Regenzeit zusammenfällt (September—März bzw. Dezember—April). Die ersten Jungen werden am Anfang der Regenzeit selbständig, und die letzten sind es höchstwahrscheinlich vor dem Ende der Regenzeit. Einiges spricht dafür, daß jedes ♀ 2 Würfe (von durchschnittlich 2 Jungen) innerhalb der Regenzeit haben kann.

12. 18 Junge wurden in Gefangenschaft geboren; weitere 34 wurden in Nestern mit ihren Müttern gefunden. Die ♀♀-Gruppen spalten sich anscheinend nicht, ehe die Jungen geboren werden (Abb. 13). Gewichtskurven wurden für 28 von der Mutter und für 3 handaufgezogene Junge aufgestellt (Abb. 22 bzw. Abb. 23). Eine kurze Beschreibung der Handaufzucht und der frühen Entwicklung wird gegeben. Die Jungen sind bei der Geburt schon ziemlich weit entwickelt, im Vergleich zu typisch nesthockenden Säugetieren, und können sich vom ersten Tag an auf kleinen Zweigen festklammern (Abb. 20b). Die Mutter trägt die Jungen im Maul und kann sie (eins nach dem anderen) zu einem neuen Nest transportieren, wenn das ursprüngliche Nest irgendwie gestört wird. Die Jungen reiten nie im Fell des Muttertiers.

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Fortschritte der Verhaltensforschung — Advances in Ethology

Herausgegeben von Priv.-Doz. Dr. Wolfgang Wickler, Max-Planck-Institut für Verhaltensphysiologie, Seewiesen/Obb.

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1971. 70 Seiten mit 37 Abbildungen. Kartoniert DM 29,—;
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8: The Ontogeny of Social Behavior in the Gray Squirrel (Sciurus carolinensis)

Von Dr. Robert H. Horwich, Brookfield/Ill.

In englischer Sprache
1972. 103 Seiten mit 70 Abbildungen und 7 Tabellen. Kartoniert DM 39,60;
für Bezieher der Zeitschrift DM 35,60

VERLAG PAUL PAREY · BERLIN UND HAMBURG

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Charles-Dominique, Pierre
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This supplement contains two independent reports of field-studies of noctur
species – one by P. Charles-Dominique on the habits of Galago demidovii
and one by R.D. Martin on Microcebus murinus (in English). The main inter
studies lies in the initial zoological relationship between the prosimians and
mination of the early phases in human evolution requires broad study of th
including the prosimians. Over and above this, the joint publication of these
highlights a number of important points. In addition to describing a num
niques for studying animals which are active at night, the two articles bring
cases of surprising similarity between the Bush-babies of Africa (Galagin
Mouse Lemur group (Cheirogaleinae) of Madagascar. In consequence, the
presented in this supplement provides some entirely new perspectives on
radiation of the Order Primates.

Ce supplément comprend deux articles distincts concernant deux espèces
nocturnes étudiées sur le terrain; l'un par P. Charles-Dominique, sur Galag
(en Français) et l'autre par R.D. Martin sur Microcebus murinus (en Anglai
tions existant entre les Prosimiens et l'Homme ajoutent un intérêt à ce
connaissance des premiers phases de l'évolution humaine nécessitant l'étud
die des Primates, Prosimiens y compris. En outre, ces deux articles publi
mettent en lumière un certain nombre de données importantes; tout en fo
aperçu sur des techniques d'étude d'animaux nocturnes, ils font ressorti
nantes similarités existant entre les Galagos d'Afrique (Galaginae) et les Mi
Madagascar (Cheirogaleinae). Les informations présentées dans ce supplém
quelques nouvelles voies pour la compréhension du début de la radiation de
Primates.

Dieses Beiheft enthält zwei unabhängige Beiträge, die über Freilandbeo
nachtaktiver Primaten berichten. Der eine, von P. Charles-Dominique (in F
beschreibt das Verhalten von Galago demidovii; der andere, von R.D. Mar
lisch), das von Microcebus murinus. Das Schwergewicht dieser Arbeiten
frühen zoologischen Verwandtschaft zwischen den Halbaffen und dem Me
Untersuchung der frühen Stadien der Menschenevolution bedarf einer ti
Analyse der Primaten, einschließlich der Halbaffen. Darüber hinaus unterstr
Beiträge eine Anzahl wichtiger Punkte: Auf der einen Seite werden Metho
ben, die das Studium solcher nachtaktiven Tiere ermöglichen, auf der a
weisen die beiden Arbeiten in verschiedenen Hinsichten eine überraschende
zwischen den Galagos von Afrika (Galaginae) und der Mausmaki-Gruppe
(Cheirogaleinae) nach. Das Tatsachenmaterial in diesemBeiheft bietet deme
eine Reihe ganz neuer Hinweise auf die frühe Verbreitung der Ordnung der